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PART A

ECOLOGY AND BIOLOGY

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PART A. ECOLOGY AND BIOLOGY

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MODERN AND HOLOCENE FORAMINIFERA IN THE CHESAPEAKE BAY REGION

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Estuaries are highly variable coastal ecosystems. Some of the variation is seasonal and some is longitudinal along the environmental gradient from the river to the sea. Foraminifers are tuned to the periodicity, and a progressive change in the composition and structure of foraminiferal faunas parallels the longitudinal ecocline, identified by the gradient in salinity.

In marshes and tributary estuaries where water is fresh, thecamoebinids comprise the microfauna. Three other marsh faunas are composed chiefly of the agglutinate species: Ammoastuta salsa, Miliammina fusca, Arenoparrella mexicana, Ammobaculites crassus *and species of* Haplophragmoides *and* Trochammina. *Their distribution is influenced by salinity and exposure. In the estuaries, where fresh and salt water mix, two faunas are characterized by:* Ammobaculites crassus, *in the middle and upper reaches where salinity is less than about 15 o/oo and the estuary is periodically freshened by river flushing, and by* Elphidium clavatum *in lower reaches and deeper channels where salinity is higher and mixing is moderate.* Elphidium, *furthermore, dominates the faunas in the lower part of Chesapeake Bay and on the inner part of the shelf. At a depth of about 25 m the* Elphidium *fauna is succeeded by a larger and more diverse fauna that may be partly relict.*

The marsh and estuarine faunas shift headward and mouthward with changing river inflow and salinity, and their changes are recorded in cores of estuarine and marsh deposits. Short-term events and paleoclimatic episodes with durations of several hundred years are superimposed on a long-term trend of decreasing salinity during the past 6,000 years as sedimentary infilling exceeded the rise in sea level.

INTRODUCTION

Chesapeake Bay, situated in the middle of the eastern seaboard of the United States, is the largest estuary in North America (Fig. 1). Within its drainage basin of 191,500 km^2 live 8 million people, and its waters must accommodate their activities and receive part of their wastes. For these reasons and because the Bay is an estuary, it is a system under stress. Being sites of rapid sedimentation, estuaries quickly lose one of their most distinctive features - the nearly unimpeded mixing of fresh and salt water. This suicidal tendency is a trait of modern-day estuaries (Russell 1967). Part of the natural stress placed on benthic organisms in estuaries is this rapid rate of deposition, particularly during floods, but the main stress is the fluctuation in solar radiation and in tidal and river inflow. Added to this is the further stress placed on the system by man. The response of aquatic plants and animals to stress is of concern, and ecological studies of Bay organisms are numerous, providing us with information useful in assessing the impact of our activities on this ecosystem that is so precariously balanced on the edge of dynamic equilibrium. This report on the distribution of foraminifera in the lower Bay, its tributary estuaries and adjacent shelf waters, representing a compilation of work done by many investigators over the past decade, is one of these studies.[1]

ENVIRONMENTAL SETTING

General

The functional classification of coastal ecosystems proposed by Odum and Copeland (1974), while not widely adopted, provides a valuable vantage point from which to examine estuaries. According to this classification based on energy input, Chesapeake Bay is a "natural temperate ecosystem with seasonal programming". Portions of the Bay and its tributary estuaries can further be categorized as "oligohaline", "medium salinity plankton" and "coastal plankton" systems. However, it is the seasonal programming of solar radiation that stamps the Bay and its tributaries with their distinctive character (Fig. 2). Because the Chesapeake is elongate and oriented north-south, the programming at the northern end has a greater amplitude than the southern end, but the phase is the same. Maximum daily, solar insolation is greater at the northern than at the southern end of the Bay and the annual range also is greater, but the total radiation received annually is, of course, smaller.

Attendant with the seasonal programming of radiation is the seasonality of surface runoff or river discharge which results from an increase in evapo-transpiration in the summer and a decrease in the winter, not from any seasonality in the

[1]Graduate and undergraduate students at the Virginia Institute of Marine Science and in the Department of Environmental Sciences (then Geology) at the University of Virginia whose work is included here are: Thomas Bingham, John Christensen, Holly Delaney, Debbie Drinker, Wilson Felder, Allen Hartwell, Ronald Hoinowski, John Hughes, Robert Meintzer, Warren Norton, Roger Plaster, Paul Sandifer and Ruth Stenmark.

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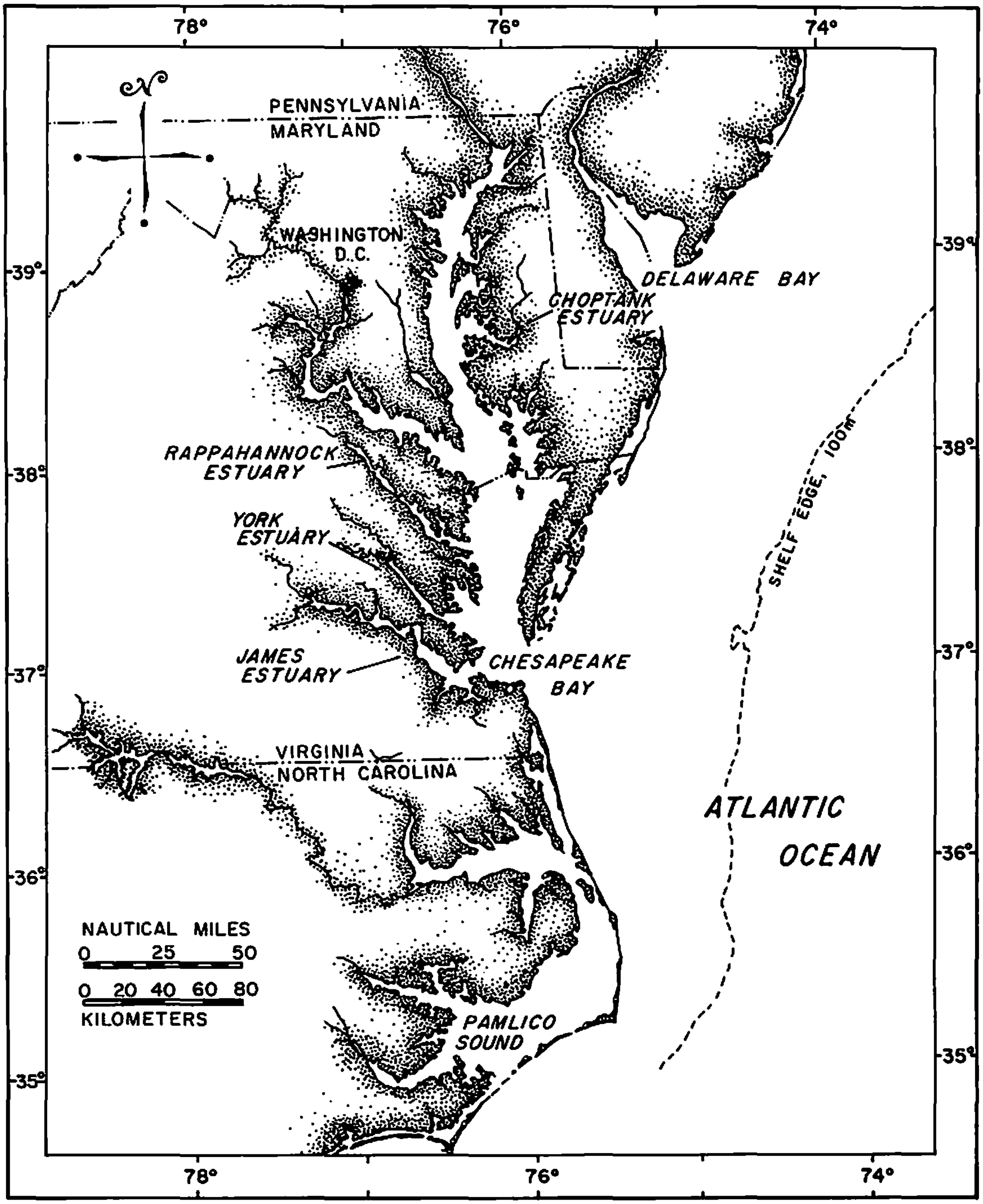

FIG. 1 Location of the Chesapeake Bay and its major tributary estuaries on the Mid-Atlantic coast of the U.S.

Table 1. Data for environmental conditions in microfaunal zones of the Chesapeake Region

ENVIRONMENTAL CONDITIONS IN THE CHESAPEAKE REGION

	ESTUARINE AND SHELF MICROFAUNAS			
	THECAMOEBINID	AMMOBACULITES	ELPHIDIUM	MIXED SPECIES, SHELF
Geographic Limits - distance downstream from fall line, km	0 - 72 (0 - 40nmi)	72 - 135 (40 - 75 nmi)	135 - 227 (75 - 126 nmi)	.(> 126 nmi)
General Area Description	Fresh water tidal river	Low-Salinity Estuary (brackish)	Intermediate salinity Estuary Entrance & Inner Shelf	High-salinity offshore shelf
Water Depth, mean/range	4.5 1.1 to 10.7	3.8 2.2 - 29.5	8.2 3.1 - 26.0	>26
Predominate bottom sediment types	Gravel, sand & mud	Mud in channel, sand and oyster shell on shoals	Sand and Mud	sand
Tide range, mean, cm	varies 48 - 90	48 - 78	78 + 90	90
Tidal currents - maximum speed, m/sec	Tidal, reversing, 0.6	Tidal, reversing 0.6	Tidal, reversing 2.1	Tidal, rotary and wind drift
Wave action	very low	low	moderate to high	moderate
Temperature*, °C	0 - 29	1 - 28	3 - 24	5 - 21
Salinity*, ‰	0.0 - 0.5	0.5 - 15	12 - 33	33 - 34
Oxygen*, ml/l	1.0 - 5.0	0.1 - 7.0	4.2 - 8.0	---
Nitrate*, µg A/l	0.4 - 262	0.8 - 94.0	0.8 - 20.0	---
Total phosphate*, µgA/l	1.57 - 21.6	0.99 - 6.6	.68 - 2.88	---
Suspended Sediment*, ug/l	5.7 - 93.0	8.3 - 177	10.0 - 35.6	---
Transparency, Secchi disc depth, m	0.2 - 1.2	.3 - 1.8	0.8 - 2.4	2.0 - 20
Chlorophyll "a" µg/l	1.8 - 120.1	1.3 - 17.3	2.5 - 15.3	---

-- Data absent * Data for near-bottom water 1 - 5 numbers indicate seasonal ranges

precipitation pattern. The region is one of more-or-less uniform precipitation throughout the year; in fact, precipitation is slightly greater in the summer than in the winter. The annual fluctuation is slightly greater in the summer than in the winter. The annual fluctuation in the discharge of the James River and in water temperature are related to the radiation program (Fig. 2). As a consequence of this seasonal programming of solar radiation which programs the evapo-transpiration cycle and determines the amount of water available for surface runoff (supplemented by melting and thawing), the salinity of the Bay water and the flushing of nutrients oscillates annually. Ellison and Nichols (1970) have demonatrated that boundaries of foraminiferal facies migrate in response to seasonal changes in salinity. Buzas (1969) and others also have shown that sizes of foraminiferal populations are clearly synchronized with seasonally programmed populations of phytoplankton. The basic tempo of the estuaries, therefore, is set by solar radiation and precipitation; secondary rhythms are provided by the tides, and limits are placed on the system by the chemistry and recent history of the drainage basin.

Seasonal oscillations of radiation set the temporal pattern for productivity of phytoplankton (Patten *et al* 1963) and benthic plants in the estuary and for intertidal grasses and sedges that abound in marshes fringing the estuary. In temperate estuaries, this production halts in the fall and is not resumed until it is triggered by increasing radiation nearly six months later. During this non-productive period, most of the plant matter produced, but not consumed, on the marshes is washed into the estuary by tidal action. Values from Odum (1959) and Mendelssohn (1973) suggest that more than 50 % of the production of *Spartina alterniflora* marshes in the Chesapeake region is washed from the marsh into the tributary creeks. This transported plant detritus and associated bacteria (Odum and de la Cruz 1967) in places may be an important energy source for certain bay organisms. Whether or not the relationship is casual, Ellison (1972) has pointed to the proximity of salt marshes and large populations of species of *Ammobaculites*. In the Chesapeake region, *Ammobaculites*-rich sediments almost invariably are also laded with plant detritus.

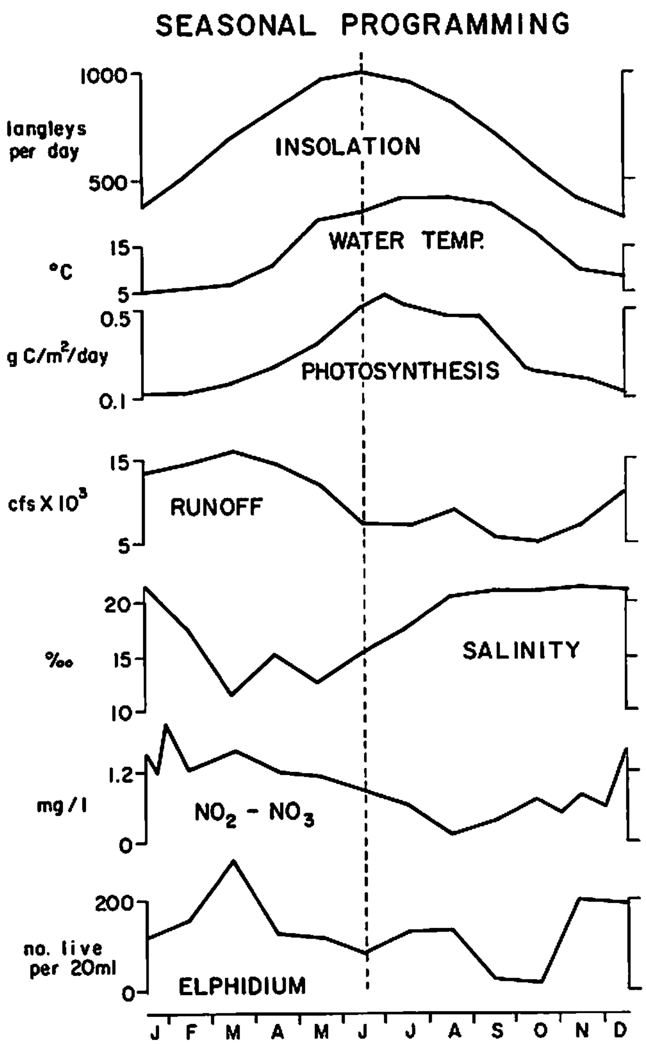

FIG. 2 Seasonal variations or "programming" of major environmental parameters in relation to seasonal changes in populations of Elphidium clavatum over an annual cycle from January (J) through December (D). Data from: List (1966), Brehmer and Haltiwanger (1966), Williams (1966), U.S. Geological Survey surface runoff data, Virginia Institute of Marine Science unpublished data on salinity distributions, Jaworski et al (1972) and Buzas (1969).

Water

The aqueous environment of the Chesapeake Bay system has been monitored for several decades (Hires *et al* 1963, Stroup *et al* 1963, Seitz 1970); consequently, the general distribution and behaviour of such standard parameters as salinity, temperature, chlorophyll and certain nutrients are reasonably well known. A summary of important environmental factors in given in Table 1.

Because the estuaries are fed fresh water at their landward ends which is tidally mixed with seawater from the seaward end, the salinity of their contained waters is intermediate, fluctuating as inputs vary. Owing partly to the mixing action of the tides and partly to the volume of freshwater inflow, the system is somewhat stratified with respect to salinity; the more salty water penetrates slightly farther up the estuaries along the bottom than at the surface. Stratification is best defined during periods of high fresh water inflow, as in late winter and early spring, and is nearly absent in the summer and fall. Weak stratification extends seaward onto the inner shelf outside the Bay. At the mouth of the Bay, the more saline water is conducted into the Bay along the bottom or in the lower estuarine layer of diverging channels - Thimble Shoals channel on the south and Chesapeake channel and two others near the northern side of the entrance into the Bay. In the summer, because fresh water inflow into and from the northern end of the Bay is drastically reduced relative to that from rivers in Virginia, the wedge of salt water moves farther north in the Bay along the eastern than along the western side. Furthermore, according to Pritchard (1968), Coriolis force deflects the incoming salt water to the right, or east side of the Bay. For these reasons, but chiefly the latter, in the lower third of the Bay a salinity gradient exists from the eastern side of the Bay (where salinity is high) across the Bay and into the estuarine tributaries. Salinity decreases most rapidly upstream in the "gradient zone" of these tributaries (Rochford 1951). Populations of foraminifera generally are larger on the eastern, more saline side of the Bay, and in the estuarine gradient zones. A longitudinal profile showing the salinity gradient from the head of the James estuary out onto the shelf is given in Fig. 3 (upper). In tributary creeks of the Eastern Shore peninsula, the upstream portions may become hypersaline in the summer when evaporation rates are elevated and fresh-water inflow is nearly non-existant. The same is true for bordering marshes.

Water temperatures range from about 1°C in the winter to 29°C in the summer, and at any particular time the waters are nearly isothermal from surface to bottom. On the shelf, bottom water is cooler than surface water, and bottom temperatures decrease offshore.

Most estuaries are characterized by a "turbidity maximum", a segment in which the concentration of suspended material is markedly high. It corresponds with the zone of near-bottom current convergence and mixing of water, and is situated in the middle to upper reaches of the estuary. Near-surface turbidity, as measured by the Secchi disc, decreases away from shore so that the water in mid-Bay or mid-

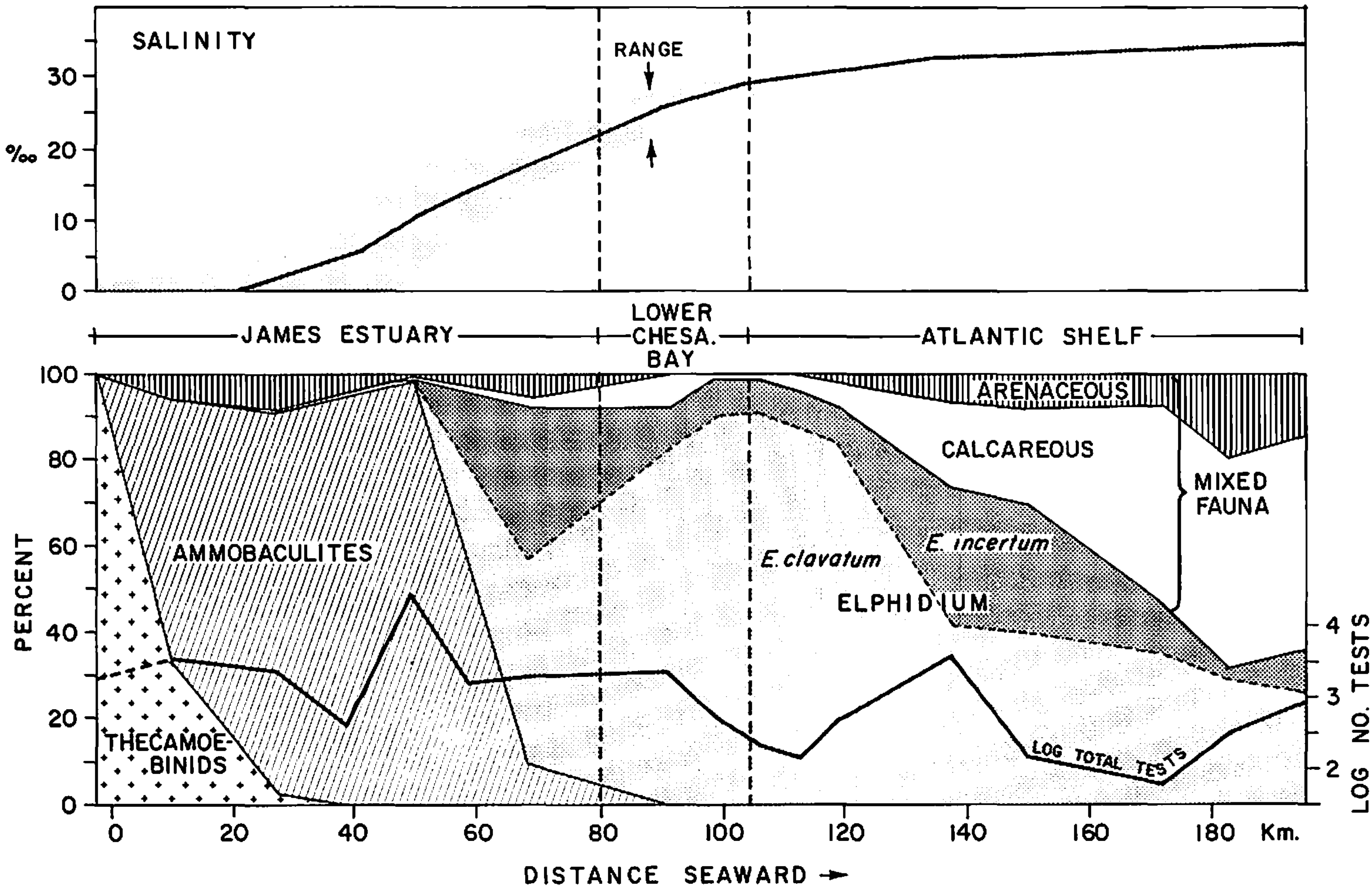

FIG. 3 Seaward change in bottom salinity (upper figure) in relation to change in foraminiferal composition (lower figure). Upper graph shows distribution of mean bottom salinity (solid line) and the annual range (stippled area). Lower graph shows percentage variation in species composition and total number of foraminiferal tests on a log scale with distance seaward from the upper James River estuary to the outer mid-Atlantic shelf off Chesapeake Bay.

estuary is more transparent than that near the margins. Near-bottom turbidity is more uniform laterally than is near-surface turbidity. Although the turbidity is partly caused by plankton, suspended sediment is by far the more important contributor.

Dissolved oxygen is generally saturated near the upper layer, but in the lower layer during the summer when biological metabolism is up and when warmer water temperatures reduce the solubility of oxygen, deep spots in the estuaries may become anoxic. Black, reduced sediments with partially pyritized diatom frustules and foraminiferal tests are evidence of this anaerobic condition. Specimens collected from these locations usually are small-sized.

Chlorophyll "A" values in the Chesapeake Bay system range from nearly zero to more than 100 microgm/L, with the higher concentrations during the winter, spring or early summer blooms and generally at more upstream stations in tributary estuaries. In the Bay, concentrations of chlorophyll "A" are commonly less than 20 microgm/L. Concentrations vary widely depending on local conditions, and it is difficult to relate chlorophyll distributions to those of benthic organisms, including foraminifera.

Tides in the Chesapeake Bay region are semi-diurnal with a tidal range of about 90 cm at Norfolk, Virginia. This, of course, matters little to benthic foraminifera in the estuary, but it is significant for species in the marshes or on the mud-flats. Intertidal foraminifera are exposed twice daily and those inhabiting the uppermost levels of the marshes are covered, or partly covered by water for only a few hours four or five times each month. Because of tidal inequalities, these few periods of submergence are more than 24 hours apart. In the summer, high temperatures and rates of evaporation add to the stress on intertidal species, and in the winter a lowered tidal plane (about 20 cm below the summer tidal plane) reduces the periods of submergence.

Bottom topography and sediment

Chesapeake Bay is an elongate estuary oriented north-south with a length of about 290 km and a width of 8 km, approximately at its northern end to more than 24 km toward the mouth (Fig. 1). With an area of 11,400 km^2 including its tributary estuaries (Potomac, James, etc.) it is the largest estuary in North America. Generally the bottom topography of the Bay deepens medially from broad

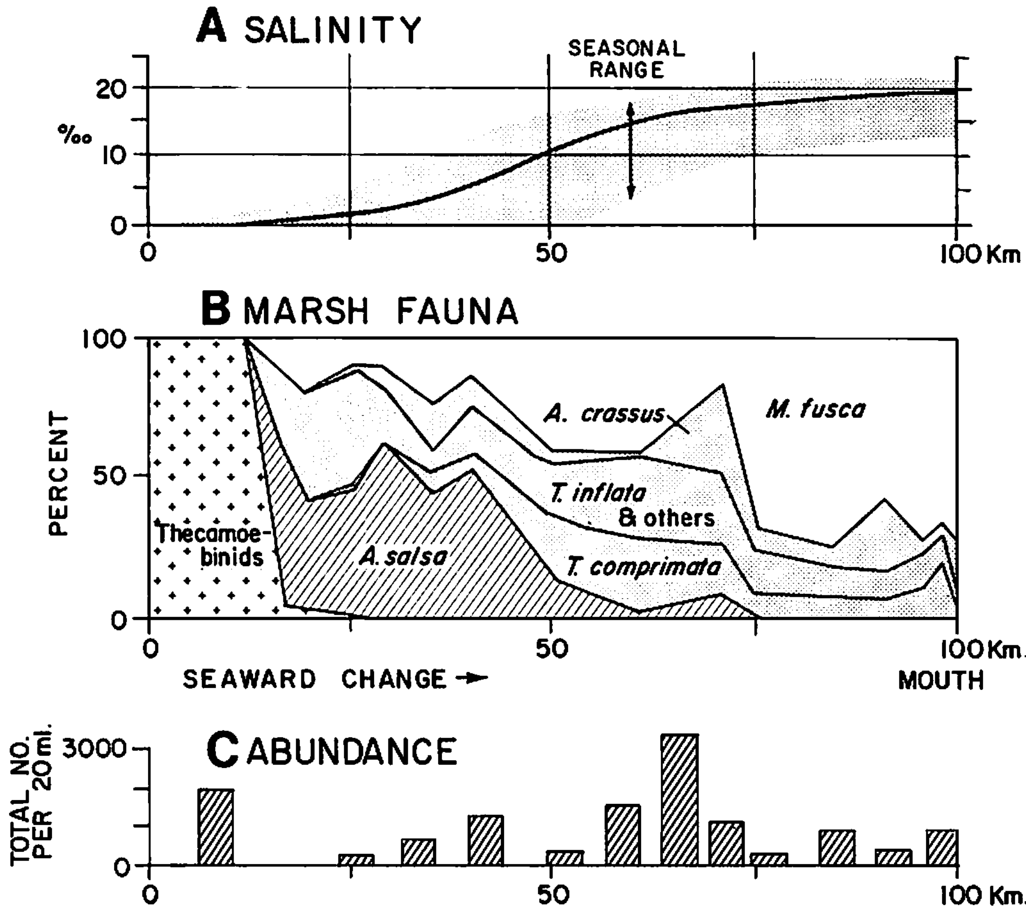

FIG. 4 Seaward change in species composition (B) and total number of marsh foraminifera (C) in relation to surface salinity (A) along the Rappahannock Estuary.

shoals on the western side and narrow shoals on the eastern side of the Bay. Medial depths are greatest in the middle and northern end of the Bay where they are 11 to 14 m. South of the York River, the middle of the Bay is from 8 to 11 m deep. Locally deeper spots, for example in the vicinity of Old Plantation Flats near the Eastern Shore, are associated with the abruptly deepening Bay floor adjacent to the eastern shoals. At and inside the entrance, across the width of the Bay, sandy shoals such as Thimble and Nautilus shoals are extensive and continuous except for two naturally maintained and two dredged channels. This shallow lens of sand, or inlet delta, extending from the Bay mouth to about 40 km above the mouth, is built of sediment carried into the Bay from the shelf by bottom currents whose net direction is bayward and net velocity is 0.1 to 0.2 knots. Maximum velocities of bayward currents along the bottom are about 2 knots, sufficient to move unattached foraminifera. The largest populations of Bay foraminifera have been found associated with this inlet delta near the Bay entrance.

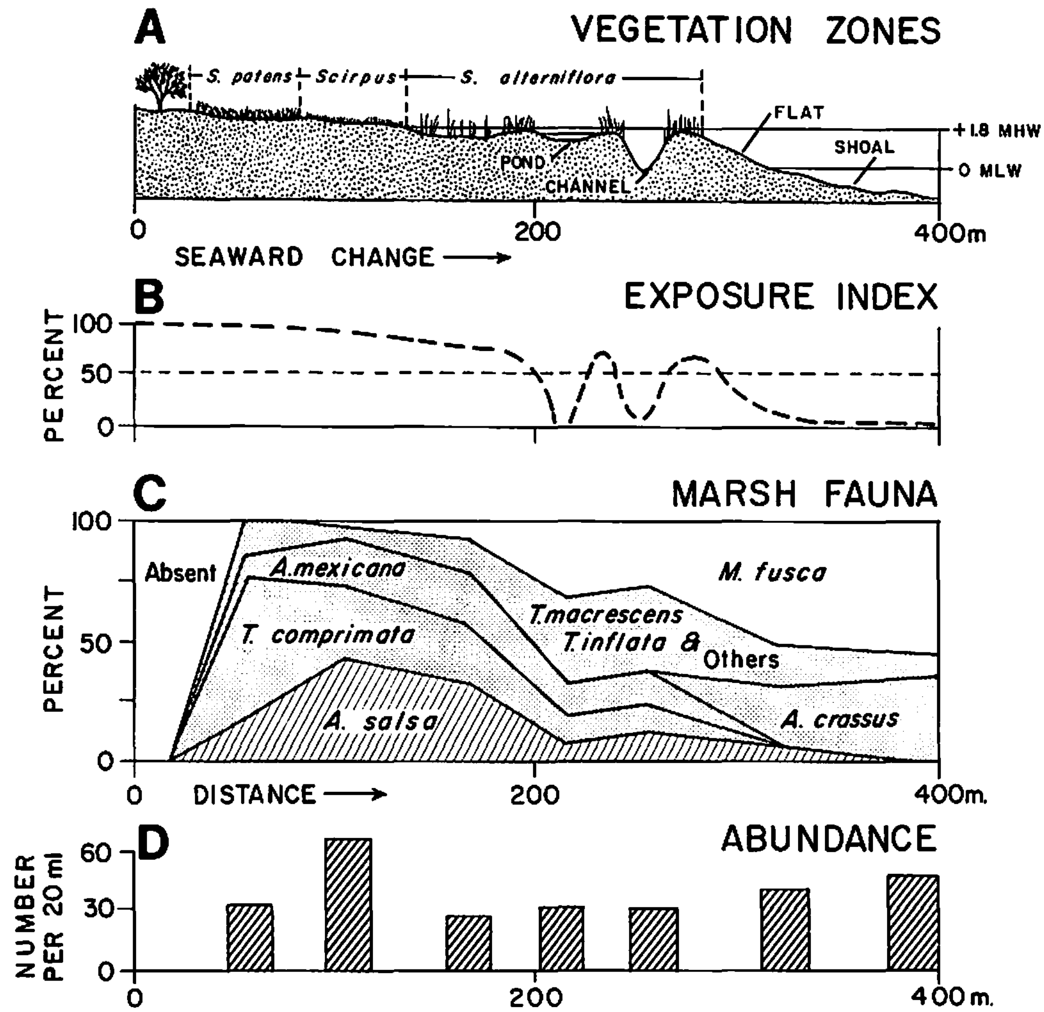

FIG. 5 Change in species composition (C) and number of live marsh foraminifera (D) in relation to vegetation zones (A) and exposure (B) across Belle Isle marsh in the middle Rappahannock Estuary. Exposure index is frequency of intertidal exposure expressed as percent.

Tributary estuaries similarly deepen into medial channels from marginal shoals (Fig. 6). These shoals, the sites of extensive oyster beds, are coarser-grained than are the channels, and slope gradually to depths of about 9 m where the bottoms steepens into the channel which in some estuaries reaches depths exceeding 27 m. At the mouth of the Rappahannock River a transverse sill partly restricts the exchange of water between the river and the Bay through the lower layer. On the other hand, highly mobile sands migrate back-and-forth where the James estuary joins the Bay.

Off the coast of Virginia and north of the mouth of Chesapeake Bay, the continental shelf is approximately 160 km wide and attains a depth of 150-180 m at its seaward edge. From the shoreline to 80 km offshore the portion included in this study, the

TABLE 2

Foraminiferal Faunas: Diversity (number of species per 20 ml sample) and population size (number of living specimens and empty tests per 20 ml sample)

	Marsh Ammoastuta	Mixed Marsh	Marsh Miliammina	Ammobaculites	Elphidium	Shelf Mixed
Diversity	10	16	16	14	16	31
Population Size	800	1,000	2,500	1,800	500[1] 600[2] 800[3]	850

[1]Tributary estuaries
[2]Chesapeake Bay
[3]Near-shore continental shelf

shelf slopes gradually at a rate of about 0.5 m/km; at the seaward edge of the study area, the slope of the shelf is steeper, nearly 2.5 m/km. This surface is crossed northeast-southwest by a series of low ridges and troughs that are believed to represent sand waves or relict Pleistocene topography drowned by rising sea level. Relief of this bottom topography is nearly 8 m, with the sediment on the inner shelf often coarsening on the ridges and becoming finer-grained in the intervening troughs. A blanket of Holocene, fine-grained sand covers the innter-shelf bottom from the shore to a distance of about 32 km offshore, at depths less than 30 m. Pilkey and Frankenberg (1964) have described a similar relict-Recent sediment boundary on the continental shelf of Georgia (see also Sen-Gupta 1976). Species composition of foraminiferal faunas appear to be related to these two sedimentary facies, and population sizes correlate with bottom topography.

Coastal drift moves predominantly southward on the surface, and bottom currents on the inner shelf move southward and landward near the Chesapeake entrance. Wave agitation in water less than 15 m deep prevents finer particles from settling and keeps the inshore water slightly turbid. Transparency of shelf water increases sharply offshore.

Bottom sediments that serve as substrate for foraminifera in the Bay and in tributary estuaries at depths greater than about 9 m are dark gray, clayey silts with more than 60 % water, and with an oxidation layer that is a thin surface film of fluid brown, clayey sediment. In places, the clayey silts are composed almost wholly of ovoid fecal pellets.

The shoals of the tributaries and of the Bay are very fine-grained to medium-grained sand partly derived from upland sources in the drainage basins of the various rivers and partly supplied by erosion of banks and bluffs of poorly consolidated sediment lying along the shores of the estuaries.

Sediments in this system are continually being re-worked by tidal currents and wave action, with much sediment being re-suspended at every tide. Reworking of this material naturally is most effective on shallow bottoms where the finer sediment is removed and the sands left on the shoals as lag sediment. Such environments offer a highly unstable, mobile substrate for benthic organisms.

Present-day rates of net coastal erosion along the Bay are about 503 m^2 per linear km of shoreline annually (Ryan 1953). Assuming an average height of 1.5 m for the 13,033 km of shoreline along the Bay and its tributaries, coastal erosion could contribute 6.5 million m^3 of sediment annually to the Bay system, enough to provide the Bay with all of its Holocene sediments (46,750 million m^3) in a period of about 7000 years. Sediments comprising the baymouth or inlet delta are nearly all fine-grained sands and the floor of the Bay in the region is especially firm and hard, even in the area of Nautilus Shoal and Middle Ground where strong currents keep the substrate in distributary channels in almost continual motion. Other distributary channels (Chesapeake, Thimble Shoal) through the inlet delta are composed of clayey silt. A 27-m deep basin offshore from Cape Henry consists of clayey silt mixed with gravel and fragments of shell. Much, if not most of the sediment comprising the inlet delta is provided by coastal currents which transport sediment along the shore from north to south.

According to Ryan's (1953) figure on total deposition in the southern part of the Bay during the past 10,000 years, the rate of sedimentation in this region is calculated to have been between 0.10 and 0.15 cm per year. This estimate is comparable with that obtained for Virginia estuaries, including the James and the Rappahannock, and for Virginia marshes.

Biological Factors

Phytoplankton. The Phytoplankton of Chesapeake Bay consists of 123 species of diatoms and 12 species of dinoflagellates (Patten *et al* 1963), with the former dominating in winter and the latter dominating in summer and fall. Closely keyed to nutrients supplied by the rivers, the phytoplankton are most abundant, most diverse and most productive on the western side of the Bay near the mouths of tributary

TABLE 3

Radiocarbon Dates from Marsh Deposits of the James and Rappahannock Estuaries

Core	Locality[1]	Material	Depth, cm	Date[2]
1B	Hunter Marsh	sandy peat, basal	90 ± 2	535 ± 95
1KM	Kennon Marsh	clayey peat	153 ± 2	880 ± 110
1KM	Kennon Marsh	sandy peat, basal	245 ± 3	1310 ± 160
2KM	Kennon Marsh	peat	323 ± 3	1465 ± 110
2KM	Kennon Marsh	peat, basal	498 ± 2	2700 ± 160
3E	Hunter Marsh	clayey peat	30 ± 2	60
2C	Hunter Marsh	clayey peat	43 ± 2	320 ± 80
3E	Hunter Marsh	clayey peat	60 ± 2	120 ± 75
2C	Hunter Marsh	peat, basal	125 ± 5	980 ± 90
3E	Hunter Marsh	clayey peat	255 ± 3	1260 ± 200*
3CM	Chippokes Marsh	clayey peat, basal	733 ± 2	4880 ± 140
3HM	Hunter Marsh	peat	576 ± 4	3310 ± 300
3HM	Hunter Marsh	peat, basal	922 ± 2	5780 ± 210
4G	Hunter Marsh	peat	385 ± 2	1735 ± 95
4G	Hunter Marsh	peat, basal	445 ± 2	3345 ± 120
5H	Hunter Marsh	clayey peat	375 ± 2	1570 ± 140
5H	Hunter Marsh	clayey peat, basal	565 ± 2	2810 ± 160

[1]Kennon Marsh, James Estuary
Hunter Marsh, Rappahannock Estuary
Chippokes Marsh, James Estuary

[2]Dates by Geochron Laboratories except for 3E by Smithsonian Institution.

estuaries. At the mouth of the York estuary, populations exceed 2.3 x 10^6 cells/L, decreasing to 1.5 cells/L at the mouth of the Bay. During summer months productivity in estuary mouths is greater than 45 mg-carbon/m^3/hr (Zubkoff *et al* 1973). Populations of foraminifera are large near the mouth of the James, but small off the mouths of the York and the Rappahannock Rivers.

Benthic Plants. Shoals of the lower bay and lower estuaries less than 3.5 m deep are covered with grass beds of *Zostera marina* and *Ruppia maritima*. Dillon (1971) estimates the productivity of *Zostera* beds to be about 0.95 gm-carbon/m^2/day, a significant contribution to the total Bay production, as well as an important habitat for a variety of consumers including foraminifera. *Zostera* stands in the estuaries often support large, healthy populations of foraminifera, particularly *Ammonia beccarii*.

Zooplankton. Since most of the primary production in the Bay is planktonic and most of this production is not directly linked to benthic organisms, grazing by zooplankton is a critical link in the flow of energy. These zooplankton populations show large seasonal changes in number and composition, with winter assemblages differing considerably from summer assemblages. Copepods, however, are nearly always dominant. Production by the copopod *Acartia tonsa* alone is estimated to be nearly half of the total primary planktonic production (Heinle 1966).

Historical factors

Any consideration of biological communities must take into account the past and future history of the habitat occupied by the community. Estuaries are aquatic systems that are the result of the Holocene rise in sea level over the past 17,000 years (Emery 1967, Wolman 1963). As sea level rose submerging the stream valleys of the Susquehanna, James and other rivers, the Chesapeake Bay estuary was formed (Hack 1957). This gradually enlarging coastal reservoir was the site of rapid infilling by sediment supplied by the rivers, as well as by river-bank erosion and sediment input from the sea. Attendant with this inundation by marine waters was the invasion of marine organisms into Chesapeake Bay, somewhat forestalled by the high rates of river discharge during glacial melting within the Bay's drainage area. Because the Bay is of relatively recent occupation by marine and brackish water organisms, habitats have not yet been finely differentiated so that communities still

TABLE 4

Paleoclimatic Episodes (after Bryson, *et al*, 1970)
and Marsh Deposit Microfaunas

EPISODE	TENTATIVE DATE, B.P.	CLIMATIC CONDITIONS[1]	MICROFAUNAS IN MARSH CORES[2]
Neo-Boreal	100	-	
Neo-Atlantic	800	+	Increased foraminifera relative to thecamoebinids (880-1310 B.P.)
Scandic	1200	-	
Sub-Atlantic	1690	+	Increased foraminifera relative to thecamoebinids (1465-2700 B.P.)
Sub-Boreal	2890	-	
	4680		
Atlantic (post-glacial optimum)		+	Increased foraminifera relative to thecamoebinids (4880-5780 B.P.)
	8450		

[1]Climatic conditions cannot be generalized satisfactorily inasmuch as a particular episode may be manifested in one area by an increase in precipitation or temperature, etc. while the same parameter decreases elsewhere. A + signifies a "moderation" in conditions; - a "deterioration" in conditions.

[2]See Figure 8 for changing percentages of foraminifera relative to thecamoebinids, and accompanying radiocarbon dates.

are composed chiefly of a few, broadly tolerant species.

DISTRIBUTION OF BENTHIC FORAMINIFERA

General

Foraminifera comprises but one element of the benthic community of the Bay ecosystem, large in number but small in total biomass. Although faunal boundaries and population sizes fluctuate seasonally with changes in environmental factors, the species composition of foraminiferal faunas is relatively distinct and stable. Therefore, the distribution of these faunas should provide useful ecological information about the Bay system. Over the past 13 years, nearly 500 samples of the topmost cm of sediment taken from cores in the Chesapeake Bay region have been subjected to foraminiferal analysis. Standard field and laboratory practices have been followed, and living specimens of foraminifera have been identified through the use of rose Bengal stain. Because empty tests are so much more numerous than living specimens, population sizes in this paper commonly refer to total numbers of specimens rather than to only living ones or to empty tests. Table 2 summarizes faunal numbers and diversity.

The community gradient (coenocline) reflects the environmental gradient (ecocline) in the estuary. Environmental parameters gradually change geographically along the length of the estuary; so, too, communities of benthic organisms including populations of foraminifera change. Associations of species of foraminifera, here termed "faunas", appear to be particularly useful in delineating segments of such gradually varying coastal ecosystems. These faunas inhabit a range of different but interrelated environments from the river to the sea acorss a salinity gradient from fresh water to water of normal marine salinity (Fig. 3). Another environmental gradient results from a change in depth across the estuary and a change in elevation across zones of different marsh vegetation.

Associated with these environmental gradients are seven foraminiferal faunas, recognized on the basis of the dominance of one or two species. The faunas consist of well-known marsh and estuarine species which are illustrated and described for the region by Ellison and Nichols (1970), Nichols and Norton (1973). Generally, distributions of individual species overlap, so that the transition from one fauna to another is gradual. According to Whittaker (1975), communities are continuously intergrading features. However, boundaries between two or three of the faunas described here are relatively sharp. Such abrupt transitions (ecotones) normally should include very diverse assemblages with species from the faunas on either side of the boundary as well as a few that are unique to the ecotone itself.

Marsh and estuarine thecamoebinid fauna

Extending from the river seaward to the salt-intrusion head of tributary estuaries, 74 km above the mouth of the James, the benthic microfauna is devoid of foraminifera, but contains a diverse assemblage of thecamoebinids. Total populations often exceed 2,000 specimens per 20 ml. The dominant species in both the estuary and fringing marshes are: *Centropyxis arenata, C. constrictus, Difflugia constricta* and *D. pyriformis*. This zone is continually freshened by river water despite ebb and flood of the tide which scours the sandy bottom around meanders. The dominant marsh plants are *Pontederia cordata* (pickerelweed), *Sagittaria* (arrowhead) and *Typha augustifolia* (cattail). The seaward change from thecamoebinids to foraminifera is rather abrupt, taking place in a narrow zone extending less than 8 km along the estuary where the bottom salinity in summer averages 0.5 °/oo (Fig. 3). However, the boundary fluctuates more than 30 km upstream or downstream in response to seasonal changes of salinity resulting from changes in river inflow.

Marsh *Ammoastuta* fauna

The *Ammoastuta* fauna inhabits river-influenced, low-salinity marshes. It extends along the estuary from the thecamoebinid fauna in fresh water seaward to the "mixed marsh" fauna in water of intermediate salinity (Fig. 4). Laterally the fauna ranges mainly from the upper limits of tidal flooding to the edge of the marsh (Fig. 5). Although species of this fauna are found farther seaward on estuary shoals and in marsh-fringed creeks, the largest populations of these species are in the middle marsh. Characteristic species of this fauna are: *Ammoastuta salsa* (dominant), *Astrammina rara* and *Miliammina earlandi*.

The annual average salinity of estuary water that floods *Ammoastuta* marshes is less than 10 °/oo and the range is from 0 °/oo to 13 °/oo. The plant *Peltandra virginica* covers low marsh banks while *Scirpus robustus* (bullrush) and *Spartina cynosuroides* (giant cordgrass) cover the high marsh, and *Typha augustifolia* grows near the upper marsh margin. The extreme intertidal exposure and the strong river influence in this zone makes survival of foraminiferal species risky. Total populations are relatively small, with fewer than 800 specimens per 20 ml. About 10 species are found in an average sample. The boundary between this fauna and the thecamoebinid fauna is relatively sharp, and it fluctuates seasonally with changes in river inflow.

Mixed marsh fauna

A mixed foraminiferal fauna inhabits marshes in middle estuarine reaches. Although river influence in this zone is diminished, marshes are subject to freshening by local runoff. The normal salinity range is 4 to 15°/oo and the annual average is about 13 °/oo. *Spartina alterniflora* (smooth cord grass) covers the low marsh while *Scirpus* sp. and *Spartina patens* (salt meadow grass) cover the high marsh.

The mixed marsh fauna is transitional between the *Ammoastuta* fauna landward and the *Miliammina* fauna seaward. Faunal boundaries are not sharp; instead the proportion of species changes gradually along the estuary. The most characteristic species are: *Tiphotrocha comprimata, Haplophragmoides hancocki, Trochammina macrescens, T. inflata* and *Arenoparrella mexicana*. Foraminiferal populations in this zone are relatively large with living populations often exceeding 4,500 per 20 ml, and total populations exceeding more than 21,000 psecimens per 20 ml. The mixed marsh fauna is comprised of 16 species, making it more diverse than the adjacent *Ammoastuta* fauna.

Lateral changes in the species composition of the mixed marsh fauna with increasing elevation above low water are recorded in a traverse across Belle Isle marsh of the middle Rappahannock estuary (Hoinowski 1969), shown in Figure 5. The low, *Spartina alterniflora* marsh is flooded at each high tide, whereas the high, *S. patens* marsh is inundated only by storm tides. Between these two plant zones, in an intermediate zone near mean high water, *Scirpus robustus* is dominant. Landward from the low to the high marsh, *Ammobaculites crassus* and *Miliammina fusca* decrease in number while *Tiphotrocha comprimata, Trochammina macrescens* amd *T. inflata* increase. Populations of *Ammoastuta salsa* peak in the intermediate, *Scirpus* zone; living populations there reach 65 per 20 ml while total populations are 5,000 per 20 ml. Diversity is greater (12 species) than in the low and high marshes.

Marsh Miliammina Fauna

The fauna dominated by *Miliammina fusca* inhabits high-salinity seaward reaches along the estuary where the salinity of the water inundating the marshes averages 16 °/oo annually and ranges from 9 to 27 °/oo. *Spartina alterniflora* covers the low marsh and *S. patens* along with *Distichlis spicata* (marsh spike grass) cover the high marsh. Extensive sections of low marsh are exposed to wave action which produces sandy sediment parallel to the shore. This is a direct contrast to the organic silty clay of the *Ammoastuta* and mixed marsh faunas.

The *Miliammina* fauna extends from the mixed marsh fauna in middle extuarine reaches to marine marsh communities of lower Chesapeake Bay and the Eastern Shore of Virgina; laterally it grades into the *Ammobaculites* fauna on the shoals of the estuaries. *Miliammina fusca* is the dominant form, comprising more than 65 % of the fauna; the remaining portion is composed of about 15 of the more ubiquitous species, including: *Ammonia beccarii, Ammobaculites crassus* and *Arenoparrella mexicana*. In lagoons contiguous to the Chesapeake Bay entrance the fauna contains numerous specimens of *Elphidium clavatum* and *Trochammina inflata*. Total populations are of modest size, largely less than 2,500 specimens per 20 ml.

Ammobaculites Fauna

The *Ammobaculites* fauna inhabits the river-influenced, low-salinity reaches of the tributary estuaries along the western side of Chesapeake Bay in Virginia. Farther north, in Maryland, this fauna extends seaward down the estuaries nearly to the Bay. In the Choptank estuary, on the Eastern

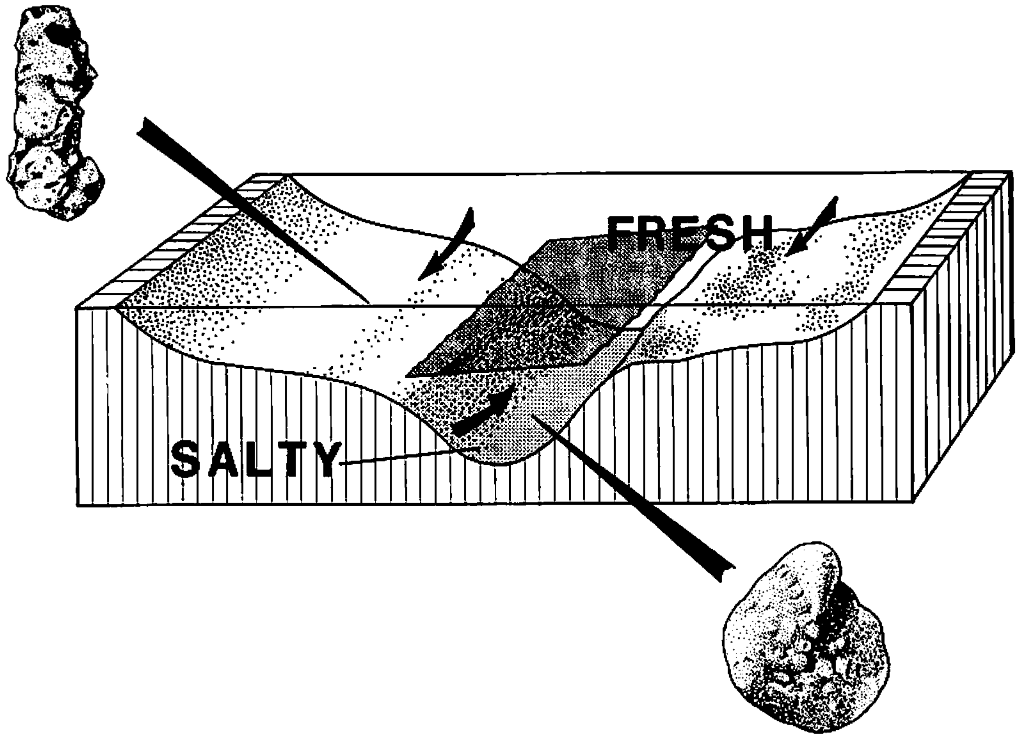

FIG. 6 Lateral change in principal faunas, Ammobaculites and Elphidium in relation to bottom topography and upper and lower, freshened and salty, estuarine layers. The boundary between layers is the level of no-net motion.

Shore of Maryland, Buzas (1969) studied assemblages that were predominantly *Ammobaculites exiguus* 8 to 16 km above the mouth of the estuary. Farther south in the Bay, small creeks draining the Eastern Shore of Virginia have well-developed faunas dominated by *Ammobaculites* extending to within 3 km of their mouths. In those estuaries where river inflow exceeds the influence of the tide and salinity stratification is established, e.g. in the James, York and Rappahannock estuaries, the *Ammobaculites* fauna is found on the shoals (less than 9 m deep), and the higher salinity, *Elphidium* fauna inhabits the deeper, medial channels (Fig. 6). The downstream limit of the *Ammobaculites* fauna is about at the position of the 14 °/oo-bottom isohaline in the Rappahannock and the 15 °/oo isohaline in the James (see also Weiss, 1976) and the upstream limit is at a salinity of 0.5 °/oo where the fauna is replaced by the thecamoebinid fauna. However, the limiting factor for the *Ammobaculites* fauna is not salinity *per se* because *Ammobaculites* and *A. dilatatus* abound in creeks on the Eastern Shore where summer salinities approach 19 °/oo. Many factors are responsible for a particular environmental setting, some of which may be more influential than salinity. This is a region of environmental stress where factors vary widely. One particular stress, suspended sediment concentration is significantly greater here than elsewhere (Table 1).

Besides the dominant *Ammobaculites*, this fauna consists of small percentages of agglutinate forms such as are found in the marshes, namely species of *Trochammina* and *Haplophragmoides*, *Miliammina fusca* and *M. earlandi*, and the calcareous *Ammoni beccarii tepida*. Tributaries on the eastern side of the Bay, draining the Eastern Shore also contain large numbers of *Ammobaculites dilatatus*. Although the number of species per 20 ml may be as many as 14, *Ammobaculites crassus* commonly comprises more than 90 % of the fauna, and the remaining 13 species collectively make up less than 10 %. The greater foraminiferal diversity at the mouths of tributary creeks suggests that either conditions are somewhat more favorable there, or that the less common species are being introduced there from the fringing marshes rather than being indigenous to the estuary. The significance of *Ammobaculites* and, to some extent, its associated species in the Chesapeake Bay region has been considered elsewhere at length (Ellison 1972).

Total populations within this fauna are large. Nichols and Norton (1968) report one sample from the gradient zone of the James estuary with over 100,000 specimens per 20 ml. Samples with more than 5,000 specimens are common in the middle stretches of the tributary estuaries. In the Eastern Shore creeks, total populations of *Ammobaculites* reach tens of thousands per 20 ml. Although living populations are 1 to 2 orders of magnitude smaller than total populations, their maxima coincide in position along the estuaries.

Elphidium Fauna

In the tributary estuaries 3 to 32 km above their mouths, throughout nearly the entire lower half of Chesapeake Bay and extending 16 to 24 km offshore, foraminiferal assemblages are overwhelmingly dominated by *Elphidium*, chiefly *Elphidium clavatum*[1]. This widespread, highly tolerant and morphologically variable species abounds in waters that range in salinity from 14 to 33 °/oo and on substrates varying from fluid mud to well-sorted, fine-grained sands. On the shelf, percentages of *Elphidium clavatum* commonly are less than 40 % in medium-grained sand and greater than 50 % in fine and very fine-grained sand.

Although as many as 30 species per 20 ml are locally present within this zone, the average number of species is 16. However, the proportion of *Elphidium clavatum* and *E. incertum* together generally exceeds 80 %. Diversity is minimum in the tributary estuaries and the Bay, increasing to a maximum on the shelf; many samples in the Bay contain fewer than 5 species. In the James, York and Rappahannock estuaries, the *Elphidium* fauna ("basin facies" of Nichols and Ellison 1967) extends seaward of the 14 °/oo isohaline. Confined largely to the channels and to the shoals near the mouths of these tributary estuaries, the *Elphidium* fauna is abruptly replaced upstream by the *Ammobaculites* fauna within a distance of from 6 to 16 km. The diversity at this transition is high at times, owing chiefly to the occurrence of other *Elphidium* species or related taxa. For example, in the Rappahannock estuary, *Elphidium galvestonense* and *Protelphidium tisburyense* were numerous in this boundary zone in 1963 but not in 1962. Owing to seasonal changes in salinity and associated factors the upstream limit of this fauna migrates up and down the estuary.

The composition of the *Elphidium* fauna in the Bay differs from that in the estuaries, chiefly in the absence of *Ammobaculites*, *Miliammina* and other species that are principally inhabitants of the upper estuary and of the marginal salt marshes. On the shelf the most important foraminifera, in addition to *Elphidium*, and *Eggerella advena*, *Trochammina squamata*, *Reophax scottii*, *Ammonia beccarii* and *Cibicides lobatulus*.

Populations of empty tests and living specimens range from nearly zero to over 15,000 per 20 ml, averaging approximately 600. In the Rappahannock estuary, total populations within this fauna average 500 per 20 ml, but range from 150 to 1,500.

Total populations in the Bay average 600 per 20 ml, but the largest are in the lower Bay east of the mouth of the James where the influence of that river is most effective in continually replenishing the food supply. Inexplicably, this is not true in the Bay off the mouths of the Rappahannock or the York. One particularly puzzling and perhaps important feature is the absence of foraminifera in mid-Bay, as determined from several surveys. The bay floor just east of the York River entrance is barren of foraminifera in places, and no foraminifera were found in several samples collected east of the mouth of the Rappahannock. There the dark muds contain little else than large numbers of needle-like frustules of the diatom *Nitzschia*. This foraminiferal, mid-Bay "desert" remains to be explained.

On the shelf, in water less than about 25 m deep, population sizes average 800 per 20 ml. The largest populations here are immediately northeast of the Bay entrance where the total number of specimens per 20 ml generally exceeds 1,000. This also is a zone of rapid current mixing. In addition, populations of over 4,000 per 20 ml found in troughs at depths of 24 to 29 m are much larger than those on the intervening topographic rises.

Shelf Mixed Species Fauna

On the continental shelf between depths of about 20 and 45 m, the foraminiferal species are numerous and vary widely in abundance and relative proportions from place to place. No single species is "dominant", i.e. none comprises 50 % of any sample population, but the most abundant species is *Elphidium clavatum*. Most of the common species (*E. clavatum*, *E. incertum*, *Eggerella advena*, *Trochammina squamata*, *Reophax scottii*, *Ammonia beccarii* and *Cibicides lobatulus*) are not unique to this fauna. Several species, however, have been found only in this zone, namely: *Cassidulina algida*, *Cornuspira* sp., *Bulimina marginata*, *Globulina* sp., *Textularia* cf. *T. candeiana*, *Bolivina pseudoplicata* and *Poroeponides lateralis*. Diversity is high, with the average number of species per 20 ml at 31, and one sample yielded 39 species; furthermore, the abundances of the various species are more uniformly distributed in this fauna than in others.

Total populations average about 850 per 20 ml and increase slightly with depth. However, none of the samples have populations as large as some of those found in shallower depths on the shelf.

The shelf bottom inhabited by the "mixed species" fauna is largely a relict surface of Late Pleistocene or Early Holocene age. The sediment is primarily residual, inasmuch as little or no sediment is being deposited there now. In fact, the principal sedimentary process operative there is scour in the elongate depressions which, in places has exposed an underlying stratum of firm clay. Quite possibly the foraminiferal assemblages found on this portion of the shelf are partly fossil and partly contemporary.

Beyond any major influence of the Bay, the shelf bottom water here maintains a salinity of about 32 °/oo, is moderately clear (Secchi disc values of 18 or more m), and ranges in temperature from about 5°C in the winter to 21°C in the summer. The water over deeper bottoms in the summer is, of course, cooler than the surface water; also offshore water is slightly cooler than inshore water in the summer, a situation that is reversed in the winter. Following Odum and Copeland (1974), this is a "coastal plankton" system that is under minimal stress and exhibits less pronounced seasonal programming than do the estuaries. Low stress leads to high diversity and numerous species niches. It is natural, then, to find diversity within this zone increasing with depth offshore.

[1]*Elphidium excavatum* (Terquem) *forma clavata* Cushman, according to Feyling-Hansen (1972).

Relationships of Foraminiferal Faunas

Vertical and horizontal marsh distributions. Species inhabiting the high marsh tolerate extremes and must, therefore, have a wide range in their horizontal distributions. For this reason it is not surprising that many species of the "mixed marsh" fauna occur in small numbers landward into fresh-water marshes and also seaward into normal marine marshes. Then, too, *Ammoastuta salsa* which increases in abundance with increasing elevation across marshes of the middle estuary also increases in abundance in upstream marshes. In contrast, *Miliammina fusca* which decreases in abundance with elevation across marshes of the middle estuary, also increases in abundance seaward. Thus, the vertical trends of dominant species are linked to horizontal trends according to the extreme range of environmental conditions, mainly salinity. Changes in foraminiferal composition along the estuary are generally parallel to begetational zones, but not necessarily dependent on them.

Estuary-shelf

The major features of the distribution of foraminiferal taxa in the estuary-shelf portion of the Chesapeake region are shown in Figure 3 (lower). From the head of the James estuary to the middle of the continental shelf, the foraminiferal faunas are dominated in turn by thecamoebinids, *Ammobaculites*, *Elphidium* and a mixture of species. Boundaries between these fauns, established where one genus, e.g. *Ammobaculites* comprises more than half of the population, are reasonably well-defined and abrupt. This is especially true of the thecamoebinid-*Ammobaculites* boundary and somewhat less so for the *Ammobaculites*-*Elphidium* boundary. On the shelf, the change from an *Elphidium*-dominated fauna to one with several co-dominants is transitional and results primarily from the progressive decrease in numbers of *Elphidium clavatum* offshore. Similarly, Buzas (1969) found that the upstream replacement of an *Elphidium* fauna by an *Ammobaculites* fauna in the Choptank River of Maryland resulted from a decrease in numbers of *Elphidium clavatum* upstream rather than from an increase in numbers of *Ammobaculites exiguus*. Such an interpretation cannot be applied indiscriminately in the Chesapeake region; in the Rappahannock estuary, the change from an *Ammobaculites* to an *Elphidium* fauna most commonly represents a decrease in numbers of one genus and an increase in numbers of the other.

The faunal changes observed along the length of the estuary and laterally across the estuaries has been discussed elsewhere (Ellison and Nichols 1970). The *Elphidium* fauna in the deepr, more saline, medial basin-channel of the estuary is replaced on the marginal shoals by the *Ammobaculites* fauna that is adapted to the less salty, near-surface water (Fig. 6). Lateral boundaries between these faunas are very sharp owing to the sudden changes in depth and the marked vertical increase in salinity from the shoals into the basin-channel; the transition occurs over a distance of a few hundred meters horizontally. In contrast, the longitudinal boundaries between faunas, even where sharp, extend over a distance of several kilometers. This arises from the fact that longitudinal mixing of water, while less effective than vertical mixing, is more effective than lateral mixing, particularly near the head of the salt-water intrusion where mixing of river water with salt water is most intense.

The distributions are modified by transportation of immature and adult forms, with specimens of *Elphidium* being moved upstream in the channels, and those of *Ammobaculites* being moved downstream over the shoals by net density currents in those directions. Specimens of marsh foraminifera also are washed into the creeks and downstream on the estuarine shoals. Studying several common estuarine species, Sandifer (1969) was unable to distinguish between settling velocities of living (stained) individuals and the empty tests, but found that all species behaved about like fine sand. These results support the contentions of other investigators (Parker, Phleger and Peirson 1953; Haven and Morales-Alamo 1968) that foraminifera may be physically transported over considerable distances. According to Sandifer, agglutinate species are slightly easier to transport than calcareous ones. Ability to attach is important to species inhabiting bottoms subject to current stress.

Faunal boundaries shift upstream and downstream in response to seasonal and long-term changes in the fresh water-salt water budget. In the Chesapeake region, increased evapo-transpiration in the summer means that less fresh water is available for river discharge into the estuaries. Consequently, the estuaries become saltier and the faunas shift upstream. Climatological changes that produce the same effects, but on a larger time scale are discussed in a later section of this paper.

Species of foraminifera on the shelf are not distributed in well-defined faunas. Delaney (1970) classified her samples into: Zone I (Nearshore, turbid zone) and Zone II (inner shelf zone) on the basis of the dominance of *Elphidium clavatum* which appears to bear some relationship with the turbidity of the water and the character of the substrate. That is essentially the classification adopted here: the inner shelf zone of Delaney corresponds with the "mixed species" fauna. Species adapted to more stable, marine conditions increase in proportion offshore, gradually replacing *Elphidium clavatum* and *E. incertum*. Species of agglutinate forms, in particular *Eggerella advena*, *Trochammina squamata* and *Reophax scottii* are increasingly important components of the offshore faunas studied.

Population sizes, while highly variable, exhibit a trend from large in the upper and middle stretches of the estuaries to small in the Bay, increasing slightly onto the shelf. The largest total populations and largest living populations are within the range of the *Ammobaculites* fauna where numbers may exceed 25,000 per 20 ml and where the average is nearly 2,000. Living specimens average an order of magnitude fewer. These numbers diminish to an average of 650 per 20 ml in the Bay and 800 to 850 per 20 ml on the shelf. The negative gradient in population size from the estuaries to the Bay suggests that the foraminiferal "carrying capacity" of the system decreases in that direction. One element of this decrease is the gradual reduction in the amount of available nutrients (total phosphorous and nitrite-nitrate) downstream and the decrease in populations of primary producers including benthic algae and phytoplankton. Optimization of resources in the estuary may demand larger, seasonal populations than in the Bay. The larger populations on the shelf may reflect the fact that this is the natural environment for *Elphidium clavatum* in the Chesapeake region whereas this species is a stranger to the estuaries, living only a marginal existence there. Large offshore populations found by Schnitker (1971) about 60 m deeper than the shallowest maximum for several species on the North Carolina shelf have been interpreted as representing fossil populations from earlier stillstands in sea level. This may also be true for populations of the shelf of Virginia.

HOLOCENE HISTORY

General

The Flandrian rise in sea level, between 15,000 and 5,000 years BP, submerged the lower stretches of the anicent Susquehanna River drainage system, producing the Chesapeake Bay and its tributary estuaries. During this sea-level rise, a time of unusually heavy river runoff, both depositional and erosional rates also must have been unusually high. As sea level rose, salt water penetrated farther into the drowned river system, bringing with it the microfaunas associated with higher salinities. This marine transgression should be documented vertically in the sedimentary record. Furthermore, extreme events as well as long-term climatic changes which affect the volume of fresh or salt water entering the estuary also should leave faunal documentation in the sediments.

If, as we have suggested, the boundaries between present-day foraminiferal faunas correlate with bottom salinity, then the past positions of these boundaries as represented faunally in cores should provide us with information concerning paleosalinities and, in turn, paleoclimatology. Of the microfaunal boundaries observed in the Chesapeake region, that between the thecamoebinids and foraminifera in the marshes, and between *Ammobaculites* and *Elphidium* in the estuaries are most closely tied to salinity. For this reason they should have greatest potential for this application. With this as a working hypothesis we have taken 12 piston cores in the Rappahannock estuary and in the James estuary along the present position of the *Ammobaculites-Elphidium* boundary, and 11 cores from several marshes across the present position of the thecamoebinid-foraminifera boundary. In addition, cores taken by the Coastal Engineering Research Center of the Army Corps of Engineers near the mouth of Chesapeake Bay have been examined (Nelson 1969).

Chesapeake Entrance

Five cores from the entrance to Chesapeake Bay have yielded limited evidence about the recent depositional history of that area. The most informative of these cores came from 14 m of water in the Chesapeake Channel. The core is 5.4 m long and shows sedimentary and foraminiferal changes through its length. Nelson recognized three paleofaunas: (1) the bottom of the core (19.5 m below present sea level) has a fauna composed of a mixture of high and low salinity species, suggesting a bay or lagoon in close proximity to the bay entrance where shelf and estuarine species could be mixed; (2) 16.8 and 17.7 m below present sea level, salt-marsh deposition is indicated by more than a meter of peat with small populations of *Arenoparrella mexicana, Ammoastuta salsa* and *Tiphotrocha comprimata* indicative of the intermediate, *Scirpus* zone of the "mixed" marsh fauna"; and (3) the upper half of the core with a fauna varying in composition vertically and suggesting an upward increase in salinity. In as much as salt marshes are intertidal, the peat with its salt-marsh foraminifera at about 17 m marks a former sea level. According to the sea-level curve of Milliman and Emery (1968) this peat should be 6000 to 7000 years old. However, radiocarbon dating of the peat gives it an age of about 11,000 years; the entrance to the Bay must, therefore, have been uplifted about 40 m during the rise in sea level.

Rappahannock and James Estuaries

Five cores from the *Ammobaculites-Elphidium* boundary in the Rappahannock and James estuaries yielded data that, if interpreted with care, can provide useful paleoclimatological information. Ambiguities arise, partly from solution of foraminiferal tests; below about 120 cm in these estuarine cores, few tests are preserved. Post-depositional decomposition of tests appears not to be restricted to calcareous species.

Whatever the ultimate cause, or combination of causes, the position of the upstream boundary of the *Elphidium* fauna has oscillated along the estuary in the recent past. Rates of sedimentation as determined from hydrographic surveys over the past century are about 0.15 cm per year. If this rate is dependable and the upper meter represents the last 600 years, there have been three periods of *Ammobaculites* dominance and two period of *Elphidium* dominance, each of about 100 years duration. Increased percentages of *Ammobaculites* relative to *Elphidium* could result from higher preceipitation, lower evapo-transpiration, or shoaling of the estuary floor.

Fresh-salt transitions in marsh deposits

The most convincing and comprehensive data on the Holocene history of the Chesapeake region comes from cores taken from marshes along the upper reaches of the James and Rappahannock estuaries.

Because modern thecamoebinids and foraminifera mark the transition between fresh and salty water, fossil specimens of these taxa in marsh deposits are useful for tracing past changes in the transition. These changes indicate the probable paleohydrologic conditions affecting the estuary during its submergent history over the past 6,000 years.

The samples were obtained at 10 to 30-cm depth intervals from 11 cores located across a 14-km reach of the fresh-salt transition in the James and Rappahannock estuaries. The deposits consist of

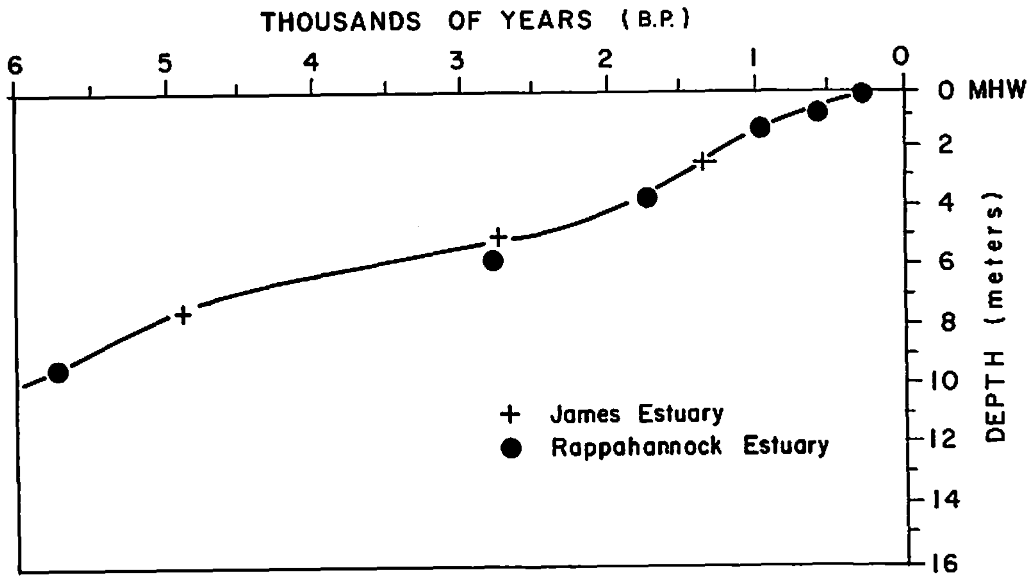

FIG. 7 Submergence curve for the upper James and Rappahannock estuaries based on radiocarbon dates of basal peat deposits.

peat and organic-rich silty clay deposited mainly in the high marsh. Preservation of the specimens is generally good. The faunas consist wholly of arenaceous species that live in the modern marshes.

The age of the marsh deposits was determined from radiocarbon dating of peat samples obtained at selected depths exhibiting marked changes in the faunas, and also at the base of marsh deposits overlying firm sand and gravel. Table 3 lists locations and ages of the samples dated.

A submergence curve, which is defined by a plot of sample age versus depth for samples from the marsh base (Fig. 7), records the accumulation of sediments deposited near high water during submergence of the estuary in the last 6,000 years. The rate of submergence proceeded at a relatively uniform rate, 0.16 cm per year. This rate is similar to rates reported for other parts of the mid-Atlantic coast (Newman and Rusnak 1965, Stuiver and Daddario 1963).

General History. In cores KM-1 and CM-1 thecamoebinid percentages generally decrease upward while foraminiferal percentages increase. This trend indicates increased freshening with time during submergence of the estuary, a trend that would appear to be contrary to the expected increase of salinity as the estuary was drowned. The increased freshening with time may result from increased sedimentary infilling that shoaled the estuary floor more rapidly than the estuary submerged. Present-day shoaling is active at the inner limit of salty water today. Shoaling not only restricts penetration of salty water from the sea but also increases mixing of fresh and salty water in the estuary proper thereby lowering the overall salinity. A slight freshening of the estuary may cause a large longitudinal shift in the fresh-salt boundary. Seaward shifting of this boundary with time also would be effected by increased river inflow.

Long-term Climatic Changes. Direct and indirect evidence for recent paleoclimatic changes have been summarized by Lamb (1971) and Bryson *et al* (1970). Although some differences of opinion exist concerning the classification and dating of the paleoclimatic episodes, several points of interest here are more or less agreed upon (Table 4).

1. The period from about 5,000 to 3,000 B.C. (7,000 to 5,000 BP), known as the "post-glacial optimum" was a time of moderate climate in the northern hemisphere, with floras and faunas displaced northward.

2. The period from 2,900 (or 2,500) BP to 1,700 BP was also characterized by mild climates and northward

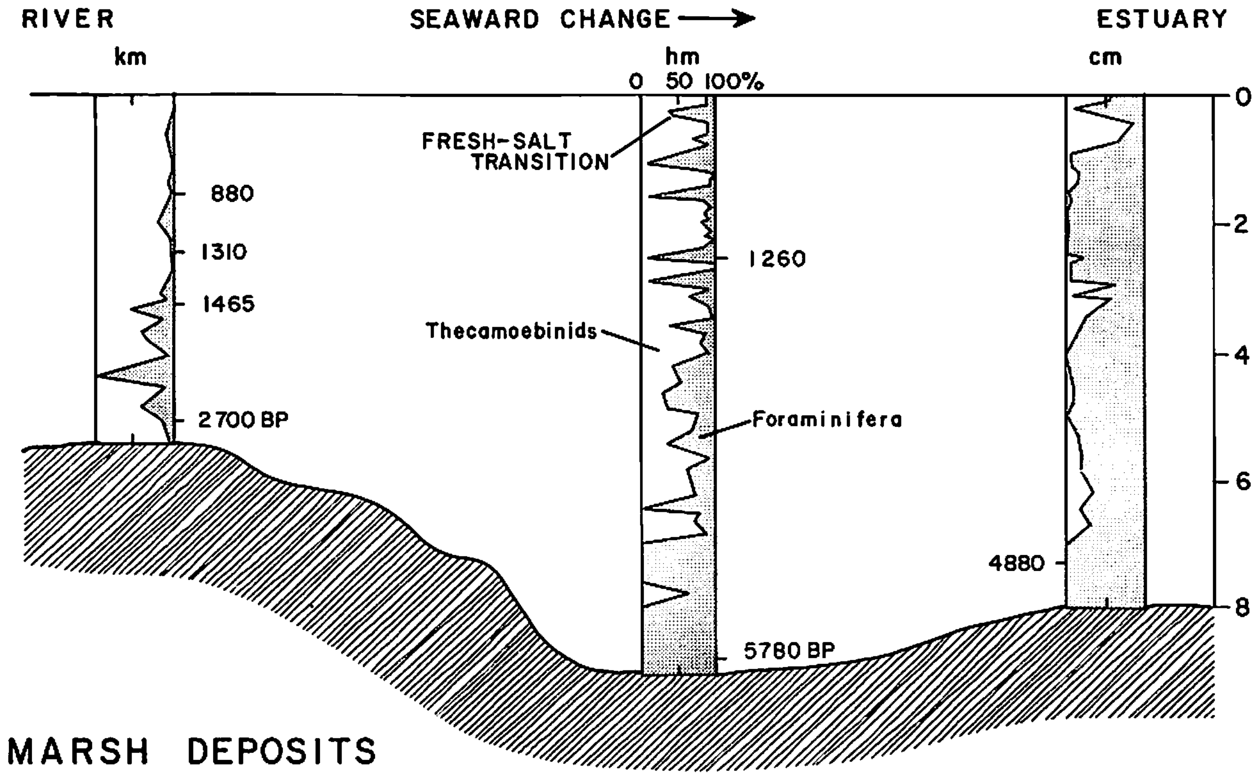

FIG. 8 Vertical variations in percentages of foraminifera and thecamoebinids in cores of marsh deposits across the present-day transition from fresh to salty water. Numbers represent radiocarbon ages of peat material. For precision of dates, see Table 3.

migrating plants and animals. This period is referred to as the Sub-Atlantic episode and is separated from the post-glacial optimum by the cooler, Sub-Boreal episode.

3. The most recent period of climatic moderation was from 1,200 to 800 BP. This Neo-Atlantic episode was preceded by a wrming, "Scandic" episode and followed by about 750 years of climatic deterioration, culminating in the Little Ice Age between 100 and 300 BP (1700 and 1883 A.D.).

Referring to Figure 8 and Table 4 we see maximum salt water intrusion at the base of core HM, dated 5,780 BP, and probably corresponding with a similar dominance of foraminiferids at the base of core CM-310. The marshes freshen markedly sometime shortly after 4,880 BP (core CM-310). It is not unlikely that this correlates with the post-glacial optimum when, with warmer temperatures and displaced frontal systems, fresh water inflow into the estuarine system may have been reduced.

Similarly, the salt water intrusion represented by increased foraminiferal numbers between 2,700 and 1,465 BP, and between 1,310 and 880 BP in core KM (and 1,260 BP in core HM) very likely correspond respectively with the Sub-Atlantic and the Neo-Atlantic episodes of Bryson. The periods between would, naturally, be times of climatic deterioration, cooler temperatures and perhaps increased precipitation or reduced evaporation. Although more data are desirable, the available information strongly suggests a correlation with established paleoclimatic episodes.

Short-Term Events. Superimposed on the long-term trend of increasing thecamoebinids with time in the last 6,000 years, there are short-term changes in the relative percentages of thecamoebinids and foraminifera in depth intervals of 10 cm. Such an interval represents an average deposition of about 80 years, or possibly deposition during a single flood, The percentage increases in foraminifera observed at depth intervals in core 3E from Hunter Marsh in the Rappahannock Estuary (Fig. 8) are indicative of salt intrusions;for example at 3.0 cm (about 1925 A.D.), 70 cm (about 1800 A.D.), 110 cm (1570 A.D.), 170 cm (1150 A.D.), 260 cm (710 A.D.), 290 cm (545 A.D.) and 350 cm (220 A.D.). The intervening intervals of high percentages of thecamoebinid suggest that the periods of freshening and salt intrusion alternated with considerable frequency. Most changes display an abrupt shift upward from thecamoebinids (fresh water) to foraminifera (salty water) and a more gradual change from foraminifera to thecameobinids. Climatic changes are not known to display such asymmetry. The inferred salinity intrusion at depth (about 1925 A.D.) corresponds to historical records of drought in the region whereas a salinity minimum at 90 cm (about 1800 A.D.) corresponds with a known period of high precipitation. The trends indicate freshening increased faster above the 100-cm depth (1600 A.D.) a trend that reflects faster sedimentation that may have accompanied deforestation and land use during and after the Colonial Period.

The trends found in the James and Rappahannock estuaries are similar to those reported by Weiss (1924) in the lower Hudson River estuary. Like the Chesapeake, foraminifera in the Hudson indicate the estuary freshened with time in the last 1,500 to 3,000 years as the foraminifera changed from chiefly calcareous to arenaceous. The maximum invasion of foraminifera in the Hudson reportedly coincides with a period of postglacial transgression 6,500 years ago. Similarly, the microfaunal composition in a core from the upper Chesapeake Bay reportedly (Owens *et al* 1974) represents more saline conditions than at present. If such trends continue over the long term, salinity should continue to decrease with infilling until freshwater marshes prevail.

SUMMARY OF CONCLUSIONS

1. The Chesapeake Bay with its tributary estuaries is a "natural temperate ecosystem with seasonal programming." The seasonality which is established chiefly by the annual variation in solar insolation is reflected in the character and distribution of microfaunal populations in the Bay system.

2. Seven microfaunas from the marshes, river-estuaries and Bay, and on the shelf are recognized on the basis of the dominance of one or a few species. These faunas, correlated with salinity, are (from the river, seaward): marsh and estuarine thecamoebinid, marsh *Ammoastuta*, "mixed marsh", marsh *Miliammina*, *Ammobaculites*, *Elphidium*, and "shelf mixed species" faunas.

3. Lateral faunal "boundaries" across estuaries and marshes generally are sharper than longitudinal boundaries. More intensive longitudinal mixing of tidal and fresh waters and more gradual changes longitudinally in environmental factors such as salinity and depth both tend to make longitudinal faunal changes more transitional.

4. Foraminiferal diversity increases seaward from the estuaries and high marshes where 10 species per 20 ml is average, through the Bay and onto the shelf where 31 species per 20 ml is average. Diversities in most of the tributary estuaries and the Bay all average 14 to 16 species per 20 ml although the species may differ. The Bay contains the least diverse fauna.

5. The sizes of total foraminiferal populations show considerable variation over small distances, but generally increase seaward from less than 1,000 per 20 ml on the high marshes to a maximum (2,000 per 20 ml) in the middle marshes and tributary creeks. Toward the mouths of the estuaries, populations become smaller (500), remaining about the same (600) through the lower Bay and increasing slightly on to the shelf (800 near-shore, 850 offshore). Living populations parallel total populations although they are one-tenth to one-hundredth the size. In mid-Bay, in an area between the Potomac and York rivers, no foraminiferal tests were found. In the marshes and the estuaries, foraminifera are found in largest numbers near the upper limits of their occurrence. In the Bay, the largest populations are associated with areas of water-mixing on the northern and southern sides of the Bay entrance. On the shelf, population size relates to bottom topography where relief may be as great as several meters. Populations there are larger in topographic swales and smaller on the adjacent rises.

6. Faunas of the marshes and in the middle and upper reaches of the tributary estuaries are composed chiefly of agglutinate species of foraminifera, whereas those in the lower estuarine reaches and the Bay, and on the shelf are predominantly calcareous species. Agglutinate forms also are numerically important in offshore faunas on the shelf.

7. Peat with a "mixed marsh fauna" in a single core from the Bay entrance documents a former sea-level position about 17 m below present sea level. Above that position, the foraminifera in the core are gradually increasing salinity and depth.

8. Microfaunal data (thecamoebinids and foraminifera) and radiocarbon ages from several cores taken from estuarine marshes provide a picture of the recent history of estuarine water budgets and the paleoclimatic history of the region. A gradual freshening of the marshes resulted from sea level being nearly stable for the past 6,000 years, and sedimentary infilling being relatively rapid. Periods of climatic moderation, as established by paleoclimatologists, are marked in the marsh cores by increased number of foraminifera relative to thecamoebinids. Short-term events, such as floods or droughts in the more recent past appear to have a 60 to 80-year periodicity.

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