LIFE HISTORY AND DEVELOPMENT OF OLIGOCENE LARGER BENTHIC FORAMINIFERA: A TEST OF THE ENVIRONMENTAL CONTROL ON HETEROCHRONY

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I. ABSTRACT

Larger benthic foraminifera (LBF) comprise a heterogeneous group of protists that typically reach more than three cubic millimeters in test volume and have complex internal morphologies. For most extant species, large size and complex tests are related to algal symbiosis. Living forms are associated with coral reefs and related oligotrophic carbonate environments, where symbiotic relationships with algae are especially advantageous. Extinct larger foraminifera are almost invariably associated with similar (paleo)environments. It has been argued on theoretical grounds (and supported by some empirical data) that in stable (*i.e.*, low energy) but stressful (*e.g.*, low light for photosymbionts) conditions, the semelparous LBF will delay reproduction, grow to larger sizes, and produce larger embryons (juvenile tests) during asexual reproduction. To test these relations, test size and embryon size of the LBF *Nummulites panamensis*, *Lepidocyclina mantelli*, *L. yurnagunensis*, and *L. undosa*, were examined along a Lower Oligocene forereef-to-deep shelf transect across Georgia, Florida, and Alabama.

The results of this study indicate that intraspecific LBF body size and embryon size are predicted to be greatest at the extremes of a species' range. At these limits, however, it is suggested that large size is attained for different reasons. At the deep end of the ecogradient, LBF delay reproduction and grow longer. Large juveniles (with much symbiont-rich protoplasm) are favored under these low light conditions. Such populations are under stress-selection. At the shallow end of the range, reproduction is also delayed (to increase either fecundity or juvenile size because of low juvenile survival in high energy conditions), but because of the optimality of the environment (*i.e.*, low stress), growth rate is normal or even accelerated. These populations are under *K*-selection. Environmental variables exert a direct influence on the life history and development of larger foraminifera. By delaying reproduction (hypermorphosis) to increase fecundity or juvenile size at the extremes of a species' range, larger intraspecific body sizes result.

II. INTRODUCTION

The relationship of heterochrony (changes in the rates and/or timing of ontogenetic processes) to life history strategies has been developed in the context of *r* and *K* selection. As summarized by McKinney and McNamara (1991, p. 268), *r*-selected populations normally inhabit highly fluctuating environments with unpredictable resources, whereas *K*-selected populations are typical of stable, crowded (*i.e.*, competitive) environments. Some life history attributes of *r*-selected organisms might include small size, early sexual maturation, semelparity, large reproductive allocation, and high numbers of small offspring. *K*-selected organisms are frequently characterized by large size, delayed sexual maturation, iteroparity, low reproductive allocation, and few, large offspring. The *r*-*K* concept represents a continuum of life history strategies. Al-

though the generality (and even validity) of the *r-K* model has been contested, it remains a useful concept (see Boyce, 1984).

As summarized by Gould (1977, p. 289-294), one of the most important life history attributes in *r-K* selection theory is the timing of reproduction. Given the primacy of reproductive timing, specific heterochronic processes would be expected to be associated with *r* and *K* strategies. Under conditions of *r*-selection, *progenesis* (early onset of sexual maturity) and *acceleration* (increased rate of development) should be common. Under conditions of *K*-selection, *hypermorphosis* (delayed onset of sexual maturity), and *neoteny* (reduced rate of development) are expected (McKinney and McNamara, 1991, p. 269).

A recent expansion of the *r-K* model has been the addition of a third end-member to the *r-K* continuum: stress ("stress adaptation" or "stress tolerance": McKinney and McNamara, 1991). Stress-selection occurs in environments that are persistently suboptimal for normal growth and function. According to Grime (1989, p.4), stress is defined as "external constraints limiting the rates of resource acquisition and growth or reproduction of organisms." For marine invertebrates, stress may include (Hallam, 1965) extremes in temperature or salinity, water turbidity and motion, nutrient and oxygen availability, organic content of substrate, solar radiation (especially for organisms harboring photosynthetic symbionts), and crowding.

McKinney and McNamara (1991, p. 377) relate stress-selection to the *r-K* model as follows:

> "Whereas *r*- and *K*-selection represent extreme poles of an axis of environmental stability (disturbance frequency), *K*- and stress-selection represent extreme poles of an axis of environmental stress (or optimality). In other words, any environment on this latter axis is predictable (stable, generally constant), but it may be predictably suboptimal for one or more parameters."

Furthermore, *K*-selection is a density-dependent natural selection (Boyce, 1984), and promotes life history characteristics in response to competition, predation, and other density-dependent pressures. Although high density may be a form of stress, stress-selection encompasses a number of other factors and may occur irrespective of population density or competition. In terms of heterochronic responses to stress, stress-selected species (just as *K*-selected species) would be expected to delay reproduction (hypermorphosis) and to grow more slowly (neoteny). The relationships between environmental disturbance and stability, *r*- *K*- and stress-selection, and the predicted heterochronic processes are illustrated in Figure 1.

The Biology of Larger Benthic Foraminifera

Larger benthic foraminifera (herein LBF) is an informal designation for numerous taxa that typically reach more than three cubic mm in test volume and have

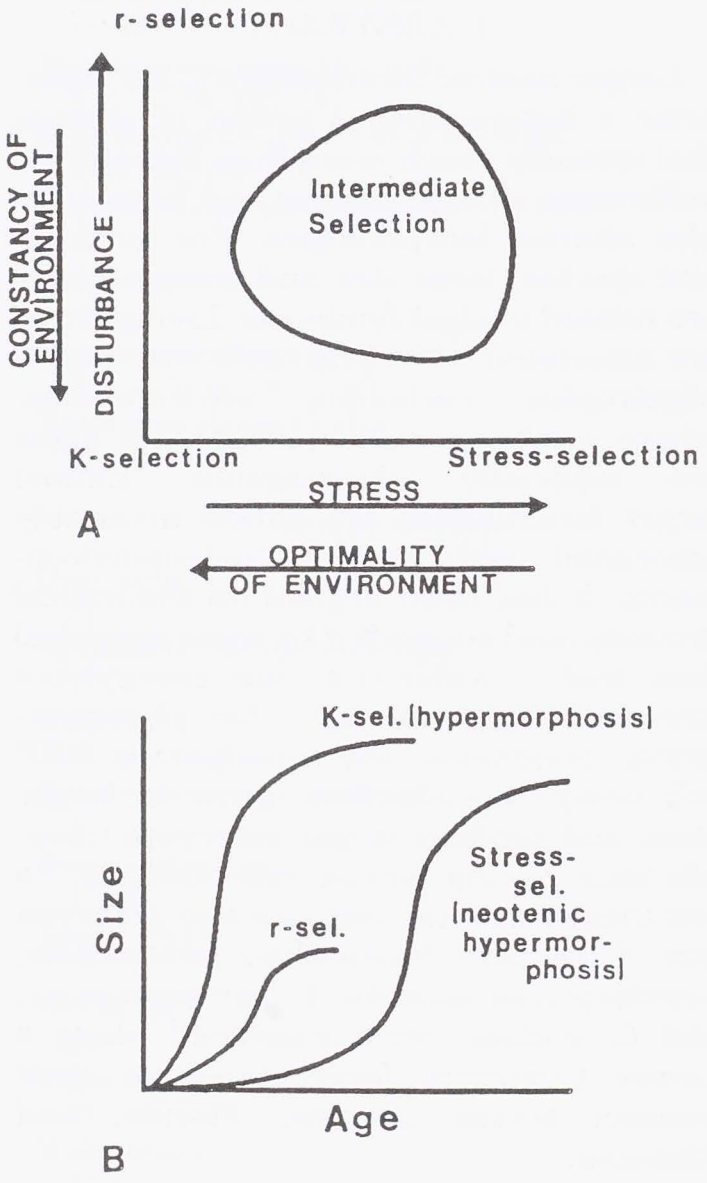

Figure 1. The relations between *r*-, *K*-, and stress-selection and ontogeny. *A.*, *r*-, *K*-, and stress-selection as three end-members along two gradients, disturbance frequency and stress (optimality). *B.*, Predicted ontogenetic curves favored by the three kinds of selection (from McKinney and McNamara, 1991, p. 379, figure 9-4).

complex internal morphologies (most foraminiferans do not exceed 1-2 mm in size: Lee and Hallock, 1987; Hallock, 1985; Ross, 1974). Algal symbiosis has been demonstrated for most modern species of LBF (symbionts include chlorophytes, rhodophytes, diatoms, and dinoflagellates: Leutenegger, 1984; Lee and Anderson, 1991), and it is generally thought that large test size is somehow related to symbiosis (which may facilitate calcification, for example; see Cowen, 1983). Likewise, the complexity of the LBF test may be, in part, a function of cytoplasmic compartmentalization and specialization (such as the housing and sheltering of symbionts in regions of optimal illumination, and away from cytoplasmic flow: Lee and Hallock, 1987; Leutenegger, 1984).

Larger foraminifera are found primarily in tropical to subtropical, oligotrophic environments. They are especially prominent in coral reefs and related facies and can be substantial sediment producers, rivaling corals and calcareous algae in their volumetric contribution (Hallock and Glenn, 1986; Hallock, 1981a; Ross, 1977). Most extinct LBF are associated with similar paleoenvironments, and are inferred to have had algal symbionts (Hallock, 1982).

Foraminifera have extremely variable life cycles (see Lee and Capriulo, 1990), which can extend up to one year or more (Ross, 1974; Lutze and Wefer, 1980). Most larger foraminifera are characterized by an alternation of generations in which a haploid *gamont* (gamete-producing) form (also called the A-generation) alternates with a diploid *agamont* (asexual) form (also called a *schizont*, or B-generation). This heterophasic life cycle frequently results in both morphologic and nuclear dimorphism. The gamont normally has a smaller test than the agamont. The agamont, however, is typically multinucleate (heterokaryotic), with one or more macronuclei controlling somatic and metabolic functions, and many micronuclei that divide to produce nuclei during schizogony (macronuclei degenerate during reproduction).

Morphologic dimorphism of the foram test is also apparent in the embryonic chambers (embryon) of both gamont and agamont. The embryon of the gamont normally consists of two large chambers (protoconch and deuteroconch; or proloculus and deuteroloculus, if part of a primary spire), and is termed *megalospheric*. These two initial chambers house the juvenile foraminiferan when first released from the parent test during asexual reproduction. The agamont, formed by the fusion of gametes, has an extremely small initial chamber (proloculus), and is termed *microspheric* (Loeblich and Tappan, 1964; Lipps, 1982).

Morphologic dimorphism in test size can be extreme in larger foraminifera, with the adult microspheric form reaching several times the size of the megalosphere. In the Permian, some fusulinid microspheres (genus *Parafusulina*) reached 10 cm in length (Dunbar, 1963), and I have verbal reports of microspheric individuals of Tertiary *Nummulites* from the Middle East reaching 12 cm in diameter (B. Carter, pers. comm.). Some fragments of *Lepidocyclina* found in the course of this study represent individuals which must have approached 7 cm or more in diameter.

In both living and fossil assemblages, microspheric individuals are typically very uncommon. Megalospheres are always disproportionally greater in number. This has led to the hypothesis of biologic trimorphism, in which it is thought that microspheric schizonts produce megalospheric schizonts, which produce megalospheric gamonts, which produce microspheric schizonts (Leutenegger, 1977). Several generations, in fact, of megalospheric schizonts are thought to precede gametogenesis in some cases. Although this theory has been disputed in the past (Rottger *et al.*, 1986), it has recently been confirmed for *Heterostegina depressa* (Rottger *et al.*, 1990).

The Ecological Significance of Test Size in Larger Foraminifera

The complexity of the LBF test records a wealth of biological information (Hottinger, 1978, 1986). However, there are three aspects of LBF test size which make it an especially useful indicator of development and reproductive strategy.

First, like most lower invertebrates, LBF have indeterminate growth. As summarized by Hallock and Glenn (1986), under favorable conditions, LBF will mature and reproduce at relatively small sizes. However, if the population is stressed by low light (necessary for symbionts),

low temperature, or other suboptimal conditions, the forams will delay reproduction and simply continue to grow. This is observed, for example, when shallow-dwelling forms are washed into deep water. Ironically, if a population contains many large individuals, conditions for growth and reproduction may have been marginal. *Within a species, test size is generally a reliable relative indicator of individual age.*

Second, LBF are semelparous. That is, during multiple fission, the entire protoplasm of the adult foram is divided among its progeny. Reproduction is a major cause of mortality among adults (Hallock, 1985; Hallock and Glenn, 1986; Hallock *et al.*, 1986). *If the adult size distribution of a population is unimodal, the size at reproduction is approximated by the peak of the curve.* This, of course, assumes that taphonomic processes have not significantly altered the assemblage.

Third, because LBF distribute all of their protoplasm to juveniles during asexual reproduction, test size is a good indicator of reproductive allocation. LBF fecundity (the number of offspring produced by a parent during asexual reproduction) is a function of test size (Hallock, 1985; Hallock *et al.*, 1986). *LBF fecundity is normally directly proportional to body size.*

In addition, the LBF megalospheric embryon (first two chambers of the LBF test) represents the juvenile foram when it was first released from the parent test. *Embryon size indicates the size of the individual foram at birth.* This can be of special significance in the study of LBF life history. Survival rates are typically very low for juvenile LBF. However, if juveniles can survive to a certain critical size (0.5 mm for extant *Amphistegina*), chances of survival to reproduction are greatly increased (Hallock, 1985). Survival is largely size-specific.

Theoretical Predictions for Fossil Larger Foraminifera

Paleontologists working on LBF have long known of the incredible amount of morphologic variation in the group (see Frost and Langenheim, 1974, p. 43). In the past, this variation, plus the desire to use LBF for biostratigraphic purposes, resulted in an excessive proliferation of taxonomic names. Fortunately, most of these names have been relegated to synonymies. This is notably true for American species, where diversity is actually quite low compared to Tethyan and Indo-Pacific faunas (particularly in the Oligocene). Few investigators, however, have tried to make ecological sense of this variability.

The initial aim of this investigation was to examine the morphological (developmental) and life history adaptations of four species of LBF along a paleoenvironmental transect in Lower Oligocene carbonates of the eastern Gulf Coastal Plain. In particular, mean adult *test size* and *embryon size* were examined.

The fossil LBF used were taken along a shallow reef-to-deep forereef and shelf paleoenvironmental gradient and are assumed to have lived under progressively less disturbed and less illuminated conditions. From the outset of this study, the following morphologic patterns were expected to be found along this paleodepth gradient:

(1) *Mean population test size should increase with depth.* This is a function of reduced solar illumination and temperature, making conditions suboptimal for growth and reproduction. But because of their indeterminate growth, by delaying reproduction the LBF grow to larger sizes. At greater depths, metabolism and growth are necessarily slowed. As Hallock (1985) has shown in her models for LBF adaptive strategies, both low juvenile growth rates and low juvenile survival favor large adult size and high fecundity. A corollary of this prediction is that the amount of post-embryonic growth (measured by equatorial chamber area) should also increase with depth.

(2) *Embryon size should increase with depth.* Increase in embryon size commonly (but by no means always) accompanies increase in test size in LBF. According to Hallock (1985), an increase in embryon size increases the chances of juvenile survival, which is typically very low in LBF. In explaining observed patterns of increasing embryon size with depth in fossil *Discocyclina*, for example, Hallock suggests that larger embryons receive more protoplasmic symbionts from the parent, thus increasing chances of survival under conditions of low light penetration. It is clear that there may be many reasons for

changes in embryon size, not all of which are understood (Drooger, 1983; and Discussion section below). As the results of the present investigation confirm, embryon size must be interpreted cautiously.

(3) *Test elaborations (such as development of pillars and pustules), selliform tests, and a decrease in length/width ratios (nummulitids) should be more common in shallow, high energy conditions.* It has been documented for both fossil and extant LBF that certain test modifications are commonly associated with high energy conditions. These are presumably adaptations for test strength, and reflect high calcification rates. Pillars, for example, (radial thickenings extending from the center of lepidocyclinid tests, manifested by rounded prominences called pustules on the test centrum) are common in high energy facies (Drooger, 1983; Frost and Langenheim, 1974, p.135-136). Selliform ("saddle-shaped") tests have been recorded for reef-dwelling populations of *Lepidocyclina undosa* from Mexico (Frost and Langenheim, 1974, p. 170). And test flattening is commonly observed as a correlate with depth (low energy) in a variety of LBF (Reiss and Hottinger, 1984; Hallock, 1979).

III. METHODS

Field and Laboratory Work

Larger foraminifera were collected (Fig. 2) during the course of field work for a regional facies analysis of Lower Oligocene strata of the eastern Gulf Coast (Bryan, 1991, 1993). Bulk samples were collected for preparation in the laboratory. Samples used include the Bridgeboro Limestone type section (Bridgeboro, Georgia); Duncan Church Beds of the Bridgeboro Limestone (Wausau, Florida); Florala Limestone (Florala, Alabama); Glendon Limestone (Jackson, Alabama); and the Marianna Limestone (Jackson, Alabama).

The diagnostic morphologic features of larger foraminifera (such as embryonic and equatorial chambers) are found *within* the test, requiring that the test be partially destroyed before measurements can be taken. Most specimens cannot be identified with certainty without such preparation. Preparation of lepidocyclinids requires that the each specimen be mounted (with resin) to a 1x3" glass slide, then ground on a frosted glass plate (as with a thin section) until the equatorial plane and embryonic chambers of the foram are in full view. Nummulitids can be split across their equatorial plane of weakness (the marginal cord) by heating the specimen over an alcohol lamp, then plunging the specimen in water. These methods are elaborated in Bryan (1991). Over 1000 individual specimens were prepared for this study.

Cross-sectional area measurements (used as a proxy for embryon volume) of nummulited and lepidocyclinid embryons were made with the aid of a digitizing tablet, binocular microscope, video camera and monitor, computer, and JAVA (Jandel

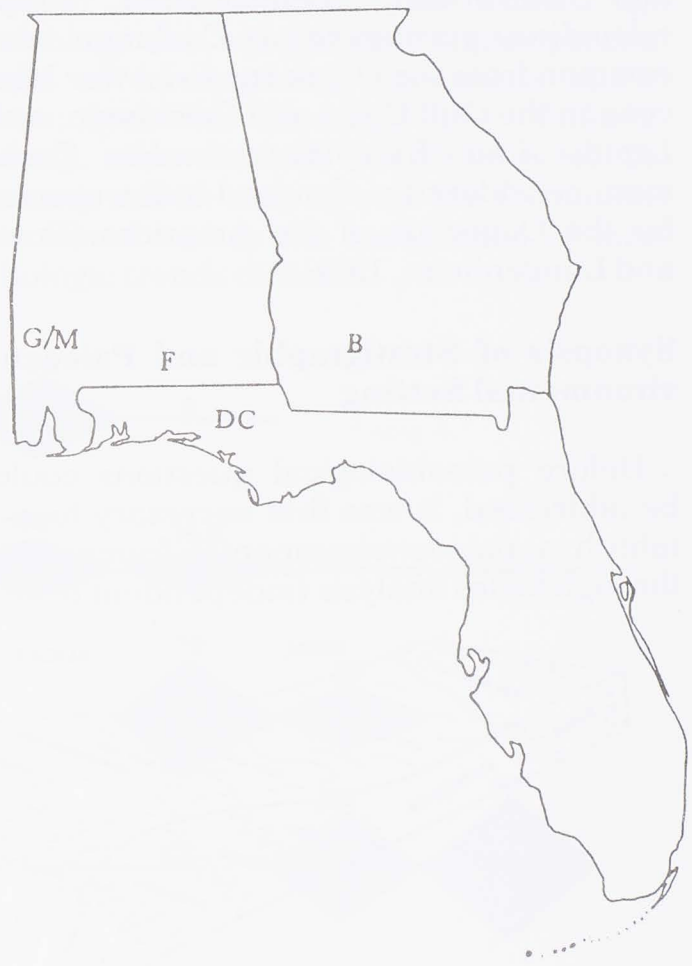

Figure 2. Locality map, eastern Gulf Coastal Plain. *G/M*, Glendon and Marianna Limestones as exposed at the St. Stephens Quarry, Washington County, Alabama; *F*, Florala Limestone type section, Covington County, Alabama; *DC*, Duncan Church Beds of the Bridgeboro Limestone, Washington County, Florida; *B*, Bridgeboro Limestone type section, Mitchell County, Georgia.

Video Analysis) biometric software package. Test diameters were measured with a digital caliper. The amount of post-embryonic, equatorial growth was calculated for lepidocyclinids, and various qualitative features (*e.g.*, presence or absence of pustules) were also taken into account (Bryan, 1991).

Larger Foraminifera Examined

Four species of LBF were examined. *Nummulites (Paleonummulites) panamensis* Cushman is the only nummulitid found in the Lower Oligocene of the eastern Gulf Coast, and is widespread in the Caribbean. Three lepidocyclinids were examined: *Lepidocylina (Lepidocyclina) mantelli* (Morton), a form common in Oligocene to Lower Miocene strata of the Gulf Coast and Caribbean; *Lepidocylina (Neprolepidina) yurnagunensis* Cushman, also common from the Oligocene to Lower Miocene in the Gulf Coast and Caribbean; and *Lepidocylina (Eulepidina) undosa* Cushman, considered a standard index species for the Oligocene of the Americas (Frost and Langenheim, 1974).

Synopsis of Stratigraphic and Paleoenvironmental Setting

Before paleobiological questions could be addressed, it was first necessary to establish a paleoenvironmental framework through facies analysis (independent of environmental inferences drawn from LBF). The interval chosen is a portion of the Vicksburgian (Lower Oligocene) section of the eastern Gulf Coastal Plain, containing LBF-rich carbonates. A full stratigraphic and paleoenvironmental analysis of this time interval is given Bryan (1991, 1993). The units used are correlative both lithostratigraphically and biostratigraphically (with the exception of the Marianna Limestone), and represent a series of laterally adjacent paleoenvironments.

The forams used in this study are from the Bridgeboro Limestone (type section), the Duncan Church beds of the Bridgeboro Limestone, the Florala Limestone, the Glendon Limestone, and the Marianna Limestone. These formations represent a transect across an extensive carbonate platform and shelf in the Gulf Coast during Lower Oligocene time. In summary, the paleoenvironments represented by this transect are: (1) coralgal shelf margin (platform-like) buildup (Bridgeboro type section), which flanked the Gulf Trough (a narrow current-swept channel stretching from panhandle Florida to central Georgia); (2) forereef coralgal limestone (Duncan Church beds, Bridgeboro Limestone); (3) deep forereef, platey coralgal limestone (Florala Limestone); (4) deep, shelf margin (ramp) bank grainstone (Glendon Limestone); and (5) mid-to outer shelf carbonate mudstone (Marianna Limestone). These facies are illustrated in the block diagram model of Figure 3.

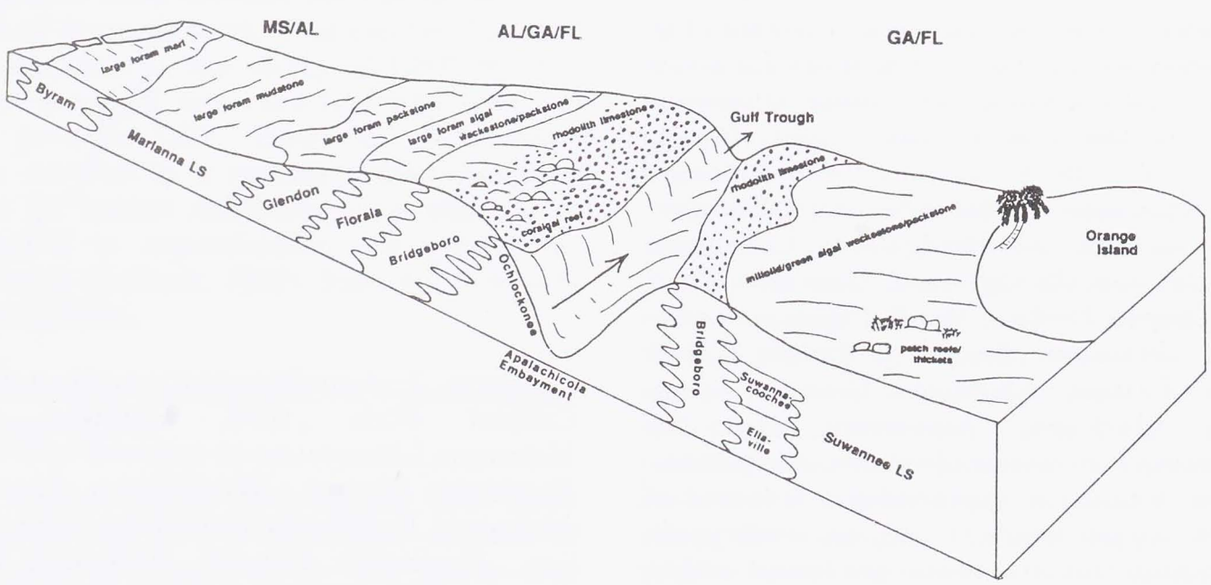

Figure 3. Block diagram reconstruction of Vicksburgian carbonate facies across the eastern Gulf Coastal Plain (from Bryan, 1991, 1993).

The lateral gradation of Bridgeboro–Duncan Church–Florala–Glendon–Marianna, represents progressively deeper paleoenvironments. The best evidence for this deepening is the local presence of massive reef corals and changes in coralline algal morphology (see Steneck, 1986). In short, the type section of the Bridgeboro contains reef corals and extensive formations of large, well-rounded rhodoliths in a grainstone matrix. The Duncan Church beds of the Bridgeboro Limestone contain only small, sub-rounded rhodoliths and algal marls. The Florala Limestone contains extensive, thin, platey red algae in a mudstone matrix. The glauconite-rich Glendon Limestone has only rare algal marls. The muddy Marianna Limestone contains no algal remains.

IV. RESULTS

Distributional and Biometric Trends

The facies distribution and relative abundance of the four LBF species are illustrated in Figure 4 and are based on the data of Table 1. From this figure, a shallow-to-deep water gradient in LBF species composition is clearly evident, and this biofacies pattern is consistent with previous reports (such as Frost and Langenheim, 1974). Biometric results are presented in Tables 2-5.

Nummulites panamensis (Table 2, Figs. 5, 6) is found almost exclusively in the Glendon and Florala Limestones. Test diameter, test width, and embryon size are significantly greater in the shallower water Florala sample. The average diameter/width ratio, however, is greater in the Glendon assemblage (3.58) than in the Florala (2.44). These observations are consistent with those of Frost and Langenheim (1974, p. 84-89) on Mexican *N. panamensis*, where compressed forms with smaller proloculi are more common in deeper water facies. The Florala assemblage also has a slightly higher percentage of microspheric specimens (2.2%) than does the Glendon (1%). Unfortunately, the limited occurrence of *N. panamensis* in only two of the formations examined makes the recognition of morphologic trends difficult.

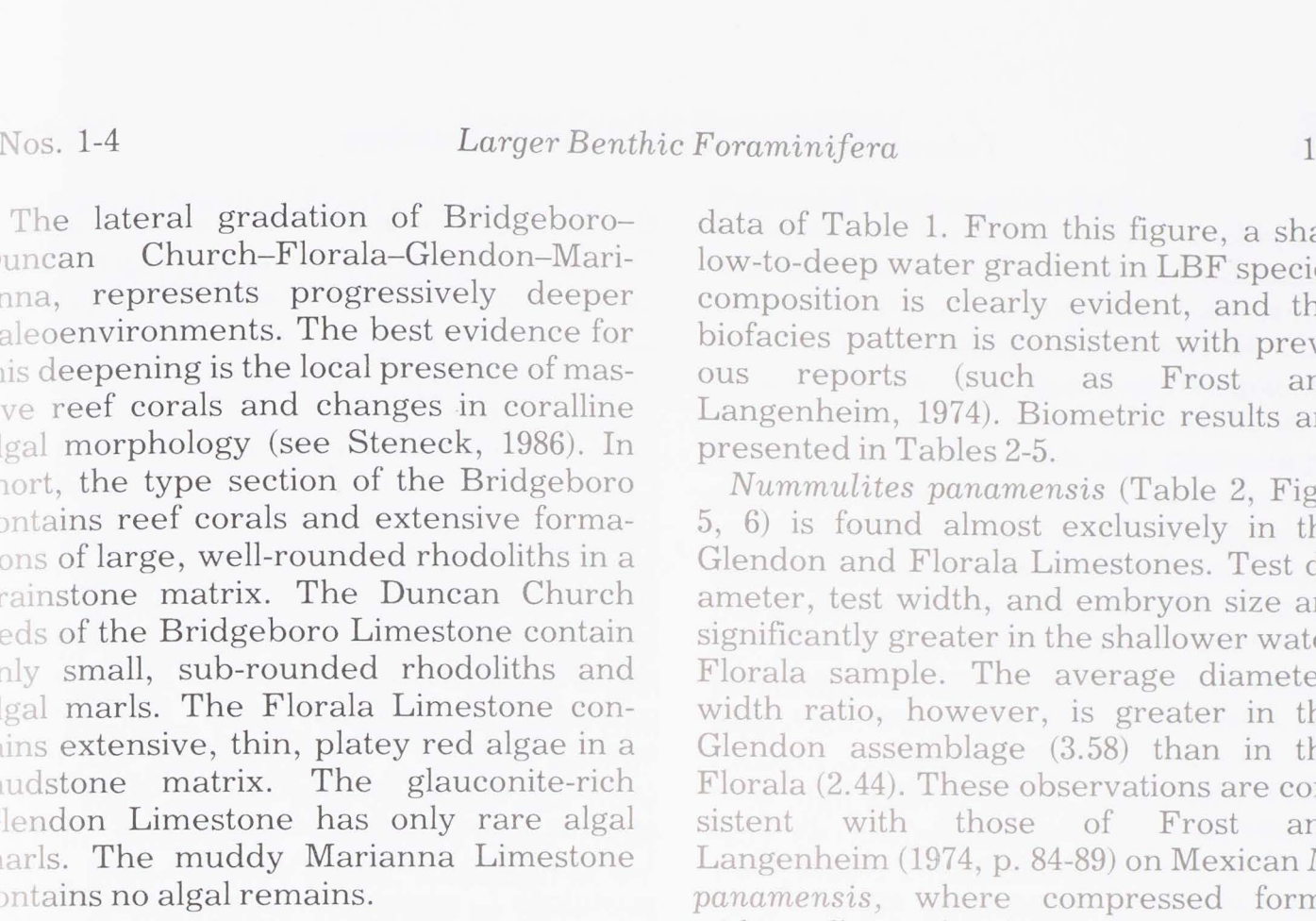

Figure 4. Spindle diagram showing facies distribution, absolute abundance, and percentage abundance of larger foraminifera taxa in the study area. Vertical scale on left for absolute abundances shown by vertical height of diamonds.

Lepidocyclina (Lepidocyclina) mantelli (Table 3, Figs. 4, 5, 6, 7) is found in all five facies, but is common only in the Glendon and Marianna Limestones. The assemblage from the deeper water wackestones of the Marianna shows significantly larger mean test size, embryon size, and post-embryon size. The Marianna assemblage also has a slightly higher percentage of microspheric specimens (8%) than does the Glendon (5.5%). Although much rarer in the Florala, Duncan Church, and Bridgeboro samples, *L. mantelli* generally has larger test size, embryon size, and post-embryon size in these facies.

Lepidocyclina (Nephrolepidina) yurnagunensis (Table 4, Figs. 4, 5, 6, 7) is found in great abundance in the Bridgeboro Limestone type section and the Duncan Church beds, and is present in fewer numbers in the Florala Limestone. Test size and post-embryon size are greatest in the Bridgeboro type section, smaller in the Duncan Church beds, and return to a larger sizes in the Florala. Microspheric specimens were found only in the Bridgeboro type section (1.7% of the assemblage). Embryon size is greatest in the Bridgeboro type section, and decreases in the Duncan Church and Florala. In the Bridgeboro type section, *L. yurnagunensis* almost always has pustules on the centrum, a feature commonly displayed by this species in high energy environments and sometimes designated by the subspecies name *morganopsis*. Specimens from the lower energy Duncan Church beds do not have pustules, and fit the description of the subspecies *yurnagunensis* (Frost and Langenheim, 1974). Pustulose and nonpustulose *L. yurnagunensis* are associated with high-energy biosparites/patch reefs and lower-energy, forereef slope biomicrites (respectively) in the Oligocene of Ja-

Table 1

Number of Specimens and Percentage Abundances of Larger Foraminifera from the Marianna, Glendon, Florala, and Bridgeboro Limestones

	Nummulites panamensis		*Lepidocyclina (Lepidocyclina) mantelli*		*Lepidocyclina (Nephrolepidina) yurnagun.*		*Lepidocyclina (Eulepidina) undosa*	
Formation:	No.	%	No.	%	No.	%	No.	%
Bridgeboro (type sect.)	0	0%	1	0.5%	174	82.5%	36	17%
Bridgeboro (Duncan Ch.)	0	0%	8	3%	168	55%	129	42%
Florala	410	79%	3	0.5%	9	2%	96	18.5
Glendon (St.Steph.)	94	33%	179	63%	0	0%	10	4%
Marianna (St.Steph.)	0	0%	100	97%	0	0%	3	3%

Total number of specimens picked per formation sample, used to calculate percentage abundances (does not include microspheres nor unidentified specimens):

Bridgeboro (type)	211
Bridgeboro (Duncan Ch.)	305
Florala*	518
Glendon	283
Marianna	103

*The original Florala Sample had 144 lepidocyclinids and 447 nummulites (=591 total). Of these, 37 lepidocyclines were unidentifiable. Therefore, 37 nummulites were subtracted from 447 (=410) for percentage calculations. (Also, the nummulite sample was split twice before a reasonable working size was obtained).

maica and Mexico (Frost and Langenheim, 1974).

Lepidocyclina (Eulepidina) undosa (Table 5, Figs. 4, 5, 6, 7) is common in the Bridgeboro type section, Duncan Church beds of the Bridgeboro, and Florala Limestone, and is found more rarely in the Glendon and Marianna Limestones. Test size, embryon size, and post-embryon size generally increase towards the Bridgeboro reef facies and decrease towards the Glendon, but radically rise again in the deep-water Marianna Limestone (although few specimens are present). Frost and Langenheim (1974, p.170-172) report that Mexican populations of *L. undosa* in shallow, high-energy reef deposits also have larger embryonic chambers than those from lower energy facies. Although *L. undosa* is frequently reported to have selliform tests (especially in reef facies), there was no evident trend of more abundant selliform tests in the Bridgeboro. Microspheric specimens are generally rare, except in the Duncan Church beds, where they compose 9.3% of the assemblage.

Potential Taphonomic Bias

A potential source of bias in this study is taphonomic alteration, particularly in high energy facies or areas of reduced sedimentation. Facies with fine grain size would predictably be less altered. While taphonomic studies of fossil LBF are not common, analysis of some modern LBF living and dead assemblages indicates that thanatocoenoses often faithfully represent the biocoenoses (Jell *et al.*, 1965; Zohary *et al.*, 1980; Reiss and Hottinger, 1984, p. 15). Nevertheless, abrasion, bioerosion, dissolution, and transport can alter assemblages (Martin and Liddell, 1991).

In high energy facies, larger sized LBF may be preferentially preserved. In the Bridgeboro Limestone (the highest energy facies) small individuals were abundant, and there is no indication of differential preservation. The same is true of all facies studied. It is concluded, therefore, that taphonomic effects have not significantly altered the assemblages. This is certainly an oversimplification, but there are no ob-

Table 2

Biometric Statistics for *Nummulites (Paleonummulites) panamensis*

Locality:	Glendon Limestone	Florala Limestone
Test Diameter (mm)		
Sample Size	96	92
Mean	1.62	1.97
Std. Dev.	0.56	0.49
Coef. Var.	0.35	0.25
t-test	t = 4.52; means are different at 0.05 level	
Test Width (mm)		
Sample Size	21	92
Mean	0.54	0.83
Std. Dev.	0.17	0.23
Coef. Var.	0.31	0.27
t-test	t = 5.47; means are different at 0.05 level	
Diameter/Width Ratio	3.58	2.44
Embryon Size (mm^2)		
Sample Size	25	75
Mean	0.01	0.02
Std. Dev.	0.001	0.02
Coef. Var.	0.14	1.0
t-test	t = 3.06; means are different at 0.05 level	

vious indications of size-sorting, at least. Still, many LBF examined in this study show signs of rounding and abrasion. Additional work on the distribution of such features (within an assemblage and across different facies) would sort out this potential source of bias.

V. DISCUSSION

A New Hypothesis

At the outset of this investigation, it was expected that both test size and embryon size would increase in deeper water facies (Fig. 8). However, this prediction was met only in part. What was not anticipated was an increase in test and embryon size as the reef (Bridgeboro Limestone) is approached. This pattern is common in *L. undosa*, *L. yurnagunensis*, and *N. panamensis* (Figs. 5, 6, 7). This discovery led to a reconsideration and expansion of the original hypotheses.

As summarized by Hallock (1985), large test size and large embryon size may essentially be adaptations for conditions of low juvenile survival. But such conditions may be found in a variety of environments, and for as many reasons. My initial premise of increasing test size and embryon size with increasing depth was too simplistic. While increased depth may indeed be unfavorable for juvenile survival (because of reduced illumination for symbionts in nutrient-poor waters), extremely shallow

Table 3

Biometric Statistics for *Lepidocyclina (Lepidocyclina) mantelli*

Locality:	Marianna Limestone	Glendon Limestone	Florala Limestone	Bridgeboro Limestone (Duncan Ch)
Test Diameter (mm)				
Sample Size	61	95	3	7
Mean	5.80	2.74	4.75	3.77
Std. Dev.	2.49	1.61	0.76	1.39
Coef. Var.	0.43	0.58	0.16	0.37
t-test:				
Mar/Glen: t = -4.32; means are different at 0.05 level				
Mar/Bbro: t = 2.11; means are different at 0.05 level				
Glen/Bbro: t = -1.64; means are not different at 0.05 level				
Embryon Size (mm^2)				
Sample Size	61	95	3	7
Mean	0.46	0.19	0.27	0.33
Std. Dev.	0.12	0.09	0.10	0.11
Coef. Var.	0.26	0.47	0.37	0.33
t-test:				
Mar/Glen: t = -17; means are different at 0.05 level				
Mar/Bbro: t = -.0029; means are different at 0.05 level				
Glen/Bbro: t = 4.15; means are different at 0.05 level				
Post-Embryonic Growth (mm^2)				
Sample Size	61	95	3	7
Mean	30.86	7.72	17.76	12.11
Std. Dev.	24.58	10.57	5.45	7.16
Coef. Var.	0.79	1.36	0.31	0.59
t-test:				
Mar/Glen: t = -0.809; means are different at 0.05 level				
Mar/Bbro: t = 1.99; means are different at 0.05 level				
Glen/Bbro: t = -1.07; means are not different at 0.05 level				

conditions, such as on a reef, may be equally unfavorable. As Hallock (1985) has found experimentally, juveniles of *Amphistegina* less than 0.5 mm in size can be dislodged from their substrate with even gentle water motion. Large embryon size may be favored in shallow, high energy conditions because too small juveniles are at risk of being dislodged from their substrate. But in deep waters, small juveniles may have insufficient protoplasmic symbionts to survive in low light conditions.

Unfortunately, previous studies do not show a consistent correlation between individual test size and embryon size. Depth-related trends have been found in some LBF, but this is not a consistent pattern (Drooger, 1983). Furthermore, it has not been established whether larger parents produce more juveniles of the same size, or fewer, larger embryons. While the former is possible, it is unlikely that increasing embryon size would proceed without some increase in adult size (Hallock, 1985). In short, the ecological significance of embryon size is not easily evaluated. Nevertheless, following the models developed by Hallock (1985), increasing test size increases individual fecundity, and is a response to high juvenile mortality. Under conditions of low juvenile survival, LBF may only be able to respond by increasing fecundity or increasing embryon size. And both strategies could occur in the same environment.

In this investigation, test size was generally found to increase in both the shallow and deeper extremes of the ranges of three out of four species (Fig. 5). Embryon size appears to show this same pattern in two of the four species (Fig. 6), but the statistical significance of this pattern is equivocal. None of the species contradicts either pattern. These data, in combination with the model of Hallock (1985), are combined to

Table 4

Biometric Statistics for *Lepidocyclina (Nephrolepidina) yurnagunensis*

Locality:	Florala Limestone	Bridgeboro Limestone (Duncan Church)	Bridgeboro Limestone (Type Section)
Test Diameter (mm)			
Sample Size	9	167	174
Mean	2.46	1.90	3.04
Std. Dev.	0.38	0.57	1.04
Coef. Var.	0.15	0.30	0.34
t-test:			
DCh/Bbro: t = 1.25; means are different at 0.05 level			
Embryon Size (mm^2)			
Sample Size	8	130	153
Mean	0.05	0.062	0.088
Std. Dev.	0.02	0.025	0.081
Coef. Var.	0.40	0.42	0.88
t-test:			
DCh/Bbro: t = 3.61; means are different at 0.05 level			
Post-Embryonic Growth (mm^2)			
Sample Size	8	131	153
Mean	4.72	2.98	7.91
Std. Dev.	1.49	1.67	5.08
Coef. Var.	0.32	0.56	0.64
t-test:			
DCh/Bbro: t = 1.06; means are different at 0.05 level			

generate a new hypothesis to predict test size and embryon size in LBF along a shallow, high energy to deep, low energy environmental gradient:

> If a species extends along a sufficient range across a shallow, high energy, high illumination-to deep, low energy, low illumination ecogradient, it is predicted that test size and embryon size will generally be larger at the extremes of this range (Fig. 9).

Shallow, high energy/well-illuminated conditions favor large adult size and larger juveniles, which can avoid being easily dislodged from their substrate (increased fecundity is another possible ecologic strategy and correlate of large size). Deep,

Table 5
Biometric Statistics for *Lepidocyclina (Eulepidina) undosa*

Locality:	Marianna Limestone	Glendon Limestone	Florala Limestone	Bridgeboro Limestone (Duncan Church)	Bridgeboro Limestone (Type Section)
Test Diameter (mm)					
Sample Size	2	10	93	128	31
Mean	7.88	3.53	3.55	5.42	5.84
Std. Dev.	4.90	2.56	1.82	3.54	2.50
Coef. Var.	0.62	0.73	0.51	0.65	0.43

t-test:
Glen/Flo: t = -0.042; means are not different at 0.05 level
Glen/DCh: t = 1.65; means are not different at 0.05 level
Glen/Bbro: t = -2.53; means are different at 0.05 level
Flo/DCh: t = 4.65; means are different at 0.05 level
Flo/Bbro: t = -5.50; means are different at 0.05 level
DCh/Bbro: t = 0.63; means are not different at 0.05 level

Embryon Size (mm^2)					
Sample Size	2	10	89	99	31
Mean	0.76	0.49	0.53	0.65	0.48
Std. Dev.	0.19	0.22	0.29	0.20	0.15
Coef. Var.	0.25	0.45	0.55	0.31	0.31

t-test:
Glen/Flo: t = 0.46; means are not different at 0.05 level
Glen/DCh: t = -2.39; means are different at 0.05 level
Glen/Bbro: t = -0.15; means are not different at 0.05 level
Flo/DCh: t = -3.29; means are different at 0.05 level
Flo/Bbro: t = -0.97; means are not different at 0.05 level
DCh/Bbro: t = -4.36; means are different at 0.05 level

Post-Embryonic Growth (mm^2)					
Sample Size	2	10	89	99	31
Mean	57.37	13.90	11.85	19.83	31.09
Std. Dev.	60.81	20.56	12.88	18.08	25.97
Coef. Var.	1.06	1.48	1.08	0.91	0.83

t-test:
Glen/Flo: t = 0.45; means are not different at 0.05 level
Glen/DCh: t = 0.098; means are not different at 0.05 level
Glen/Bbro: t = -1.90; means are not different at 0.05 level
Flo/DCh: t = 3.45; means are different at 0.05 level
Flo/Bbro: t = -5.37; means are different at 0.05 level
DCh/Bbro: t = -2.70; means are different at 0.05 level

low energy/low light conditions also favor large adult size and large juveniles, which inherit many symbionts from the parent test (necessary in low light conditions). Thus, large test and embryon size are predicted at the limits of a species' range, but for different reasons. Smaller test and embryon sizes will be expected in intermediate areas that favor reproduction in minimal time.

Some comments regarding these generalities must be given here. First, this prediction is for intraspecific variability. Interspecific patterns may show different features. *Lepidocyclina yurnagunensis* and *L. undosa*, for example, are both common in the Bridgeboro Limestone, but *L. undosa* is a much larger species than *L. yurnagunensis* in both test and embryon size. *Lepidocyclina yurnagunensis* almost certainly had a different reproductive schedule and potential rate of population increase than did *L. undosa*.

A problem with testing the revised hypothesis is that many species appear to have a limited range. *Lepidocyclina mantelli*, for example, is restricted to relatively deep shelf areas (although it occurs in low numbers in other facies), while *L. yurnagunensis* is primarily a reef dweller (Fig. 4). Such limited ranges may in part reflect host-specific adaptations of symbionts. As shown by Leutenegger (1984) for some modern LBF, hosts with chlorophycean symbionts are restricted to shallow water, those with dinophyceans or rhodophyceans occur between 0-70 meters depth, and LBF with diatom symbionts extend from 1-130 meters depth.

Further testing of the revised hypothesis here would require a finer-scale sampling scheme in conjunction with carbonate microfacies analysis. The ecologic range of each species should be determined with as much precision as possible to confirm whether the bimodal size trend is consistent. In addition, morphologic data bearing on growth rate would be useful. The larger individuals found at each extreme of the species range should grow at different rates.

Life History, Heterochrony, and Environmental Stress

The results of this investigation can be profitably interpreted using the concepts of heterochrony and environmental stress. Relative to most foraminifera, LBF have been considered "*K*-strategists" because of their protracted reproductive cycles, brooding of asexually-produced young,

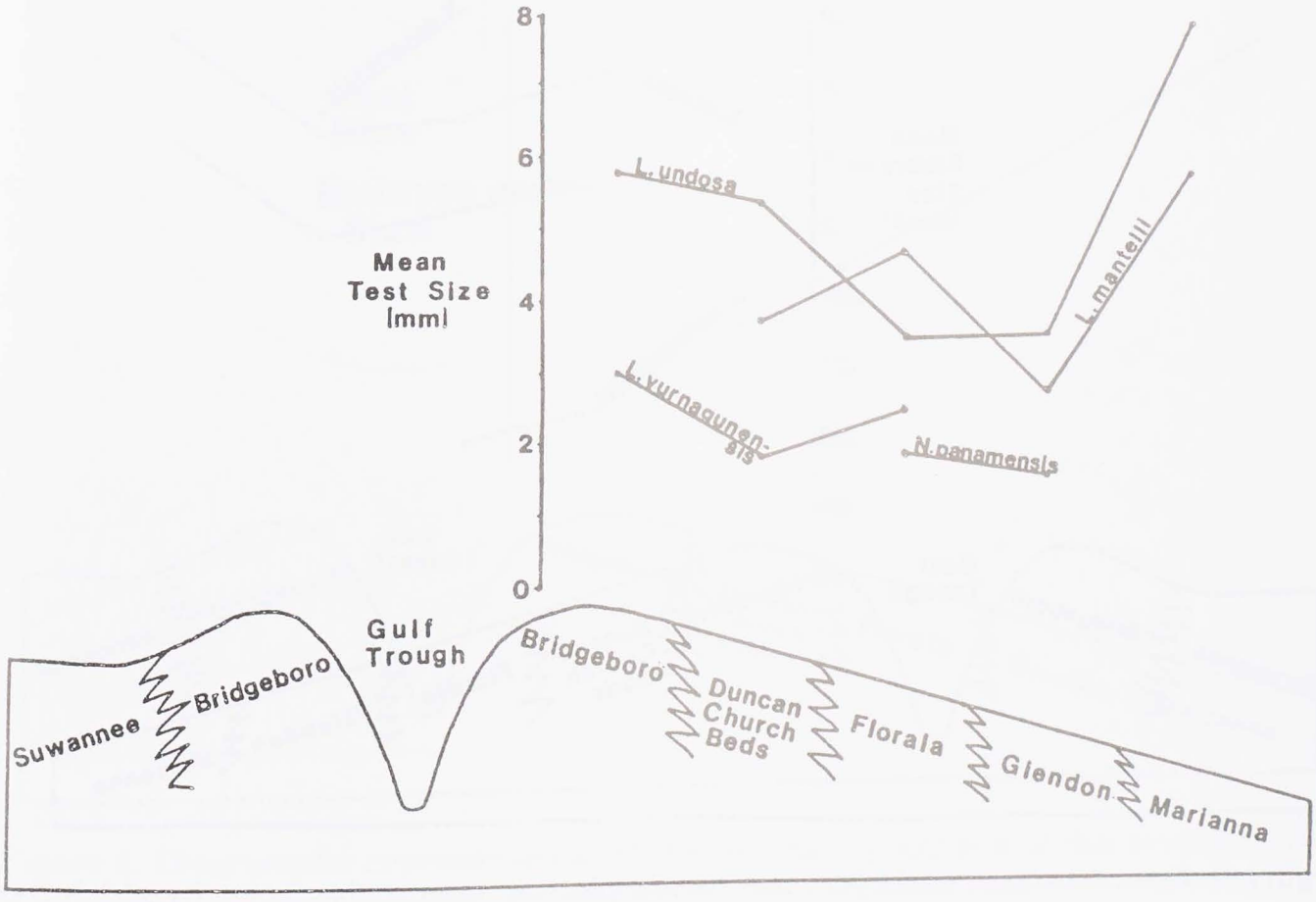

Figure 5. Species mean test size plotted against the facies in which it occurs.

slow growth, growth to large size, and occurrence in relatively stable environments (Hottinger, 1982, 1983). But at a finer scale of analysis, stress adaptation may also be evident.

Along the shallow, high energy/high illumination to deep, low energy/low illumination gradient, differences in growth rate and reproductive schedule should occur. At the shallow end, high light intensity and water energy facilitate relatively rapid growth. This environment and its resources, however, are not ephemeral, so there is no advantage to reproducing early (as would an *r*-strategist). Also, selection for either larger, or more, juveniles requires reproduction at large sizes. Growth is prolonged and reproduction delayed, but test calcification is efficient (producing robust, ornamented tests). Large size is thus reached by *hypermorphosis*. Such populations are *K*-selected relative to deeper populations.

In deeper waters, low light reduces the efficiency of algal symbiont photosynthesis and test calcification, and selection is for large juveniles that inherit much symbiont-rich protoplasm from the parent. Like the shallower populations, growth is prolonged, but at a slower rate. Large size is thus attained by hypermorphosis, but with a reduced rate of growth and perhaps less efficient calcification of the test. These populations are stress-selected.

As illustrated in Figure 10, these two developmental extremes represent endmembers along a gradient of environmental *optimality* and *stress*. Environmental *disturbance* is not, strictly, a variable. Although a high energy coral reef might be considered a frequently disturbed environment, it is comparatively stable (seasonally) and does not fluctuate rapidly in food resources, temperature, salinity, etc. Therefore, life history strategies normally associated with *r*-selection are not found.

VI. CONCLUSIONS

For the symbiont-bearing larger foraminifera, primary stress factors are low light intensity and water energy. In oligotrophic, tropical to subtropical waters, light intensity and water energy are generally inversely related to water depth. The results of this study suggest that along a gradient of environmental stress and optimality (a depth gradient), intraspecific LBF body size and embryon size are pre-

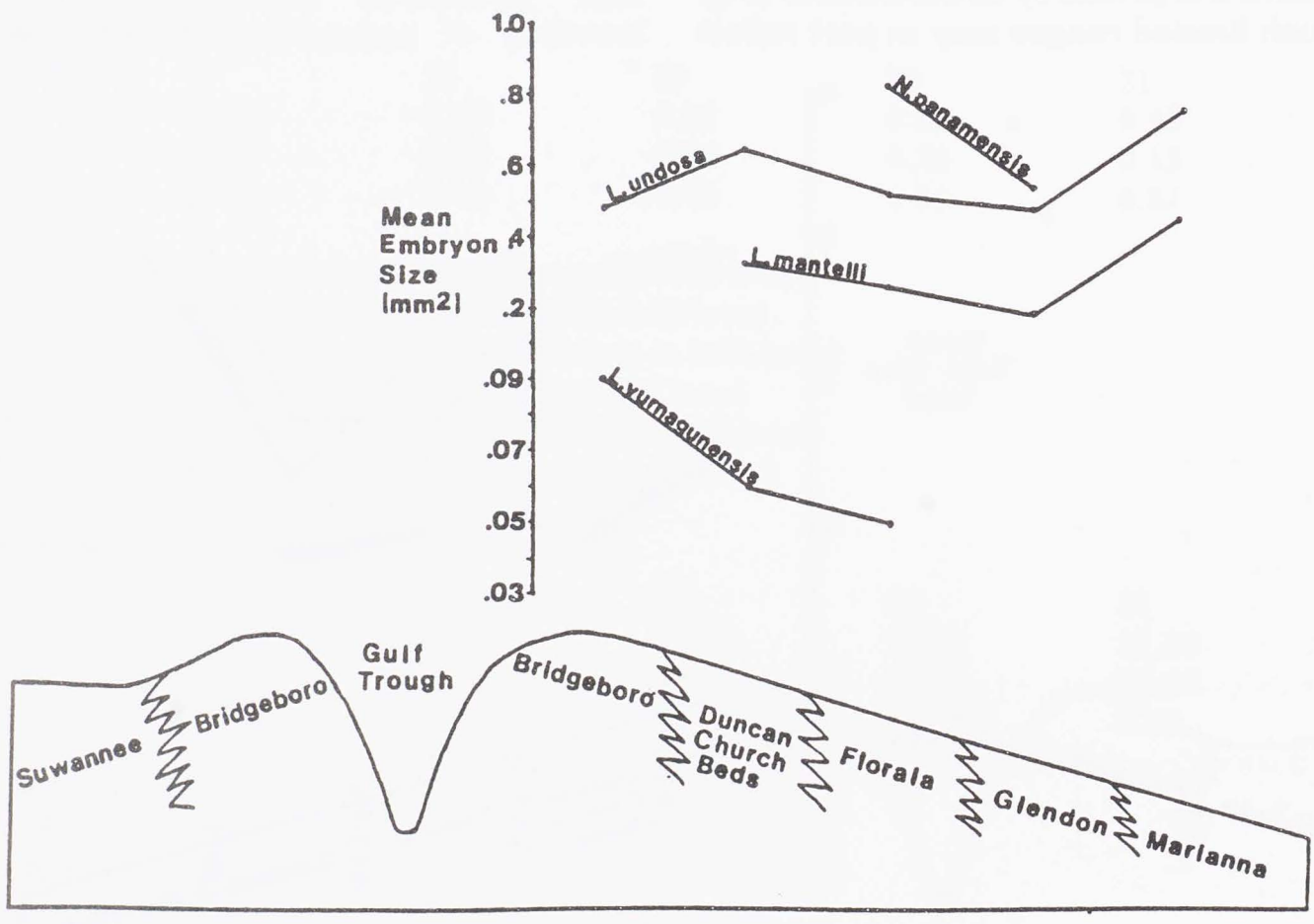

Figure 6. Species mean embryon size (area) plotted against the facies in which it occurs.

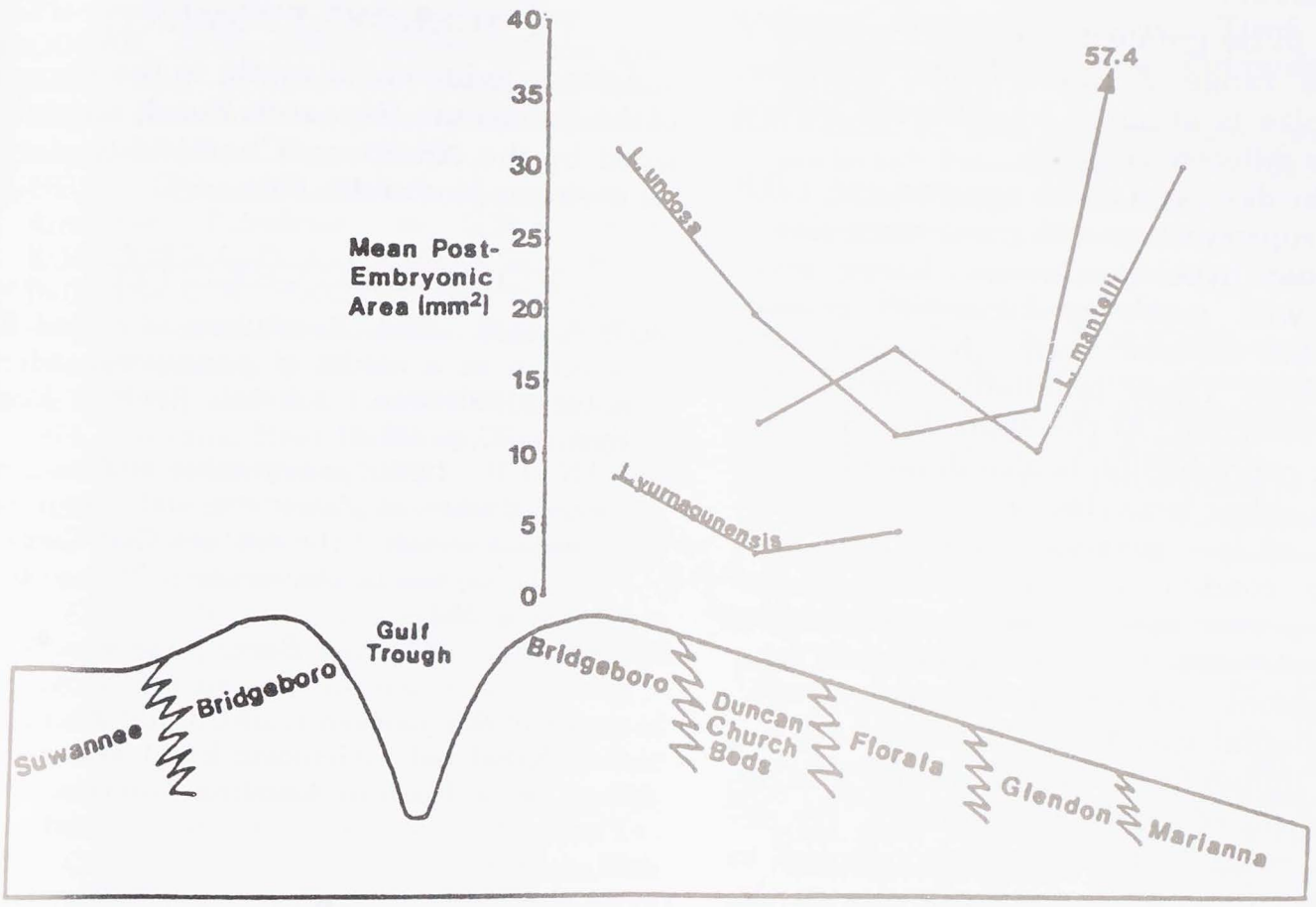

Figure 7. Species mean post-embryon size (area) plotted against the facies in which it occurs.

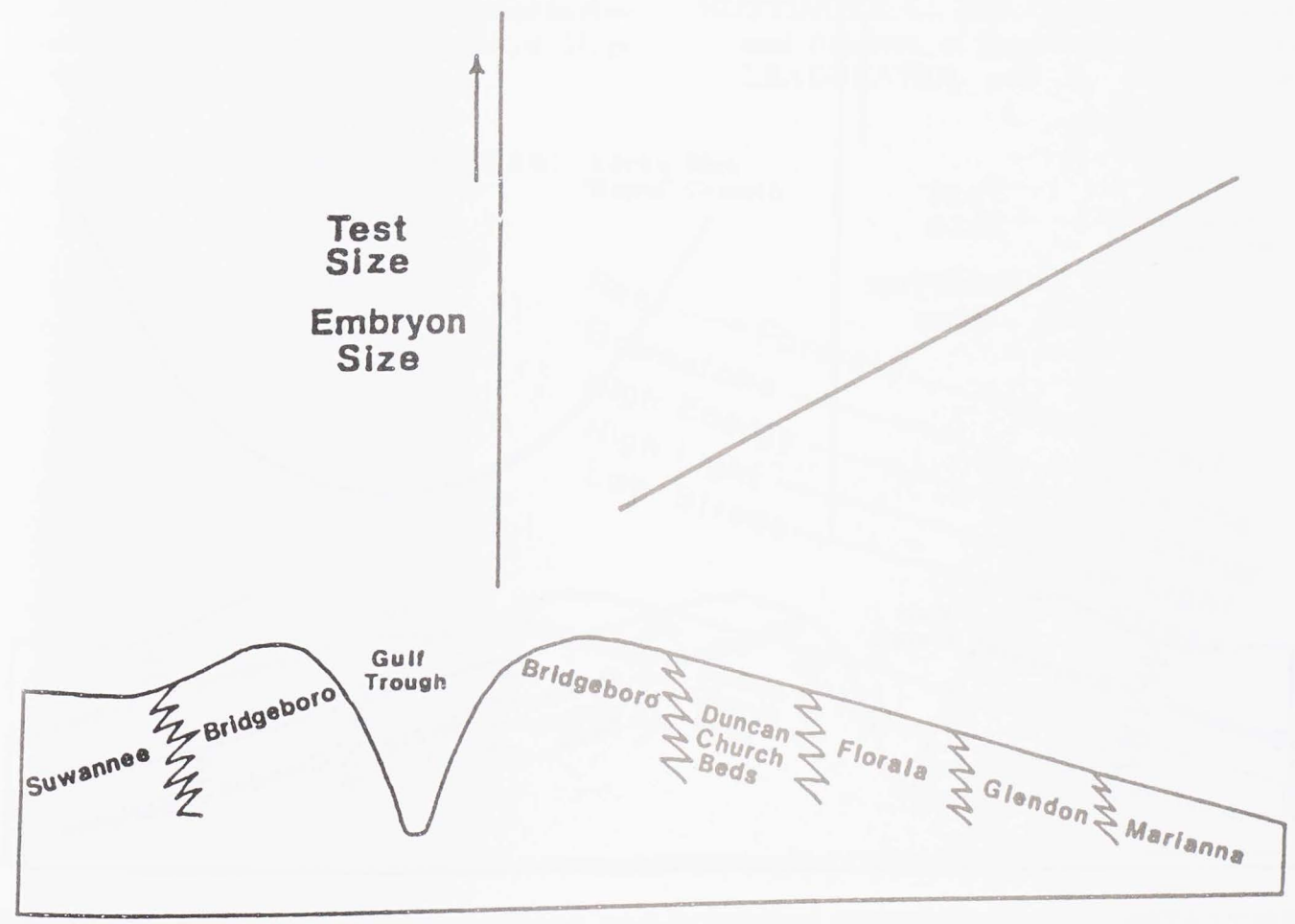

Figure 8. Diagramatic representation of the original hypothesis of this investigation. It was expected that both test size and embryon size would increase with depth along the paleoenvironmental gradient.

dicted to be greatest at the extremes of a species' range. At these limits, however, large size is attained by different means and for different reasons.

At the deep end of the ecogradient, LBF delay reproduction and grow more slowly (neotenic hypermorphosis). Large juveniles (with much symbiont-rich protoplasm) are favored under these low light conditions. These populations are under stress-selection. At the shallow end of the range, reproduction is also delayed (to increase either fecundity or juvenile size because of low juvenile survival in high energy conditions), but because of low stress, growth rate is normal or even slightly accelerated (hypermorphosis). These populations are under *K*-selection. Environmental variables, therefore, exert a direct influence on the life history and development of larger foraminifera. By delaying reproduction (hypermorphosis) to increase fecundity or juvenile size at the extremes of a species' range, larger intraspecific body sizes result.

VII. ACKNOWLEDGMENTS

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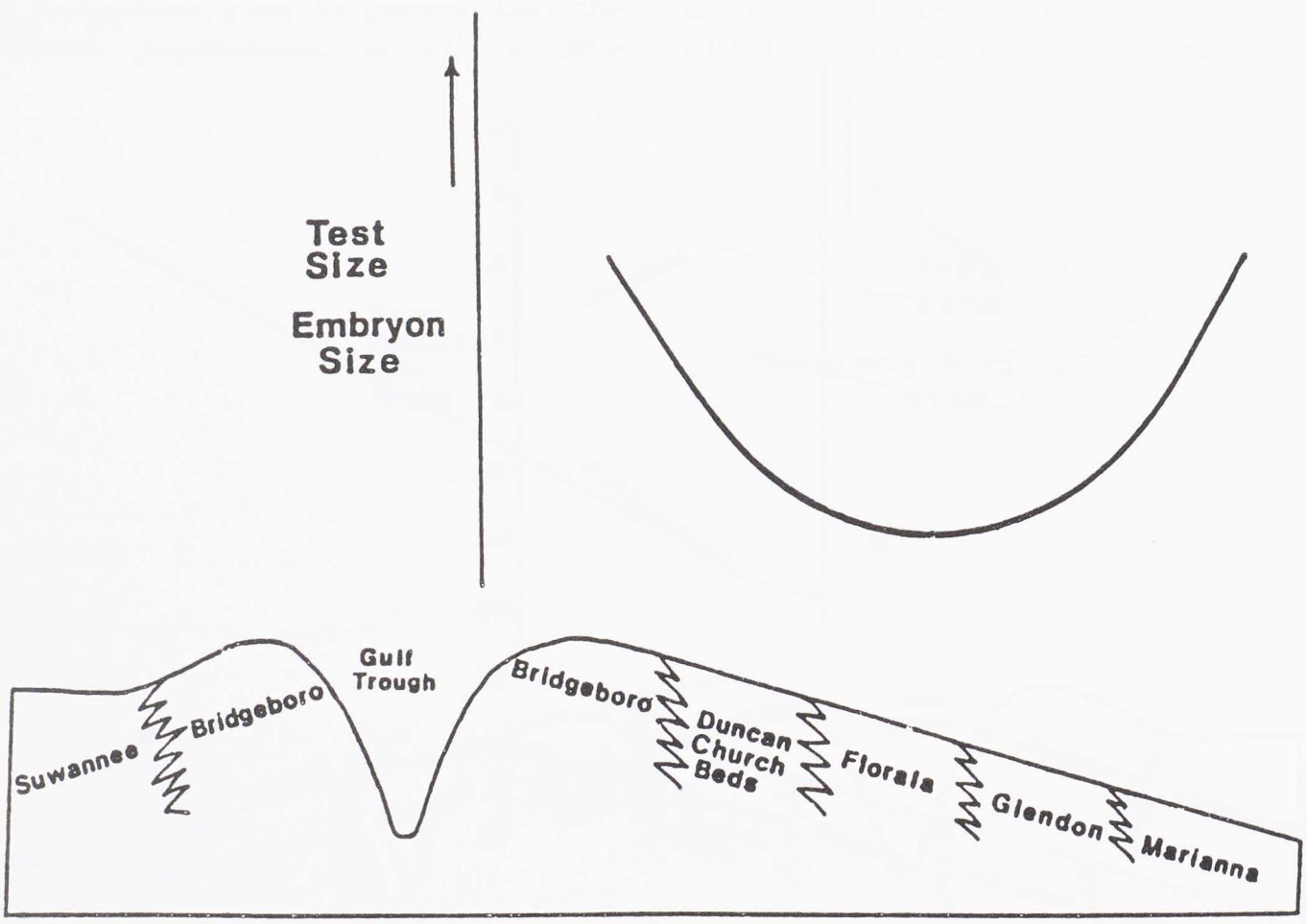

Figure 9. Diagramatic representation of the new, modified hypothesis generated by the data of this investigation. It is predicted that a species' test size and embryon size will increase at both extremes of its range along a shallow to deep paleoenvironmental ecogradient.

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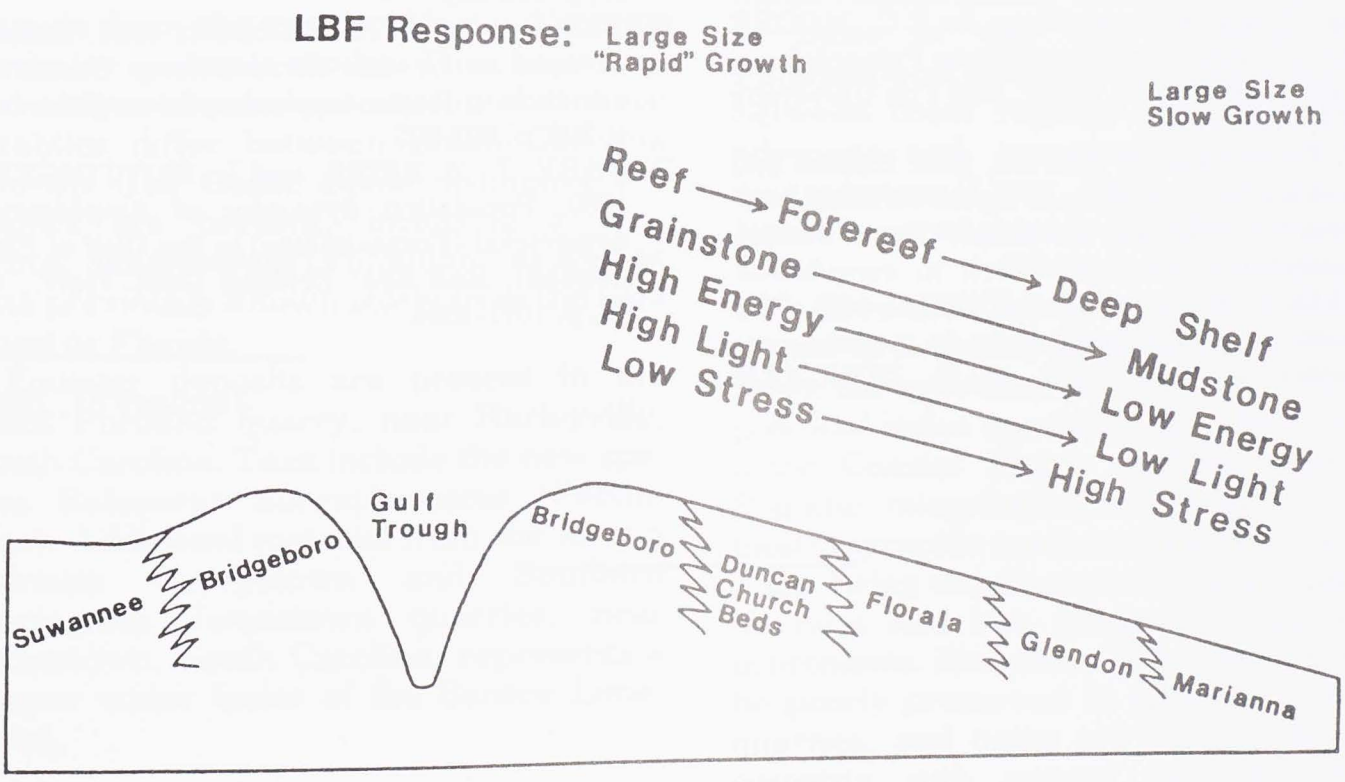

Figure 10. Environmental conditions and predicted morphologic and developmental response of larger foraminifera along the Lower Oligocene paleoenvironmental gradient in the eastern Gulf Coastal Plain.

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