

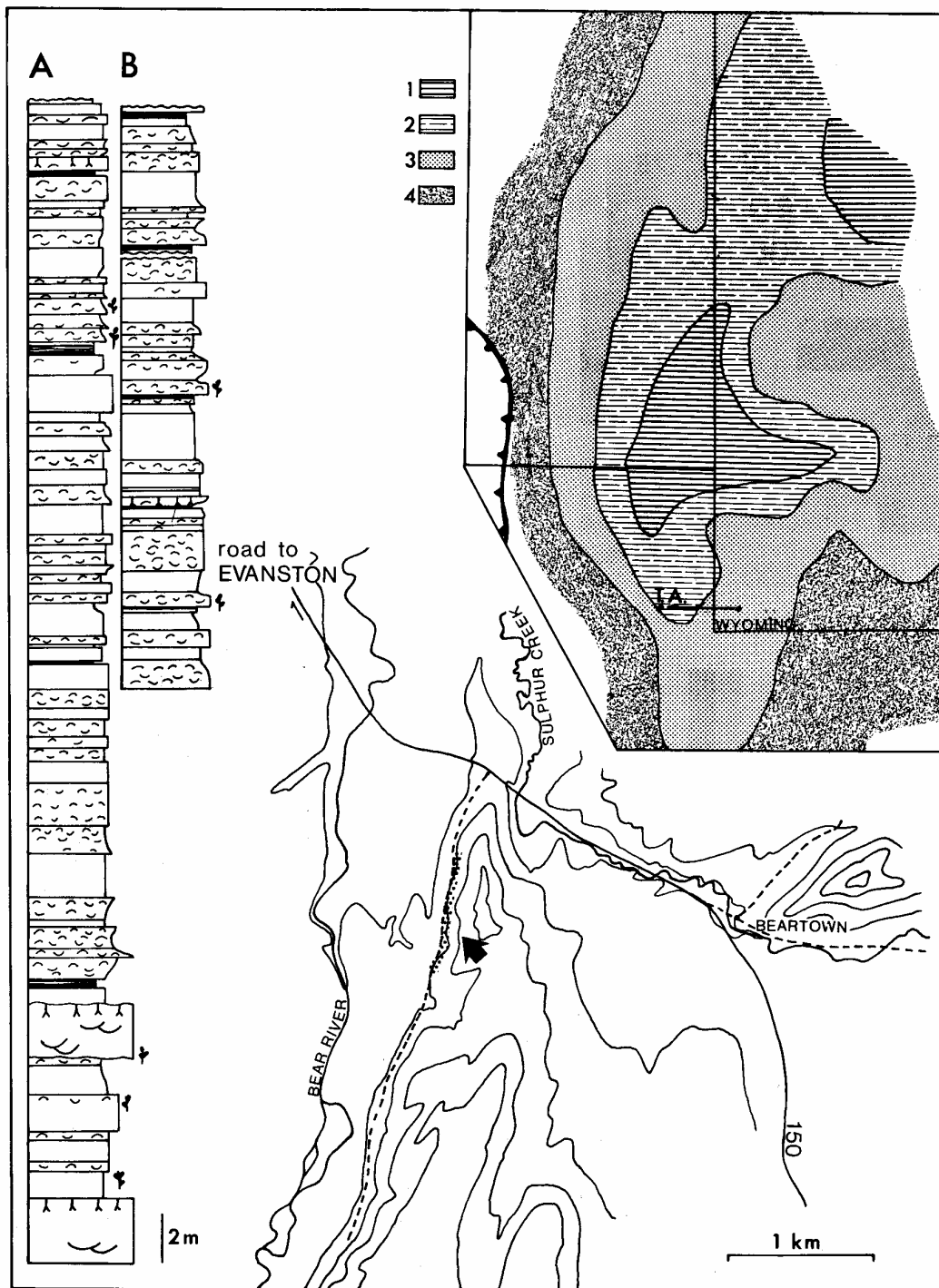
PALAEOECOLOGY OF MARGINAL MARINE SEDIMENTARY CYCLES IN THE ALBIAN BEAR RIVER FORMATION OF SOUTH-WESTERN WYOMING

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ABSTRACT. The Middle to Late Albian Bear River Formation of south-western Wyoming includes a cyclic sequence of fine-grained sediments with numerous shell beds comprised of abundant, low diversity fresh- and brackish-water faunas. These record the initial marine transgression of the Cretaceous in this region (Skull Creek-Kiowa tectono-eustatic cycle) and are interpreted as part of an extensive embayment with limited marine influence. Biostratigraphic data suggest low rates of sedimentation, frequently shifting environments, and, in the coquinas, reworking by storms to account for mixing of meso- to oligohaline and freshwater faunas. Five discrete, repetitive benthic associations are documented for the freshwater and two associations with four subsets for the brackish-water facies. They were controlled in their distribution largely by substrate, temperature, and oxygen levels in freshwater and by substrate and salinity in brackish water. Size/frequency curves of brackish species document seasonal fluctuations in salinity (tertiary cycles). Repetitive successions of facies and faunas record regressive sequences (secondary cycles), whilst fluctuations in the relative dominance of fresh- or brackish-water conditions within bundles of regressive sequences reveal a still higher order of cyclicity (primary cycles) within the Bear River Formation. These cycles are partly of climatic origin, partly autocyclic.

DURING the early Cretaceous (middle Late Albian), a narrow seaway which extended from the Proto-Gulf of Mexico to the Circum-Boreal Sea was first established in the Western Interior Basin of North America (Eicher 1960), and has been named the Skull Creek Seaway by McGookey *et al.* (1972, p. 200). Near its centre, grey to black, finely laminated, commonly organic-rich shale facies (e.g. Thermopolis Shale, Mowry Shale) characterize the seaway. Toward the west, these offshore marine facies grade into a zone of marginal facies representing deposition in estuaries, lagoons, and bays. These in turn grade further west into deposits of low-lying flood plains (text-fig. 1). Isotopic studies suggest that even in the centre of the seaway subnormal salinity existed during Skull Creek time. The Middle to Late Albian Bear River Formation represents the western marginal marine facies deposited early in transgression of the northern arm of the Skull Creek Sea (e.g. Young 1969) before a connection was established across Colorado with the warm-water incursion of the Interior Seaway from the Gulf of Mexico. The Bear River Formation comprises fluvial channel and overbank sandstones and, in its centre, lagoon or bay fill sequences of shales, siltstones, and silty carbonates. They contain, in places, low-diversity but highly abundant molluscan-dominated faunas indicative of fresh- and brackish-water conditions. The depositional environments of these fine-grained facies, and especially of the numerous small-scale sedimentary cycles within them, are poorly understood.

The Bear River Formation overlies the non-marine Smoot Formation of the Gannett Group and is in turn overlain by marine shales of the Aspen Formation. Towards the south-east, along the depositional strike, rocks of the Bear River Formation grade into those of the Dakota Formation (e.g. Horstman 1966). Due to widespread thrusting, which commonly cuts the Bear River, the thickness of the formation is difficult to evaluate. It is usually given as 175 to 1750 m, depending on the region (e.g. Stanton 1892; Veatch 1907; Wilmarth 1938). The type section (Stanton 1892, fig. 1) is near the site of the former Bear River City, about 12 miles south-east of Evanston in south-western Wyoming. This section, first described by Meek (1873) and interpreted in more detail by Stanton



TEXT-FIG. 1. Locality map, palinspastic palaeogeography, and section of part of the Bear River Formation at the Bear River Locality in south-western Wyoming. T.A.: type area; (1) offshore marine shale; (2) near-shore mud, sand, and shale; (3) marginal mud and sand; (4) non-marine sand and mud. The thrust symbol denotes position of the Willard-Paris thrust. Section B is stratigraphically higher than section A. For key of symbols, see text-fig. 2. Palinspastic reconstruction after Royse *et al.* (1975).

(1892), is now very poorly and incompletely exposed. A largely complete, freshly exposed section exists along a gravel road leading south past Myers Reservoir (text-fig. 1) 1.5 miles to the west of the type section and about 0.5 miles east of Bear River. This section, subsequently referred to as the Bear River Reference Section, displays in its middle to upper part thin coals, carbonaceous shales, siltstones, thin sandstones, and thin, resistant beds of silty limestone which contain well-preserved fossils representing the characteristic 'Bear River fauna' (Stanton 1892). Cyclic sedimentation and palaeoenvironments are reflected at three different levels of magnitude by both facies and faunas in this part of the section. Second-level cycles are most obvious. Within each secondary cycle the facies change up-section from shelly silts and silty limestones, to silty and carbonaceous shales, to coals, and finally to silty or marly freshwater limestones. The benthic fauna changes accordingly in composition from brackish-water-dominated associations to freshwater-dominated associations. It is the purpose of this paper to analyse the fauna ecologically, to describe in detail the cyclic changes of the facies and faunas, and to speculate on the origin of these cycles at all levels of development.

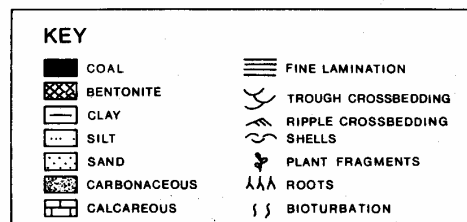
HISTORY OF RESEARCH

Although frequently discussed in the second half of the last century, little modern work has been done on the Bear River Formation. The rocks were discovered by Engelmann in 1859 near the mouth of the Sulphur Creek (type area), and first mentioned by Meek and Engelmann (1860). In 1869 Hayden gave them the name Bear River Group, after the nearby Bear River. In the following twenty-five years, there was a lively debate about the age of the rocks. Originally thought to be Eocene in age (Meek and Engelmann 1860; Meek 1860), their Cretaceous age was only gradually recognized (e.g. Engelmann 1876; White 1891). Stanton (1892) established beyond doubt the Cretaceous age of the rocks and their position below the Colorado Formation. White (1895) reviewed earlier literature, in particular the age controversy, described in detail the faunas, discussed aspects of their ecology, and concluded that the Bear River Formation was 'deposited in a brackish water lake or sea which was more or less completely cut off from open marine waters' (pp. 68-69).

Stanton (1892) had already recognized the occurrence of the Bear River fauna at other localities in south-western Wyoming (e.g. Twin Creek, Ham's Fork, Cokeville) (see also Veatch 1907). Later on rocks with similar faunas were discovered as far as northern Wyoming (e.g. LaRocque and Edwards 1954; Wanless *et al.* 1955) and, in part, described as westward equivalents of the Bear River Formation (Rubey 1973). Due to the lack of index fossils the age question was not yet settled and, in the middle of this century, the discussion was continued by Yen (1952, 1954) who, noting the similarity of the Bear River *Pyrgulifera* to those from Cenomanian localities in Europe, assumed a Cenomanian age for the rock unit, while Cobban and Reeside (1952) assigned the Bear River Formation to the Middle Albian *Inoceramus comancheanus* zone. Today, a Middle to Late Albian age is generally accepted on grounds of facies relationships, and the Bear River Formation is thought to correspond in parts to the Thermopolis Shale (e.g. Eicher 1960; Haun and Barlow 1962; Young 1969; Kauffman *et al.* 1976).

THE BEAR RIVER REFERENCE SECTION

Along the dirt road leading from U.S. 150 toward Myers Reservoir, a large part of the Bear River Formation is exposed. The rocks are overturned and faulted several times so that it was not possible to measure one continuous section. The lower part of the exposure consists of greenish to reddish clays and silts with lenticular intercalations of silt- and sandstones and rare layers of silty limestone. Fossils are very rare and consist of poorly preserved freshwater gastropods. The environment is most likely a low-lying coastal or flood plain dotted with lakes and small streams. This sequence is overlain by a series of silts, shell beds, highly carbonaceous shales with thin coal-seams, and impure limestones (text-fig. 1). Fossils are abundant at numerous horizons, often forming



TEXT-FIG. 2. Key to symbols used in text-figs. 1, 12-17, 19.

shell beds or beds of shell hash. Only the lower portion (42 m) and part of the upper half (20 m) of the fossil-rich strata were measured in detail, the remaining part being identical. The fossiliferous beds are finally overlain by unfossiliferous silty shales.

Facies types. Fine-grained sandstones occur near the base of the measured section only. They have an erosive base and exhibit, in places, large-scale trough cross-bedding and small-scale ripple cross-bedding. Occasionally, levels with rip-up clasts are present near the base. The tops of the sandstones are rooted and occasionally bioturbated (small vertical tubes and *Chondrites*-like traces).

Siltstones do not exhibit any sedimentary structures, but are sometimes bioturbated. They are usually rich in plant debris and occasionally contain scattered shells or thin shell bands.

Silty clays and clayey silts are widespread and can be subdivided into the following types: (a) laminated shales indicative of little or no disturbance of the sediment/water interface. Rarely, thin shell bands are intercalated. (b) Carbonaceous silty clays and clayey silts with a high percentage of plant debris. (c) Blocky silty clay and clayey silt, unfossiliferous or with scattered shells only. All three types may contain thin bands of jarosite.

Shell beds are very common and represent the following three types: (a) beds of shells and shell hash; the matrix is silty clay or clayey silt. Carbonized plant fragments are common in some beds. Shells are usually of brackish-water origin and largely disarticulated. (b) Beds of shelly silty limestone or calcareous siltstone. Most shells are of brackish-water origin. Disarticulated shells dominate, although sometimes individuals are found in life position. Beds of type a and b may have an erosive base and vary in thickness laterally. (c) Beds of shelly silty limestone or marly siltstone. Most shells are small gastropods of freshwater origin. Frequently the beds are highly carbonaceous and may contain coal fragments; occasionally they are rooted.

Coal-seams several centimetres in thickness occur throughout the section. They usually alternate with thin layers of highly carbonaceous silty clay.

Bentonite layers are common. In the measured section, twenty-three layers have been encountered, the thickest measuring 25 cm. Occasionally they have an irregular base.

Facies sequence. The vertical succession of the various facies types is not random, but cyclic. As a rule, the base of each cycle is characterized by thin, bioclast-supported shelly limestone beds, less frequently by shelly silty clay. These may alternate with beds of silty clay and clayey silt in which shells are scattered or absent. At this level poorly fossiliferous siltstones may also be found. Then follows a zone of carbonaceous silty clays, sometimes laminated and often associated with thin coal-seams. Intercalated between these and often terminating the cycles are beds of mud-supported silty or marly limestones that frequently contain plant or lignite fragments and sometimes roots. The cycles range from 50 (a very incomplete cycle) to 500 cm in thickness, most of them being 150 to 300 cm thick.

Fauna. The fauna of the Bear River Formation is generally of low diversity but high abundance and this is also true of the Bear River section. The faunas from the type locality and other localities were first described by Meek (1860, 1870a, b) and more fully by White (1895), but not all Meek's species have been found (for list of species see Table 1). In addition, some are interpreted here as representing only variants of one and the same species. For example, *Corbula engelmanni* Meek (White 1895, p. 40, pl. 4, figs. 10-11) is clearly the juvenile form of *Ursirivus pyriformis* (Meek). Similarly the two species of *Pyrgulifera* (*P. humerosa* and *P. stantoni*) described by White (1895, p. 55, pl. 8, figs. 1-11; pl. 9, figs. 1-8) are here considered only variants of the same species (as also recognized by White) with *P. humerosa* Meek having priority. A similar case can be made for *Mesoneritina naticiformis* (White) and *M. stantoni* (White), the latter being regarded as a junior synonym of the former.

Later descriptions of the macrofauna, in particular the gastropods—although from other localities—are by Yen (1951, 1954). The microfauna and microflora were described by Jones (1893), White (1895), and more recently by Peck (1951) and Peck and Craig (1962). The latter authors list thirteen species of ostracods and charophytes from the Bear River Formation. Palynological investigations were carried out by Tingey (1978).

In the Bear River section gastropods dominate in number of species (twenty) and in abundance. Both fresh- and brackish-water species are present, as is the case among the less diverse bivalves (seven species). In most cases, fresh- and brackish-water species are found in the same bed, but beds with only freshwater or only brackish-water faunal elements are also present. In many beds several species of ostracods and charophytes occur.

It was soon recognized that the Bear River Formation represents a marginal marine environment and White (1895) distinguished clearly between a freshwater and a brackish-water fauna. The assignment of ancient species to a certain salinity regime is particularly difficult in the case of the Bear River fauna where mixing plays a significant role. Criteria such as the preferred occurrence with undoubtedly freshwater forms (e.g. unionids) or brackish-marine forms (e.g. *Crassostrea*, *Ursirivus*, *Brachidontes*) were used to establish the broad salinity range

TABLE 1. List of species found in the Bear River Formation at the Bear River Locality. Familial classification of gastropods based mainly on Yen (1951, 1954)

FRESHWATER		
Bivalves:	Unionidae	<i>Loxopleurus belliplicatus</i> (Meek) <i>Protelliptio (Plesielliptio) vetustus</i> (Meek)
Gastropods:	Valvatidae	<i>Valvata praecursoris</i> (White)
	Viviparidae	<i>Lioplacodes stachei</i> (White)
		<i>Viviparus couesi</i> White
		<i>Campeloma macrospira</i> Meek
	Neritidae	<i>Mesoneritina naticiformis</i> (White)
	Amnicolidae	<i>Parateinostoma occultum</i> (White)
		<i>Parateinostoma latense</i> (White)
		<i>Parateinostoma</i> cf. <i>P. altispirale</i> Yen
		' <i>Tornatellina?</i> ' <i>isocline</i> White
	Pleuroceratidae	<i>Pachychiloides cleburni</i> (White)
		<i>Pachychiloides turriculus</i> (White)
		<i>Pachychiloides chrysalis</i> (Meek)
		<i>Pachychiloides chrysalloideus</i> (White)
<i>Pachychiloides macilentus</i> (White)		
	<i>Goniobasis</i> sp.	
Cyclophoridae	<i>Pseudarinia</i> sp.	
Lymnaeidae	<i>Lymnaea nitidula</i> (Meek)	
BRACKISH WATER		
Bivalves:	Corbiculidae	<i>Veloritina durkeei</i> (Meek)
	Corbulidae	<i>Ursirivus pyriformis</i> (Meek) corbulid sp. A
Gastropods:	Mytilidae	<i>Brachidontes multilingera</i> (Meek)
	Ostreidae	<i>Crassostrea soleniscus</i> (Meek)
	Pleuroceratidae	<i>Pyrgulifera humerosa</i> (Meek)
	Ellobiidae	<i>Rhytophorus meeki</i> White
		<i>Zapytchius haldemani</i> (White)

of doubtful species. Thus *Pyrgulifera humerosa* is regarded as a brackish species (in contrast to Yen 1952; LaRocque and Edwards 1954) as is *Rhytophorus meeki* (see Table 1).

The vertical distribution of the fauna, like the sediment, reveals a cyclic pattern; within a cycle the relative abundance of freshwater forms in individual beds invariably increases towards the top. At the base, shell beds are dominated by brackish-water bivalves whilst at the top brackish-faunal elements are usually missing or do not constitute more than 5% of the fauna, the rest being small freshwater gastropods and unionid bivalves.

SIGNIFICANCE OF ENVIRONMENTAL CONDENSATION FOR THE PALAEOECOLOGICAL INTERPRETATION OF MARGINAL MARINE FAUNAS

Palaeosynecological interpretation of faunas requires that they have undergone only minimal disturbance. This is particularly true of marginal marine faunas where environments and faunas may change drastically across short lateral distances and transport lead to mixing of communities from different biotopes. On the other hand, relatively uniform marginal marine environments such as large protected lagoons and bays may exhibit only insignificant lateral faunal mixing (e.g. Peterson 1976). Of far greater importance in such environments is a process called environmental condensation (Fürsich 1975), whereby faunas representing different environments in time are telescoped into one stratigraphic horizon. Prerequisite for such a process is a low rate of sedimentation and rapid change in environmental parameters such as seasonal or larger scale fluctuations in

salinity in connection with monsoonal type climates or variations in freshwater discharge of rivers. Under such circumstances fresh- and brackish-water to marine faunas, both autochthonous and partly even in life position, can become mingled in one single bed.

The recognition of environmental condensation is relatively easy where ecologically incompatible faunas such as marine and freshwater elements are mixed. If this mixing involves faunas representing different brackish-water regimes, it is more difficult to recognize. Interpretation of such condensed faunas as relics of a single former community will lead to erroneous conclusions with regard to faunal composition, diversity, and evenness and consequently to incorrect ecological inferences (see also Peterson 1977).

Recognition of environmental condensation is therefore crucial for any ecological analysis of Recent and ancient faunas. The following features may facilitate the recognition of environmental condensation:

- (1) differences in sediment fill of shells;
- (2) preservational differences (e.g. degree of abrasion, breakage, encrustation) where they are not due to differences in life habits (such as infaunal versus epifaunal);
- (3) a less pronounced repetition of assemblages;
- (4) ecological incompatibility; and
- (5) morphological differences among individuals of the same species, such as co-occurrence of dwarfed and normal-sized, or thin- and thick-shelled individuals.

Environmental condensation played a significant role in shaping the faunal assemblages of the Bear River Formation.

BIOSTRATINOMIC AND SYNECOLOGICAL ANALYSIS OF THE BENTHIC FAUNA

Methods of study

Most of the fossiliferous part of the exposure was measured in detail and eighty-six bulk samples representing over 10,000 specimens of the benthic fauna were collected. The samples were broken up in the laboratory and the fossils counted as described in Fürsich (1977). In addition, the percentage of fragmentation among shells was noted and the right/left valve ratio calculated. Where possible, the size of the dominant faunal elements (*Ursirivus*, *Pyrgulifera*, *Veloritina*) was measured. Two aspects of faunal diversity were calculated: species



TEXT-FIG. 3. Typical example of *in situ* reworked shell bed. Bear River Reference Locality. Polished section, $\times 1$.

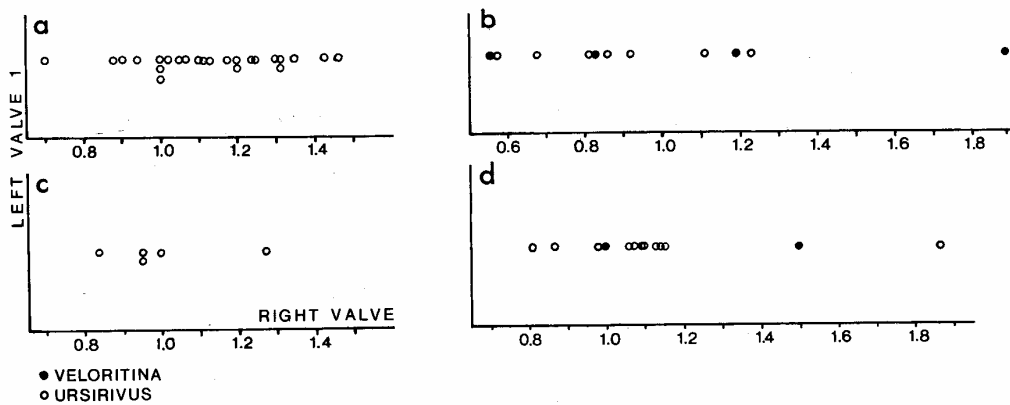
richness, expressed by the number of species present, and evenness which was calculated as $D = 1/\sum p_i^2$ whereby p_i is the relative frequency of the i th species (MacArthur 1972, p. 197). As diagenetic distortion of the fauna can be excluded with confidence (aragonitic faunal elements are invariably preserved, although aragonite has been replaced by calcite or silica) and selective transport was not a major factor, the fossil assemblages can be regarded as relics of former communities. Samples from individual beds frequently contain both fresh- and brackish-water elements, which were analysed separately.

Biostratinomy

The most conspicuous features of the Bear River Formation are the shell beds. Varying in thickness between 3 and 40 cm, they are usually packed with shells of bivalves and gastropods (text-fig. 3). Most shells are disarticulated; only 4 to 12% of brackish-water bivalves in the various associations (see below) are still articulated. This figure is higher for freshwater unionids: over 90% may still be articulated in individual samples. Only very rarely are individuals encountered in life position: the unionids *Loxopleurus* and *Protelliptio* occur predominantly in growth positions within two beds, the corbulid *Ursirivus* in another. In most shell beds a large proportion of the fauna is fragmented, in particular small specimens. In shell beds dominated by brackish-water bivalves estimated fragmentation percentage is generally in the range of 75 to 95; only rarely the percentage is 10 to 50. In contrast, shell beds dominated by freshwater elements have a lower fragmentation percentage, usually between 50 and 75, occasionally even zero.

The dense packing in most shell beds is expressed by a variety of biofabrics. Particularly common are nesting (text-fig. 3) or small-scale oblique imbrication. In contrast to the usual random orientation of shells within the shell bed, shells exhibit a preferred convex-up orientation near the top. The size range of shells and shell fragments is very large in most shell beds and individual species show often bi- or even polymodal size/frequency distribution patterns. The right/left valve ratios of dominant faunal elements (*Ursirivus*, *Veloritina*) are surprisingly close to 1 in most samples (text-fig. 4).

The matrix of many shell beds is not homogeneous. For example, in a silt or clayey-silt matrix, silty carbonaceous clay may be found under shells, in pockets, or as thin discontinuous or rarely continuous layers.



TEXT-FIG. 4. Right/left valve ratios of *Ursirivus pyriformis* and *Veloritina durkeei* in samples representing four subsets of the brackish-water *U. pyriformis* association. Minimum count per sample, 25. a, *U. pyriformis*/*Pyrgulifera humerosa* subset; b, *U. pyriformis*/*V. durkeei* subset; c, *P. humerosa* subset; d, *U. pyriformis*/*Crassostrea soleniscus* subset.

Discussion

At a first glance the shell beds appear to have undergone extensive transport resulting in significant distortion of original benthic communities. The high percentage of fragmentation, the largely disarticulated valves, and mixing of fresh- and brackish-water faunas as well as biofabrics clearly indicate reworking of the shells. However, the biostratigraphic data do not support extensive lateral transport: lack of size sorting, bimodal size/frequency distributions, and the right/left valve ratios all favour within habitat reworking. Faunal mixing was most likely caused by rapidly changing environmental conditions rather than by lateral mixing, and accentuated by local reworking. The case for environmental condensation is strengthened by the occurrence, in some of the shell beds, of 3- to 5-mm thick layers of silty clay that contain only freshwater species whilst the remainder of the bed consists of largely or only brackish-water species. During preparation of the shell beds, these thin layers could not be separated effectively from the rest, leading to samples that exhibit a mixed fauna.

Another example of environmental condensation is a bed of shelly dark-grey silty clay in which large *Pyrgulifera* and articulated *Ursirivus*, some in life position, are found between a host of small disarticulated *Ursirivus* and freshwater gastropods. In this case, at least three different environmental situations are recorded: a freshwater environment represented by the *Lioplacodes stachei* association (see below); a marginal brackish environment represented by juvenile members of the *Ursirivus pyriformis* association that were killed off before reaching maturity; and a more favourable brackish environment in which members of the *U. pyriformis* association reached normal adult size.

Differences in the matrix and faunal composition within single shell beds show that they represent a period of time during which sedimentation regime and environmental conditions changed at least once, if not several times. The extensive reworking was most likely caused by waves in connection with storms. Accordingly, the shell beds are interpreted to represent an environment below fair weather, but above storm-wave base, and thus not exposed to constant reworking as evidenced by the lack of widespread abrasion and the, albeit rare, individuals preserved in life position.

As the biostratigraphic analysis shows, the fauna has not undergone significant lateral transport and can be taken to represent relics of former benthic communities. Two problems, however, remain. First, how far did the extensive breakage act selectively, thereby distorting the original relative abundance of taxa with hard parts? Apart from *Brachidontes multiliniger* and *Crassostrea soleniscus* all brackish-water species have relatively thick shells and even small specimens appear fairly sturdy. The likelihood of fragmentation not only depends on shell size and thickness, however, but also on shell structure and crystal size, and it is very difficult to evaluate the combination of these features with regard to breakage. Observations on shell beds indicate, as one would expect, that small individuals have indeed undergone more breakage than large ones (see Hallam 1967) and thus distorted size frequency curves to some degree. The fact that in twenty out of twenty-four samples of the *U. pyriformis* association right valves are more numerous than left valves, although usually only barely so, probably does not reflect selective transport as the species is nearly equivalved; it is more likely that left valves were slightly more prone to fragmentation than right valves.

No differences with regard to fragmentation were noted between *Veloritina*, *Ursirivus*, and *Pyrgulifera*. In the case of the extremely thin *Brachidontes* and the thin to moderately thick *Crassostrea*, differential breakage was taken into account when the relative abundance of species was established. Nearly all freshwater gastropods were small and thin shelled, in contrast to the large and thick-shelled unionids. However, in both groups the percentage of fragmented shells was relatively low and apparently none of the two groups experienced preferential breakage, except that in most gastropods parts of the aperture and last whorl were damaged.

The second problem is the vertical mixing of different communities which may drastically alter faunal composition and diversity (e.g. Peterson 1977; Fürsich 1978). The fresh- and brackish-water faunas are separated relatively easily, but what about environmental condensation within the fresh- or brackish-water regime? Of the eight brackish-water species only three (*Ursirivus*, *Veloritina*, and *Pyrgulifera*) are abundant, two more occur in moderate to low numbers (*Brachidontes*, *Crassostrea*), whilst the remaining three are rare. The three abundant species and *Crassostrea* recur in sets with different relative abundances and these sets have been grouped into associations. The low and fairly

constant diversity, the lack of preservational differences, and ecological links between species (e.g. the large size of *Veloritina* in the *U. pyriformis*/*C. soleniscus* subset as opposed to its predominantly small size in the *P. humerosa* subset) do not favour extensive environmental condensation within the brackish regime. Furthermore, the salinity range represented by the brackish fauna is thought to be relatively small.

In the freshwater fauna five recurring sets of species were recognized, four of which are closely related and differ largely in the relative abundance of dominant species. There is no evidence to suggest or discount condensation of different faunas.

THE BRACKISH-WATER FAUNA

As has been demonstrated above, the benthic fauna of the Bear River section represents relics of former communities. In the following, five repetitive sets belonging to two associations (Table 2) are

TABLE 2. Composition of the brackish-water associations and subsets. EC—epifaunal cemented; SI—semi-infaunal; SHI—shallow infaunal; EM—epifaunal mobile; S—suspension-feeder; H—herbivore; HD—herbivorous detritus-feeder.

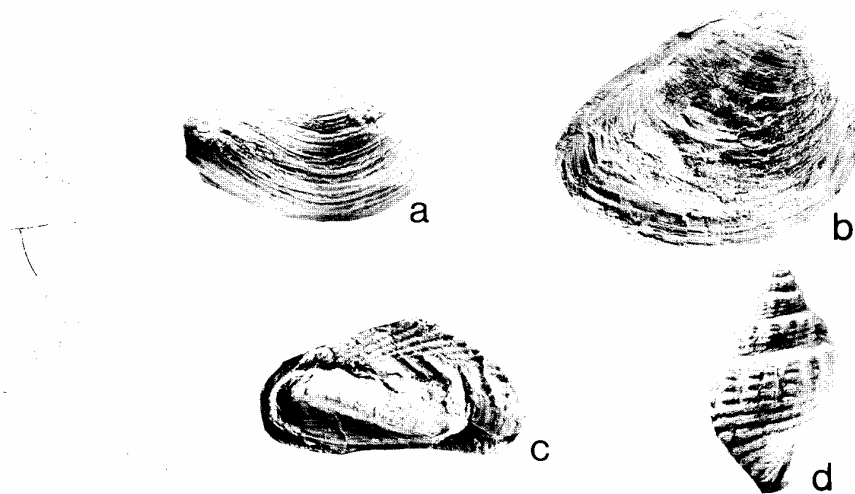
	Rel. abundance	Presence percentage	Rank position	Life habit	Feeding mode
A. <i>Crassostrea soleniscus</i> association (1 sample; 73 specimens)					
<i>C. soleniscus</i>	100	100	1-0	EC	S
<i>Ursirivus pyriformis</i> association:					
B. <i>U. pyriformis</i> / <i>C. soleniscus</i> subset (11 samples; 1054 specimens)					
<i>U. pyriformis</i>	66.0	100	1-1	SHI	S
<i>Veloritina durkeei</i>	15.4	100	2-4	SHI	S
<i>Pyrgulifera humerosa</i>	13.5	100	2-7	EM	HD
<i>C. soleniscus</i>	3.4	100	3-8	EC	S
<i>Brachidontes multilinigera</i>	0.8	18.2		SI	S
C. <i>U. pyriformis</i> / <i>V. durkeei</i> subset (8 samples; 907 specimens)					
<i>U. pyriformis</i>	67.8	100	1-1	SHI	S
<i>V. durkeei</i>	21.3	100	1-9	SHI	S
<i>P. humerosa</i>	10.2	87.5	3-0	EM	HD
<i>B. multilinigera</i>	0.4	25		SI	S
<i>Rhytophorus meeki</i>	0.1	12.5		EM	H
corbulid sp. A	0.1	12.5		SHI	S
D. <i>U. pyriformis</i> / <i>P. humerosa</i> subset (24 samples; 2,154 specimens)					
<i>U. pyriformis</i>	69.6	100	1-0	SHI	S
<i>P. humerosa</i>	22.1	100	2-0	EM	HD
<i>V. durkeei</i>	7.4	70.8	3-1	SHI	S
<i>B. multilinigera</i>	1.3	20.8		SI	S
corbulid sp. A	0.2	4.1		SHI	S
<i>Zaptychius haldemani</i>	0.04	4.1		EM	H
<i>R. meeki</i>	0.04	4.1		EM	H
E. <i>P. humerosa</i> subset (13 samples; 761 specimens)					
<i>P. humerosa</i>	75.9	100	1-0	EM	HD
<i>U. pyriformis</i>	20.1	92.3	2-2	SHI	S
<i>V. durkeei</i>	4.2	76.9	3-2	SHI	S
<i>B. multilinigera</i>	2.9	38.4		SI	S
<i>R. meeki</i>	0.6	15.4		EM	H
corbulid sp. A	0.3	7.7		SHI	S

briefly described and interpreted ecologically with particular regard to their salinity ranges. The sets were defined by using presence/absence as well as relative abundance data. The dominant faunal elements are shown in text-fig. 5.

The Ursirivus pyriformis association

The U. pyriformis/C. soleniscus subset. Represented by eleven samples and 1,054 specimens, this subset is dominated numerically by the corbulid *U. pyriformis*, followed by the corbiculid bivalve *V. durkeei* and the gastropod *P. humerosa*. *C. soleniscus* represents only 3.4% of the fauna, but is present in each sample. The mean number of species is 4.3. Only 4.4% of the bivalves are articulated and fragmentation varies between 75 and 95%. The subset occurs in shell beds; the matrix ranges from clayey silt to silty micrite. In one sample, coal fragments were common. The mean right/left valve ratio was 1.18 for both *Ursirivus* and *Veloritina* (text-fig. 4). The size distribution of *Ursirivus* was measured in four samples and was invariably bimodal with one peak at 4–6 mm height and the other, broader, at 18–24 mm. Both peaks were pronounced in three cases, while in the fourth the larger size range dominated by far. For *Veloritina* and *Pyrgulifera*, the size distribution could be established in one case each; the two species also exhibit a bimodal distribution pattern with peaks at 3–6 and 15–21 mm in diameter (*Pyrgulifera*), and 5–10 and 25–40 mm height (*Veloritina*). In both cases the larger size group dominated. *Veloritina* reaches a relatively large size in most samples. *Brachidontes*, occurring only in two samples, reached its largest size within the Bear River section within one sample, but is small in the second. In the eleven samples of the subset, freshwater faunal elements ranged from 0 to 25% of the total fauna with a mean of 6.6%.

The U. pyriformis/V. durkeei subset. A second subset occurring in eight samples with 907 specimens was also dominated by *U. pyriformis*, followed by *V. durkeei*. *P. humerosa* occurs in seven of the eight samples and constitutes 10.2% in terms of relative abundance. The remaining three species (*B. multilinigera*, *Rhytophorus meeki*, and the corbulid sp. A) are rare and occur only in few of the samples. The mean number of species in the association is 3.4. Of the bivalves, 11% are articulated; the fragmentation percentage ranges from 50 to 95 and is 90 for most samples. The sediment is either clayey silt, silty clay, or silty limestone (in one case with plant fragments) and the shell density is high in all cases. The mean right/left valve ratio is higher than in the preceding subset, both for *Ursirivus* (1.26) and *Veloritina* (1.51), in the latter case possibly indicative of either selective transport or breakage.



TEXT-FIG. 5. Dominant brackish-faunal elements of the Bear River Formation. a, *Ursirivus pyriformis* (Meek); b, *Veloritina durkeei* (Meek); c, *Brachidontes multilinigera* (Meek); d, *Pyrgulifera humerosa* (Meek); all $\times 1$. Bear River Reference Locality.

The size/frequency distribution of *Ursirivus* is bimodal in four cases with the smaller size group usually more pronounced; in one case, only one peak, at 3–6 mm is present. A similar pattern (one bimodal, one unimodal) is exhibited by *Veloritina*. *Brachidontes* is small to tiny in all samples. *Veloritina* exhibits a wide size range except in one sample where all individuals are tiny. In this particular sample, all other faunal elements are equally of small size. The percentage of freshwater elements in the total fauna of each sample ranges from 0 to 60 with a mean of 13.1.

The U. pyriformis/P. humerosa subset. The *U. pyriformis/P. humerosa* subset is very widespread in the Bear River section, represented by twenty-four samples and over 2,000 individuals. *U. pyriformis* is by far the dominant species followed by *P. humerosa* and *V. durkeei*. The remaining four species are rare (corbulid sp. A and the gastropods *Zptychius haldemani* and *R. meeki*) or encountered occasionally (*B. multilinigera*). The mean number of species is 3.1.

Of the bivalves, 11.5% are articulated; percentage of fragmentation varies from 30 to 95 and in most samples is close to the latter. In one sample, *U. pyriformis* was found in life position. The mean right/left valve ratio of specimens of *Ursirivus* is 1.18 with individual values ranging from 1.0 to 1.41 (text-fig. 4). The sediment range in which the *U. pyriformis* subset occurs is like that of the two preceding subsets except that about 16% of the samples occur in silt. About 20% of the sediments are carbonaceous containing either plant debris or wood fragments.

The size/frequency distribution of *Ursirivus* could be established in eighteen samples. Except in one case, where only small individuals are present, the curves are bimodal. Both size clusters are either roughly equal or show a dominance of smaller forms. The size/frequency distribution of *Pyrgulifera* was unimodal in one case, most specimens belonging to the 12 to 21 mm size range, and polymodal in a second case with peaks at 3–6 mm (pronounced), 12–15 mm, and 24–27 mm in diameter. *Ursirivus* and *Pyrgulifera* are generally large, whilst *Veloritina* is small in some samples and occurs in a wide size range in others. In some samples, all specimens of *Ursirivus* are small as are all other faunal elements. *Brachidontes* is tiny in one sample, but relatively large in others. The relative abundance of freshwater elements in samples ranges from 0 to 89.5% with a mean of 19.9%.

The P. humerosa subset. Seven hundred and sixty-one specimens in thirteen samples constitute the subset which is strongly dominated by the pleuroceratid gastropod *P. humerosa*. *U. pyriformis* is also common, occurring in all but one sample. The remaining four species (*V. durkeei*, *B. multilinigera*, *R. meeki*, and corbulid sp. A) are all uncommon or rare. In individual samples, two to five species occur; the mean number of species is 3.3. Of the bivalves, only 9.5% are articulated. The right/left valve ratio of *Ursirivus*, measured in five samples, is extremely close to one (mean 1.1) with individual values ranging from 1.0 to 1.33. The percentage of fragmented shells varies from 10 to 95 but is usually between 50 and 90.

Most samples occur in argillaceous silt or calcareous siltstone; some are found in silt, silty clay, or siliceous fine sandy siltstone. Two samples were rich in plant debris; bioturbation (*Chondrites*-like burrows) was encountered in one case.

In three samples, the size/frequency curves of *Ursirivus* were bimodal, with small specimens strongly dominating. In contrast, *Pyrgulifera* was represented predominantly by large specimens, three out of the four samples having a bimodal distribution pattern, the fourth a unimodal one. In general, specimens of *Ursirivus* often did not reach maximum size. Specimens of *Brachidontes* and *Veloritina* are small or tiny in all except one sample. Freshwater elements constitute from 1.5 to 87% of the total fauna of individual samples with a mean of 51.6.

The Crassostrea soleniscus association

Only represented by seventy-three specimens in one sample, the *C. soleniscus* association nevertheless appears to represent a true recurring association, as it has been mentioned from several horizons at different localities in the Bear River Formation, usually in thin, mono-, or near monotypic shell layers. At the Bear River locality, *C. soleniscus* alone occurs near the top of the measured section in a silty clayey limestone. The oysters occur in thin patches not more than 10 cm high and are preserved *in situ*. Over two-thirds of the shells are articulated and encrust each other. Life orientation of the specimens was horizontal to oblique. The shells of *Crassostrea* are thin to moderately thick and relatively small (most specimens being less than 7 cm in height). In contrast to most Recent or fossil oyster patch reefs, the shells are not encrusted or bored. There is no freshwater fauna associated with the oysters.

Discussion

Apart from the monotypic *C. soleniscus* association, the remaining four sets of species are similar in composition and are best grouped within a single association, the *Ursirivus pyriformis* association.

Within this major association, however, the relative abundance of individual species varies considerably. Samples in which *Ursirivus* strongly dominates are found as well as samples in which *Pyrgulifera* accounts for more than 80% of the fauna. *Crassostrea* occurs only in some samples. *Veloritina* accounts for a quarter of the individuals in some samples, but is rare in others.

Among marine ecologists there are two schools: one which regards marine benthic communities as discrete entities with sharp boundaries, and one which recognizes only species gradients and regards communities as artificial subdivisions of such gradients (e.g. Mills 1969). Community boundaries are usually shaped by the nature of environmental gradients. Sharp gradients such as the sudden change from a soft to a hard substrate will result in discrete community boundaries, weak gradients in turn will result in gradual replacement of species and therefore at most in blurred boundaries.

Within the brackish-water faunas from the Bear River relative abundance and, to some extent, species composition changed along a gradient of an overriding ecological parameter. In an attempt to learn more about this parameter, the *U. pyriformis* association was subdivided into four subsets which are artificial in that they grade into each other, but are interpreted as occupying different positions along a continuous environmental gradient. Thus, we do not suggest that these subsets represent relics of discrete communities. They are simply the means by which we can illustrate changes in community composition and structure along an environmental gradient. Indeed, that these subsets appear to have occupied different positions along an environmental gradient is supported by the fact that size/frequency distribution, size range, diversity, and percentage of freshwater elements in samples differ systematically between the various subsets.

Autecology. All species could apparently tolerate low salinities as indicated by their close association with non-marine sediments and faunas.

Ursirivus pyriformis (text-fig. 5a) is a nearly equivalve corbulid with a tapering posterior. This, and the presence of a shallow pallial sinus (Vokes 1945) suggests that the bivalve lived as a shallow burrower in the sediment with the anteroposterior axis in a more or less vertical position. Like other corbulids it was a suspension-feeder. Corbulids have several adaptations (such as being able to close their valves very tightly) to withstand environmental fluctuations, especially with regard to salinity, oxygen level, and temperature (e.g. Lewy and Samtleben 1979) and are consequently eurytopic. This is true not only of Recent, but also of fossil species which are particularly common in marginal marine environments (e.g. Fürsich 1981) where they typically occur in large numbers in low diversity assemblages. Being slow burrowers they are preferentially found in low-energy environments with fine-grained substrates, and this was clearly also the preferred habitat of *U. pyriformis*.

Corbulid sp. A is a small, 3–4 mm long species that exhibits the sharp posterior ridge seen in many corbulid species. As no hinge line was seen, a generic designation was impossible. Most likely this fairly rare species lived, like other corbulids, as a shallow infaunal suspension-feeder.

The corbulid bivalve *V. durkeei* (text-fig. 5b) belongs to a family whose Recent members either live in fresh or brackish waters. The pallial line of this trigonal species is posteriorly truncated and the species most likely possessed a pair of short siphons and lived as a suspension-feeder close to the depositional interface. Species of *Veloritina* and *Corbicula* are characteristic of marginal marine environments elsewhere in the Cretaceous of the Western Interior Basin (e.g. in the Fox Hills Formation of northern Colorado) and may there form monotypic shell beds. In the Bear River Formation, *V. durkeei* is generally less abundant than *Ursirivus* or *Pyrgulifera*.

The oyster *Crassostrea soleniscus* lived in small clusters as an epifaunal-cemented suspension-feeder. Elsewhere (e.g. in the Cenomanian Woodbine Formation of Texas; Stephenson 1952) it reaches a considerably larger size and may form extensive patch reefs. The relatively small and thin valves of the Bear River occurrence as well as the small size of the patches most likely indicate that there the species lived close to the limit of its environmental range.

B. multilinigera (text-fig. 5c) is extremely thin-shelled and consequently frequently fragmented. Judging from its cross-sectional shape, it appears to have lived semi-infaunally as an endobysate suspension-feeder. The small to tiny size of most specimens compared with occurrences elsewhere in the Cretaceous suggest a largely unfavourable environment for this species.

Of the three gastropods regarded as having lived in brackish rather than freshwater, *P. humerosa*

(text-fig. 5d) is by far the most abundant, whilst *R. meeki* and *Z. haldemani* are rare. *P. humerosa* most likely fed on plant detritus. Little is known about the ecology of Mesozoic gastropods and more detailed interpretation would be speculative.

Nature of environmental gradients. It is clear that the fauna lived on or in a moderately soft substrate. No specific substrate preferences have been noted, but all associations occur in a range of fine-grained substrates, and individual species appear to have been fairly eurytopic. The scarcity of sedimentary structures, the presence of laminated shales, and the fine-grained nature of the sediments indicate a low-energy environment except when, during storms, the wave base was lowered and shells accumulated in beds. This does not necessarily imply a great water depth. On the contrary, the presence of root horizons and coal layers suggests deposition in water depth of less than 5 m for most of the time.

Other environmental parameters exerting a major influence on the distribution of benthic faunas are the oxygen level, variations in food supply, temperature, and salinity. There are no indications of anoxic conditions at or near the sediment/water interface with the possible exception of the laminated, often carbonaceous silty clays and clayey silts that are usually devoid of fauna and may well represent periods of poor oxygenation. Variations in temperature are difficult to assess, but may have been pronounced in the shallow extensive water body represented by parts of the Bear River Formation. Such variations would favour eurytopic, opportunistic species, but exclude most stenotopic forms. Variations in food supply, characteristic of estuaries, are apparently less pronounced in lagoons, which are frequently rich in nutrients (e.g. Mee 1978). Marginal marine environments are strongly influenced by extreme salinity values or salinity fluctuations. The close association of freshwater and marine species in the Bear River Formation shows that salinity was the major factor controlling distribution and growth of the benthic fauna possibly amplified by fluctuations in temperature, resulting in a high stress environment. Coal beds, freshwater gastropods, unionid bivalves, and the absence of features indicative of hypersaline conditions suggest that salinity values were lower than normal marine and that one end of the salinity spectrum was represented by the freshwater environment. As stenohaline faunal elements are totally lacking (this is true also of the microfauna where foraminifera are absent and only fresh- and brackish-water ostracods occur) the highest salinity values probably were considerably below normal marine values. This is not surprising as even the offshore Skull Creek Seaway supported only a restricted fauna possibly influenced by low salinities (e.g. Eicher 1962). Considering the very low species diversity of all samples, it is safe to assume that the faunas did not live in waters of a salinity much higher than the mid-mesohaline regime (about 12‰).

Distribution of the fauna along the salinity gradient. Within meso- and oligohaline regimes of Recent estuaries, the fauna can be classified as euryhaline opportunists or estuarine endemics with freshwater species encroaching within the 1 to 2‰ range (Boesch 1977). Considering that *U. pyriformis*, *V. durkeei*, and *P. humerosa* are confined to the marginal marine Bear River environments and are not known from anywhere else in North America, it is most likely that they were endemic within this salinity range and specifically adapted to life in lowered and fluctuating salinity regimes. This is corroborated by the fact that all these species reach a large size and are fairly thick shelled. In contrast, *B. multilinigera* and *C. soleniscus* are known to occur in more saline waters elsewhere and, when occurring in the Bear River Formation, are relatively small and thin-shelled. They may be more correctly classified as euryhaline opportunists close to their environmental limit.

Using information on absolute size of individual taxa in connection with data on species richness and evenness, it is possible to arrange the five sets of species along a salinity gradient (text-fig. 6). Accordingly, the *U. pyriformis*/*C. soleniscus* subset occupies the upper end of the salinity scale, followed by the *U. pyriformis*/*V. durkeei* and *U. pyriformis*/*P. humerosa* subsets. These three subsets and the monospecific *C. soleniscus* association are thought to have occupied the lower part of the mesohaline regime, whilst the *P. humerosa* subset occupied the oligohaline regime. Within this proposed sequence the evenness declines as does species richness (except in the case of the *P. humerosa* subset). *Ursirivus* and *Veloritina* decrease in maximum size towards lower salinity whereas the size of *Pyrgulifera* remains unchanged. The proposed arrangement of associations is

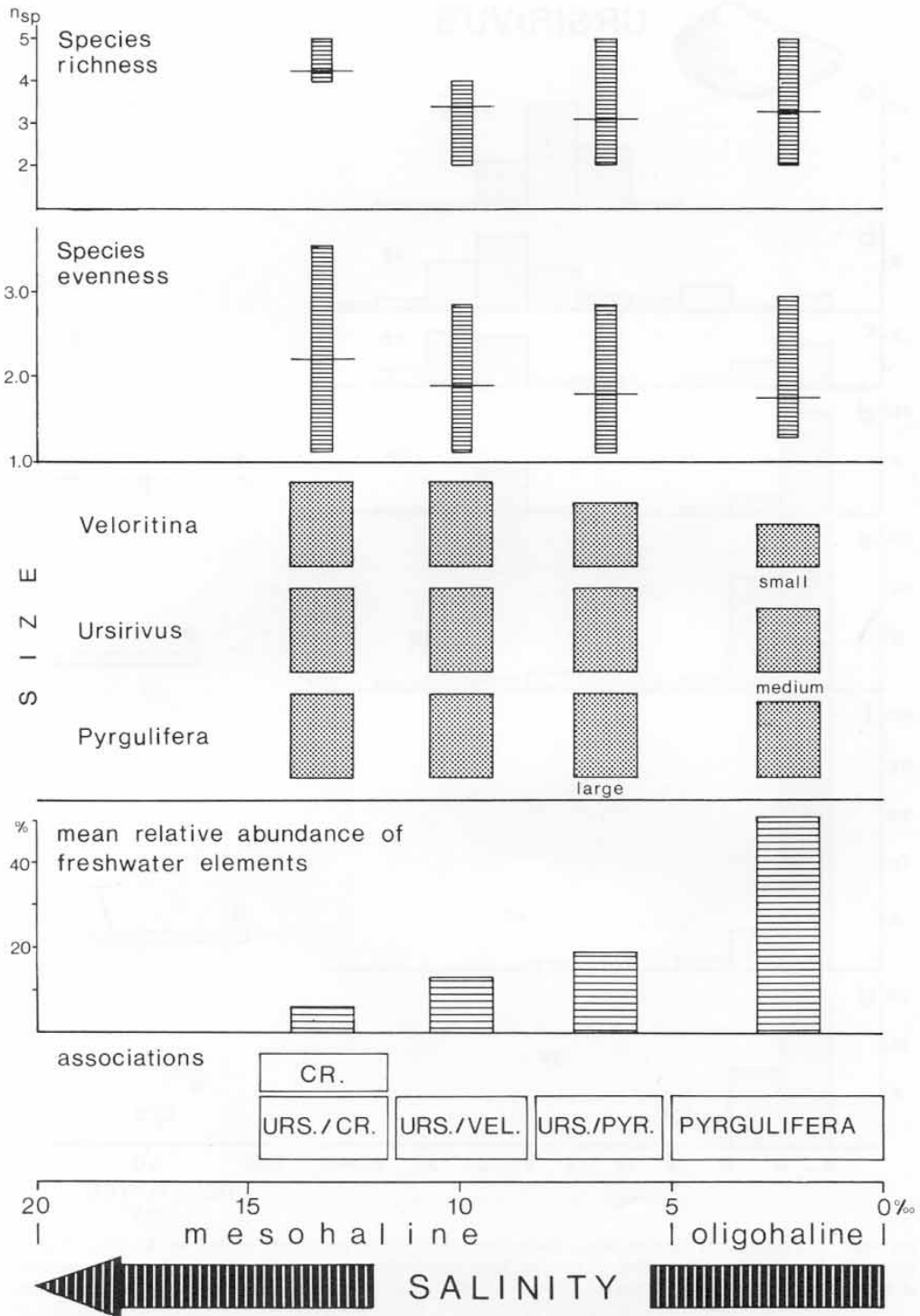
corroborated by the increase of the mean percentage of freshwater elements along the gradient, thus substantiating the decrease of marine influence. The exact position, along this gradient, of the *C. soleniscus* association is difficult to establish. According to its species richness and evenness values, it would have to occupy the zone closest to the freshwater edge. However, this seems unlikely, as *Crassostrea* was not found outside the *U. pyriformis*/*C. soleniscus* subset. The monospecific oyster patches more likely occupied a position near the upper part of the salinity range. The lack of other species may be caused by other factors than salinity. For example, the biogenic hard substrate would have prevented burrowers such as *Veloritina* and *Ursirivus*.

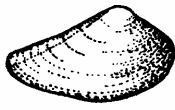
Lowered salinities versus salinity fluctuations: the significance of size/frequency curves. Recent environments rarely exhibit long-term stable salinity reductions. Fluctuations may be seasonal (variations in river discharge, monsoon-like rainy seasons), diurnal (caused by tides), or random (e.g. caused by tropical rain storms, removal of barriers). Interpreting size/frequency distribution patterns of dominant taxa, the wave length and amplitude of such fluctuations can be estimated. Text-fig. 7 shows variations in the size/frequency pattern of *Ursirivus*. *Veloritina* and *Pyrgulifera* show similar curves. The pattern is bimodal or unimodal and small or large individuals may dominate. The first mode is in the size classes 0–9 mm (*Veloritina*) or 3–9 mm (*Ursirivus* and *Pyrgulifera*), whilst the second mode lies between 24 and 40 mm (*Veloritina*), 15–27 mm (*Ursirivus*), and 12–21 mm (*Pyrgulifera*). The second size group is nearly always broader than the first one. The first mode most likely represents juveniles, whilst the second mode reflects adult populations. The size/frequency distributions do not include post-larval mortality, as those shells were too small to be recovered during the mechanical breaking up of the samples. Some individuals may be stunted, exhibiting extreme crowding of growth lines, but the majority are not. Compared with data from Recent bivalves (e.g. Hallam 1967) the smaller size group most likely represents one season's growth. Samples with only the smaller size group present thus consist of individuals that were killed after roughly one year. The reason for the death was probably a drastic reduction in salinity and this would imply strong seasonal salinity fluctuations.

Size/frequency distribution patterns with a strong dominance of juveniles in the population can also be caused by biological factors, in particular predation. An example to indicate that predation may play a significant role in marginal marine environments is the high abundance of blue crabs feeding on oyster banks in Chesapeake Bay (Levinton 1982, p. 345). Within the Bear River faunas signs of predation are extremely rare (some cases of repaired shells have been found). Predators such as starfish are unrepresented by isolated skeletal elements. The second important group preying on mollusks are crustaceans, in particular crabs. They usually leave marks on the shell when prying them open which should be preserved in the fossil record. Apart from the very rare cases of repaired shells—obviously representing unsuccessful attacks by predators such as crabs—no shell damage indicative of predation was encountered. Another indication that at least some individuals were not killed by predation is that they are still articulated. Finally, the occasional occurrence of severe growth restrictions in larger individuals at the size represented by the juvenile peak (text-fig. 8) strongly suggests that environmental rather than biological factors caused the death of many individuals after one season's growth.

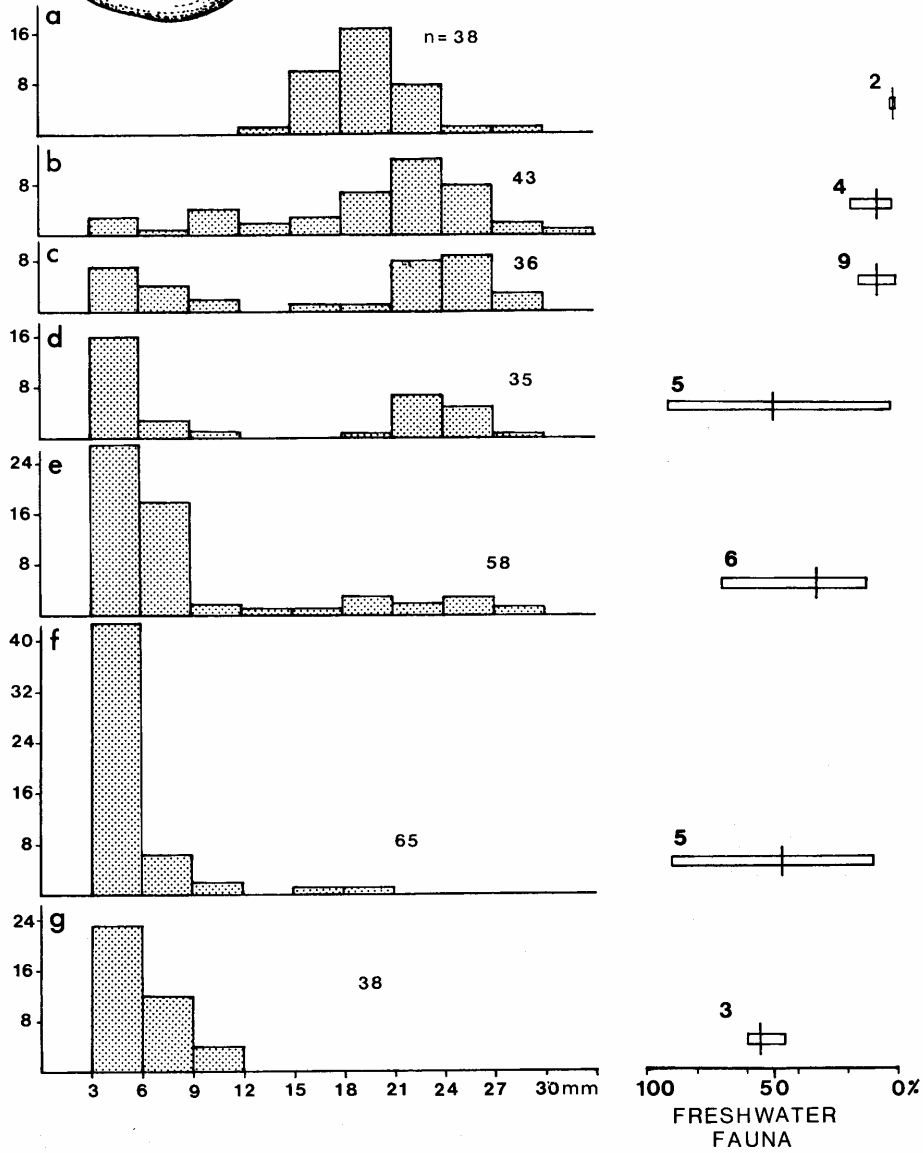
Another explanation of the size/frequency pattern would be migration of individuals from a nursery area to their adult habitat. This is apparently common among shallow water and intertidal

TEXT-FIG. 6. Inferred distribution of brackish-water associations along a salinity gradient. Note that species richness, evenness, and size of dominant species decline, whilst the relative abundance of freshwater elements in individual beds increases. For species richness and evenness both ranges and means are given. CR.: *Crassostrea soleniscus* association; URS./CR.: *U. pyriformis*/*C. soleniscus* subset; URS./VEL.: *U. pyriformis*/*Veloritina durkei* subset; URS./PYR.: *U. pyriformis*/*Pyrgulifera humerosa* subset; PYRGULIFERA: *P. humerosa* subset.

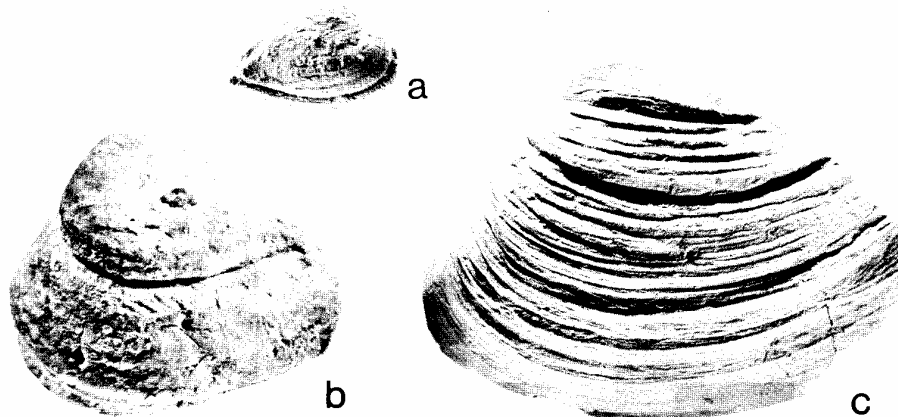




URSIRIVUS



TEXT-FIG. 7. Examples of size/frequency histograms of *Ursirivus pyriformis* related to the percentage of freshwater faunal elements in individual samples. Each histogram is representative of several samples (numbers at right side of text-fig). Note that the relative increase of large individuals is matched by a decrease in the relative abundance of freshwater faunal elements.



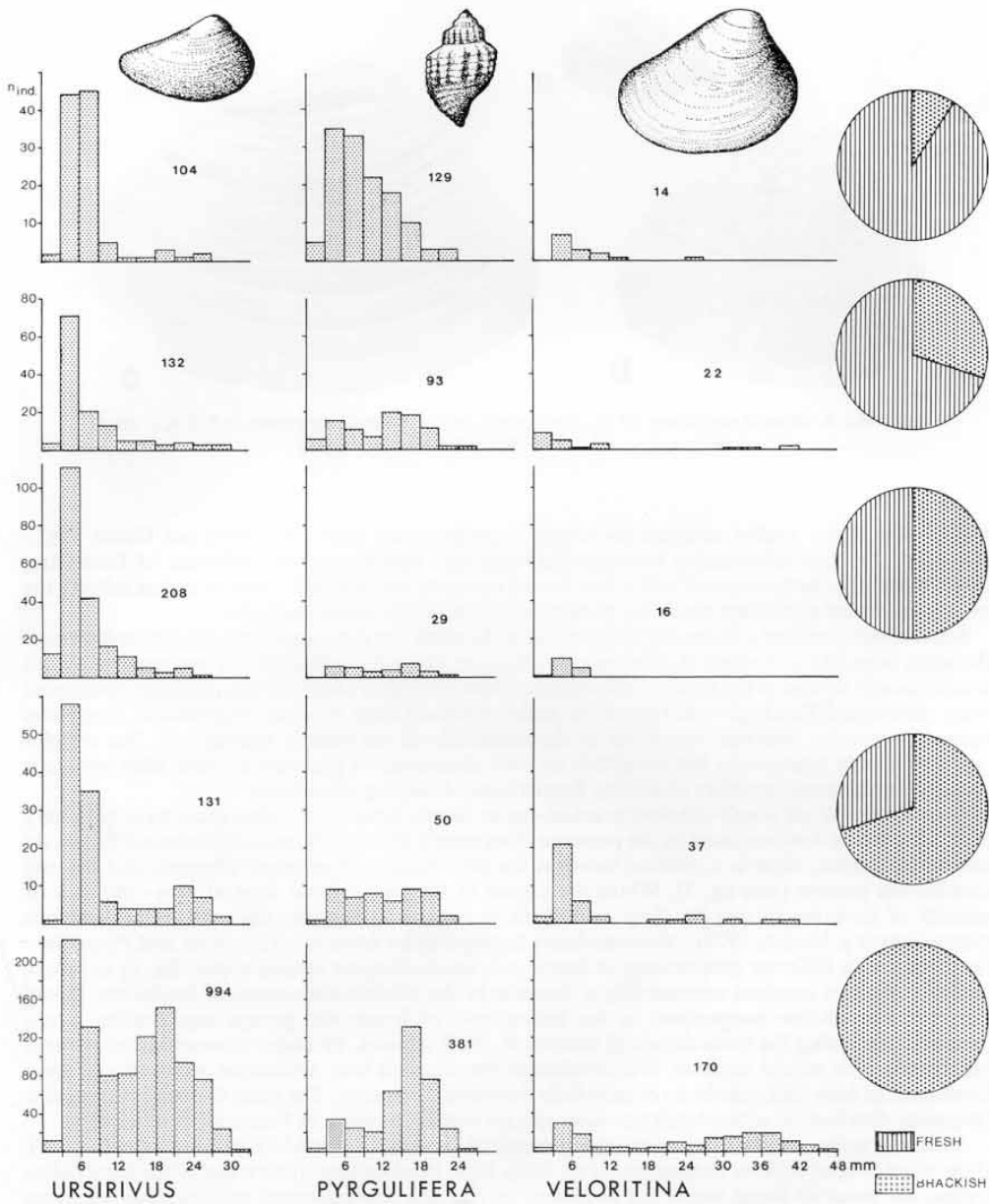
TEXT-FIG. 8. Growth restriction in *Ursirivus pyriformis*. *a*, juvenile specimen, $\times 3.5$; *b*, *c*, adult specimens, $\times 3.2$. Bear River Reference Locality.

species and by no means confined to mobile organisms (for recent summary see Cadée 1982). However, the clear relationship between size/frequency distribution and influence of freshwater (expressed by the percentage of freshwater faunal elements; see text-figs. 7 and 9) makes salinity the overriding factor explaining mortality patterns of the brackish-water mollusks.

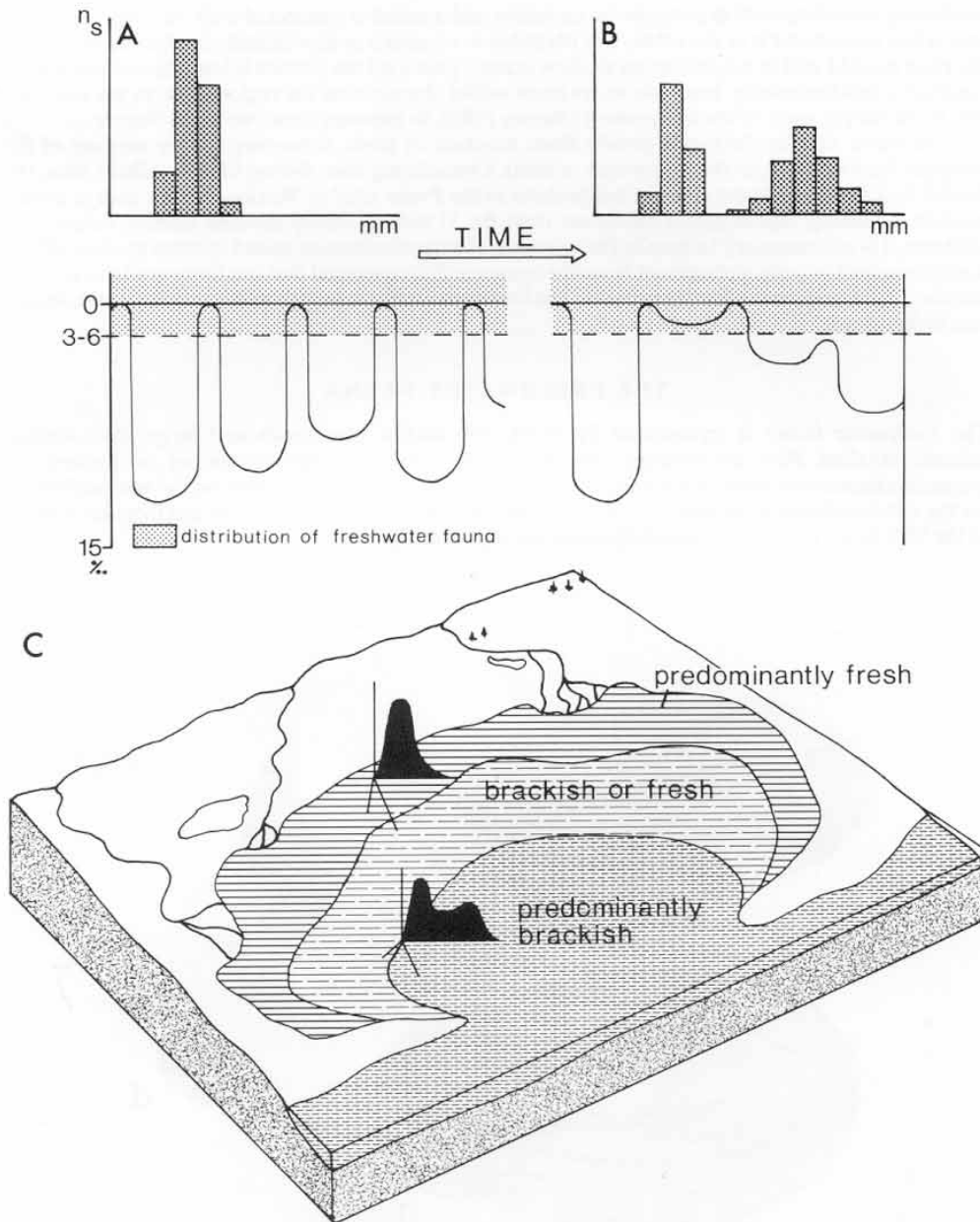
Some samples exhibit a unimodal distribution at the adult size range or a bimodal distribution with the adult population strongly dominating. In this case, the salinity fluctuation was apparently not severe enough to lead to the death of all animals. However, these samples have probably undergone some differential breakage resulting in an under-representation of small individuals. Numerous intermediate cases illustrate variations in the amplitude of the salinity fluctuations. No samples represent single generations but hundreds or even thousands of generations, and what we see is therefore the cumulative effect of salinity fluctuations of varying amplitudes.

In order to kill off a well-adapted brackish-water fauna, freshwater influx must have been very high. This can be demonstrated by the presence of an essentially autochthonous freshwater fauna. As one would expect, there is a relation between the percentage of freshwater elements and the size distribution pattern (text-fig. 7). Whilst the curves in text-fig. 7 show signs of bias—the lack or scarcity of juveniles in text-fig. 7*a-c* is difficult to explain in samples that represent numerous generations (e.g. Hallam 1972)—the cumulative histograms for *Ursirivus*, *Veloritina*, and *Pyrgulifera* from beds with different proportions of fresh- and brackish-water elements (text-fig. 9) are more realistic. Along a gradient representing a decrease in the relative abundance of freshwater faunal elements, the relative proportion, in the histograms, of larger size groups representing adults increases. Assuming the same degree of distortion, in all samples, by under-representation of small individuals, this would indicate that conditions for survival into adulthood were clearly more favourable in beds that exhibit no or only little freshwater influence. The main factor governing size frequency distribution of the brackish-water species would therefore be fluctuations in salinity.

Assuming salinity fluctuations to be largely seasonal, the following model is proposed (text-fig. 10): If the amplitude of salinity fluctuations were fairly high, ranging from freshwater to the mesohaline regime, the brackish fauna would not be able to survive and be represented only by juveniles. Were the fluctuations less pronounced, the brackish-water fauna might be able to survive seasonally reduced salinity values and be represented by juveniles and adults. Less pronounced fluctuations near the brackish/freshwater interface may also favour the establishment of a freshwater fauna over a longer period of time (text-fig. 10*b*). Text-fig. 10*c* presents a model of the water body most easily



TEXT-FIG. 9. Cumulative size/frequency histograms of the dominant brackish-water species arranged according to percentage of freshwater faunal elements in the same bed.

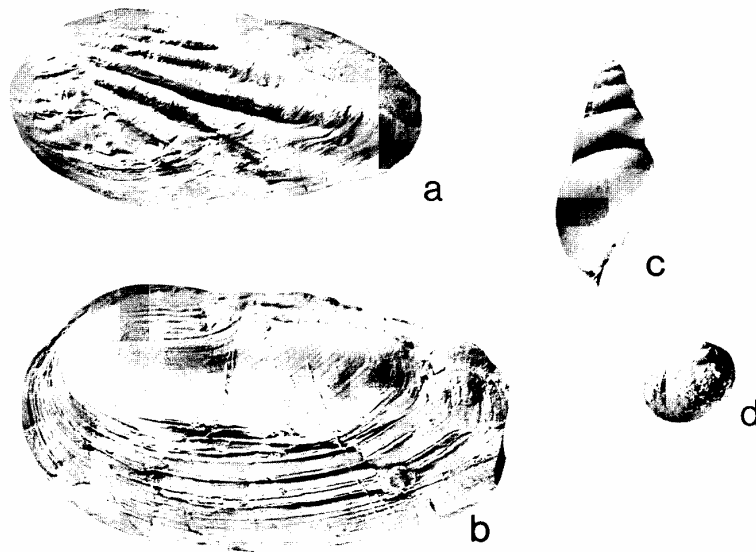


TEXT-FIG. 10. Model of the relationship between seasonal salinity fluctuations and size/frequency distribution of brackish-water species in an extensive embayment. A, model of salinity fluctuations and resulting histogram indicative of complete juvenile mortality; B, model of less regular salinity fluctuations resulting in histogram indicative of 'normal' juvenile mortality; C, palaeogeographic model of salinity zonation within an extensive embayment lacking barriers.

producing such distribution patterns: an extensive embayment is connected with the open sea at one end, while rivers enter it at the other. It is plausible to assume a predominantly freshwater mass near the river mouths and in neighbouring shallow areas—provided the climate is humid to subhumid. In contrast, a predominantly brackish-water mass would characterize the region close to the open sea and in the deeper parts of the embayment (Barnes 1980). In between these two areas there would be a zone in which salinity fluctuates greatly from brackish to fresh, depending on the amount of the seasonal freshwater input (be it by rivers or rain). Considering that, during Middle Albian time, the Skull Creek Seaway did not connect southwards to the Proto-Gulf of Mexico, but the area in southwestern Wyoming represented a cul-de-sac (text-fig. 1) with generally lowered salinity values even offshore, it is not necessary to invoke the existence of extensive barrier island systems to close off the highly brackish to fresh embayment from the open sea. It is envisaged that a salinity gradient without barriers could have been effective provided the freshwater influx was high and mixing of water masses was insignificant.

THE FRESHWATER FAUNA

The freshwater fauna is represented by small, thin-shelled gastropods and large, thick-shelled unionid bivalves. Five associations and one assemblage have been recognized on grounds of presence/absence and relative abundance of important taxa (Table 3). A modified χ^2 test performed on the relative abundances indicates that the associations are significantly different from each other at the 99% level. Dominant faunal elements are shown in text-fig. 11.



TEXT-FIG. 11. Dominant faunal elements of the freshwater. *a*, *Loxopleurus belliplicatus* (Meek), $\times 1$; *b*, *Protelliptio vetustus* (Meek), $\times 1$; *c*, *Lioplacodes stachei* (White), $\times 3$; *d*, *Mesoneritina naticiformis* (White), $\times 3$. Bear River Reference Locality.

TABLE 3. Composition of the five freshwater associations. EM—epifaunal mobile; SI—semi-infaunal; H—herbivore; S—suspension-feeder.

	Relative abundance	Presence percentage	Rank position	Life habit	Feeding mode
A. <i>Lioplacodes stachei</i> association (6 samples; 815 specimens)					
<i>L. stachei</i>	84.8	100	1.0	EM	H
<i>Mesoneritina naticiformis</i>	4.4	100	2.8	EM	H
<i>Protelliptio vetustus</i>	4.8	50		SI	S
<i>Campeloma macrospira</i>	3.4	33.3		EM	H
<i>Loxopleurus belliplicatus</i>	1.1	16.7		SI	S
<i>Parateinostoma occultum</i>	0.5	33.3		EM	H
' <i>Tornatellina</i> ' <i>isoclina</i>	0.5	33.3		EM	H
<i>Lymnaea nitidula</i>	0.4	33.3		EM	H
<i>Parateinostoma latense</i>	0.1	16.7		EM	H
B. <i>Lioplacodes stachei</i> <i>P. occultum</i> association (3 samples, 477 specimens)					
<i>L. stachei</i>	68.8	100	1.0	EM	H
<i>Pachychiloides macilentus</i>	21.9	100	2.3	EM	H
<i>Parateinostoma occultum</i>	5.2	100	2.7	EM	H
<i>P. latense</i>	2.9	100	4.0	EM	H
<i>Valvata praecursoris</i>	0.2	33		EM	H
<i>M. naticiformis</i>	0.2	33		EM	H
<i>Pachychiloides cleburni</i>	0.2	33		EM	H
<i>Protelliptio vetustus</i>	0.2	33		EM	H
C. <i>L. stachei</i> <i>Pachychiloides macilentus</i> association (14 samples, 2,607 specimens)					
<i>L. stachei</i>	71.1	100	1.2	EM	H
<i>Pachychiloides macilentus</i>	9.9	100	2.8	EM	H
<i>M. naticiformis</i>	10.3	85.7	3.4	EM	H
<i>Protelliptio vetustus</i>	2.5	64.3		SI	S
<i>V. praecursoris</i>	2.1	57.1		EM	H
<i>Goniobasis</i> sp.	0.8	14.3		EM	H
<i>C. macrospira</i>	0.7	42.8		EM	H
<i>Loxopleurus belliplicatus</i>	0.6	64.3		SI	S
<i>Viviparus couesi</i>	0.5	21.4		EM	H
<i>Lymnaea nitidula</i>	0.4	28.5		EM	H
<i>Parateinostoma occultum</i>	0.3	14.3		EM	H
<i>P. latense</i>	0.3	21.4		EM	H
<i>Pachychiloides cleburni</i>	0.1	7.1		EM	H
D. <i>M. naticiformis</i> <i>L. stachei</i> association (8 samples, 1,016 specimens)					
<i>M. naticiformis</i>	70.1	100	1.0	EM	H
<i>Lioplacodes stachei</i>	19.1	100	2.1	EM	H
<i>P. macilentus</i>	4.9	100	3.1	EM	H
<i>C. macrospira</i>	1.4	25		EM	H
<i>Protelliptio vetustus</i>	1.2	37.5		SI	S
<i>Pachychiloides cleburni</i>	1.1	25		EM	H
<i>Loxopleurus belliplicatus</i>	0.3	25		SI	S
<i>V. couesi</i>	0.3	25		EM	H
<i>P. chrysalis</i>	0.3	25		EM	H
<i>Lymnaea nitidula</i>	0.2	12.5		EM	H
<i>Parateinostoma occultum</i>	0.2	12.5		EM	H
E. <i>Pachychiloides chrysalis</i> association (4 samples; 692 specimens)					
<i>P. chrysalis</i>	53.5	100	1.5	EM	H
<i>M. naticiformis</i>	19.9	100	2.2	EM	H
<i>P. cleburni</i>	19.4	100	2.5	EM	H
<i>P. macilentus</i>	7.2	100	3.7	EM	H
<i>P. chrysalloideus</i>	1.0	25		EM	H
<i>Lioplacodes stachei</i>	0.4	50		EM	H

The Lioplacodes stachei association

In six samples with 815 specimens, the viviparid gastropod *L. stachei* represents over 80% of the fauna. Six other gastropods occur in low to moderate numbers (*Mesoneritina naticiformis*, *Campeloma macrospira*, *Parateinostoma latense*, *P. occultum*, *Lymnaea nitidula*, *Tornatellina isoclina*), only one of them (*M. naticiformis*) in all collections. Apart from the viviparid *C. macrospira* all gastropods are small to tiny (most of them not exceeding 1 cm in height). In contrast, the two species of unionids, *Protelliptio vetustus* and *Loxopleurus belliplicatus*, are large, measuring between 4 and 6 cm in height. They are more abundant than in other freshwater associations accounting for 4.8% (*P. vetustus*) and 1.1% (*L. belliplicatus*) in terms of relative abundance. The number of species varies from three to six; the mean number of species is 4.2.

Of the unionids, 50% are articulated. Percentage of fragmented shells ranges from 10 to 95, and in most samples is between 20 and 50. The association occurs in a range of sediments; in silty clays, silt, and, above all, in silty marls and limestones. Two samples are highly carbonaceous containing either coal fragments or plant debris. The percentage of brackish-water faunas in the total fauna ranges from 0 to 82, with a mean value of 15.3.

The Lioplacodes stachei/Parateinostoma occultum association

Three collections with 477 specimens were grouped in this association. *L. stachei* is the dominant species, followed by the pleuroceratid gastropod *Pachychiloides macilentus*. Two amnicolid gastropods, *Parateinostoma occultum* and *P. latense*, are also present in each sample, albeit in lower numbers. Three more gastropods (*Valvata praecursoris*, *M. naticiformis*, and *Pachychiloides cleburni*) are rare, as is the unionid *Protelliptio vetustus*. The number of species varies from five to six (mean 5.3). Fragmentation of shells ranges from 10 to 90%. Two collections are from argillaceous silt, the third from carbonaceous marly siltstone. The percentage of brackish-water elements in the total fauna ranges from 1.5 to 10.1 (mean 9.6%).

The L. stachei/Pachychiloides macilentus association

This is the commonest association in the freshwater regime, represented by 2607 specimens in fourteen collections. *L. stachei* is the dominant element followed by *M. naticiformis* and *P. macilentus*. Only *L. stachei* and *P. macilentus* occur in all samples. Eight gastropods occur rarely or sporadically only (Table 3), among them the relatively large *Viviparus couesi* and *C. macrospira*. Both unionid species are present with *Protelliptio vetustus* (2.5%) being far more common than *Loxopleurus belliplicatus* (0.6%). The number of species varies from four to nine with a mean of 6.1. 60.7% of the unionids are still articulated. Between 10 and 90% of the shells are fragmented (in most samples, however, not more than 20 to 50%). The fauna occurs in marly silts or calcareous siltstones. Over half the beds are carbonaceous with either abundant plant debris or coal fragments. In one case rootlets occur. The percentage of brackish elements of the total fauna of individual samples ranges from 0 to 85, with a mean of 15.6.

The M. naticiformis/Lioplacodes stachei association

In eight collections with 1016 specimens the neritid gastropod *M. naticiformis* dominates in terms of relative abundance followed by *Lioplacodes stachei* and *Pachychiloides macilentus*. The three species occur in all collections while six other gastropods (*P. chrysalis*, *P. cleburni*, *Parateinostoma occultum*, *Lymnaea nitidula*, *C. macrospira*, and *V. couesi*) and the two unionids are rare and occur only in one to three samples. The number of species varies from four to eight (mean 5.1). Only 25% of the unionids are articulated. The percentage of fragmentation ranges from 20 to 90 and most commonly is around 75%. In most samples the sediment is argillaceous silt, less commonly marly or calcareous siltstone. Nearly half the samples are carbonaceous containing plant debris or coal fragments. The percentage of brackish-water elements in individual samples is relatively high, ranging from 1.3 to 74%, with a mean of 38.9%.

The Pachychiloides chrysalis association

The *P. chrysalis* association differs drastically in species composition from the other associations. Found in four samples and represented by 692 specimens; it is dominated by the pleuroceratid gastropods *P. chrysalis*, *P. cleburni*, *P. macilentus*, and the neritid *M. naticiformis*. These four species occur in all samples, while the rare *Lioplacodes stachei* and *P. chrysalloideus* are found in only one or two collections. The number of species ranges from four to six (mean 4.8). Unionids are absent from this association. Fragmentation varies from 30 to 90%. The sediments are carbonaceous, non-calcareous, and range from argillaceous silt to silt and fine sandy siliceous siltstone. Two of the samples are bioturbated. The burrows consist of branching tubes, 1 mm in diameter, which are filled with dark, clayey silt. They resemble *Chondrites*, but their branching pattern is more irregular. The percentage of brackish forms within individual samples ranges from 6.9 to 24.7 (mean 16.9).

The Valvata praecursoris and corbulid sp. A assemblages

Found only in one sample, it is not known whether these assemblages represent recurrent associations. Occurring in low density in dark-grey shaley silty clay together with thin streaks of comminuted shell debris, the freshwater assemblage appears to be autochthonous. It consists of six species of small gastropods, with the tiny *V. praecursoris* most abundant (58.5%), followed by the amnicolid *Parateinostoma* cf. *altipsirale* (15.4%), the pleuroceratids *Pachychiloides chrysalis* (10.8%), and *P. chrysalloideus* (9.2%). *M. naticiformis* and *Parateinostoma occultum* account for the remaining 6.1%. Fish scales are found occasionally in the sediment that also contains a brackish-water assemblage (33% of the total fauna) that is dominated by the small corbulid bivalve sp. A (31.2%), followed by *Veloritina durkeei* (28.1%), *Brachidontes multilinigera* (25%), and *Ursirivus pyriformis* (15.6%). The two corbulid species are small, *Veloritina* and *Brachidontes* tiny.

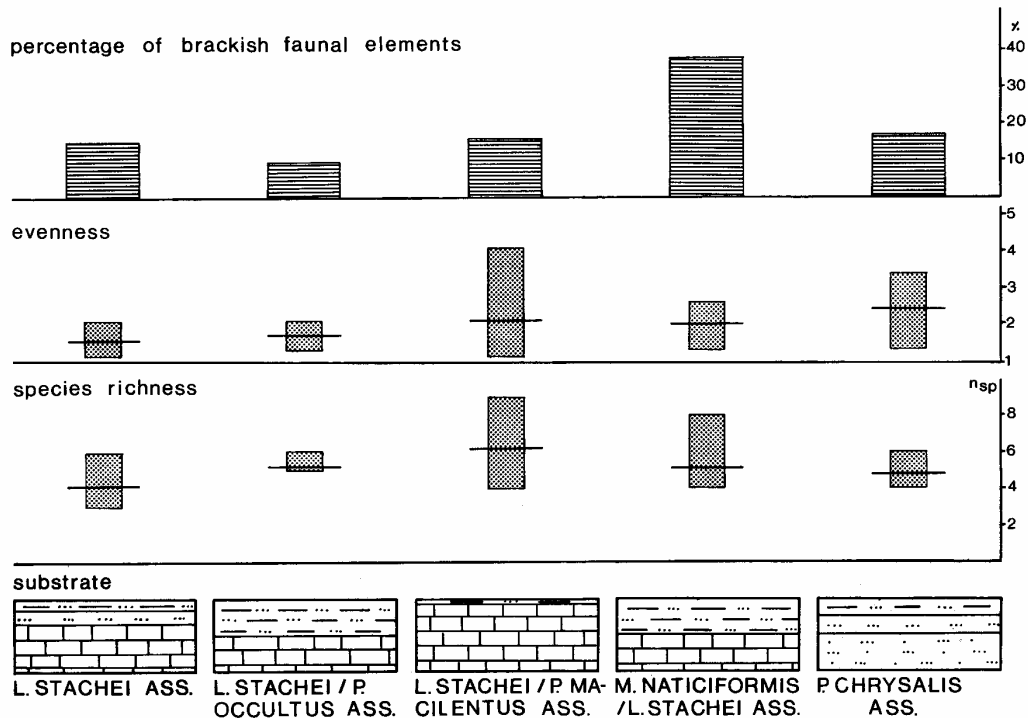
Discussion

Autochthonous nature of the freshwater associations. Few biostratigraphic data are available to indicate transport or the lack of it in the freshwater fauna. In most samples, unionid bivalves are predominantly articulated and in two cases they have been found in life position. Although transport of recently dead articulated unionids downstream into a nearshore area might appear plausible, it is unlikely considering the large and thick shells of both species (see also White 1895). The thin-shelled gastropods similarly underwent only little lateral transport, if any. The fragile shells would break very easily and the percentage of shell fragments would be much higher than it is. In most gastropods the aperture is damaged, but that can be explained by *in situ* reworking. Furthermore, the autecology of several species (see below) indicates that the fauna lived in the embayment and was not transported downstream from rivers. Finally, the pronounced relationship of some freshwater associations to silty limestones cannot be explained by transport. The freshwater fauna is therefore regarded as autochthonous or, at the most, parautochthonous.

Autecology. The unionids *Loxopleurus belliplicatus* and *Protelliptio (Plesielliptio) vetustus* exhibit features such as curved ventral margins and a well-expanded posterior which are more typical of species living in large lakes than in swiftly flowing rivers (e.g. van der Schalie 1938; Eager 1948; Tevesz and Carter 1980). Little is known about the life habits of Recent unionids and even less about fossil forms. It is, however, likely that both species lived partially buried in the sediment. Similarly, ecological studies of fossil freshwater gastropods are scant and little information is available. Most likely, all freshwater gastropods of the Bear River section were herbivorous, feeding either on live algae or on plant detritus. Recent members of the families represented by Bear River species vary considerably in their salinity requirements. For example, most members of the family Neritidae inhabit marine to brackish habitats at present day, but the genus *Neritina* tends to invade freshwater. A very transitional position is also assumed for the Cretaceous *M. naticiformis* as it occurs in large numbers where the percentage of brackish-water faunal elements is relatively high. This species is considered to have been able to live not only in freshwater, but also in oligohaline waters. Recent amnicolid gastropods also invade brackish water. How far this was true of the Cretaceous *Parateinostoma* is unknown. Recent members of the family Valvatidae and Viviparidae, although able to live in waters with a salinity of 2–3 permille (e.g. Ankel 1936) are typical representatives of freshwater environments and it appears safe to assume a similar habitat for Cretaceous species. In viviparids, the mantle cavity shows many features which may be associated with a muddy habitat (Fretter and Graham 1962, p. 594). This also fits the habitat preference of the Cretaceous *Viviparus couesi*. *Lymnaea nitidula* belongs to the freshwater pulmonate family Lymnaeidae and is the only representative of this group at the Bear River section.

In analysing similar faunas from the Cretaceous of Lincoln County, Wyoming, Yen (1951) concluded that they lived in relatively shallow, low-energy environments with an abundant aquatic vegetation. A freshwater assemblage from the Bear River Formation at Fossil Cut, south-east of Evanston (Wyoming), was interpreted by him (Yen 1954) as having lived in the lower part of the littoral zone (7–10 m deep), in a more or less closed and quiet bay with rich vegetation.

Analysis of the associations. Four of the five associations are closely related, with *Lioplacodes stachei* being present in moderate to high numbers in all samples. However, as in the case of



TEXT-FIG. 12. Evenness, species richness, and substrate relationships of the five freshwater associations. For key of substrate see text-fig. 2.

Ursirivus-dominated brackish associations, the relative abundance of species is thought to reflect subtle differences in the environment. Text-fig. 12 shows some ecological features of the five associations such as species richness, evenness values, and substrate relationships. All associations exhibit low species richness and evenness values suggesting that the faunas did not live under optimal conditions. However, they cannot be arranged along an environmental gradient as in the case of the brackish-water faunas. Faunal composition and diversity were probably influenced by several factors, not necessarily related. Substrate conditions appear to have influenced faunal distribution to some degree. Thus, the *Pachychiloides chrysalis* association occurs in coarser sediments than the others and the substrate was never calcareous. This biotope may have been close to river mouths and a slightly higher energy level than in the other associations probably prevailed. In contrast, the *Lioplacodes stachei*/*P. macilentus* association occurs nearly exclusively in calcareous siltstones or silty marlstones.

Another factor governing faunal distribution was *salinity*. According to Remane and Schlieper (1971) some freshwater species are able to tolerate waters of the oligohaline or even lower mesohaline regime. Segerstråle (1957, p. 779) records a number of freshwater gastropods from the Baltic Sea which live in oligo- or even low mesohaline coastal waters. Many of them are greatly reduced in size. Even some unionid bivalves tolerate salinities up to 3‰ in parts of the Baltic Sea (Segerstråle 1957; see also Remane 1958 for summary of the salinity tolerances of freshwater organisms). It is therefore

likely that several freshwater gastropods from the Bear River Formation could tolerate at least short-term small-scale salinity fluctuations. This may have been particularly true of *M. naticiformis* (see above). Consequently, the *M. naticiformis*/*L. stachei* association is thought to have lived closest to the brackish-water edge and was able to survive short-term incursions of oligohaline waters. This implies that there might have been a spatial and temporal overlap of members of this association with members of the oligohaline *Pyrgulifera humerosa* subset. The position of the *M. naticiformis*/*L. stachei* association close to the freshwater/brackish-water interface is supported by the relatively high percentage of brackish-water faunal elements in the total fauna as compared to that of other associations.

The *L. stachei* association appears to have lived furthest away from the freshwater/brackish-water interface: in three out of six samples no brackish faunas occur, in two more the brackish fauna accounts for less than 10%, and only in one sample is the brackish fauna very abundant (81.5%).

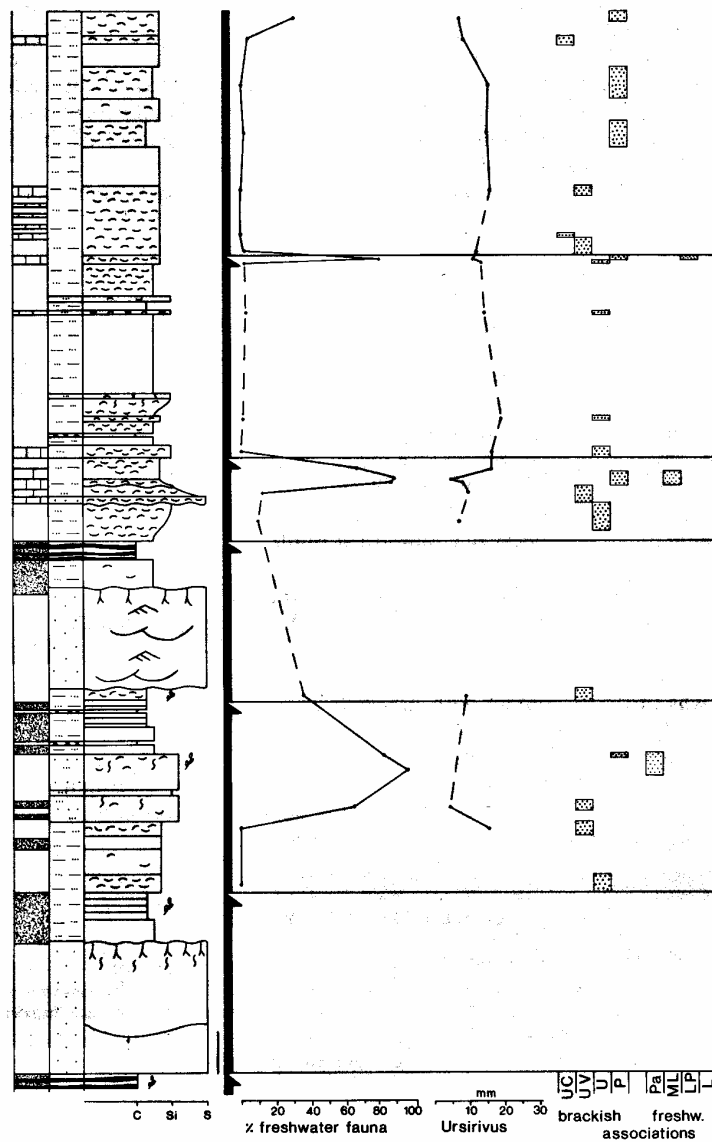
Other factors not readily recognized from the substrate must have exerted a strong influence on the freshwater fauna. Most likely they were water chemistry (e.g. concentration of Ca-ions), temperature and oxygen level. High temperature fluctuations combined with periods of poor oxygenation are very common in large, very shallow-water bodies, restricting the fauna to eurytopic species. That it was a high stress environment can also be demonstrated by the size of several faunal elements. At Shell Hollow, a locality of the Bear River Formation several miles north-west of Evanston (Wyoming), the gastropods *L. stachei*, *Pachychiloides chrysalis*, *P. chrysalloideus*, and *P. macilentus* were about 20 to 25% larger than at the Bear River locality (Shell Hollow data from unsorted collections in the Henderson Museum of the University of Colorado at Boulder). This implies that at least these species (data on other freshwater gastropods were not available) did not grow to their maximum size at the latter locality. Low oxygen conditions were most likely responsible for the small to minute size of all specimens in the *Valvata praecursoris* and corbulid sp. A. assemblages, which occur in a dark-grey laminated silty clay.

Summary of depositional environment. The freshwater faunas lived in a large shallow body of freshwater that was in direct contact with brackish water. Most associations lived in low-energy environments on soft substrate that was richly vegetated. The close association of coal-seams and freshwater faunas indicate that water depth was extremely shallow. Only one association appears to have preferred a somewhat higher energy level and coarser substrate, probably close to the rivers emptying into the embayment. The embayment was subject to fluctuations in temperature and oxygen levels that restricted the fauna to eurytopic species.

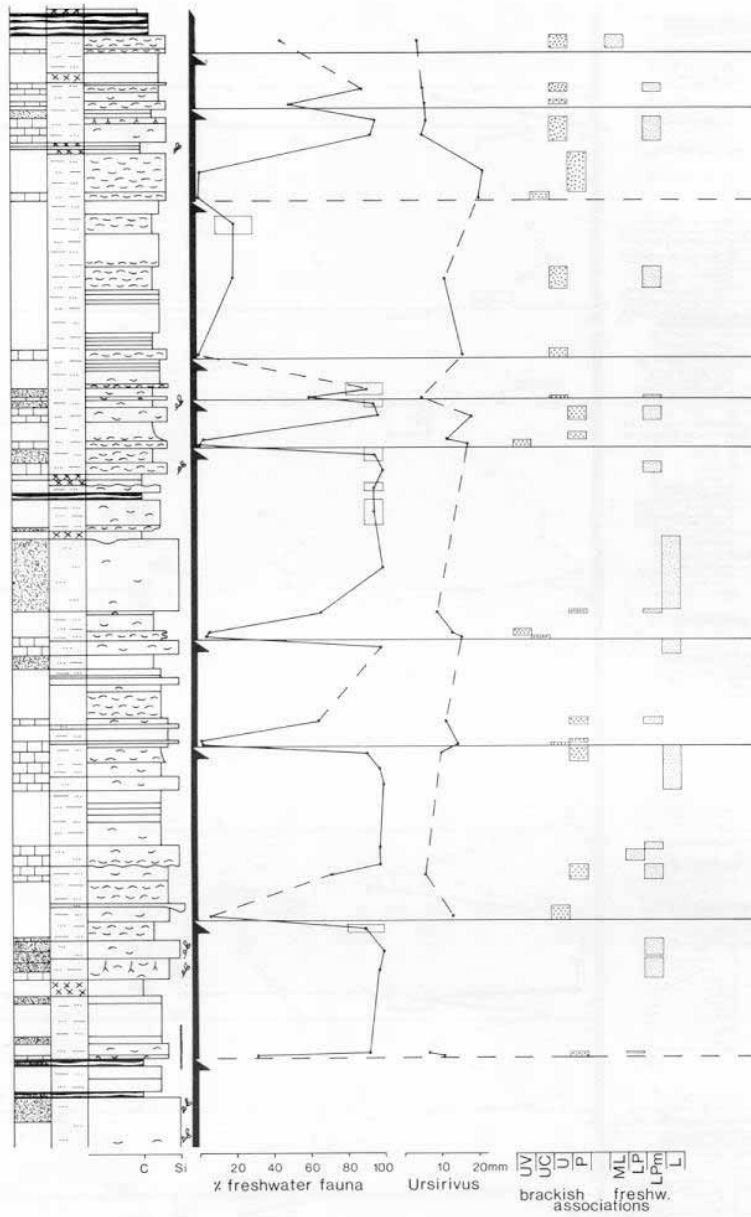
ANALYSIS OF CYCLES

In the Bear River section both sediment and benthic faunas occur in cycles. The base of each cycle is defined by shell beds dominated by brackish-water fauna, the top by coals, highly carbonaceous sediments and/or calcareous beds dominated by freshwater faunas. The boundaries between cycles are marked by the drastic change in the proportion of fresh- to brackish-water faunal elements. Text-figs. 13-15 show the lithological change, the variation in the proportion of fresh- to brackish-water species, the variation in mean size of the dominant brackish-water species (*Ursirivus*) and the distribution of fresh and brackish-water associations throughout the Bear River section. Although quantitative data are not available for each bed, the pattern is quite clear and can be interpreted as a series of regressive sequences each followed by relatively rapid transgressive pulses. In most cases, the transgressive phase did not leave any sedimentary or faunal record, but occasionally the change from freshwater-dominated faunas at the top of a cycle to brackish-water-dominated faunas at the base of the next cycle is represented by intermediate stages: part of the transgressive phase. The amplitude of the cycles may vary. Beds with exclusively brackish-water faunas may grade into beds with only freshwater elements at the top of each cycle. Alternatively, beds at the base may already exhibit a strong freshwater influence and beds at the top may still have a high percentage of brackish-water elements. Even where no faunas are preserved, the regressive nature of the cycles can be demonstrated easily: thus, at the base of text-fig. 13, carbonaceous sediments intercalated with thin seams of coal are overlain by a fine-grained channel sandstone which is bioturbated and rooted at the top and overlain by silty clays that grade into highly carbonaceous shales. This sequence can be interpreted as fluvial channel sands giving way to overbank deposits and finally swamps. Strong

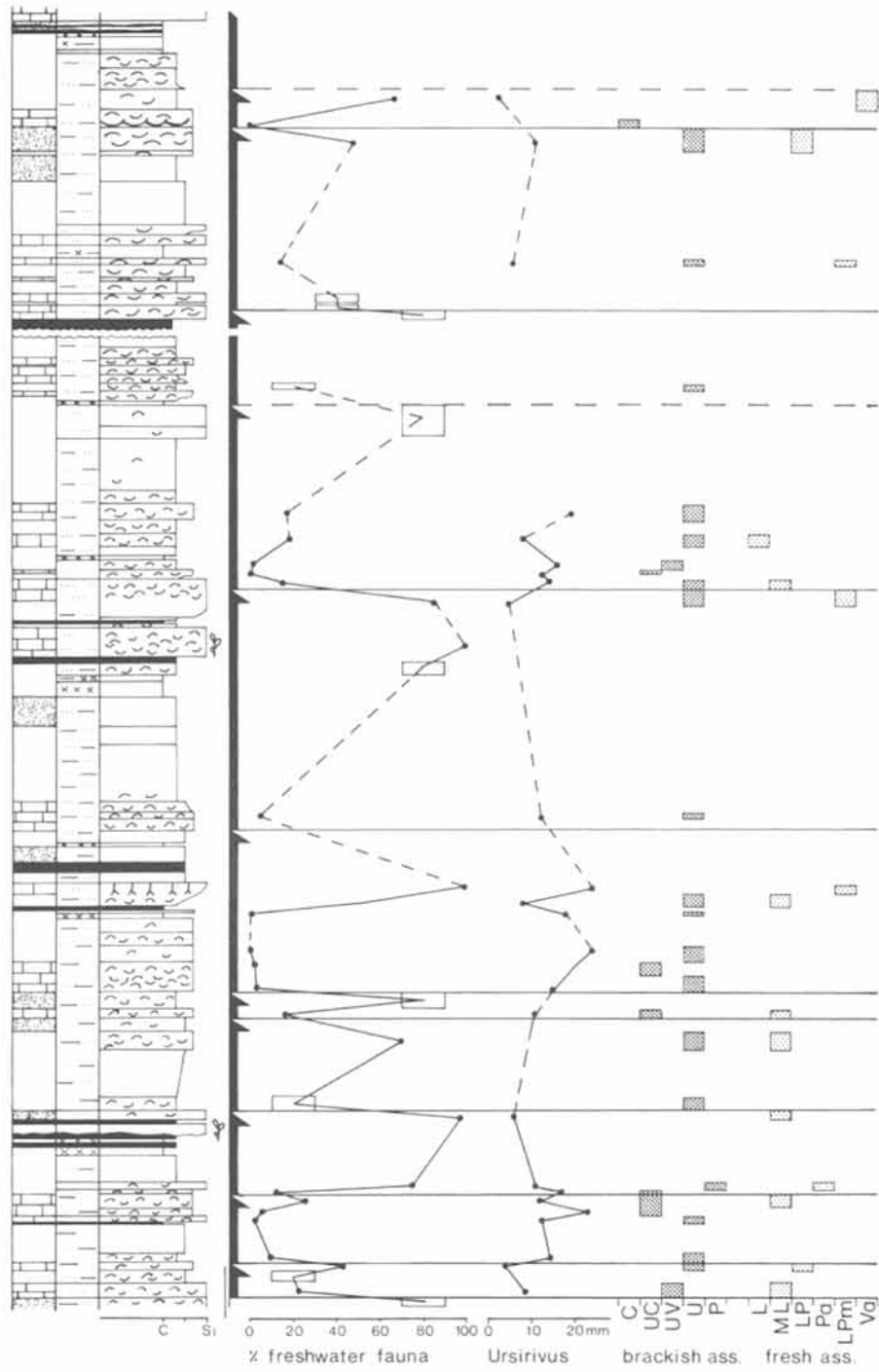
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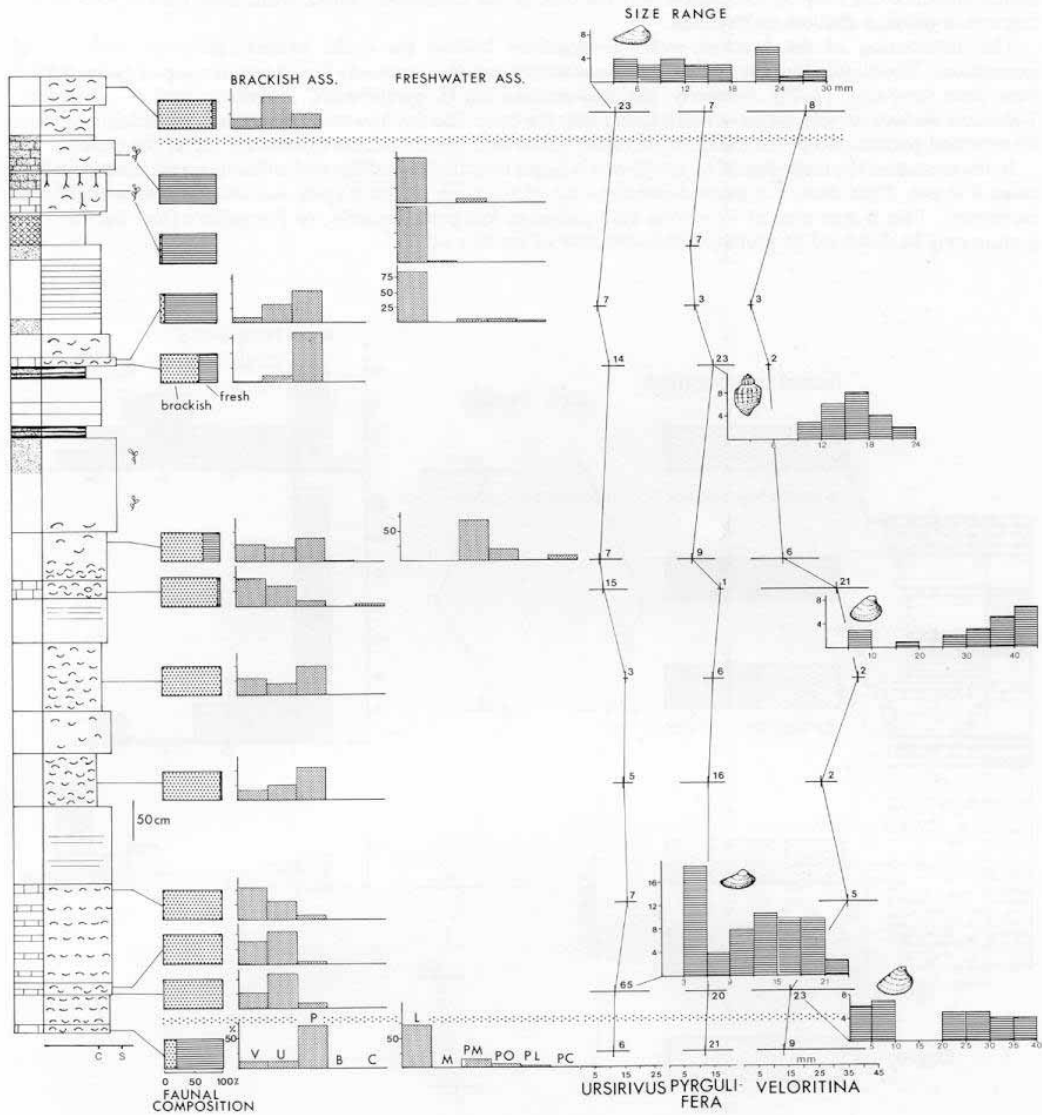
TEXT-FIG. 13. Sedimentological and palaeoecological data (percentage of freshwater faunal elements, mean size of *Ursirivus pyriformis*, and distribution of benthic associations) of the Reference Section of the Bear River Formation. For key to symbols see text-fig. 2. C—clay; Si—silt; S—fine-sand; C—*Crassostrea soleniscus* association; UC—*Ursirivus pyriformis*/*C. soleniscus* subset; UV—*U. pyriformis*/*Veloritina durkeei* subset; UP—*U. pyriformis*/*Pyrgulifera humerosa* subset; P—*P. humerosa* subset; Pa—*Pachychiloides chrysalis* association; ML—*Mesoneritina naticiformis*/*Lioplacodes stachei* association; LP—*L. stachei*/*Parateinostoma occultum* association; L—*L. stachei* association; LPm—*L. stachei*/*Pachychiloides macilentus* association; Va—*Valvata praecursoris* assemblage. Empty rectangles are semi-quantitative field estimations of the percentage of freshwater elements.



TEXT-FIG. 14. Continuation of section of text-fig. 13.



TEXT-FIG. 15. Upper part of marginal marine section at the Bear River Reference Locality. For key to symbols see text-fig. 2. Note disruption of section near top due to faulting.

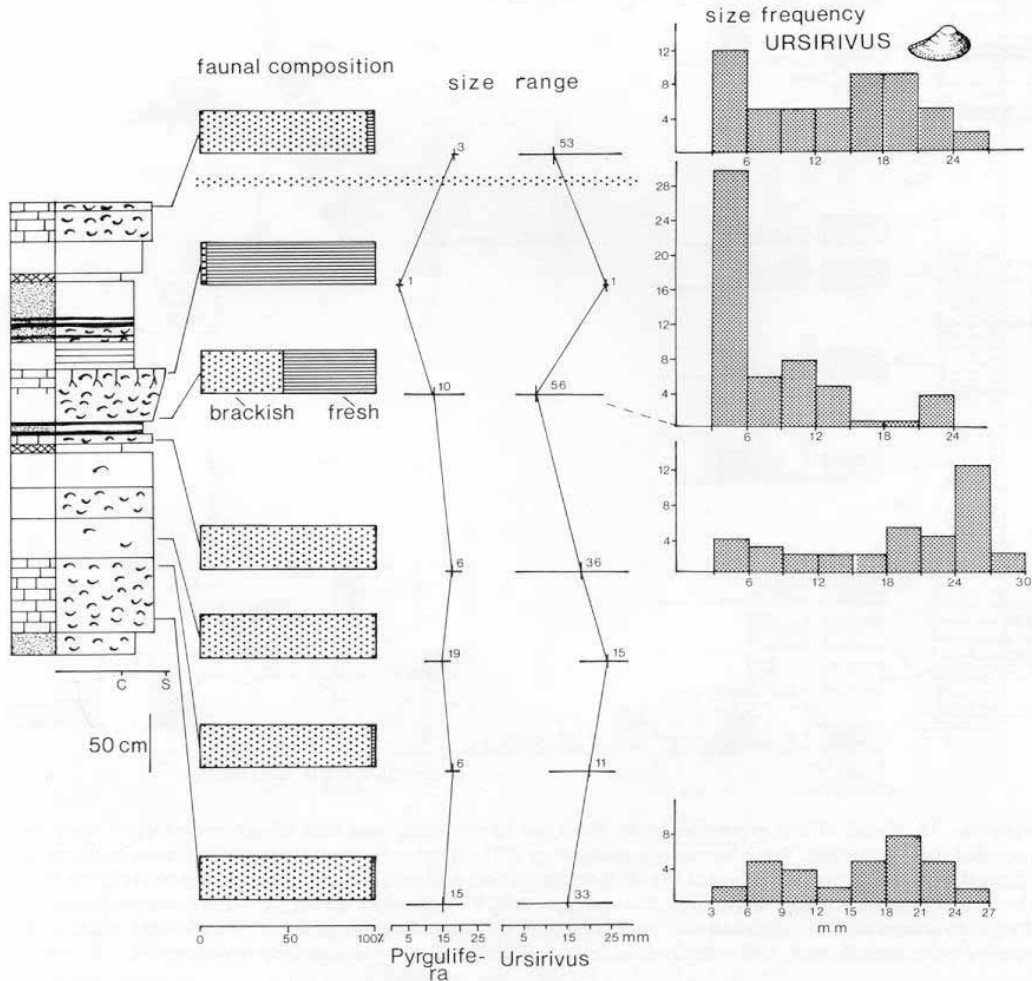


TEXT-FIG. 16. Detail of one regressive cycle. Both top of preceding and base of succeeding cycle have been included for comparison. Note increase in percentage of freshwater elements, changes in faunal composition, changes in the mean size of dominant brackish-water species, and size/frequency histograms towards the top of the cycle. For key to symbols see text-fig. 2. c—clay; s—silt; V—*Veloritina durkeei*; U—*Ursirivus pyriformis*; P—*Pyrgulifera humerosa*; B—*Brachidontes multiliniger*; C—*Crassostrea soleniscus*; L—*Lioplacodes stachei*; M—*Mesoneritina naticiformis*; PM—*Pachycholoides macilentus*; PO—*Parateinostoma occultum*; PL—*P. latense*; PC—*P. cleburni*.

fluvial influence can only be recognized near the base of the measured section, while most other cycles record regression within a shallow embayment.

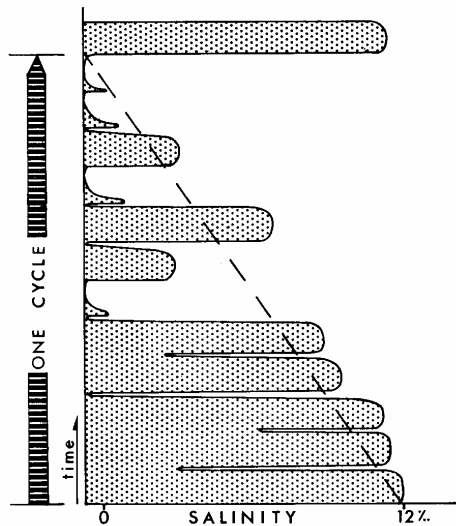
The distribution of the brackish-water associations follows the cyclic pattern, although with several exemptions. The oligohaline *Pyrgulifera humerosa* subset is more commonly found near the top of cycles than at their base (text-figs. 13-15). Similarly, the mid-mesohaline *U. pyriformis*/*C. soleniscus* and *U. pyriformis*/*Veloritina durkei* subsets are more often found near the base. The freshwater associations show a fairly random distribution pattern except for the *L. stachei* association that usually occurs toward the top of the cycles.

In thirteen cases the mean size of *U. pyriformis* is larger near the base of the cycles than towards the top; in four cases it is not. Thus there is a general size decrease of *Ursirivus* within a cycle, notwithstanding a significant variability. This is true also of *Veloritina* and, although less pronouncedly, of *Pyrgulifera* (text-fig. 16). The picture may be distorted by preferential destruction of smaller valves.



TEXT-FIG. 17. Detail of one regressive cycle including base of the next cycle. Note increase in percentage of freshwater faunal elements, changes in the mean size of *Pyrgulifera* and *Ursirivus*, and dominance of juvenile individuals of *Ursirivus* near top of the cycle. For key to symbols see text-fig. 2.

The lack of an anticipated neat correlation between changes in size and benthic associations and the regressive cycles can be explained by the overprint of seasonal fluctuations on the cyclic pattern. The resulting pattern is therefore one of interference of two cycles of different magnitudes. In text-fig. 17 the size/frequency distribution of *Ursirivus* within one cycle is plotted as are mean size of *Pyrgulifera* and *Ursirivus*. As expected a strong peak of juveniles indicative of mass mortality during freshwater interludes shows up when the percentage of fresh-water faunas among the total fauna increases. However, there are also several examples of high juvenile mortality among the brackish-water species near the base of cycles where the percentage of freshwater faunas is low. In these cases the freshwater phase killed the brackish fauna, but did not last long enough for the establishment of a freshwater fauna. Similarly, presence of adult *Ursirivus* in time-averaged brackish-water populations of beds dominated by freshwater elements can be explained by occasional less severe salinity reductions which enabled the brackish fauna to survive for more than one season.



TEXT-FIG. 18. Model illustrating the overprint of seasonal cycles on the salinity reduction within one regressive cycle. Note that in reality thousands of seasonal cycles may be involved instead of the twelve shown here.

Text-fig. 18 presents a model of the salinity changes within cycles combining seasonal fluctuations with a general reduction in salinity. Both parameters can be reconstructed by using size/frequency data, proportion of fresh- and brackish-water faunas in one bed, and the nature of the brackish associations.

The cycles in text-figs. 13-15 vary in thickness, but also according to the dominant salinity regime. Groups of cycles in which brackish conditions dominate for most of each cycle followed by a short period of dominantly freshwater conditions alternate with groups where the brackish-water dominated phase is short and fresh-water conditions prevail for most of the time. The groups are composed of two to four cycles. Unfortunately for several cycles the data are insufficient to allow a more precise description of this feature. It seems, however, that yet another order of cyclicity is recorded by the fauna, but not by any features of the sediment.

INTERPRETATION OF CYCLES

Cyclicity recorded in the sedimentary or fossil record is either caused by climatic factors, by movements of the earth's crust in the broadest sense (be it by spreading of mid-oceanic ridges or small-scale tectonic movements), or by factors connected with mechanisms of sediment transport and deposition within basins (e.g. articles in Merriam 1964, Duff *et al.* 1967, Einsele and Seilacher 1982).

There can be little doubt that the seasonal cyclicality found in the Bear River section, expressed by the size/frequency curves of brackish-water organisms, is of climatic origin and records the alternation of dry and wet seasons similar to monsoon seasons in today's tropical and subtropical belts. This is in agreement with Tingey (1978) who, based on palynological data, postulated a subtropical to warm temperate climate for south-western Wyoming during the middle and late Albian.

The origin of the secondary cycles can be less easily assessed. What is recorded is the gradual infilling and freshening of a large embayment. The tectonic hypothesis would require rhythmic pulses of subsidence that would lead to a rapid transgression across the embayment and subsequent gradual infilling with sediment. Another variation of the tectonic model assumes increased uplift of the hinterland (ancestral Rockies) which would result in increased supply of sediment to deltas. Reworking of sediments by longshore currents would then lead to increased formation of barrier bar systems which could restrict marine influence in the embayment and finally seal it off completely. However, there are no signs of extensive barrier systems along the shorelines of the Skull Creek Seaway which apparently was bordered by very low-energy shore-lines. Moreover, the regressive cycles in the embayment are not coarsening-upward cycles, though an increase in the rate of sedimentation toward the top of the cycles is indicated in many cases by the decrease in the thickness and abundance of shell beds and by the lower density of shells within them.

Assuming a climatic origin of the cycles, with an increase of rainfall, there should be increased run off and consequently increased erosion and sediment supply to coastal waters. The same process of increased formation of barrier bars could then operate as in the tectonic model. As mentioned before, however, the existence of extensive barrier sands is unlikely. Increased rainfall could have resulted in a more extensive sheet of freshwater across the embayment and caused a long-term shift of the freshwater/brackish-water interface towards the open sea.

The third possibility is that the regressive pattern is autocyclic, caused by the switching of major distributaries within a deltaic system. This would cause sediment influx into the embayment to cease and, assuming subsidence to continue, would result in rapid transgression. From the available evidence it is impossible to decide which model is correct. An autocyclic explanation for the regressive sequences is, however, the simplest model and is therefore favoured.

The cause of the primary cyclicality, which is characterized by the relative duration of fresh- to brackish-water conditions within secondary cycles, is even more open to speculation. It may have been the result of climatic or tectonic factors, possibly expressed by slight eustatic fluctuations in sea-level. In this case, an allocyclic mechanism is more likely.

Text-fig. 19 presents a summary of the three orders of cycles. Whilst the tertiary cycles represent fluctuations on the scale of 10^0 years, the secondary cycles probably are in the range of 10^3 to 10^4 years, and the primary cycles possibly present periods of 10^4 to 10^5 years. Unfortunately, biostratigraphic and chronostratigraphic control on the Bear River section is not available. The time ranges for the three orders of cycles must therefore be regarded as very tentative. To what extent the primary cyclicality, should it prove to be of climatic origin, can be related to cycles of the earth's orbit (Milankovich 1930) remains unknown.

CONCLUSIONS

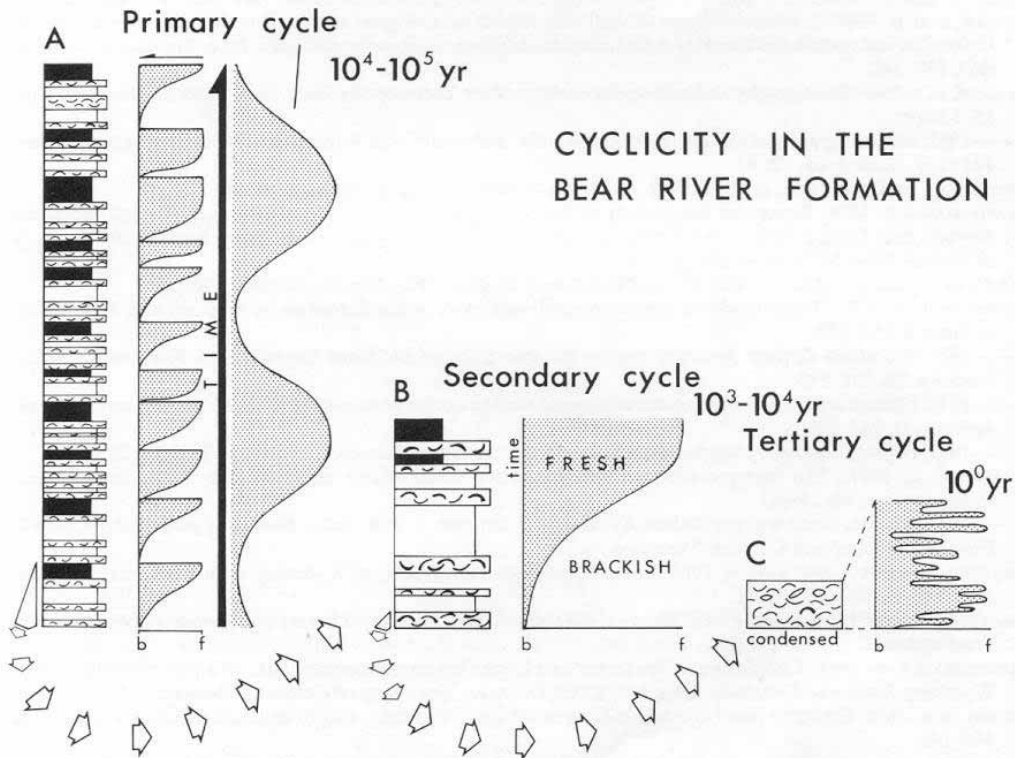
1. Part of the Bear River Formation represents an extensive embayment in which fine-grained sediments ranging from silty clays to silts and silty limestones accumulated in a predominantly low-energy environment. Within this sequence, numerous shell beds with a highly abundant but low diversity fresh- and brackish-water fauna of bivalves and gastropods occur.
2. Biostratigraphic data favour local reworking by storms rather than lateral transport by currents as the origin of the shell beds. Mixing of fresh- and brackish-water faunas in the same bed was caused by rapidly shifting environments and not by mixing of faunas from neighbouring habitats.
3. Sedimentological and palaeosynecological analyses demonstrate the presence of cycles that start with shell beds of predominantly brackish origin and end with thin seams of coal or beds of silty limestone dominated by freshwater faunal elements.

4. Two benthic associations, one of them with four subsets, are recognized in the brackish-water fauna. They can be arranged along a salinity gradient ranging from mid-mesohaline (about 12‰) to the freshwater edge. Along this gradient, species evenness and richness drops and most faunal elements decrease in size.

Five associations are recognized in the freshwater fauna. They are dominated by small gastropods, exhibit some substrate control, and, at least in one case, were probably able to invade oligohaline waters.

5. Size/frequency distribution patterns of the brackish bivalves *Ursirivus*, *Veloritina*, and the gastropod *Pyrgulifera* point to strong seasonal salinity fluctuations which, in many cases, caused a high juvenile mortality.

6. Altogether, three orders of cycles are recognized in the Bear River section of probably the following magnitudes: (a) 10^0 years (seasonal), recorded by size/frequency curves within shell beds; (b) 10^3-10^4 years, expressed by regressive sedimentary sequences and a consistent change from brackish to freshwater-dominated biota; and (c) 10^4-10^5 years, expressed by the dominance of fresh or brackish conditions within bundles of regressive sequences. Whilst the tertiary (seasonal) cyclicality is of climatic origin, the nature of the secondary cycles is probably autocyclic. The origin of the primary cyclicality remains unclear.



TEXT-FIG. 19. The three orders of cycles in the Bear River Formation at the Bear River Reference Locality. The terms primary, secondary, and tertiary cycles are used in order to avoid confusion with first, second, and third order cycles of Vail *et al.* (1977). *b*—brackish; *f*—freshwater.

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