

ENVIRONMENTAL STABILITY AND MORPHOGENETIC
RELAXATION IN BRYOZOAN COLONIES FROM THE EDEN
SHALE (ORDOVICIAN, OHIO VALLEY):
A DEVELOPMENTAL EXPLANATION OF STABILITY -
DIVERSITY - VARIATION HYPOTHESES

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ABSTRACT

ENVIRONMENTAL STABILITY AND MORPHOGENETIC RELAXATION IN BRYOZOAN COLONIES FROM THE EDEN SHALE (ORDOVICIAN, OHIO VALLEY): A DEVELOPMENTAL EXPLANATION OF STABILITY-DIVERSITY-VARIATION HYPOTHESES

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Growth features that are morphogenetically regulated provide a developmental insight into the genetic-morphologic paradox of stability-diversity-variation hypotheses. Morphogenetic systems within Ordovician bryozoan colonies are recognized through morphologic gradients that allometrically changed in "field potential" through astogeny. This developmental regulation is additionally documented by means of newly recognized monarchic zooids at field centers, a test of position effect on zooidal differentiation, and a test of field induction and suppression as a distance effect. For each species, least squares regression analysis permits the measurement of the rates of field growth, and the residual variance from regression measures morphogenetic relaxation, a facultative response to environmental differences. In four stratigraphically pervasive species in the Eden Shale the level of morphogenetic relaxation is homogeneous within species, but varies significantly across taxa. The two species with the highest residual variability fit the concept of r-selected opportunistic species and are most abundant in communities of lowest diversity. The other two species have much lower residual variance, fit the concept of K-selected equilibrium species, and are

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most abundant in the communities of highest diversity. Within-colony variability is higher in the opportunistic rather than in the equilibrium species, indicating that the higher morphologic variability observed in unstable environments is non-genetic in nature and not the result of higher genetic polymorphism. Equilibrium species in stable environments have lower levels of morphologic deregulation whose relationship to genetic diversity could not be conclusively tested with the available data. However, several genetic mechanisms, such as maintenance of developmental homeostasis through heterozygosity, are available to explain the apparently negative correlation of genetic and morphologic variability.

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A DISSERTATION

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To Betty and
my Parents

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INTRODUCTION

Hypotheses concerning the relationship between environmental stability, morphologic variability and genetic polymorphism have considerable potential in providing more ecologically based explanations for many episodes in the history of life, as well as simplifying a great number of other paleontological problems. Stability-diversity-variation models (Ashton and Rowell, 1975) have predicted that communities in unstable environments have low levels of taxonomic diversity and high morphological variation within species. Opinions have differed, however, as to the relationship of genetic variability within species to morphologic variability across stability gradients. Levins (1968), in his "niche-variation" model, predicted on theoretical grounds that a population's genetic variation should be positively correlated with the degree of fluctuation of environmental parameters, so that species inhabiting unstable environments would be characterized by high levels of both genetic and morphologic variation, while low levels of both would be expected in stable habitats. Several other authors have supported this hypothesis, based upon the variability of morphologic features or protein polymorphism (Van Valen, 1965; Bretsky and Lorenz, 1970; Powell, 1971; Burns and Johnson, 1971; Grassle, 1972; Grassle and Sanders, 1973; Levinton, 1973; Lorenz, 1973; Rothstein, 1973; Soulé et al., 1973; Johnson, 1973). The only previous assessment of stability-diversity-variation models in a paleontological context (Ashton and Rowell, 1975) failed to reveal any relationship, based upon the comparison of

coefficients of variability of eight cranidial features of seventeen Late Cambrian trilobite species across a diversity gradient. The authors viewed their failure to find any differences in variability as the result of a dearth of attributes capable of illuminating potential differences.

The work of Ayala, Valentine et al. (1975a, b, c), based upon protein polymorphism in extant benthic marine invertebrates, indicates a possible paradox; genetic variability within species was observed to be positively correlated with taxonomic diversity and, presumably environmental stability, while the opposite trend was observed for morphologic variability (Doyle, 1971, 1972; Schopf and Gooch, 1971, 1972; Gooch and Schopf, 1973; Somero and Soulé, 1974; Valentine and Ayala, 1974). High genetic variability, therefore, appears to be characteristic of species exhibiting low levels of morphologic variation.

Developmental deregulation possibly provides an explanation of this conflict: through greater complexity in regulatory rather than structural genes, species in unstable environments could facultatively deregulate development in all individuals, thereby conferring high morphologic variation within species in which the choice of developmental pathway would be ecophenotypically rather than genetically determined. Conversely, species in stable environments could have more canalized development and therefore exhibit more constant within-species morphology. Higher genetic polymorphism could be maintained within the latter species, either because the value of deregulated development in stable environments would be adaptively neutral, or because constant morphology is better achieved through the "greater ability of the heterozygote to stay within the norms of canalized development" (Lerner, 1954; Eldredge and Gould, 1972).

The morphogenetic fields of Ordovician trepostome bryozoan colonies provide a test of this hypothesis in the fossil record. Their "ontogeny"

is not simply growth-related, but is developmentally regulated and has components of variation both within and among species. Very similar developmental fields or gradients in living organisms are known to be regulated by specific growth hormones. It is possible that these bryozoan fields give access to an important regulatory sector of the genome. Changes in "field potential" resulted from both colony growth and environmental conditions. Separation of these two sources of variability and a comparison of the latter component with taxonomic diversity provides a developmental insight into the nature of the genetic-morphologic paradox. It is the purpose of this paper to document the existence and characteristics of morphogenetic regulation in fossil bryozoan colonies from the Eden Shale (Ordovician, Ohio Valley), and to compare levels of developmental deregulation with the taxonomic diversity, and by inference with the environmental stability, of the communities in which they lived.

MORPHOGENETIC SYSTEMS IN ORDOVICIAN BRYOZOAN COLONIES

Introduction. - Gradients of substances are responsible for much cellular differentiation beginning during embryogenesis and continuing until maturity. Differentiation along a gradient can be a process of selective genetic expression in response to changing concentration levels of substances diffused away from the point of origin. The establishment of the existence of this type of regulation requires that polar points (field centers) and potential fields (zones of influence) be recognizable and testable. These criteria, and others as well, have been recognized in the morphogenesis of both living and fossil cheilostome bryozoans (Bronstein, 1939; Dzik, 1975), for fossil trepostome bryozoans (Anstey and Pachut, 1976; Anstey et al., 1976), hydroids (Burnett, 1966; Braverman and Schrandt, 1966), graptolites (Urbanek, 1973

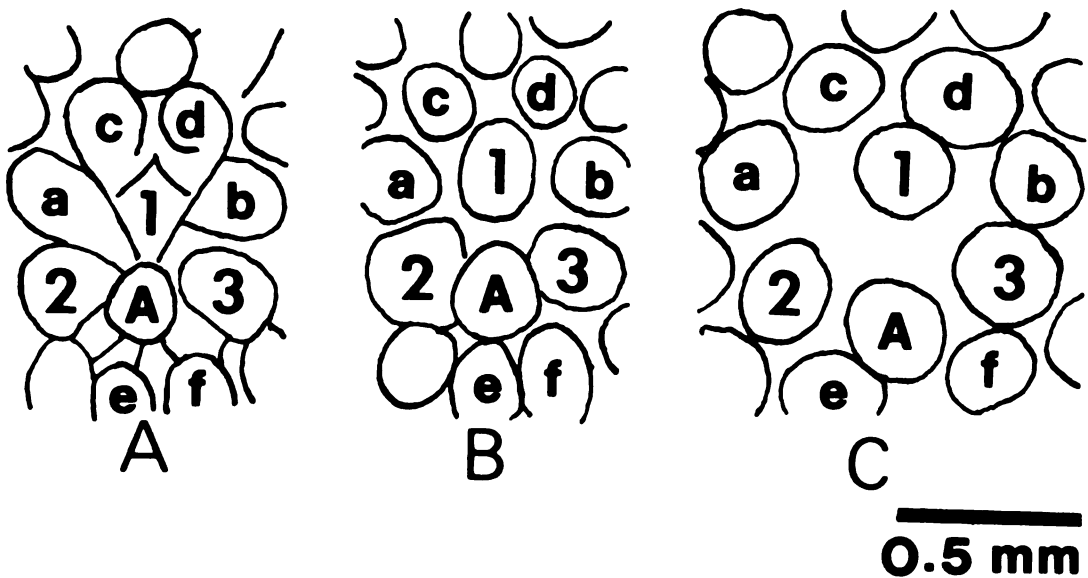


Figure 1: Zooidal arrangement in the ancestrular and monticular regions of *Prasopora conoidea*. A. Transverse section through the ancestrula (A), first generation of zooids (1-3) and second generation (a-e). B. Transverse section through the same area as in A, but at a slightly higher level. C. Transverse section through the same area as in A and B, but at a level 1.5 mm higher in the zooarium; the structure of the primary zooids at this level is indistinguishable from a monticule. All figures redrawn from Cumings (1912): A, from Plate 19, Figure 5; from Plate 19, Figure 6; C, from Plate 21, Figure 31.

inter alia), fossil crinoid stems (Seilacher et al., 1968), mammalian molars (Van Valen, 1962; reviewed in Gould and Garwood, 1969), for the spacing of punctae in fossil brachiopods (Cowen, 1966), and for the morphogenesis of a variety of living animals and plants (reviewed by Bonner, 1974).

The recognition of morphogenetic fields in Paleozoic stenolaemate bryozoans has been centered around the structure and spatial arrangement of structures called monticules. These structures are surficially expressed as regularly arranged prominences of polymorphic zooecial chambers. Specialists have generally recognized the polymorphic character of the zooids in these small clusters (Boardman and Cheetham, 1973, p. 156; Utgaard, 1973, p. 324; Astrova, 1973, p. 4; Banta et al., 1974). However, utilizing detailed computer mapping around several monticules from a colony of Amplexopora filiosa (D'Orbigny), Anstey et al. (1976) demonstrated, at least in the species studied, more or less radial gradients in zooecial morphology centered on the monticules. Computer mapping also showed that field boundaries could be objectively determined by the change in slope of the morphologic gradient going from one monticule to another, and that a large number of brown bodies (preserved polypide degeneration remnants) were located along the field boundaries. They also showed, within four other species, that the fields gradually enlarged themselves with colony growth, and that the polar zooidal clusters, or monticules, grew larger as the polar points became more widely separated. In this paper the most critical evidence for polar regulation from previous work is restated, and new information is presented as well.

Monarchic control. - The recognition of a special monarchic zooid or pseudoancestrula within each monticule was casually made by Cummings

Figure 2: Monticular structure in tangential sections in eight genera of Ordovician trepostome bryozoans. A. Hallopora nodulosa, IU8975.41024. B. Amplexopora septosa, IU8976.17005. C. Heterotrypa ulrichi, IU8976.25007. D. Peronopora vera, IU 8974.1001. E. Generalized zooid pattern, using the same symbols as Figure 1. F. Balticoporella whitfieldi, IU8975.38001. G. Batostoma jamesi, IU8974.1004. H. Stigmatella clavis, IU8972.3008. I. Eridotrypa mutabilis, IU8974.1004. Monarchic zooids marked by stars. All thin sections are in the paleontological collections of Indiana University.

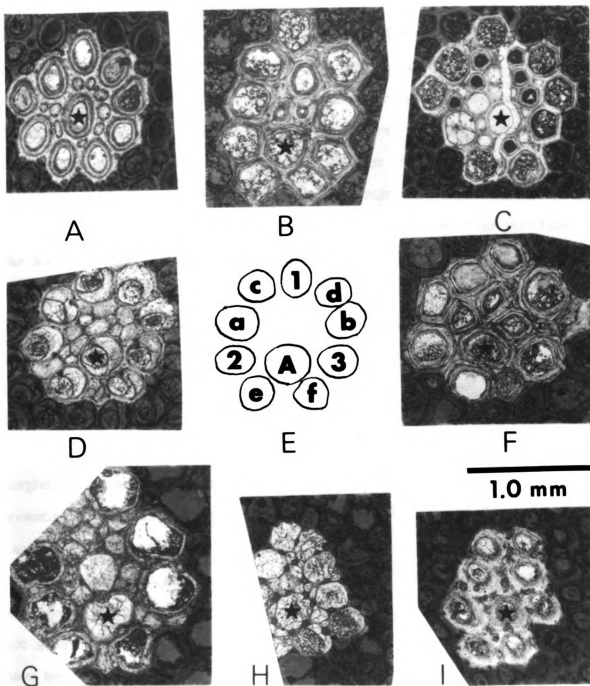


Figure 2

(1912, p. 366) and by no one else since; he observed the same arrangement of zooid types in both the zone of earliest colony development from the founding zooid or ancestrula, and within a monticule of the Ordovician trepostome Prasopora conoidea (Figure 1). The structure within each monticule repeats, with some modification, the structure of the zone of early development, including a special zooid within the monticule that "mimics" or replicates the ancestrula. In several species examined for this study, including one of Prasopora and eight other genera from the Eden Shale, one large zooid within each monticule has been observed to be in the same spatial arrangement with respect to the other monticular zooids as the ancestrula of the entire colony is positioned with respect to the first nine or so zooids that were budded from it (Figure 2). In very small disklike colonies (50-100 zooids) examined for this study, the ancestrula and its surrounding ring of nine or so polymorphic zooids form, in essence, the first monticule of the colony. The zooids outside of the initial monticule display radial morphologic gradients, identical to those mapped in Amplexopora filiosa. Thus, the morphologic gradients in the zone of early astogeny are polarized on the ancestrula, just as the gradients in the zones of later development (astogenetic repetition) are polarized on the monarchic zooid (pseudo-ancestrula) in each monticule (Anstey and Pachut, 1977). As zooidal arrangement in trepostome monticules may vary, the monarchic zooid cannot always be easily identified. Several recognition criteria, however, have been found to be useful in combination if not alone: 1) the monarchic zooid is usually larger in diameter than any other monticular zooid, 2) small zooids in the monticular center (frequently termed mesopores) are commonly smaller near the monarchic zooid and become

Figure 3: Monticular structure in longitudinal sections of six genera of Paleozoic trepostome bryozoans. a, b. Amplexopora filiasa, MSU1001. c. Peronopora vera, IU8976.19007. d. Heterotrypa urlichi, IU8976.21024. e. Hallopora nodulosa, IU8975.15009. f. Generalized zooidal pattern, using same symbols as in Figure 1. g. Atactoporella variant, IU8974.2004. h. Tabulepora penerudis, IU6004.111b. Specimen illustrated in a and b is in the paleontological collection of Michigan State University; all others are in the paleontological collection of Indiana University. Horizontal bar in each illustration is 0.5 mm.

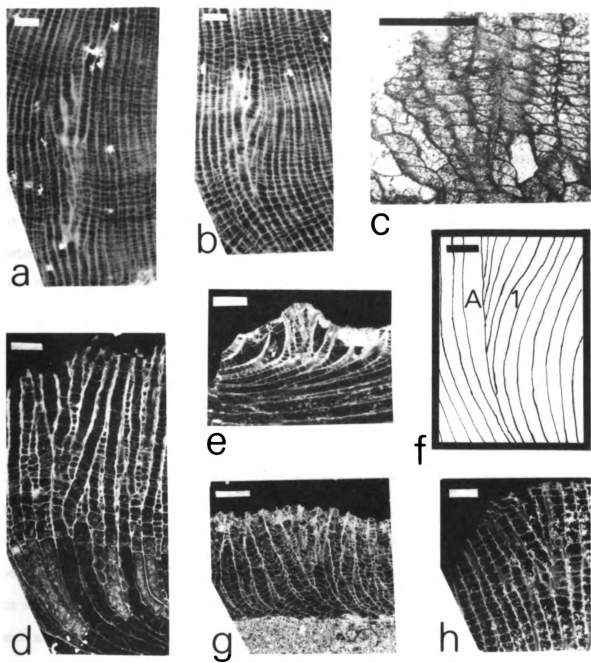


Figure 3

larger away from it; the opposite size gradient has also been observed as well as a radial structure resembling the spokes of a wheel, 3) the monarchic zooid is usually offcenter in the monticule, although its position varies taxonomically, and 4) monticules are generally bilaterally symmetrical and fan-shaped, with the monarchic zooid at the fan apex; the very large zooids (termed by some authors megazooecia) around the margin of the central cluster are regularly arranged in symmetric pairs, one member on either side of the monticular axis, duplicating the pattern of early astogeny (Figure 3). These patterns can be illustrated in at least six families of Paleozoic bryozoans and possibly in a Recent heteroporid (Figures 1-4). There is, therefore, a strong analogy between the function of the monarchic zooid of a trepostome monticule and that of the siculozooid of the graptolite morphoregulatory systems demonstrated so carefully by Urbanek (1973, summarizing a series of earlier papers) through "natural experiments" provided by damaged and regenerated colonies.

Position effect within a field. - Inferences have been made concerning the reproductive, feeding, and sanitation functions of the polymorphic zooids within monticules (Banta et al., 1974, inter alia). The control of reproductive differentiation by a morphogenetic field has been illustrated in the colonial hydroid Podocoryne (Braverman, 1963) in which the reproductive zooids form only in the center of the colony, and asexual feeding zooids occupy the periphery. As the colony grows marginally, the sexual center expands by the progressive differentiation of the asexual zooids caused by an increase in field strength (potential). Urbanek (1973) has postulated reproductive differentiation of graptolite zooids as a position effect along a morphogenetic gradient arising from

Figure 4: Monticular structure in surficial views of Ordovician and Recent colonies. A. Peronopora vera, IU8976.30001. B. Amplexopora septosa, IU8976.30002. C. Heteropora sp., BMNH1889,1.1.G (Port Elizabeth). A and B are in the collection of Indiana University; C is from the British Museum (Natural History), photograph courtesy of Paul D. Taylor, University of Durham. Above each photograph is a slightly enlarged diagrammatic drawing of the monticular pattern, using the same symbols as in Figure 1. Third generation zooids marked by an x. Small zooids in monticular center are shaded. Vertical bar in each photographic illustration is 1.0 mm.

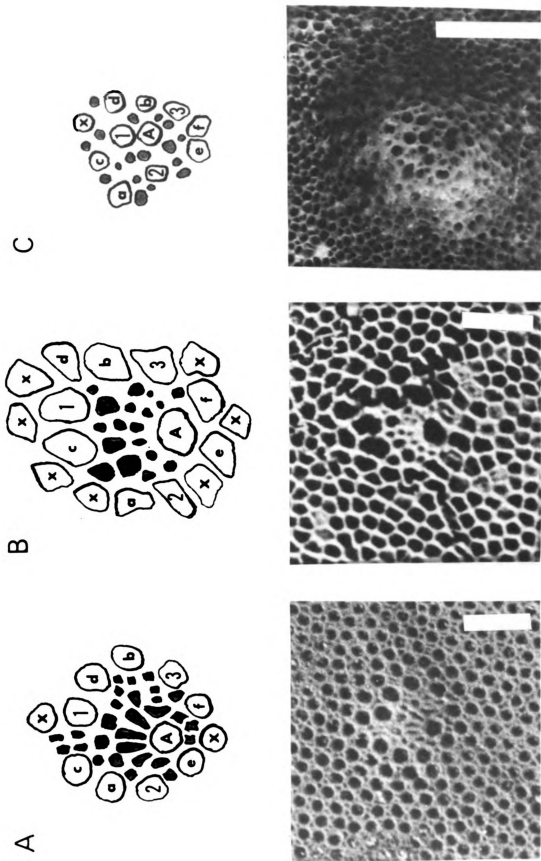


Figure 4

the siculozoid. The position effect on polymorphic differentiation of zooids in a morphogenetic field can be tested only in bryozoans having monticular budding. In such colonies, the monticule functions as a meristem, and as new buds arise at the growth pole, older zooids are displaced outward in the field. The position effect on zooids can be tested directly by tracing the actual history of specific zooids through serial thin sections or peels. In the trepostome Amplexopora filiasa, the vertical development of five zooids was traced through nine serial tangential peels cut at 0.5 mm intervals (Figure 5). All of these were monticular polymorphs at the lowest level (9); three (2, 3, 5) were the very small variety of polymorphs found in the monticular center, and two (1, 4) were the very large polymorph characteristic of the monticular border. All three of the very small ones greatly increased in size through only one level, and all eventually became standard nonmonticular autozooids (above level 6).

In the trepostomes, zooid migration takes place within morphogenetic fields as a consequence of zooidal budding within growth centers (monticules or branch tips). New zooids displace older ones outward in the field, producing a form of morphogenetic movement induced by growth at the polar point. To document the lateral movement away from a monticule during zooidal ontogeny, the spatial position of the five zooids of figure 5 were mapped through the same nine levels; all originate in a monticule and are gradually displaced away from it (Figure 6), inducing the morphologic differences shown above. These growth displacements are likewise observable in longitudinal section (Figure 3). Polymorphism may be induced by the displacements of zooids within a field, but also by displacement of the fields themselves, discussed below. This test

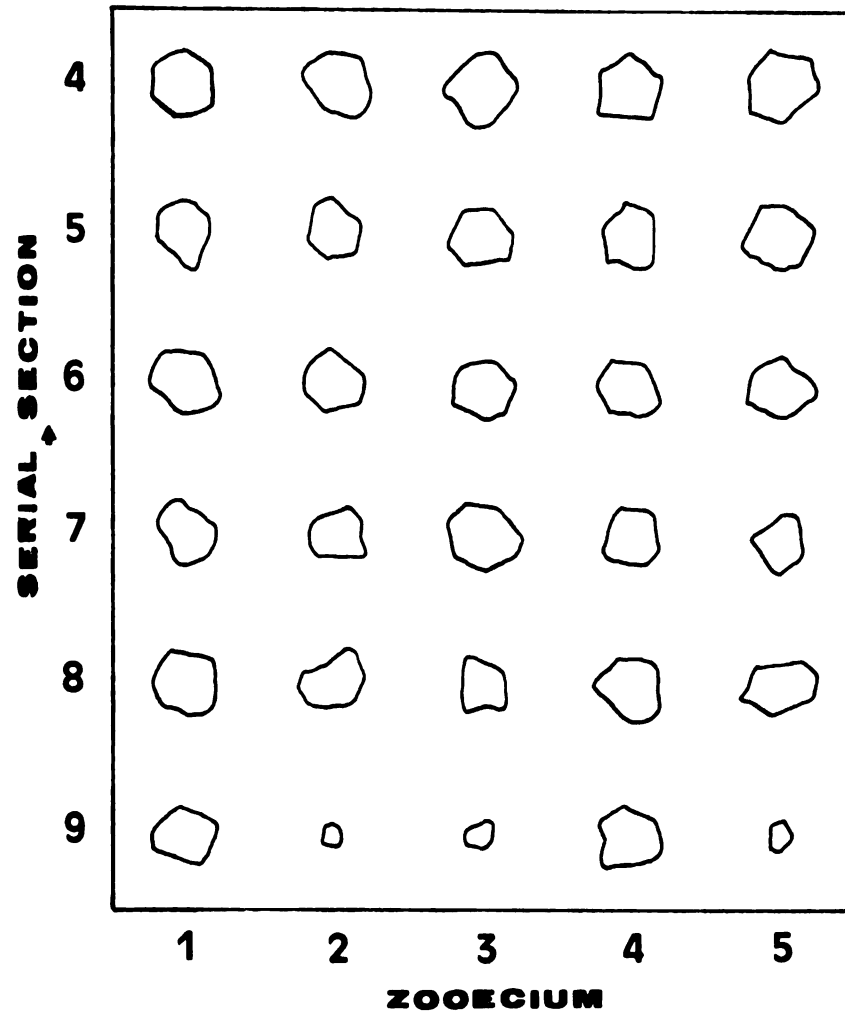


Figure 5: Changes in zoecial outline of five zoecia from a monticule of *Amplexopora filiosa*, MSU1001.4-1001.9, through six serial acetate peels cut at 0.5 mm intervals. Zooecium 1, level 4, is 0.20 mm in maximum diameter.

demonstrates that polymorphic differentiation is a function of position in a morphogenetic field. The newly budded individuals are initially very small, undergo a dramatic size increase, and then decrease in size thereafter as they migrate from the monticular pole toward the field's periphery.

Preliminary observations indicate that the monarchic zooid is, at least in several species, the only zooid that is not displaced out of its original position, remaining in the same general location, even through successive lamellar growth zones of accretionary colonies (Anstey and Pachut, 1977). This unique quality partially indicates its dominance over the morphogenetic field, and if the fields are maintained by the release and diffusion of a growth hormone (as, for example, in plant phyllotaxis), then the monarchic zooid is the most likely source of that substance. In addition, it is the locus of zooidal budding within monticules in certain taxa (Figure 3), implying that asexual reproduction within a colony is also a function of this polymorph.

Field growth. - Morphogenetic field size (potential) in these colonies is not static; it changes allometrically during colony growth (astogeny). In a massive lamellar colony of Amplexopora filiasa (illustrated by Delmet and Anstey, 1974, Figure 1), the thickness of each lamellar growth zone is very significantly correlated with the mean radius of the morphogenetic fields at the top of each zone (Figure 7). This colony, about 8 cm thick, experienced 17 cycles (probably seasonal) of growth, each of which added another layer of skeletal material to the massive zoarium. This correlation indicates that, after an exponential increase in field size within each growth zone, the fields deteriorated. Because the field strengths achieved at the end of each growth cycle are

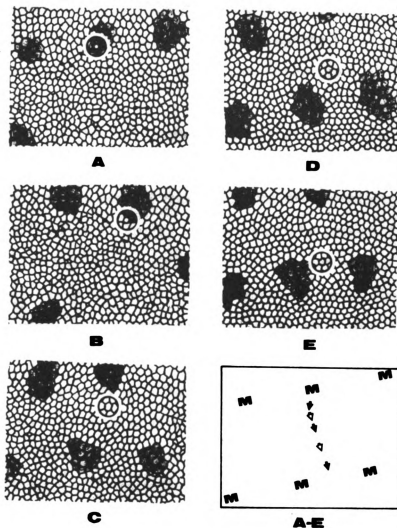


Figure 6: Lateral displacement of a monticular zooid in *Amplexopora filiosa*, MSU1001.5-1001.9, through five serial acetate peels (A-E) cut at 0.5 mm intervals. Generalized displacement pattern illustrated at lower right; monticules marked as M. Shaded regions in A-E are monticules; displaced zooid centered within circle. Each illustration represents an area 3.7 mm by 5.0 mm.

completely non-monotonic through the zoarium, the fields must have disappeared at the end of each cycle, and their buildup begun de novo at the onset of the next. This type of field growth suggests the diffusion of a morphoregulatory substance rather than other types of field maintenance.

Monticules are absent in the lower part of each growth zone, and generally appear about 2 mm above the base of each zone. In the lower part of each layer (the immature zone or endozone), the differentiating morphogen, by extrapolation from figure 7, is inferred to be present in concentrations below a critical level; differentiation of zooids into monticular polymorphs is concomitant with the appearance of the exozone (mature zone) and presumably reproductive maturity in the upper part of each layer.

Field initiation and suppression. - One of the most conventional observations regarding monticules is that of their generally hexagonal spacing over a colony surface, an effective space-filling strategy with the morphogenetic implication of a distance effect. Cowen (1966) inferred regulation in the insertion of hexagonally spaced brachiopod punctae, but could not test it because the fields remained static after insertion. Because the monticular fields grow within the colony, and the colony itself may not be able to expand uniformly in all directions, the fields locally interfere with one another, resulting in the suppression of some fields and the actual disappearance of a monticule. Local irregularities in field arrangements develop, and new monticules actually appear in relatively empty areas (Figure 8). This suggests that threshold levels are required to induce new fields in interareas that have become too large, and likewise for field suppression in areas that have

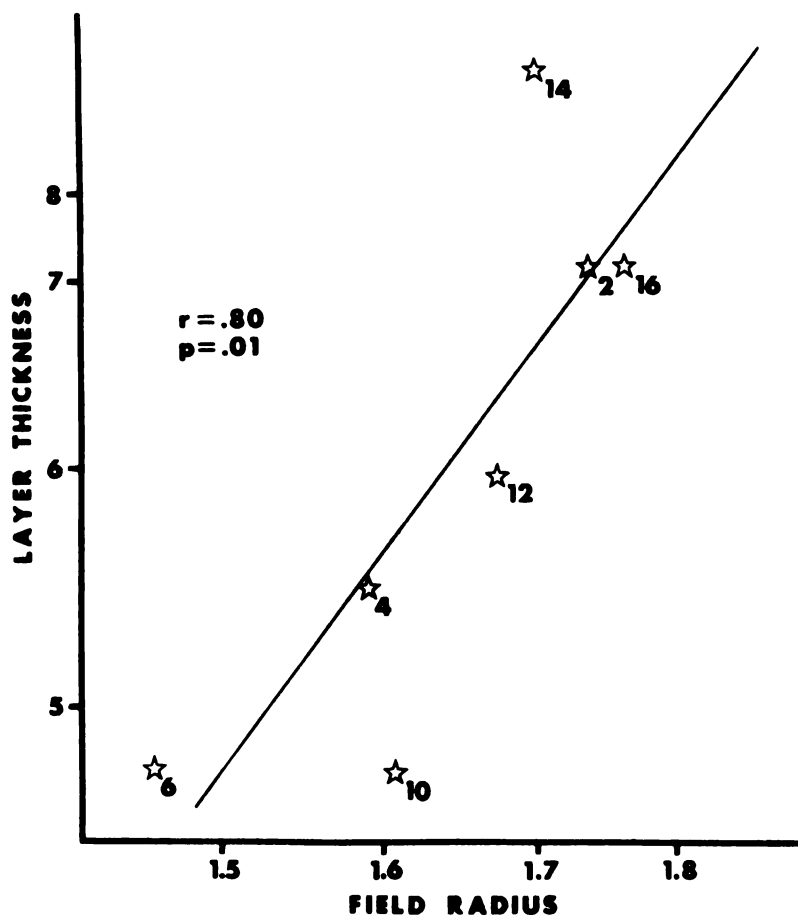


Figure 7: Correlation of the thickness of lamellar growth zones in *Amplexopora filiosa*, MSU1001, with the mean radius of subcolonies at the top of each zone. Means computed from 48 radii measured from the calculated center of gravity of each subcolony; layer means based on from 2-21 subcolonies per thin section, and 2-4 thin sections per layer. Stars indicate growth zones within the zooarium, numbered in sequential order.

become too crowded. The histories of 41 specific fields were traced through five serial acetate peels in A. filiasa (Figure 8). The closest observed spacing between field centers in this interval was 1.24 mm, and the largest 4.24 mm (mean, 2.27 mm). The close spacing of 1.24 mm was measured between fields 11 and 14 (Figure 8) at the 1.0 mm depth, above which, between the 1.0 and 0.5 levels, field 11 was suppressed. The large spacing of 4.24 mm was measured at the 0.5 level, between field 6 and an unnumbered field, above which a new field was induced in the interarea which appeared at the 0.0 level. The cross-sections in figure 8 illustrate the induction of new fields (2, 10, 3, 4, 8, 9) in empty interareas, and the suppression of an old field (11) in a crowded region. The budding of new zooids in the field centers of this colony caused lateral displacement of the monticules and their fields, so that some of the fields illustrated (5, 7) are displaced into and out of the cross-sectional planes. Field suppression and induction imply that the zooids in the areas affected must be repolarized toward the new field arrangement. These patterns illustrate the inhibitory and polarizing effects of the field agent. It can be concluded that, in the absence of the inhibitor, any autozooid could become a monarchic zooid and institute a field of its own. Conversely, in the presence of too much inhibitor a monarchic zooid could produce a normal polypide and become a normal autozooid polarized towards the nearest monticule. Therefore, the morphogenetic agent could be considered either an inhibitor with respect to monarchic zooids, or an inducer with respect to autozooids.

Regeneration. - Anstey et al. (1976, Figures 8, 9) and Anstey and Pachut (1976) have shown that brown bodies, the residues of polypide degeneration, occurred in Amplexopora filiasa mostly in zooecia near the

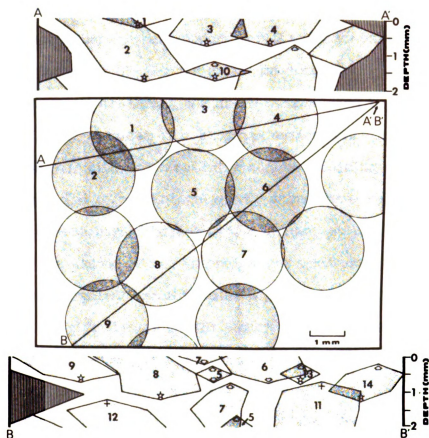


Figure 8: Induction and suppression of monticular fields through five serial acetate peels cut at 0.5 mm intervals in Amplexopora filiosa. Center, plan view of 13 monticular fields at uppermost level. Cross sections along transect A-A' and B-B' shown above and below plan view, respectively. Monticular fields represented by the mean intermonticular spacing in all five peels. Areas of no data are vertically lined. Stars, loci of field induction; crosses, loci of field suppression; arrows, loci of field displacement. Cross sections are drawn without vertical exaggeration.

boundaries of the monticular fields. A few anomalous zones were observed wherein all the zooecia contained brown bodies except those in the monticules. Such zones provide further support for the former existence of these morphogenetic systems. They occur at random locations within the colony's repetitive growth layers and are thus unrelated to seasonal growth. They most likely resulted from external environmental perturbations (e.g. starvation) with the monticular zooids remaining unaffected, possibly because some kind of physiologic gradient ran parallel with the morphogenetic one, concentrating the colony's resources at the polar points. Therefore, the source of the morphogenetic substances would be unaffected, and the gradient could be maintained. The observed regeneration of the extramonticular zooids supports this contention: the size and shape of an individual skeletal chamber did not change after regeneration, and must have been dependent upon its position in the field polarized on the monticule (Anstey et al., 1976). The regenerated zooids adopted the form (and inferred functions) of their defunct predecessors in the same zooecium above several layers of mass degeneration in A. filiasa, indicating that the gradients were stable enough to be maintained, even though most of the colony's autozooids had experienced degeneration.

In summary, evidence for the existence of a regulatory system in Ordovician bryozoan colonies includes: 1) radial morphologic gradients in zooecial morphology polarized on each monticule, 2) the presence of a monarchic zooid or pseudoancestrula within each monticule that provides a specific point of origin for each morphogenetic field, 3) a position effect for polymorphic differentiation with respect to the monarchic zooid, 4) nonlinear (allometric) growth of fields, suggesting

diffusion as a likely cause of field maintenance, 5) a distance effect for the induction of new fields and suppression of old ones, illustrating the polarizing and inhibitory effects of the field agent, and 6) the maintenance of morphogenetic fields following an episode of mass degeneration not at the end of a normal growth cycle.

MEASUREMENT OF DEVELOPMENTAL RELAXATION

Genetic basis. - In many organisms, gradient or field characteristics, including morphogen concentration, diffusion rate, threshold levels and so on, appear to be involved in the localization of differentiated cells or body parts, and pattern formation in general. Therefore, environmentally or genetically induced changes in these characteristics could produce different phenotypes. Genetic alterations of the basic gradient or field pattern have the capacity to cause changes in the rates and amounts of growth, in the localization, degree of expression, or even the presence or absence of particular cellular (or intracolony) differentiations (Child, 1941). Such quantitative alterations of basic gradient patterns may explain growth and form differences in related species, its recognition thus assuming importance in phyletic reconstruction (as, for example, in heterochrony). Underlying genetic changes need not be complex or extensive, however. It has been suggested (DeBeer, 1958, ch. 3; Gould, 1968, p. 92; Wilson, 1976) that general developmental rates may be regulated by simple genetic mechanisms, minor alterations potentially having substantial phenotypic effects. Valentine and Campbell (1975) have applied the concept of gene regulation to explain the major advances in animal evolution, viewing evolutionary changes as expansions or repatterning of the regulatory portions of the

genome rather than changes in structural genes. It is plausible that similar controls may represent a measurable aspect of the regulatory phenotype on which natural selection has acted, a conclusion which Urbanek (1973, p. 498) reached regarding graptolite phyletics. The morphogenetic field dynamics of bryozoans are capable of producing significant differences in colony form, both within and among species. This study seeks to determine whether or not relaxation of these developmental systems is in any way correlated with environmental stability (as measured by taxonomic diversity). To test this hypothesis, the developmental variation of the bryozoan assemblages of the Eden Shale (Ordovician, Ohio Valley) will be compared with taxonomic diversity.

Measurements. - A preliminary investigation (Anstey et al., 1976) illustrated significant correlations among field size, colony size, and monticular diameter in four species of Eden trepostomes. These relationships indicated that field dynamics were related to overall colony form and monticule size. Therefore different growth rates of the fields could produce colonies having different stature, erectness, and polymorphic ratios. In each of the four stratigraphically pervasive Eden species (Heterotrypa ulrichi, Hallopora nodulosa, Amplexopora septosa, and Peronopora vera) twenty measures of monticular diameter and intermonticular distance (i.e. field diameter) were obtained from each colony, allowing the calculation of colony means. These means were subsequently converted to natural logarithms to remove non-linear effects, as allometric field growth had been previously established. Colony size (branch diameter or frond thickness) measures were not utilized because of low reliability caused by differences in colony growth forms and multiple growth increments (as in Amplexopora), thickness variations along the

length of branching colonies' axes, and deformation resulting from sediment compaction. Additionally, the species Peronopora vera, which has a very thin endozone, would possess diameter measures varying totally with the realized stage of astogeny. Monticule and subcolony (field) sizes, on the other hand, are measurable irrespective of growth form and circumvent such problems.

The developmental pattern of each species and the degree of deviation from a strictly canalized development (developmental relaxation) may be measured through least-squares regression analysis: the calculated regression line itself estimates the "standard" developmental pathway, and the residual variance from regression measures the degree of relaxation from normal development. Additionally, the slope (allometric exponent) estimates the relative rates of growth, and the value of the Y-intercept provides the size of the monticules at a field diameter of 1 mm (the log of 1 mm is zero). From the slope an indication of polymorphic ratios and general colony form may be obtained. Samples from each of the four species listed above were subjected to regression analysis, yielding within-species statistics (Table 1). Developmental relaxation values (residual variances) were converted into standard deviations for comparative purposes.

Results and inferences. - For each species (Table 1) a significant correlation between monticule and subcolony size was obtained, confirming the developmental character of field growth. Both the relative growth rate (allometric exponent or slope) and monticule size, at a field diameter of 1 mm (Y-intercept), differ among species so that different species have different overall growth forms. The scatter of points within a species represents the deviations from normal development

Table 1. Species growth rates, developmental relaxation, and intra-specific character variability.

Species	N	R	P	AE	YI	DR	IV
Peronopora vera	38	.5990	.01	.7860	.6339	.11718	4.65
Amplexopora septosa	55	.5744	.01	.7212	.7052	.12124	8.20
Hallopora nodulosa	43	.5782	.01	.4663	.8790	.15241	5.78
Heterotrypa ulrichi	66	.3963	.01	.6521	.7836	.21823	6.72

N: number of specimens. R: correlation coefficient. P: significance level of correlation. AE: allometric exponent ($\log \text{mm} / \log \text{mm}$); proportional to colony growth rate. YI: y-intercept; proportional to monticular size at a field diameter of 1 mm. DR: developmental relaxation; square root of residual variance from regression. IV: mean percent intraspecific variability of the 80 two-state characters used by Anstey and Perry (1973, Tables 2-5, pp. 17-20).

(Figure 9); those lying along the regression line are representative of the "normal" developmental pathway (astogeny) while deviations from this trend are inferred to reflect ecophenotypic deregulation. Although these species overlap one another in the specific aspects of development being measured, each species is sufficiently distinct in terms of slope, intercept, and residual variance, implying that each displays a certain degree of developmental homostasis.

The strength of the correlations suggests that these systems were functionally important; across the four species, a highly significant correlation is obtained between monticule and field size ($r = .70$, $p = .01$). As these species represent four different families, such a developmental economy must have a high degree of generality in describing trepostome morphogenesis, and has implications in the areas of functional morphology, autecology, and phyletics that are undeveloped in this study.

COMPARISON OF DEVELOPMENTAL RELAXATION WITH DIVERSITY

Sampling and diversity indices. - Taxonomic diversity has been considered to be one of the more important aspects of community organization and structure. Indices are reasonably sensitive to such ecologic parameters as the number of ways and how evenly the environment is partitioned among species and, therefore, how effectively it is being utilized by the community (Lorenz, 1973). Margalef (1968) has further summarized the implications of diversity measures as being an expression of the possibilities of constructing feedback mechanisms. Based upon these ideas, diversity should be proportional to food chain length, the degree of symbiosis, and the possibility of negative feedback control,

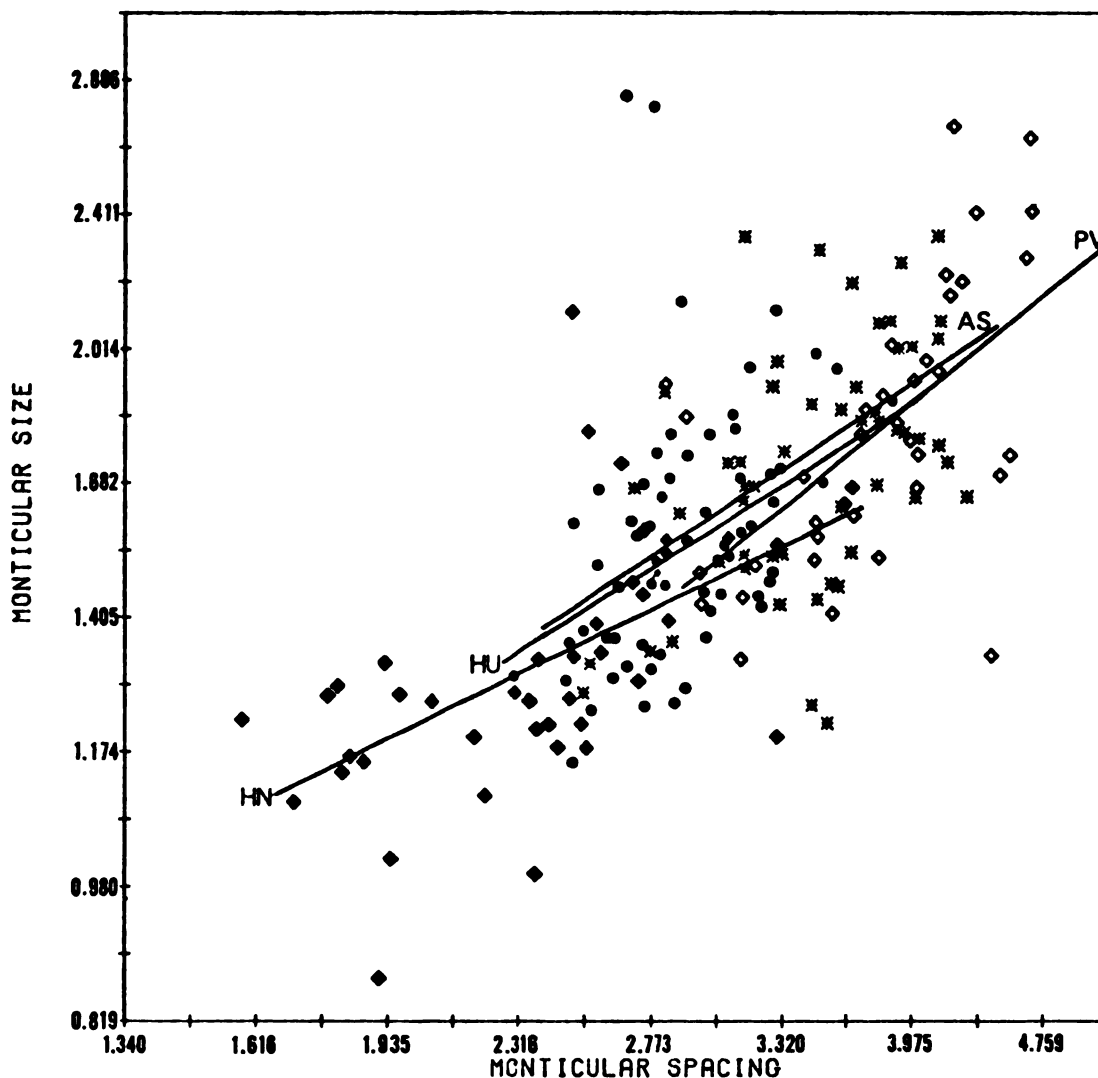


Figure 9: Developmental regression and variability in the four pervasive Eden trepostome species. The length of each regression line equals the range of values for the species. Circles, HU, Heterotrypa ulrichi; solid squares, HN, Hallopore nodulosa; asterisks, AS, Amplexopora septosa; open squares, PV, Peronopora vera; all values are in mm. Values of the slope, intercept, and developmental variability are listed in Table 1.

thus causing a reduction in oscillations and increasing stability when diversity is high (Odum, 1971).

In order to assess diversity, the collections of Anstey and Perry (1973), utilized above, and additional unsectioned material in the paleontological collections of Michigan State University were censused. Locality data is listed and figured in Anstey and Perry (1973, Appendix 1, p. 77; Figure 1, p. 8); all measured sections included recognizable formational boundaries to exclude any "floating" sections. Samples were obtained from strictly in-place materials throughout the lateral extent of each collecting interval. The separation of specimens from matrix was accomplished through kerosene immersion and washing through nested sieves; materials that passed through the 2 mm sieve were discarded. External debris was removed ultrasonically and as the taxonomy of these materials had previously been worked out on a numerical basis by Anstey and Perry (1973), external identification was possible. The species involved have several externally observable diagnostic features. All materials (over 6000 colony fragments) were so identified using a dissecting microscope.

The high degree of fragmentation of the resulting material would have led to systematic overestimation of diversity if simple numbers of colony fragments had been used. An additional size bias would also enter: of the dominant species present, Heterotrypa ulrichi and Hallopora nodulosa were considerably smaller in estimated living colony size than Amplexopora septosa and Peronopora vera. To circumvent these potential biases, species' skeletal volumes from each of 21 sampling intervals were determined by water displacement (Table 2). This yielded a measure of relative skeletal biomass, presumably proportional to resource uptake in filter-feeding organisms and more closely approximating the actual

Table 2. Relative species' biomass measured in cm³.

Species	1-01	1-03	2-13	5-14	5-14	5-23	Sampling interval										6-09	6-30			
							5-18	5-17	5-15	4-01	3-11	3-09	3-04	3-03	6-21	6-19			6-15		
<u>Heterostypa ulrichi</u>	148	129	343	7	2	25	23	5	11	4	-	9	10	20	94	435	52	148	22	30	2
<u>Heterostypa nodulosa</u>	44	25	25	23	144	13	30	.2	4	12	35	71	42	44	9	12	6	1	.5	1	.3
<u>Ampelocera septosa</u>	13	-	3	1	20	10	163	9	19	-	11	3	13	23	22	101	.7	75	-	5	69
<u>Peronopora vera</u>	22	23	11	2	5	14	-	6	2	.3	10	6	2	23	84	20	4	22	2	5	17
<u>Baccharis jamesi</u>	-	-	5	.5	-	15	-	-	-	-	-	-	-	-	-	7	-	-	2	46	-
<u>Dekania aspera</u>	6	1	-	-	-	-	-	-	-	-	-	-	-	1	1	2	4	3	-	-	-
<u>Balticoporella whitfieldi</u>	-	-	-	-	-	2	-	12	1	-	-	-	-	-	-	-	-	-	-	-	257
<u>Stigmatella clavus</u>	-	-	-	-	-	-	2	-	-	.5	1	-	-	-	-	-	-	-	-	-	-
<u>Ascioporella typicalis</u>	-	-	-	-	-	-	-	2	.5	-	3	-	-	-	-	-	-	-	-	-	-
<u>Eridictyia mitabilis</u>	-	-	-	-	-	-	-	-	-	-	76	-	-	-	-	-	-	-	-	-	-
<u>Prasopora simulatrix</u>	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-
<u>Coastellaria florida</u>	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
<u>Ceramatorcids</u>	16	9	19	5	.2	14	-	10	75	-	-	2	1	2	4	5	5	94	38	25	-
Totals	254	197	406	38.5	171.2	93	218	44.2	112.5	16.8	141	91	69	113	215	584	70.7	340	64.5	112	345.3

community relationships (Lloyd and Ghelardi, 1964). Macrofossils other than bryozoans were very minor in abundance in the intervals sampled except for the brachiopod Onniella which was as common as any of the trepostome species, and in some intervals, fragmented crinoid columnals.

In this study, Brillouin's equation, based upon information theory, is utilized as a measure of taxonomic diversity rather than the more widely used Shannon index. The reasons for this are: 1) Brillouin values are determined, not estimated, with a standard error of zero; Shannon values are an approximation of Brillouin's, 2) Kaesler and Brondos (1975) have found that Shannon's index is a biased estimator of diversity, always resulting in overestimation, and suggested the use of Brillouin's equation for paleontological purposes, and 3) the Brillouin equation is ideally suited for studies such as the present one wherein collections may be treated as discrete entities and not as subsets of larger populations (Pielou, 1974).

The Brillouin equation measures the information content per symbol of a message composed of N symbols of s different kinds, of which N_j are of the j^{th} kind as follows (Pielou, 1969, p. 232):

$$H = \frac{1}{N} \cdot \frac{\log N}{(N_1!N_2!\dots\dots\dots N_s!)}$$

The base of the logarithm employed in this study is 2, H being expressed as bits per individual.

This index, like Shannon's, confounds simple species diversity and species evenness, a measure of how equally (numerically) species are represented in a community (Pielou, 1974). A finite collection has maximum evenness and diversity when individuals are distributed among the species as evenly as possible. A separate measure of evenness, also

termed "dominance concentration" (Whittaker, 1964) and "equitability" (Lloyd and Ghelardi, 1964), is therefore desirable as communities of similar diversity may exhibit different patterns of species distribution. The ratio of observed diversity to the maximum possible diversity for the same number of species was suggested by Pielou (1966) for this purpose:

$$J = H/H_{\max} \quad \text{where,}$$

$$H_{\max} = \frac{1}{N} \log \frac{N!}{\{[N/s]!\}^{s-r} \{([N/s] + 1)!\}^r}$$

and,

N = total of importance values (e.g. number, biomass, productivity)

s = number of species

$[N/s]$ = integer portion of N/s

$r = N - s[N/s]$

A related measure, inversely proportional to diversity, is ecological dominance. Its importance as a separate index resides in the fact that not all of the organisms present in a community exert the same influence over the nature and function of the entire community (Odum, 1971). In general, a few species or groups of species disproportionately affect energy flow owing to their numbers, size, productivity, and other factors. Relative importance additionally tends to cross taxonomic lines, involving organisms belonging to widely differing groups. An index of dominance based upon relative resource utilization measures (i.e. biomass) may closely approximate the degree to which the energy flow of a community is controlled by one or several species. Such an index is defined by Odum (1971, p. 144) as:

$$c = (n_1/N)^2$$

where, n_1 = importance value for each species (e.g. numbers, biomass, productivity), and

N = sum of importance values.

Therefore, c is proportional to the sum of each species' importance to the community as a whole.

Species dominance and opportunism. - Examining these indices (Table 3) in more detail reveals several previously unobserved aspects of the Eden Shale communities. Species dominance measures indicated that domination was consistently attributable to three species: Heterotrypa ulrichi, Hallopora nodulosa, and in a few instances to Balticoporella whitfieldi (Pachut and Anstey, 1977). Intervals of lowered dominance (less than 50%) exhibited more equal abundances of up to ten additional species (Table 2). The latter range of dominance values was subdivided into three statistically differing levels whose correlations across sections are shown in figure 10. The three "dominating" taxa exhibit several of the relative abundances and distributional characteristics listed by Levinton (1970, p. 76) as useful in recognizing opportunistic (r-selected) species: 1) random orientation and lack of size sorting in individual beds, but a tendency toward size-group aggregations of the dominant species (see Waage, 1968, p. 162), 2) limited areal distribution, beyond which the horizon is unfossiliferous (Waage, 1968), 3) individual species aggregated into clusters (especially if sessile), 4) presence of species in thin but widespread isochronous horizons, indicative of a brief invasion, 5) species found abundantly in several otherwise distinct faunal assemblages (eurytopic), 6) species appearing in great abundance in a facies with which it is not usually associated,

Table 3. Diversity indices and weighted developmental relaxation for Eden Shale sampling intervals.

Unit	SP	PO	DIV	EVN	DOM	WDR
1-01	27.85	75.6	1.57	0.71	0.38	0.15737
1-03	31.35	82.4	1.09	0.64	0.52	0.17541
2-13	28.20	90.6	0.71	0.34	0.75	0.18612
5-44	32.75	78.0	0.86	0.88	0.44	0.12028
5-41	35.80	85.3	0.67	0.49	0.69	0.14815
5-38	40.15	43.0	1.85	0.97	0.18	0.07376
5-23	55.05	24.3	0.92	0.66	0.58	0.13341
5-18	64.65	38.9	1.42	1.00	0.22	0.03014
5-17	65.40	14.2	1.00	0.65	0.52	0.01578
5-15	67.40	95.0	0.53	1.00	0.56	0.15731
4-01	85.45	24.8	1.29	0.70	0.41	0.02208
3-11	0.65	87.9	0.62	0.50	0.69	0.14887
3-09	5.80	75.4	0.92	0.81	0.47	0.14627
3-04	13.10	56.6	1.53	0.96	0.28	0.14261
3-03	14.30	47.9	1.47	0.74	0.35	0.15551
6-21	29.50	76.5	1.20	0.47	0.55	0.18543
6-19	31.20	82.0	0.95	0.65	0.52	0.16075
6-15	35.75	43.8	1.60	0.88	0.32	0.09389
6-11	38.25	34.9	0.73	0.95	0.53	0.03010
6-09	40.25	27.7	1.57	0.86	0.28	0.02579
6-30	49.60	75.1	0.89	0.61	0.60	0.00802

Unit: codes used by Anstey and Perry (1973). SP: stratigraphic position of sampling intervals in meters below Eden-Dillsboro contact. PO: percentage of opportunistic species. DIV: Brillouin Diversity index. EVN: species evenness. DOM: species dominance. WDR: weighted developmental relaxation of species occurring in sampling interval.

7) a species numerically dominates an assemblage by 85-100%. Specifically, characteristics 1, 2, 3, and 7 apply to the species of Hallopora, Heterotrypa and Balticoporella in the Eden Shale.

MacArthur (1960) distinguished between opportunistic (eurytopic) and equilibrium (stenotopic) species. Opportunists are generally small, unspecialized, r-selected species capable of rapid population expansion as a result of elevated birth rates, enhanced larval survival, short generation length and generality with respect to resource utilization. They are common in unpredictable environments and areas with unoccupied or newly opened niches, and are usually not constrained by density-dependent factors such as oxygen level, food supply or living space. Equilibrium species, on the other hand, are larger, more stable, K-selected taxa, inhabit more uniform or predictable environments and maintain their numbers near the carrying capacity of the environment by producing the minimum number of offspring to ensure survival. Hallam (1972, Figures 4-8, p. 74) graphically illustrated the patterns of variation in the abundances of both opportunistic and equilibrium species: equilibrium species maintain small or moderate population sizes while undergoing minor oscillations in abundance through time; conversely, opportunists are characterized by abrupt oscillations resulting either in very low or extremely high numbers of individuals in response to ecological opportunities hindering or favoring proliferation. Therefore, consistent extreme domination of communities by the same taxa suggests that such species were opportunistic.

This premise was tested by calculating the percentage of the total biomass of each sampling interval accounted for by the three possibly opportunistic species (Tables 2 and 3). Two statistically different

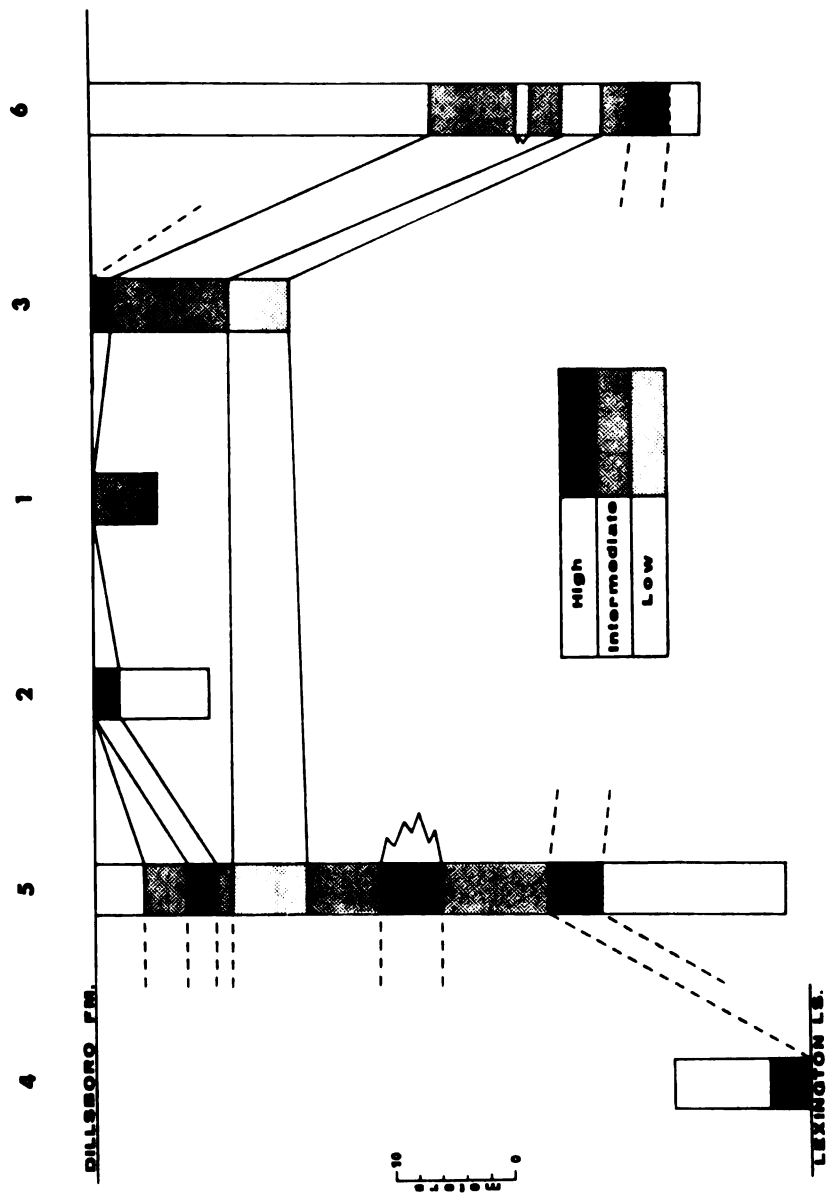


Figure 10: Levels of species dominance across 6 sections of the Eden Shale. Correlations are inferred. Levels are based on the statistical subdivision of ranked dominance values of the 21 sampling intervals listed in Table 3.

($t = 10.25$, $p = .01$) subsets of sampling intervals resulted: a group whose total biomasses were at least 75% made up of the three opportunists; and a subset wherein less than 57% of the biomass was attributable to the opportunists and which contained more equal abundances of up to 8 additional taxa (Table 2). This dichotomy bears out the presence of opportunistic species in the Eden Shale. The subgroup of sampling intervals characterized by equilibrium species was further subdivided to yield a total of three levels of opportunism whose patterns across sections are illustrated in figure 11A. It is proposed that the opportunists' advantages could have been related to a greater physiologic tolerance of physical changes in the environment which greatly enhanced larval survival. Simply elevating birth rates would have had little direct influence on population bursts as average fecundity (hundreds or thousands of reproductive individuals per colony) could easily have accounted for continually large populations if larval mortality had been slight (Levinton, 1970).

Taxonomic diversity. - In contrast to dominance and opportunism, Brillouin diversity shows a highly mosaic pattern in the Eden Shale (Figure 11B). Rollins and Donahue (1975) summarized community characteristics and recognized three successional levels; opportunistic (immature), mature (equilibrium), and relict-mature communities. Through time, maturity and stability tend to increase (Valentine, 1969; Levinton, 1970). Sharp changes in stress conditions, however, would have the effect of producing a quantum change in stability, stenotopic taxa being rapidly winnowed, and thus reducing the probability of their being preserved. The general absence of monotonic gradients of increasing community stability (diversity) in the Eden (Figure 11B) suggests that

Figure 11: Levels of species opportunism (A) and taxonomic diversity (B) across 6 sections of the Eden Shale. Correlations are inferred. Levels in each instance are based upon the statistical subdivision of ranked values of opportunism and diversity listed in Table 3.

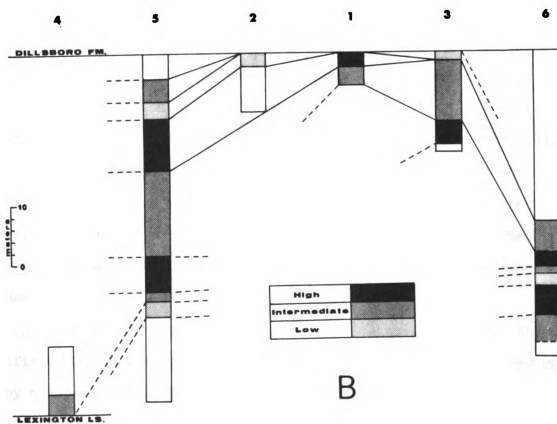
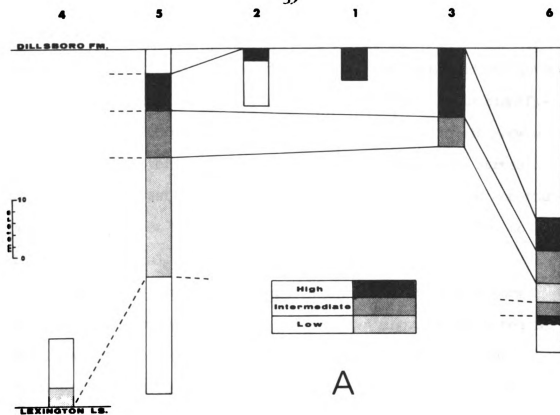


Figure 11.

fluctuations in limiting factors may have been quite sudden.

Therefore, monotonic trends in both species dominance and the percentage of opportunists are observable within the Eden, and the latter trend is especially distinct. Although Brillouin diversity is significantly (negatively) correlated with both quantities, its levels show a pronounced mosaic pattern probably owing to abrupt changes in stress conditions. In contrast, the monotonic trends in dominance and opportunism most likely persist because those measures are less sensitive to low level environmental fluctuations.

Developmental relaxation and homeostasis. - If such a dichotomy in their adaptive strategies existed, differences might be predicted in the developmental strategies of the opportunists and equilibrists. Opportunists, adapted to unstable environments, should display less canalized development than the equilibrists. To ascertain if statistically significant differences existed among the four pervasive species, a homogeneity of variance test was performed. Significant inhomogeneity ($F_{\max} = 3.47$, $p = .05$) was present, indicative of differing degrees of developmental relaxation in these taxa.

Examining each species' value of developmental relaxation (Table 1), one finds that Peronopora vera and Amplexopora septosa have the lower values, whereas Hallopora nodulosa and Heterotrypa ulrichi have higher values. This accords well with qualitative observations of the morphology of Peronopora, which is the least variable in overall form (bilaminate, frondescent).

These values are independent ($r = .13$, $p = .43$) of the average intra-specific variability of the 80 two-state characters (Table 1) examined by Anstey and Perry (1973, Tables 2-5, pp. 17-20). Relaxation of

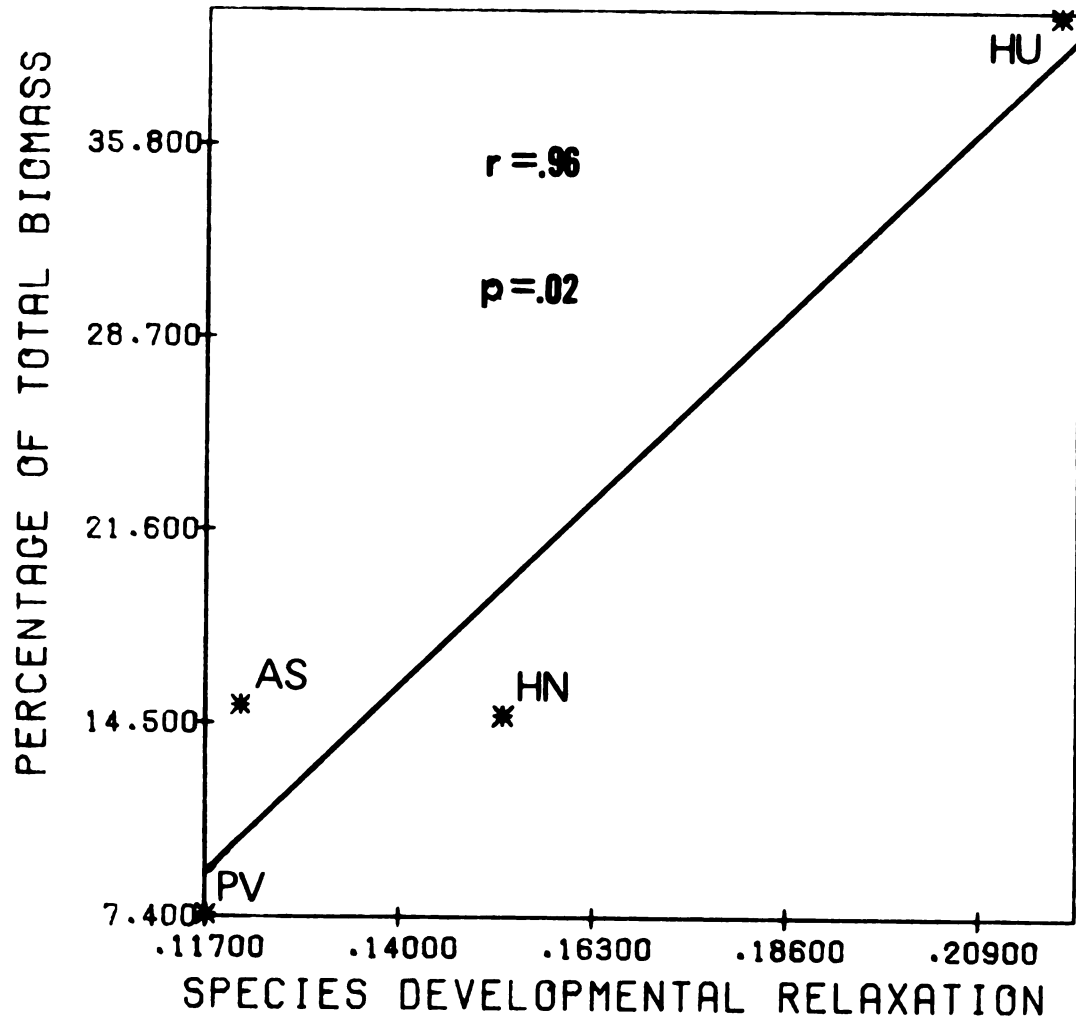


Figure 12: Correlation of developmental relaxation within species and the percentage of total Eden biomass. HN, Hallopora nodulosa; HU, Heterotrypa ulrichi; AS, Amplexopora septosa; PV, Peronopora vera.

morphoregulatory restraints, therefore, does not appear to be genetically linked to these phenetic traits, although these traits were successfully used by Anstey and Perry in the taxonomic discrimination of a diverse group of trepostomes.

Developmental homeostasis is, therefore, present to varying degrees in these taxa. It apparently functioned by canalizing development, buffering the bryozoans against deviations in astogeny which could have eventually resulted in reduced overall fitness. It is by definition, inversely proportional to the degree of developmental relaxation, being highest in Peronopora vera and lowest in Heterotrypa ulrichi.

Both Heterotrypa ulrichi and Hallopora nodulosa have been considered to be opportunistic, while Amplexopora septosa and Peronopora vera have the attributes of equilibrium taxa. Levels of developmental relaxation support these assertions (Table 1): Heterotrypa and Hallopora possess the highest levels with correspondingly lower homeostasis. In particular, Heterotrypa ulrichi, which has the highest range of variability and the lowest level of homeostasis of any of the four, must have been capable of withstanding extremes in environmental conditions through substantial developmental deregulation. Further evidence for opportunism is obtained through an evaluation of allometric exponents (or slopes), and Y-intercepts (Table 1). The opportunists are characterized by a lower field growth rate and have proportionately larger monticules (and more of them) than the equilibrium species. If hypotheses concerning the presence of reproductive individuals in the monticules are valid, then opportunistic colonies would have had a higher ratio of reproducers to feeders. Equilibrists, on the other hand, would have a much lower ratio of reproducers to feeders, in accord with their being attuned to effective resource

Table 4. Genetic variability in living benthic marine invertebrates tested at 15 or more genetic loci *.

Species	Number	Average Percent of Loci Heterozygosity	Source
1. <u>Asterias vulgaris</u> Verrill	26	1.1	Schopf & Murphy, 1973
2. <u>Cancer magister</u> Dana	29	1.4	Hedgecock & Nelson, unpublished
3. <u>Asterias forbesi</u> (Desor)	27	2.1	Schopf & Murphy, 1973
4. <u>Liothyrella notorcadensis</u> Jackson	34	3.9	Ayala et al., 1975
5. <u>Homarus americanus</u> Milne-Edwards	37	3.9	Hedgecock & Nelson, unpublished
6. <u>Crangon negricata</u> (Stimpson)	30	4.9	Ibid.
7. <u>Limulus polyphemus</u> (Linne)	25	5.7	Selander et. al., 1970
8. <u>Upogebia pugettensis</u> (Dana)	34	6.5	Hedgecock & Nelson, unpublished
9. <u>Callinassa californiensis</u> Dana	38	8.2	Ibid.
10. <u>Phoronopsis viridis</u> Hilton	39	9.4	Ayala et. al., 1974
11. <u>Crassostrea virginica</u> (Gmelin)	32	12.0	W. W. Anderson, unpublished
12. Asteroidea, four deep-sea species	24	16.4	Ayala et. al., 1975
13. <u>Frieleia halli</u> Dall	18	16.9	Valentine & Ayala, 1974
14. <u>Ophiomusium lymani</u> Thompson	15	17.0	Ayala & Valentine, 1974
15. <u>Tridacna maxima</u> Roding	37	21.6	Ayala et. al., 1973; Campbell et. al., 1975

* After Valentine (1976, p. 86)

utilization rather than reproduction. If such inferences are correct, the estimated productivity of the opportunists should be higher than that of the equilibrists. Figure 12 indicates that this appears to be so; the opportunists account for a proportionately higher percentage of the Eden's skeletal biomass in spite of being the two smallest taxa in terms of individual colony size, an additional attribute of opportunistic species (Rollins and Donahue, 1975; Schoener, 1969).

Developmental relaxation and diversity. - Ayala et al., (1975a) noted that the recent brachiopod Liothyrella notorcadensis is rather variable morphologically while exhibiting low genetic polymorphism. In contrast, the deep-sea brachiopod Frieleia halli is quite variable genetically but possesses little morphologic diversity. A paradox thus becomes apparent; phenotypic and genotypic variability may be inversely related. In living populations, genetic variability may be directly assessed through an analysis of enzyme polymorphism utilizing the technique of starch-gel electrophoresis (see Ayala et al., 1972 for methodology). Table 4 summarizes the available data in genetic variation in extant benthic marine invertebrates, expressed as the percentage of loci at which an average individual is heterozygous where 15 or more loci were examined. As correlative data on resource stability is as yet unavailable, diversity measures have been employed as first-order approximations (Valentine, 1971, 1972, 1976). A highly significant positive correlation (Figure 13) between average heterozygosity and the average diversity of associations in which the species ranges today results (see Valentine, 1976, pp. 89-90), indicating a trend of increasing genetic variability with increasing stability. Such a relationship (Table 5) is contrary to the expectations of the Bretsky-Lorenz model, but

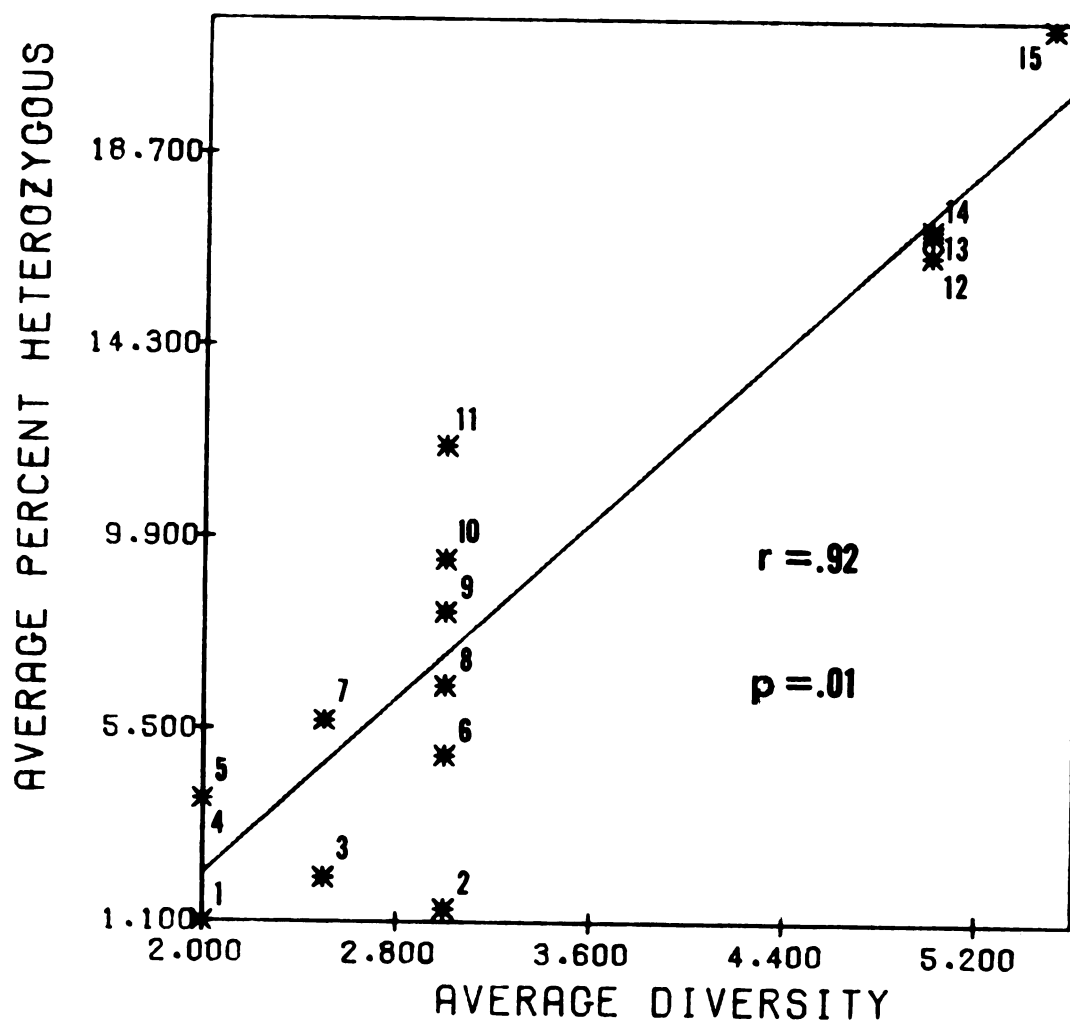


Figure 13: Correlation of the average percent heterozygous and average diversity of inhabited associations for extant benthic marine invertebrates tested at 15 or more genetic loci. Numbers refer to the species listed in Table 5.

consistent with the predictions of Ayala et al. (1975a, b, c) and Valentine and Ayala (1974).

Additional supportive data is available from pelagic organisms; Somero and Soulé (1974) found diversity and heterozygosity to be positively associated in 13 species of marine teleosts, while Ayala et al. (1975c) and Valentine and Ayala (in press) noted that, in three species of krill (Euphausia), average heterozygosity was negatively correlated with trophic resource seasonality. Doyle (1971, 1972) found considerable variability in three species of ophiuroids from the deep-sea considering only 4 to 6 loci, and Schopf and Gooch (1971, 1972) and Gooch and Schopf (1973), also examining deep-sea populations, found genetic polymorphism to be significantly high at 4 to 15 loci in small populations of eight species.

As colonial organisms, bryozoans offer the possibility of partitioning their morphologic variability into within-colony (ecologic, polymorphic, or developmental) and between-colony (genetic) components of variance (Schopf 1976). Schopf and Dutton (1976), for the recent cheilostome Schizoporella errata, and Farmer and Rowell (1973), for the Paleozoic crustoporate Fistulipora decora, found within-colony variance to be greater than between-colony variance. Schopf (1976) attributed this to gradients in environmental stability; forms in variable environments exhibited variation assignable to ecophenotypic rather than genetic causes, while the reverse appeared to be true for stable habitats.

For the bryozoans of the Eden Shale, the relationship between developmental relaxation and taxonomic diversity (stability) may be assessed in two ways: 1) through an examination of opportunistic and equilibrium species abundances, and 2) through a weighted average value

Table 5. Aspects of the major stability-diversity-variation models

Model	Habitat	Genetic Variability	Polymorphism	Selection	Homeostasis	Niche Size	Speciation Tendency
Bretsky - Lorenz *	Stable	Low	Low	Homo-	Low	Narrow	High
	Unstable	High	High	Hetero-	High	Broad	Low
Ayala - Valentine **	Stable	High	High	Hetero-	High	Narrow	Low
	Unstable	Low	Low	Homo-	Low	Broad	High

* Bretsky and Lorenz (1969, 1970)

** Ayala et al. (1975a, b, c), Valentine (1976)

of developmental relaxation for each sampling interval. It was shown above that the opportunistic species (Heterotrypa ulrichi and Hallopora nodulosa) exhibited higher levels of developmental relaxation than the equilibrium species (Amplexopora septosa and Peronopora vera). Therefore, high percentages of opportunists should represent environments favoring greater developmental relaxation (variability), whereas a preponderance of equilibrium species would be indicative of developmental restraint (canalization).

A weighted average of developmental relaxation, based upon relative biomass contributions of the above four taxa follows similar logic. However, inasmuch as the biomass of an interval may have substantial contributions from up to nine other taxa having the characteristics of equilibrium species, but whose levels of developmental relaxation were not measurable due to small sample sizes, corrections were made to counteract a consistent overestimation of the overall developmental relaxation. To accomplish this, the developmental relaxation value of each of the four measurable taxa was multiplied by their biomasses, summed, and divided by the total biomass of the sampling interval (Table 3). This has the effect of lowering the weighted value of intervals containing substantial numbers of equilibrists while leaving the values for highly dominated intervals unchanged. Four intervals were deleted: 5-18, 6-30, and 5-17, 6-11, dominated by Balticoporella and undifferentiated ceramoporoids respectively, which appear to have been opportunists but whose developmental relaxation values have not been calculated.

Figures 14 and 15 illustrate significant correlations between the percentages of opportunistic and equilibrium species in each sampling interval and species diversity and evenness of distribution, respectively,

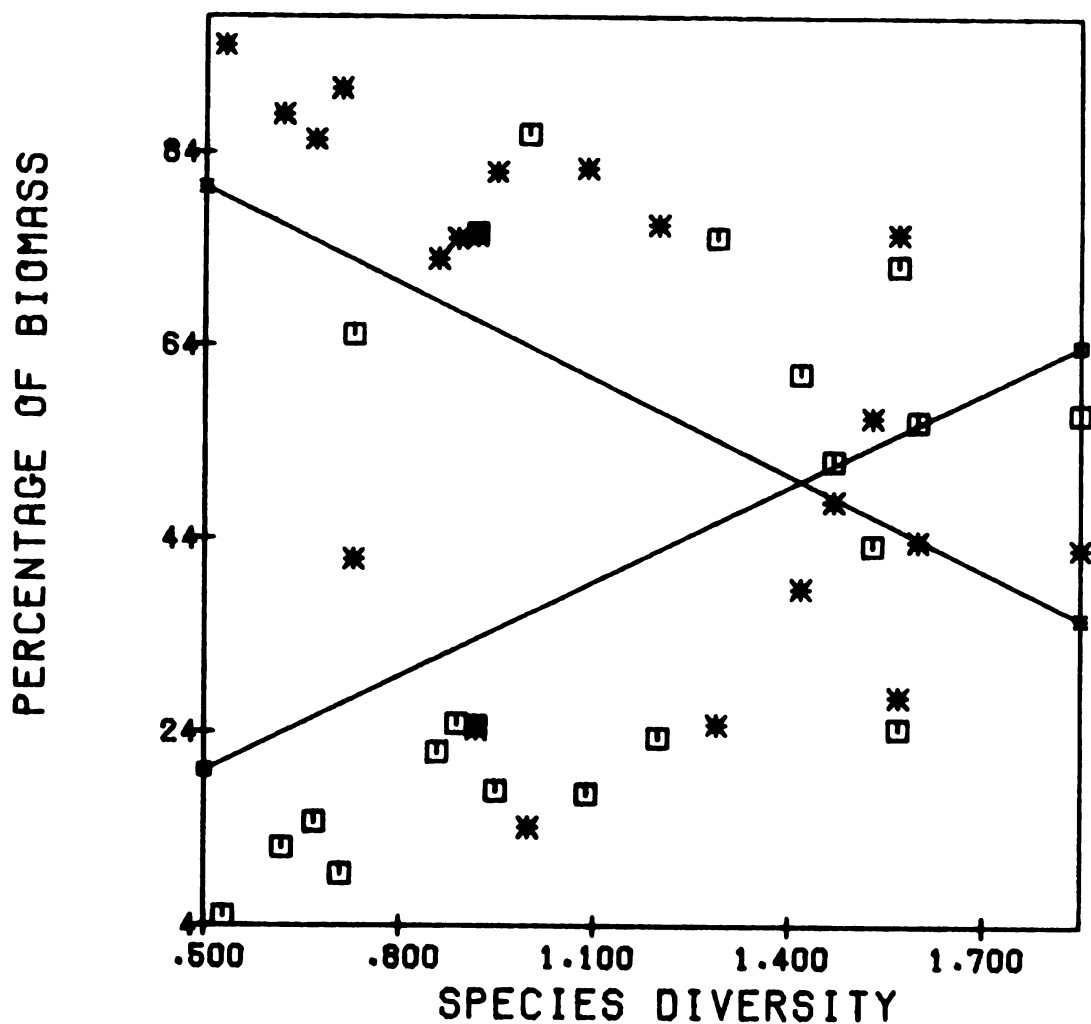


Figure 14: Correlations of the percentages of opportunistic and equilibrium species with taxonomic diversity. Asterisks denote opportunists ($r = -.50$, $p = .01$); squares, equilibrists ($r = .48$, $p = .01$).

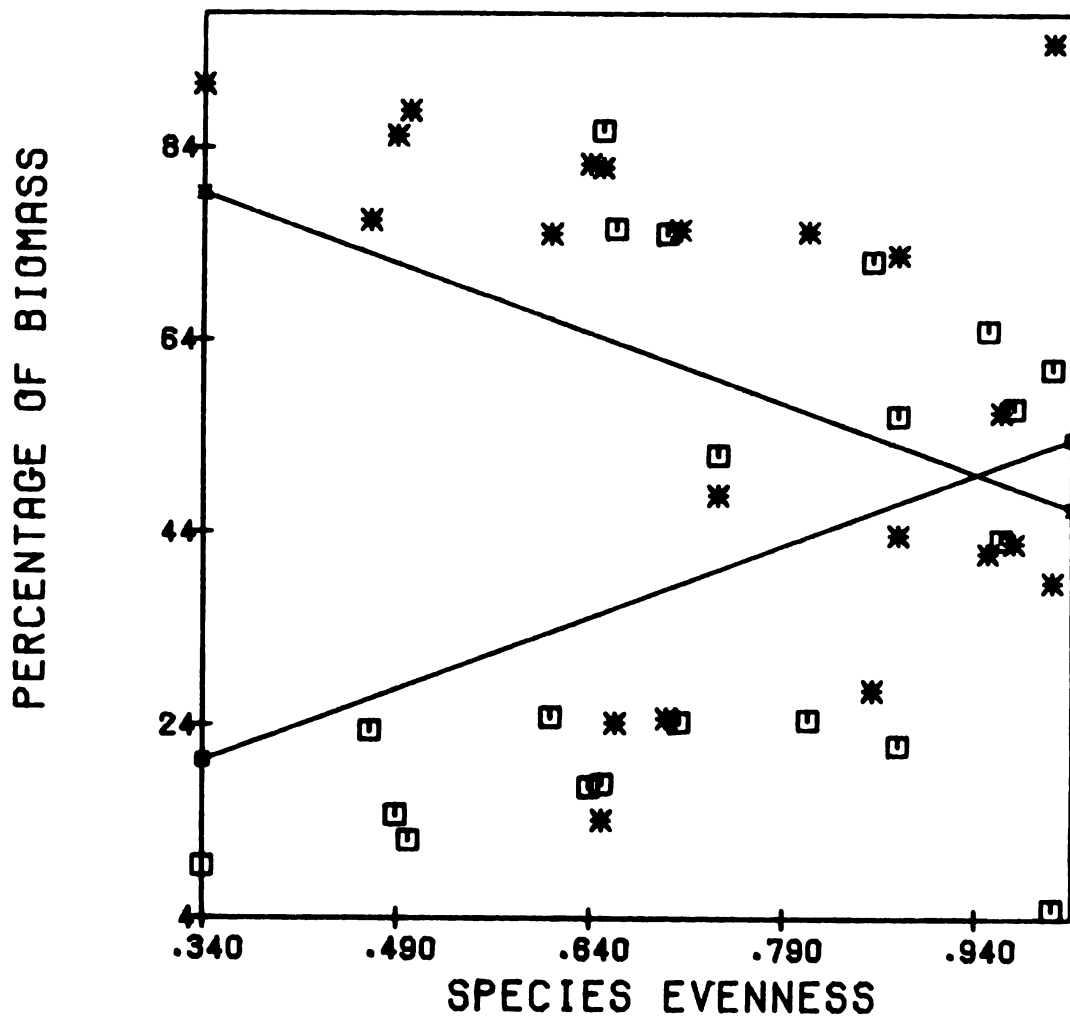


Figure 15: Correlations of the percentages of opportunistic and equilibrium species with species evenness. Asterisks, denote opportunists ($r = -.37$, $p = .05$); squares, equilibrists ($r = .37$, $p = .05$).

while figures 16 and 17 indicate similar relationships between taxonomic diversity and evenness, and weighted developmental relaxation throughout the Eden Shale. Through their wider ranges of developmental responses, opportunists characterize the lower diversity (more unstable) habitats where they dominate biomass. Conversely, higher diversity (more stable) regimes favor a more even distribution of taxa and greater niche subdivision by equilibrium species.

Developmental relaxation is, therefore, negatively associated with diversity and, presumably, stability. The genetic-morphologic paradox remains to be explained. For the two extant species so compared to date (the brachiopods Liothyrella notorcadensis and Frielella halli), genotypic and phenotypic variability were inversely related. In the Eden Shale bryozoans, the values of developmental relaxation measure departures between-colonies from "normal" development. The variability within-colonies provides a test of the genetics of deregulation. The intra-colonial variability is not of a genetic nature because each colony is a clone, and every zooid is genetically identical to all the others; it must be attributable to developmental deregulation at the subcolony level.

Within-colony variability was estimated for each species by calculating an average coefficient of variability based on 10 to 15 colonies, and 20 measures of monticular spacing from each zoarium. Measured colonies were the same as those utilized for the calculation of between-colony developmental relaxation; the within-colony variances employed are normalized for astogeny because all fields on each colony were measured at the same astogenetic stage.

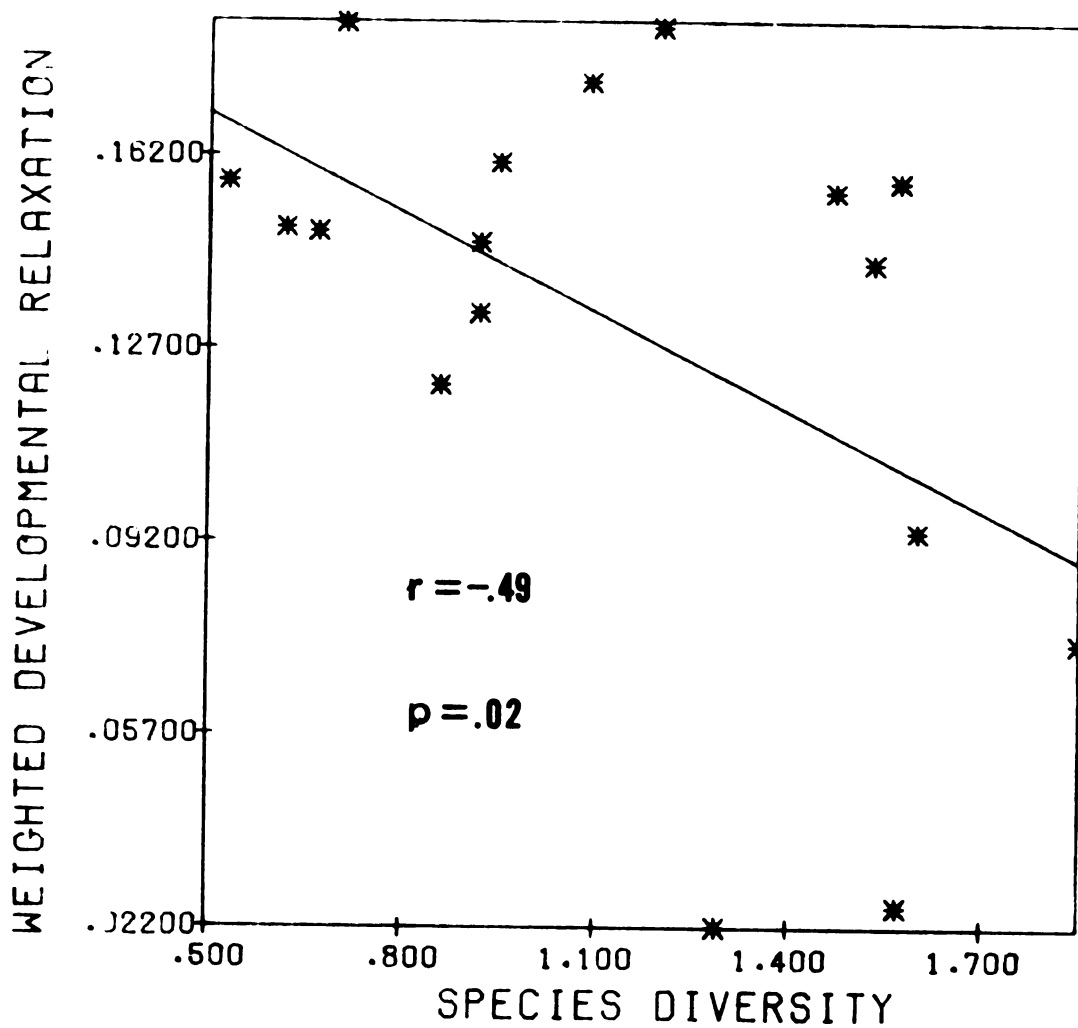


Figure 16: Correlation of weighted developmental relaxation and taxonomic diversity in 17 of the 21 Eden sampling intervals. Intervals 5-17, 5-18, 6-11, 6-30, possibly dominated by additional opportunists, omitted as their developmental relaxation values could not be calculated.

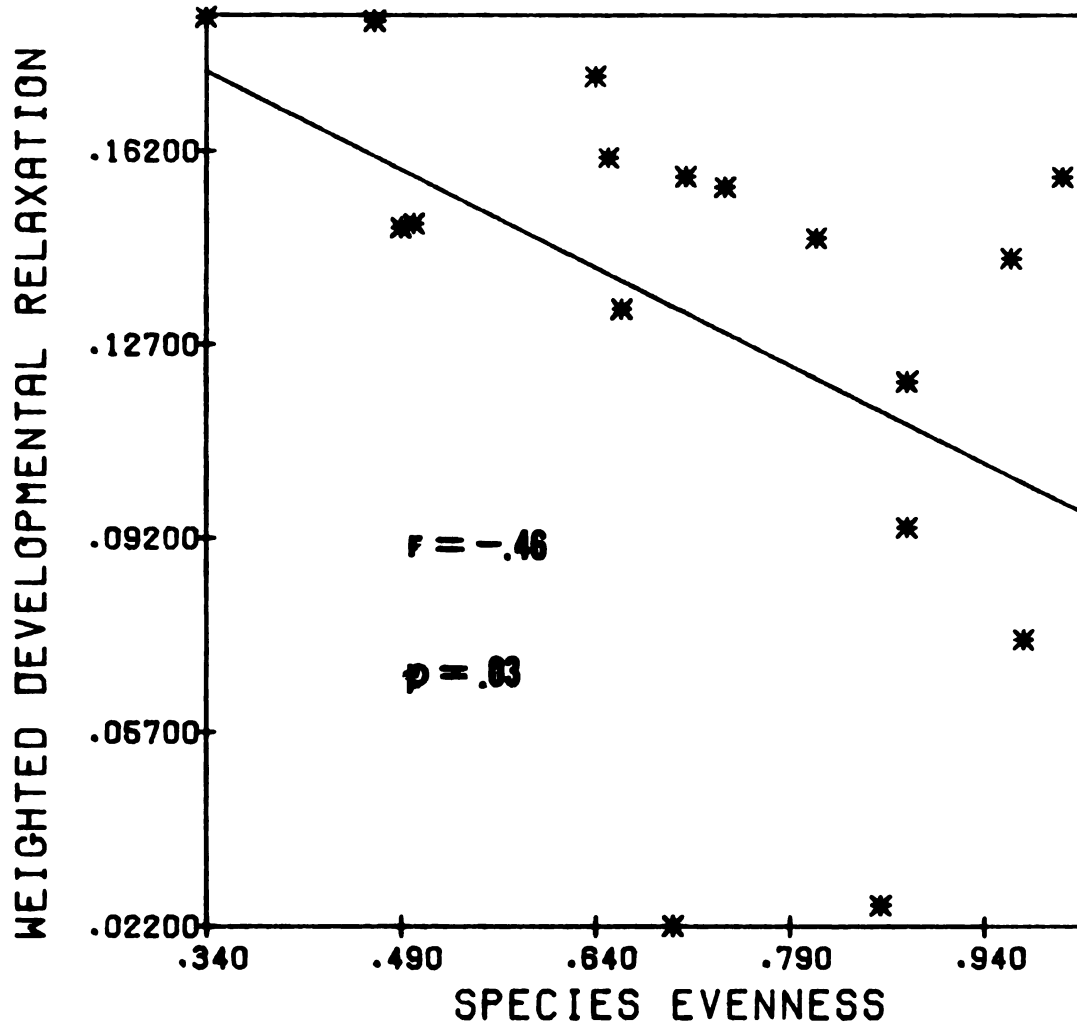


Figure 17: Correlation of weighted developmental relaxation and species evenness in 17 of the 21 Eden sampling intervals. Omitted intervals are the same as those in Figure 16.

The opportunistic species, Heterotrypa ulrichi (CV = 19.25) and Hallopora nodulosa (CV = 19.44), have higher within-colony variability than the equilibrium species, Amplexopora septosa (CV = 16.61) and Peronopora vera (CV = 16.01). This result indicates that developmental deregulation is correlated with the non-genetic variability within colonies; therefore, the higher morphological variability observed in unstable environments is concluded to be non-genetic in nature and not the result of higher genetic polymorphism. Conversely, stable habitats favored the development of communities of equilibrium species having lower levels of morphologic deregulation. Whether species in stable environments have higher levels of genetic polymorphism cannot be conclusively tested with the available data. However, several genetic mechanisms, such as the maintenance of developmental homeostasis through heterozygosity, are available to explain the apparently negative correlation of genetic and morphologic variability.

CONCLUSIONS

- 1) Evidence for the existence of developmental regulation in Ordovician bryozoan colonies includes: a) radial morphologic gradients in zooecial morphology polarized on each monticule, b) the presence of a monarchic zooid or pseudobancestrula within each monticule that provides a specific point origin of each morphogenetic field, c) a position effect for polymorphic differentiation with respect to the monarchic zooid, d) nonlinear (allometric) growth fields, suggesting diffusion as the likely cause of field maintenance, e) a distance effect for the induction of new fields and suppression of old ones, illustrating the polarizing and inhibitory effects of

the field agent, and f) the maintenance of morphogenetic fields following an episode of mass degeneration not at the end of a normal growth cycle.

- 2) For each of the four stratigraphically pervasive Eden species, colony growth rates and the proportion of monticular to extra-monticular zooids differs, resulting in different overall growth forms. Additionally, the degree of developmental relaxation is homogeneous within species but varies significantly across taxa.
- 3) The two species with the highest levels of developmental relaxation (Heterotrypa ulrichi and Hallopora nodulosa) fit the concept of r-selected, opportunistic species, and are most abundant in the communities of lower diversity and evenness. The other two species (Amplexopora septosa and Peronopora vera) have much lower levels of developmental relaxation, fit the concept of K-selected equilibrium species, and are most abundant in the communities of higher diversity and species evenness.
- 4) A major cause of the negative correlation between morphologic variability and environmental stability is apparently related to the selection of species having different levels of morphological regulation in different environments.
- 5) Within-colony variability is higher in the opportunistic rather than in the equilibrium species, indicating that the higher morphologic variability observed in unstable environments is non-genetic in nature and not the result of higher genetic polymorphism. Species in stable environments (equilibrium species) have lower levels of morphologic deregulation whose relationship to genetic diversity could not be conclusively tested with the available data.

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