

Bryozoan Colonial Growth-forms as Paleoenvironmental Indicators: Evaluation of Methodology

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Bryozoans have played a significant ecological role in many shallow marine benthic communities since the Ordovician and are important contributors to carbonate sediment production in many modern cool-water marine environments. Correlation between bryozoan colonial growth forms and environments in which the organisms lived allows for the application of growth forms as paleoenvironmental indicators. This can be done as either (1) a characterization of regional environmental or distributional data within a comprehensive study; or (2) as a predictive tool applied in an unknown setting using limited data. A number of workers have demonstrated this potential in biological, paleontological, and sedimentological studies. Growth-form distributions established independently from, and later compared to, environmental factors provide for the greatest predictive utility. Problems encountered in methodology need to be addressed before bryozoan colonial growth forms can achieve their full potential as paleoenvironmental indicators. Methodological problems include those associated with specimen abundance versus species richness, numeric versus volumetric frequency, relative versus absolute abundance, and changes within growth forms among localities versus changes among growth forms within localities (facies). A procedure is proposed that combines species richness and specimen abundance, as well as information about distributions within growth forms and within localities, into a single, comparable data set. An example is provided using bryozoans from the cool-water Lacepede Shelf of southern Australia.

INTRODUCTION

Correlation between a bryozoan's colonial growth form and the environmental conditions in which the organism lives (substrate, water energy, sedimentation rate, etc.) provides the potential for growth forms to be used as paleoenvironmental indicators (Stach, 1936). These concepts have been employed in environmental studies by biologists in modern settings, as well as by paleoecologists and sedimentologists using fossil material from throughout most of the Phanerozoic (Appendix 1).

Bryozoan colonial growth-form analysis is of interest to marine biologists, paleontologists, and sedimentologists because Bryozoa is a major, mostly marine phylum that has played a significant ecological role in many shelf and upper slope communities since the Ordovician. Bryozoans have a rich fossil record throughout most of the Phanerozoic, contributing skeletal carbonate to the sedimentary record, not uncommonly in rock-forming quantities. Today, bryozoans are a dominant faunal component of benthic communities (up to 80%) in regions of modern cool- and cold-water (<20°C) carbonate deposition (Wass et al., 1970; Nelson et al., 1988; James et al., 1992).

Numerous studies of bryozoan growth forms (Appendix 1) have employed a wide variety of qualitative and quantitative methods and ecological concepts in order to compare growth-form distributions and to make environmental interpretations. The increasing number of potentially incompatible quantified approaches calls for an evaluation of the methodology as a whole. Although methodological problems do exist, the utility and value of certain bryozoan colonial growth forms as paleoenvironmental indicators in specific settings is real and worthy of pursuit. Qualitative approaches to growth-form analysis are potentially valid as well, but are not considered here.

The complexity of the discussion presented in this paper is a direct consequence of the complexity of the topic at hand. This complexity should not necessarily make bryozoan growth-form analysis inaccessible to the non-specialist. On the contrary, the intent of this paper is to provide the information needed for individuals to make informed decisions in order to structure their own studies. A simplified methodology may be adequate for one's specific needs, but workers should be cognizant of the characteristics of the parameters that they have selected.

The primary goal of this paper is to evaluate quantitative methods of data collection, compilation, and analysis of bryozoan growth forms using simplified examples. Based on these observations, solutions to some methodological problems are proposed, and a *standardized methodology* is suggested. This standardized method is then applied to empirical bryozoan data from the Lacepede Shelf of southern Australia. It is not the goal of this paper, however, to provide a comprehensive evaluation of growth-form classification schemes and associated ecological assumptions, although these factors must be considered in the general framework of the topic.

Growth-Form Classification

Bryozoan colonial growth-form classification schemes have varied through time both in the composition of their

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categories (forms included and their relationship to each other) and on the concepts upon which they are based. Examples include characterization of forms associated with distinctive genera (e.g., *Celleporiform* Canu and Bassler, 1920; Harmer, 1926; and Stach, 1936); classifications based on geometry and construction (e.g., *flat robust branching* Nelson et al., 1988; Bone and James, 1993; Smith, 1995); and classifications based on ecological principles (e.g., *runners* McKinney, 1986; McKinney and Jackson, 1989).

There is a need for a revised, comprehensive growth-form classification that includes ecological considerations for all valid forms ever described (most schemes were developed for local faunas). In bryozoan growth-form analysis, a paradox exists between the need for a comprehensive growth-form classification that includes information required to make meaningful ecological interpretations (life-mode classification), versus the desire to have the methods accessible for those with minimal knowledge of the organism's biology. A revised classification should, however, incorporate relationships between bryozoans and their substrates, which is an important ecological character that has been under-represented in previous schemes.

A modified bryozoan growth-form classification, including only those growth forms observed in the Lacepede Shelf South Australia (Appendix 2) is presented here (Fig. 1). This classification is based on three hierarchical categories (1) attachment mode (cemented, rooted, unattached); (2) colony construction; and (3) colonial geometry. This classification is intended to apply equally to modern cheilostomes and cyclostomes, but is not meant to be a new, comprehensive classification as discussed above (considerations for which are beyond this text).

Regardless of their relative value as paleoenvironmental indicators, standardized terms and concepts for bryozoan colonial growth forms provide a very practical method for specialists and non-specialists alike to categorize and compare their bryozoan specimens in a useful way. Even if growth-form names are used only as descriptive terms for groups of bryozoans in a study, the additional information, beyond simply "Bryozoa", is of value to all concerned (e.g., Shubber et al., 1996).

MODELS FOR GROWTH-FORM STUDIES

In early work (Stach, 1935, 1936, 1937; Brown, 1952), growth-form analyses were qualitative, based on general empirical and intuitive ecological observations and interpretations. Although the very nature of qualitative studies make them difficult to test rigorously, this approach evidently has merit and deserves more detailed investigation in its own right. Qualitative methods are not, however, discussed here.

Cheetham (1963) and Lagaaij and Gautier (1965) established quantitative approaches to growth-form analysis. The basic structure of these studies is to quantify the relative importance of each growth-form type at each sample locality (geographic sample site in modern marine setting, stratigraphic level-unit in geologic setting). Each sample locality has a specific litho-biofacies attributed to it prior to the analysis. Comparisons of importance among growth forms at various litho-biofacies (or other parameters such

Attachment	Construction - Orientation	Zoarial Geometry	abbrev.
Cemented	Unilaminar	solid substrate	CUss
		flexible substrate	CUfs
		hollow cylinder	CUhc
	Multilaminar	encrusting massive	CMem
	Erect	cylindrical branches	CEcb
		unilaminar branches	CEub
		bilaminar branches	CEbb
fenestrate sheet		CEfs	
Rooted	Articulated	cylindrical branches	RAcb
		unilaminar branches	RAub
		articulated zooids	RAzo
	Rigid	encrusting sheet	RRes
		branches	RRbr
		bilaminar sheet	RRbs
		fenestrate sheet	RRfs
		cone-disc	RRcd
Free Living	Motile	disc	FLmd

FIGURE 1.—Hierarchical growth-form classification based on observed Lacepede Shelf bryozoan taxa (after Nelson et al., 1988; Bone and James, 1993; and Smith, 1995).

as substrate type or sedimentation rate, etc.) are made by plotting results in pie-diagrams, histograms, or cumulative frequency plots (e.g., percentage of each growth form in facies X). Variations on this theme, "importance" of growth form versus "facies", have been employed in growth-form analyses in modern and geologic settings in most of the studies listed in Appendix 1. It should be noted, however, that greatest predictive value from comparisons between growth forms and ecological controlling parameters is achieved if the distribution of the bryozoans has been established independently, and not based on the ecological parameter itself (see "Covariance of Ecological Parameters" section).

Bryozoan colonial growth-form analysis can be used in two roles (1) to summarize and characterize regional environmental data within a primary, detailed study; and (2) as a predictive tool, using information from primary studies in applications to unknown settings with limited data.

Summary and Characterization

Growth-form analyses have proven their ability to summarize and characterize regional ecological distributions (Appendix 1). Comparison between the results from empirical growth-form data in this study, and species-level distributions in Hageman et al. (1995, 1996), clearly shows a strong ecological correlation between growth form and species-level distributions.

TABLE 1—Broader environmental factors characterized by and correlated with ecological controlling parameters (e.g., increasing water depth is typified by changes in temperature, light, and water chemistry). Controlling parameters can vary independently from broader factors and independently from other controlling parameters. Bryozoan growth-form distributions are of greatest predictive value when compared directly to ecological controlling parameters.

Broader environmental factors	Ecological controlling parameters
water depth	nutrients
latitudinal gradient	temperature
physiography	light
ecosystem	H ₂ O chemistry
depositional system	turbidity
litho-biofacies	substrate type
regional currents	wave/current energy
	sedimentation rate
	predation
	competition

Once the distribution of bryozoan growth forms has been characterized for a region (morphologic changes correlated with a range of local ecological controlling parameters, Table 1), the known distribution has a high predictive value when applied to additional samples collected from settings within the same region, but from unknown environmental conditions. For example, a known growth-form distribution can be used to allocate unknown specimens correctly to their environmental setting using multivariate methods. The predictive value for ecologically controlling parameters is greatest when unknown samples are collected from a setting with a range of environmental and ecological parameters closely related to those that were used in the original characterization (prediction *within* the model).

Predictive Tool

Pragmatically, most non-specialists are not interested in compiling their own, comprehensive bryozoan census for every setting they study. They generally want to evaluate a single sample (rock specimen, facies, stratigraphic unit) and make environmental predictions based on summaries and characterizations (predictive models) from studies listed in Appendix 1 (e.g., see Shubber et al., 1996).

Predictive ability *outside* of the model (unknown samples collected from regional settings outside those used to establish known growth-form/environment distributions) is still viable, but with much less resolution. Comprehensive growth-form studies produce a wealth of data; indeed, it is difficult to know how to interpret and apply them all simultaneously (see empirical example herein). If one were to identify one locality, even from within one of these comprehensive studies, and ask a third party to assign it to a physiographic province based only on the typical pie diagrams or histograms, it would be a difficult prospect. Nevertheless, all of the required data are present for sensitive multivariate methods to make the correct assignment. For predictive utility it is more practical to establish general guidelines about gross trends easily observed in the data.

ENVIRONMENTAL INFERENCES FROM GROWTH FORMS

Bryozoan growth forms have been correlated with broader environmental factors such as water depth. Control over the distribution of growth forms can more precisely be attributed to individual ecological controlling parameters. Ecological controlling parameters are the local physio-chemical environmental states and biological interactions experienced by the bryozoan colony (Table 1). Although broader environmental factors, such as water depth, are generally correlated with ecological controlling parameters (e.g., light intensity), controlling parameters can vary independently from broader factors and independently from other controlling parameters. For example, a dark, tannin-rich surface-water cap derived from terrestrial run-off into protected (calm water) Tasmanian estuaries, induces "deep water" conditions and accompanying "deep water" bryozoan growth forms in less than ten meters water depth (Gowlett-Holmes, pers. comm.).

Assumptions have been made in previous bryozoan growth-form studies about (1) the significance of ecological controlling parameters (Table 1) that allow for dominance of a growth form in an environmental setting versus ecological parameters which restrict a growth-form's distribution (i.e., is abundance/dominance more important than absence, relative to simple presence?); (2) the role of morphologically plastic species (intraspecific variation) versus morphologically conservative species (interspecific variation); and (3) relationships among ecological parameters controlling morphologic variation. It is beyond the scope of this paper to evaluate fully the ecological significance of each of these assumptions, but basic concepts are discussed below. More information about ecological controls over growth-form distributions is undoubtedly needed. However, a lack of understanding about specific mechanisms involved does not nullify the premise of growth-form and environmental associations (cf., evolutionary theory and biostratigraphy).

Dominance versus Restriction

Optimal environmental settings are intuitively obvious for many bryozoan growth forms (e.g., delicate, erect forms in calm water; robust encrusting forms in high-energy settings). For any given environmental setting, a specific growth form may be considered as: (1) dominant; (2) present but not dominant; or (3) absent. Beginning with Stach (1936), most studies have emphasized correlation between a growth-form's *dominance* and its environmental setting. However, relatively little is known about the ecological controls that restrict growth forms in their non-optimal environments. For example, if absence (or non-dominant presence) is ultimately the result of differential competitive success or resistance to predation (rather than strict environmental tolerance), then parameters controlling the distribution of the overall community must be considered. Parameters controlling the *restriction* of growth-form distributions are likely to be as complex and variable among groups as those that allow for their dominance.

Growth-form dominance undoubtedly reflects relative success in a given environment and is, therefore, of value in paleoenvironmental interpretations. Ultimately, how-

ever, information about growth-form restrictions may allow for even greater ecological inferences.

Intraspecific Versus Interspecific Variation

Bryozoan species can be separated into two groups based on the degree to which individual colonies can modify their morphology (growth form) in order to adapt to local environmental conditions (Stach, 1935, 1937). Some bryozoan species are morphologically plastic, with growth-form expression varying from encrusting unilaminar sheets, to erect bilaminar sheets, to broad bilaminar branches, to delicate cylindrical branches (e.g., *Caleschara denticulata*). Thus, with morphologically plastic species, growth-form variation among environments is *intraspecific*. Other bryozoan species are morphologically conservative, with each species having a certain, genetically controlled, growth form. Thus, with morphologically conservative species, growth-form variation among environments is *interspecific*.

Previous quantitative growth-form studies have emphasized morphologically conservative forms (e.g., Gautier, 1962; Lagaaij and Gautier, 1965; Cook, 1968; Cheetham, 1971; Moissette, 1993), with the suggestion that plastic species are relatively rare. However, McKinney and Jackson (1989) report that 24% of 1430 Atlantic species surveyed exhibit morphological plasticity. It is likely that plastic forms are of value in bryozoan growth-form studies as well. It may be of value to distinguish between morphologically plastic and conservative forms and to evaluate their (different?) distributions. The changing proportion of morphologically plastic versus conservative forms (intra-specific versus interspecific variation) among regional settings may also be of ecological significance.

Covariance of Ecological Controlling Parameters

Primary factors that contribute to the distribution of bryozoan colonial growth forms are (1) nature of the substrate; (2) water current and wave activity; (3) sedimentation rate; (4) water depth, which is likely a proxy for some combination of temperature, light, chemistry, and nutrients; and (5) predation and competition for substrate (Cheetham, 1966; Schopf, 1969; Hancock, 1980; Nelson et al., 1988; Bone and James, 1993; Hageman et al., 1996). All of these factors are themselves interrelated; that is, they covary. For example, Stach (1936) emphasized bathymetric controls in his original interpretations, providing specific depth ranges for given growth forms. He noted, however, variation in his bathymetric ranges based on the influence of currents.

Single environmental factors should not be evaluated outside the context of others when developing models in which growth forms are to be used as predictive tools. Growth-form distributions should not be established using any other *a priori* distribution (e.g., not simply derived from lithofacies distribution). As a rule, growth-form distributions should be established *independently* from causal factors (e.g., Hageman et al., 1995) and then later compared to all of the factors described above.

Other Considerations

This paper deals primarily with methods and concepts involved in developing actualistic models for bryozoan growth-form distributions based on living material. Other factors, not addressed here, that need to be considered before bryozoan growth forms can be applied uniformly in geologic settings include (1) differential taphonomic histories among growth forms that can alter original patterns (Smith and Nelson, 1994); (2) changes in growth-form dominance and community structures through geologic time (McKinney and Jackson, 1989; Lidgard and Jackson, 1989; Lidgard et al., 1993); (3) methodological problems associated with applications in a stratigraphic context; and (4) objective evaluation of the predictive utility of existing actualistic models. Problems associated with these factors are not insurmountable, but need to be given careful consideration before bryozoan colonial growth forms can be used consistently to make paleoenvironmental interpretations.

METHODOLOGY

Methodological differences among workers present difficulties in interpretation of bryozoan colonial growth-form studies. There are many logical and theoretically valid methods in which a single data set can be compiled and interpreted. Variable methods arise from the four fundamental options in data evaluation: (1) changes within growth forms versus changes within localities; (2) species richness (number of species present) within growth form versus simple growth-form abundance; (3) absolute, indexed, and relative abundance; and (4) volumetric versus numeric abundance. Indeed, workers have employed a variety of these methods, making their studies and conclusions difficult to compare (e.g., Stach, 1936; Brown, 1952; Gautier, 1962; Cheetham, 1963, 1971; Lagaaij and Gautier, 1965; Cook, 1968; Labracherie and Prud'Homme, 1966; Askren, 1968; Cuffey, 1967; Ceretti and Poluzzi, 1973; Braga, 1979; Moissette, 1993).

For each of these approaches, there are *practical* and *theoretical* considerations. For example, sedimentologists with limited taxonomic knowledge are restricted to analyses based on abundance of general growth forms alone. Alternatively, bryozoan taxonomists have the option of introducing additional complexity based on the number of species within each growth form. The discussion below highlights some of the fundamental differences between methods of compiling growth-form data, and, where possible, provides suggestions for the most pragmatic method.

Standardized Sampling

For any study to have significance, comparisons between locality data must be based on standardized samples. Ideally samples should be standardized in bulk (i.e., equal volumes or weights of bulk samples, say 250 g. per locality). Statistical comparisons of data derived from bulk samples of unequal/unknown volume/weight are of little value.

To a degree, comparative locality data can also be standardized by standardizing sampling effort. For example, if

a fixed time interval is given to picking and sorting each size fraction from all samples (say, one hour per fraction), then relative abundance can be indexed in a standardized fashion (i.e., all taxa have equal likelihood of being recognized as absent, rare, common, abundant). As discussed below, this level of resolution has the ability to efficiently recognize robust trends.

Absolute, Indexed, and Relative Abundance

The most direct and accurate way to represent growth-form abundance is to literally count every specimen present in each growth-form type for each locality (or make volumetric or weight measurements). This can be done by a comprehensive survey of every specimen in a fixed volume of sediment. Problems of dealing with fragmentary material and limitations of data collection in terms of demands on time must still be addressed.

Abundance can also be estimated or indexed (e.g., 0 = absent, 1 = rare, 2 = common, and 3 = abundant). Investigations on repeatability of data indexing (Hageman et al., 1996) indicate that, although somewhat subjective among workers, indexing of abundance can be remarkably consistent for individual workers. In addition, unpublished tests of data manipulation (data sets of Lagaaij and Gautier, 1965; Hageman et al., 1996) indicate that robust distributional trends observed with raw data are also evident with indexed data. Considerations for increased data-collection efficiency versus acceptable information loss makes abundance indexing an attractive alternative.

Growth-form distributions can also be reflected by their relative abundance, such as the percentage of the bryozoan fauna at a single locality made up of a given growth form (Fig. 2A). Relative abundance data provides a convenient method by which to make standardized comparisons. It is important to note, however, that relative abundance can be derived in two ways (1) calculated from absolute or indexed data; or (2) estimated or measured directly during data compilation. The distinction is important because, with directly compiled data, the model used to evaluate the data (within growth forms versus within localities) is dictated *a priori*. If relative abundances have been calculated or estimated using one model (within growth forms or within localities), data *cannot* be converted to, or compared with the other model (unless totals for absolute abundance are provided). Therefore, absolute or indexed abundance (Table 2A) is the most desirable form of data compilation because all other analyses can be calculated from it for later comparisons (Table 2B, C). The same principles apply to data using species richness.

Volumetric versus Numeric Abundance

Because of inherent differences among growth forms (size and construction), it is difficult to quantify (or even qualify) abundance. The question is one of numeric abundance versus volumetric abundance. Evaluations can be based on the number of specimens (fragments) or on volumetric differences between groups. For example, it seems unlikely that three sub-millimeter thick segments of *Cel-laria tenuirostris* (Rooted Flexible articulated cylindrical branches) with hundreds of segments per colony should

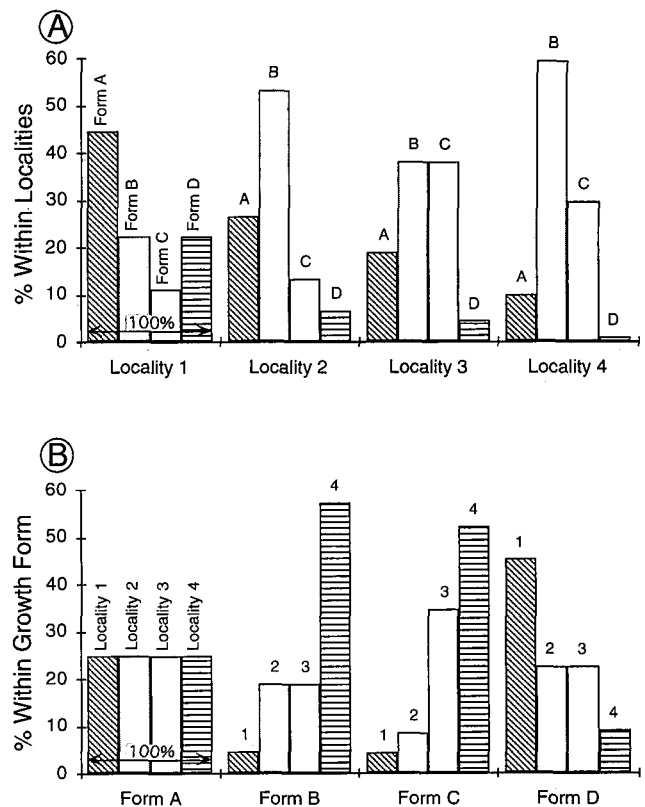


FIGURE 2—Comparison of bryozoan growth-form distributions analyzed within localities and within growth forms. (A) Relative abundance of bryozoan growth forms within each of four localities (1, 2, 3, 4; each locality totals 100%; Table 2B). (B) Relative abundance within each of four growth forms (A, B, C, D) taken across different localities (each growth-form totals 100%; Table 2C).

have three times the ecological significance of a single 25 cm² fragment of a *Adeona grisea* (large Rooted Rigid fenestrate sheet) from a single colony. Alternatively, is skeletal volume/weight an absolute measure of "importance" (cf. a very large, but lightly calcified *Bugula* relative to a small, but more heavily calcified *Adeona*)? These problems are not as great when comparisons are made within growth forms; thus, the value of indexed abundance values scaled within growth forms. For example, the abundance of *Cel-laria tenuirostris* could be indexed at a given locality based on all occurrences of similar forms in the study.

Weight Percentages and Petrographic Estimates

Weight percent of CaCO₃ can be used if pristine skeletal material is involved. Pore-filling cements and matrix can, however, strongly bias measurements (even recent material). Estimates of bryozoan abundance based on simple areas from thin sections (point counts) are not advised, due to the geometric complexity of growth forms and difficulties involved in volumetric estimates of even simple shapes (Flugel, 1982).

Changes within Growth Forms Versus Changes within Localities

Correlation between growth-form dominance and local ecological controlling parameters is the fundamental ar-

TABLE 2—Example of four hypothetical growth forms from four localities. (A) Raw abundance data (count or volume in fixed amount of sediment). (B) Relative abundance of growth forms *within localities* (Fig. 2A). (C) Relative abundance *within growth forms* distributed among localities (Fig. 2B); (D) Data combined to account for both within growth forms and within localities (Figs. 3, 4), derived from Table 1A using Equation 1.

	(A) Raw abundance data						(B) % Within localities				
	Form A	Form B	Form C	Form D	Sum		Form A	Form B	Form C	Form D	Sum
Locality 1	20	10	5	10	45	Loc. 1	44	22	11	22	100%
Locality 2	20	40	10	5	75	Loc. 2	27	53	13	7	100%
Locality 3	20	40	40	5	105	Loc. 3	19	38	38	5	100%
Locality 4	20	120	60	2	202	Loc. 4	10	59	30	1	100%
Sum	80	210	115	22							
	(C) % Within growth form					(D) Combined index					
	Form A	Form B	Form C	Form D		Form A	Form B	Form C	Form D		
Locality 1	25	5	4	45	Loc. 1	56	11	10	101		
Locality 2	25	19	9	23	Loc. 2	33	25	12	30		
Locality 3	25	19	35	23	Loc. 3	24	18	33	22		
Locality 4	25	57	52	9	Loc. 4	12	28	26	5		
Sum	100%	100%	100%	100%							

gument that allows for the application of bryozoan colonial growth forms to environmental analyses. However, there are two fundamental ways in which variations of growth-form dominance can be evaluated (1) changes within localities; or (2) changes within growth forms. The first addresses the question for a single locality, which growth form is most important? The second addresses the question for a single growth form, at which locality is it most important?

Virtually every previous study (Appendix 1) has employed the first method, which emphasizes the relative differences within localities/facies (i.e., among bryozoan growth forms at each sample sight), largely because data are naturally examined by localities. For example with the raw data (Table 2A), each locality (row) is examined separately. The relative importance of each of the four growth forms (A-D) is then determined as percentages of each locality's bryozoan fauna (Table 2B, Fig. 2A).

The second method documents the relative importance within each growth form as it changes among different localities. For example, with the raw data (Table 2A), each growth form (column) is examined separately. The relative importance of the growth form at each of the four localities (1-4) is then determined, as percentages of the total occurrence of the growth form at all four localities (Table 2C, Fig. 2B).

Comparison of Figures 2A and B illustrates that these two methods of data compilation and analysis provide different information about the correlations between growth forms and localities. For example, when data are compared within localities (Fig. 2A), Growth-form A is the dominant growth form at Locality 1, and Growth-form A is itself proportionally most important at Locality 1. Whereas, when data are compared within growth forms (Fig. 2B), Growth-form D is the dominant form at Locality 1 and Growth-form A is evenly distributed among all localities.

These results are not contradictory; rather they contribute to an even greater understanding of the relationships between bryozoan growth forms and environmental conditions than either do alone. If only one method is em-

ployed, however, workers should clearly acknowledge their methodology so others can make appropriate comparisons.

Combined within Growth Form and within Locality Index

A major problem associated with interpreting growth-form distributions is that dominant growth forms, and localities with abundant faunas, overshadow the numerically less-dominant constituents. However, growth forms with less abundance and fewer localities with overall fewer specimens, may have proportionally greater changes (and more ecological information) through their distributions than dominant forms and localities. The method proposed below accounts for these different relative proportions, and scales them so that changes can be compared on the same index.

This approach evaluates the occurrence of a single growth-form/locality combination (e.g., Growth-form D at Locality 1, cell D1 = 10, Table 2A) and simultaneously asks two questions. First, how important is combination (D1) relative to occurrences of all other bryozoans at Locality 1? Secondly, how important is combination (D1) relative to occurrences of Growth-form D at all other localities?

This is accomplished by dividing the cell D1 for Growth-form D at Locality 1 (D1=10, Table 2A) by the product of the total bryozoans at Locality 1 (45) and the total within Growth-form D (22). These are then multiplied by 100² to scale values to a magnitude of around 0 to 100. For example (Table 2D), the combined index for Growth-form D from Locality 1 equals

$$[10 / (45 * 22)] * 10,000 = 101$$

This method allows comparison of data by either within growth forms or within localities using a single, combined index derived from the original data set (Fig. 3, Table 2D).

The formal equation for this is

$$K_{ij} = [R_{ij} / (\Sigma_i * \Sigma_j)] * 100^2 \text{ (Eq. 1)}$$

where K_{ij} is the combined index for the observation from

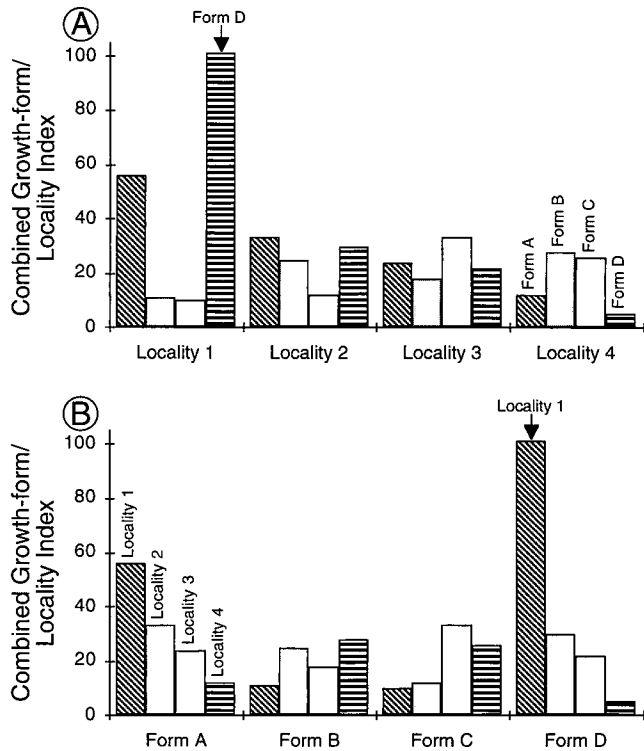


FIGURE 3—Relative abundance of growth forms based on combined data, within growth forms and within localities derived with Equation 1 (Table 2D). (A) Relative abundance of four growth forms within each of four localities. (B) Relative abundance within each of four growth forms from four localities. With combined indexed data, the value of Locality 1/Growth-form D (A), is equal to that of Growth-form D at Locality 1 (B).

locality i , and growth-form j ; R_{ij} is the raw abundance data for locality i , and growth-form j ; Σ_i is the total number of specimens from locality i ; and Σ_j is the total number of specimens of growth-form j in the study.

When within growth form and within locality distributions are combined (Fig. 3), they produce results that differ from either distribution taken separately (Fig. 2A, B). However, combined indices (weighted by total abundance among both localities and growth forms) have an additional benefit in that the strongest overall correlations between growth forms and localities can be identified directly. For example, Locality 1/Growth-form D (Fig. 3A) is the exact same value as Growth-form D/Locality 1 (Fig. 3B), both = 101 from Table 2D. If the combined index values in Table 2D are plotted in rank order (Fig. 4), the most significant locality/growth-form correlations are evident. In this example, it is clear that Locality 1/Growth-form D, and Locality 1/Growth-form A are most significant.

Questions such as “which growth form is most important for Locality 2?”, or “at which locality is Growth-form C most important?” can be answered directly from Figure 4 (Growth-form A and Locality 3, respectively).

Species Richness versus Abundance

The fundamental premise involved in the application of bryozoan growth forms to environmental analysis is that bryozoan colonies with growth forms most adapted to giv-

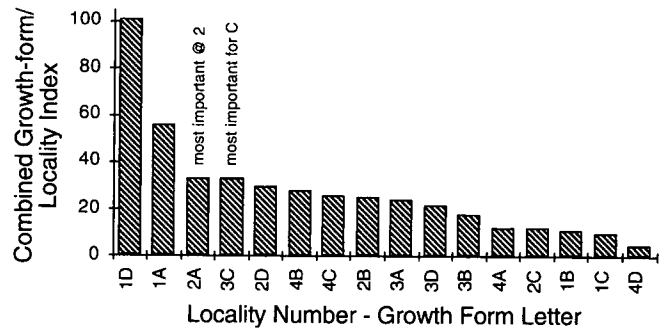


FIGURE 4—Histogram of sorted (ranked), combined growth-form/locality indexed data (Table 2D) for distribution of four growth forms (A, B, C, D) and sample localities (1, 2, 3, 4). Increasing values indicate stronger correlations between growth forms and localities.

en environmental conditions will be most successful in that setting. Previous workers have defined success as either simple growth-form *abundance* (an ecomorphic approach) or by the *number of species* within each growth form (species richness = taxic approach). Biologists have long struggled with the ecological meanings, significance and comparability of these two measures of success. For example, the relative importance is unclear in the comparison of two faunas, one composed of a few species, all of which are abundant versus a second fauna with many species all of which are represented by only a few individuals.

Selection of a method for growth-form analysis (specimen abundance or species richness), carries implicit endorsement of an ecological model, even if its meaning or context is poorly understood. Stach (1936, p. 65) viewed relative abundance as the more important factor. Cook (1968) and Schopf (1969) were the first (independently) to employ species richness within growth forms in environmental analyses, though without comment on their rationale.

It is clear, however, that analyses using data based on species grouped into their colonial growth forms provides distributional patterns (ecological information) with *less resolution* than patterns based on primary species distributions alone (cf. the empirical example in this study with Hageman et al., 1995, 1996). Thus, the influence of component species distributions appears to have a greater ecological resolution than the distribution of growth forms based on gross abundance alone. Given this information, it is unclear why one should go to the trouble of differentiating species, only to lump the data into ecomorphs (unless the primary interest is the ecomorphs themselves). Nevertheless, methods of incorporating species richness into growth forms are discussed here for the sake of comparison and completeness.

Diversity Indices

Ecologists have developed numerical methods to combine information about specimen abundance and species richness for a given locality or region into a single, combined index. Ecologists call this combined abundance/species richness index a measure of *diversity*. A number of methods for calculating diversity indices have been proposed, e.g., Shannon-Wiener index, Simpson index (Pie-

TABLE 3—Combined, average specimen abundance plus species richness. For example, the average indexed abundance value for Form I $(1+2+2+3)/4 = 2$. To this value, the number of species ($n = 4$) is added to obtain a Combined Index value of $(2+4) = 6$.

	Form I				Form II		Form III
	A	B	C	D	E	F	G
Locality 1	1	2	2	3	1	1	3
Av. abundance		2			1		3
Species #		4			2		1
Combined		6			3		4

lou, 1974), and Fisher's α (Fisher et al., 1943). These methods have not been applied to bryozoan growth-form analysis, but could potentially resolve some of the problems discussed here. One of the limitations of diversity indices is that most only account for proportional differences in abundance between species, within growth forms. That is, a growth form with two equally rare species would be treated the same as a growth form with two equally abundant species. A method of combining specimen abundance and species richness, which accounts for absolute differences is presented next.

Average Abundance plus Species Richness

This method does not fulfill the optimal statistical qualities of a proper diversity index, but its direct method of calculation and ability to reveal robust trends in the data, makes this method attractive to non-specialists. In this method, the average abundance is calculated for all species of a given growth form, from a single sample locality. The number of species for the growth form present at the locality is then added to the average indexed abundance. Thus, if a growth form has four species (Table 3, Form I), with indexed abundance values of 1, 2, 2, and 3, they have an average value of $(1+2+2+3)/4 = 2$. To this value, the number of species ($n = 4$) is added to obtain a Scaled Index value of $(2+4) = 6$.

The *average abundance plus species richness* method is more sensitive to changes in species richness than it is to the absolute number of species in any given setting. Species richness is increasingly emphasized over extreme range changes in species number.

Other Methods of Combining Abundance and Species Richness Data

Specimen abundance can be calculated for each locality as a percentage of the entire study. Likewise, species richness can be calculated for each locality as a percentage of all occurrences in the study. For each locality/growth-form combination, these values can be summed (% abundance + % species present). This *combined percentages* method has not been employed previously; however, this approach of comparing relative species percentages has been used by several authors (e.g., Schopf, 1969).

In an alternative method (*summed combination*), each species is treated independently and a value for its relative abundance (index or percentage) can be assigned individually for each species. These individual species-abun-

dance values can be summed for all species within a growth form at a single locality. This provides a single value for all species within a growth form at a given locality. For example, if Growth-form I has four species, with indexed abundances of 1, 2, 2, and 3, then the combined value of the growth form at that locality would be the sum of the combination $(1+2+2+3) = 8$. This approach has been applied by several authors (e.g., Moissette, 1993; Moissette and Saint Martin, 1995).

The *combined percentages* and *summed combination* methods are attractive because they are easy to tabulate and have a direct logic behind them. However, both methods heavily bias the species richness side of the equation. For example, in the *combined percentage* method, the relative weight given to each species is closely tied to the total species richness. Using this method, it is improper to compare results of two studies based on faunas with different species richness. The *summed comparison* method is more sensitive to absolute number of species, than it is to changes in species richness. The relative importance of species richness increases disproportionately as the number of species increase (i.e., the more species there are, the proportionally greater importance is placed on each species).

Other Considerations

Raw data (not indexed) can be treated in a number of ways to make the two methods (abundance and species richness) more comparable. If there are extreme differences in the scale of either abundance or species richness within localities and growth forms, then all of the data should be transformed to a logarithmic scale before analyses, e.g., $[\log(x+1)]$. This will help eliminate the disproportional emphasis inherent in wide-ranging data (i.e., meet assumption of additive effects of factor levels in parametric tests). In addition, strong relationships between sample size and observed species richness (e.g., Koch, 1987) should be considered when making comparisons between studies.

EMPIRICAL EXAMPLE

Although the multiple methods of compiling data presented here may seem academic or even pedantic, these considerations are serious, both methodologically and ecologically. The method outlined below combines theoretical considerations for *species richness* and *abundance*, plus the *within growth form* and *within locality* distributions.

This example uses empirical data from a study of the distribution of 88 bryozoan species from 16 localities on the cool-water Lacepede Shelf, southern Australia (Fig. 6; Hageman et al., 1995, 1996). In those studies the distribution of 88 bryozoan species was documented on the shelf and upper slope. Cluster analysis was used to assign the 16 localities to six assemblages which correspond to physiographic provinces on the shelf. The same 88 bryozoan species are here assigned to growth forms (Appendix 2). After growth-form data are indexed (combined abundance/species richness and combined with growth form/locality), growth-form data are then analyzed with cluster analysis. Results between growth form and primary species distributions are then compared. Although significant

TABLE 4—Combined, average specimen abundance plus species richness from Lacepede growth forms. Calculations derived from indexed abundance data for 88 species (Hageman et al., 1996, Table 1) assigned to growth forms (Appendix 2). Combined index obtained by average specimen abundance plus species richness within each growth form for each sample locality. Abbreviations from Figure 1.

Forms	Sample locality numbers															Sum	
	A-5	A-7	A-11	B-4	B-9	B-61	B-63	O-3	O-59	O-73	O-1	O-64	O-74	S-75	S-76		S-107
CUss	2	4	4	7	7	7	8	8	8	9	13	10	10	8	6	5	114
CUfs	5	5	0	7	5	5	5	7	4	7	8	8	6	7	7	4	88
CUhc	4	0	0	8	0	0	4	7	6	7	8	6	7	5	7	6	73
CMem	0	0	0	7	7	6	5	7	5	7	5	7	7	0	0	0	62
CEcb	0	2	0	5	6	7	6	7	9	9	9	12	11	9	10	7	108
CEub	5	5	0	8	7	9	7	8	8	9	12	14	12	9	12	6	127
CEbb	5	4	0	9	8	8	8	7	8	9	7	9	9	5	7	5	106
CEfs	3	2	0	8	7	6	8	6	6	9	6	8	8	4	2	3	85
RAcb	9	8	2	10	9	11	8	9	10	11	11	12	12	10	9	6	147
RAub	3	6	2	5	6	8	6	0	7	6	6	7	8	7	7	2	85
RAzo	12	11	4	9	7	11	10	9	10	12	10	12	12	11	10	7	157
RRes	0	0	0	2	0	5	0	6	5	5	7	7	8	4	5	2	55
RRbr	0	2	0	5	6	4	2	7	6	7	7	7	7	4	6	4	74
RRbs	4	2	2	6	7	5	5	5	7	7	9	7	6	10	9	5	94
RRfs	5	2	0	6	5	6	7	5	5	7	6	6	7	3	0	0	70
RRcd	0	6	0	0	6	4	4	5	7	5	9	13	9	11	12	10	101
FLmd	7	8	4	4	0	2	0	6	7	8	7	11	9	9	4	0	86
Sum	62	66	18	104	92	104	91	109	117	133	139	153	148	115	110	71	

trends are highlighted, this study is intended as an example of methodology and not as a comprehensive study of Lacepede bryozoan growth forms. The following is a proposed standardized methodology for treating growth-form data.

Survey and Split

Initially, the bryozoan fauna was surveyed to determine the growth forms present and the overall species richness (Appendix 2). Formal species names were not assigned to all morphs (i.e., as many species-level groups as possible were identified within growth forms and given known species names or labeled sp. A, sp. B, etc.).

Indexing Abundance

The abundance of each species-level group was indexed (0 = absent, 1 = rare, 2 = common and 3 = abundant) at each sample locality relative to occurrences of the species at all samples. Lacepede data were originally indexed on a scale of 0 to 6, which proved to be more detail than needed to produced observed patterns (Hageman et al., 1996, fig. 1).

Combining Species Richness and Abundance

For each growth form, the indexed abundances of all its member species from each locality was averaged. This average abundance was added to the number of species in the growth form/locality, as in the example from the "Average Abundance plus Species Richness" section of this paper (Table 3). This results in a primary data matrix reflecting the combined species richness and abundance of 17 growth forms from 16 sample localities (Table 4).

Combining within Growth Form and within Locality Distributions

Equation 1 from the "Combined within Growth Form and within Locality Index" section of this paper was applied to the data matrix in Table 4. This results in a matrix of values that are scaled to account for distributions both within growth forms and within localities (Table 5). This data matrix allows for direct comparisons between relative correlations within both growth forms and localities (larger value = greater correlation).

Analysis of Data Set

This data set (Table 5), which is the result of combined indexed abundance and species richness and combined within growth-form and locality distributions, can be evaluated using any number of standard statistical methods. Cluster analysis is used here to establish relationships among the sample localities based on their growth-form composition (Fig. 5).

The 16 sample localities were clustered into four groups using Average Linkage Cluster Analysis (Fig. 5). These four groups correspond to their members physiographic position (facies) in the sample region (Fig. 6, Inner Shelf-A, Inner Shelf-B, Outer Shelf, and Slope). Physiographic regions corresponding to these groups are characterized below, and compared with the six bryozoan assemblages recognized from species-level distributions of the same, original data set (Hageman et al., 1996). The only difference between the assemblages based on cluster analysis of growth-form distributions and those based on species-level distributions is that the Outer Shelf and Slope groups were split further, into four discrete groups, using species-level information. Thus, some resolution is lost with growth forms relative to primary species distributions, but the overall patterns remain strong.

TABLE 5—Relative importance of growth forms scaled to account for their distributions within growth forms and within localities. Combined specimen abundance and species richness data (from Table 4) are scaled to account for their relative importance both within single localities and within individual growth forms, using Equation 1; A = Inner Shelf, B = Inner Shelf B, O = Outer Shelf, S = Slope. Data used for cluster analysis (Fig. 5). Abbreviations from Figure 1.

Form	Sample locality numbers															
	A-5	A-7	A-11	B-4	B-9	B-61	B-63	O-3	O-59	O-73	O-1	O-64	O-74	S-75	S-76	S-107
CUss	2.8	5.3	19.1	5.9	6.7	6.2	7.3	6.6	6.1	6.1	8.0	5.6	5.7	5.7	4.4	5.8
CUfs	8.3	8.0	0.0	7.7	6.2	5.5	6.2	6.7	3.9	6.0	6.2	6.2	4.6	6.9	6.7	6.4
CUhc	8.9	0.0	0.0	9.9	0.0	0.0	6.0	8.8	6.4	7.2	7.9	4.9	6.5	6.0	8.7	10.6
CMem	0.0	0.0	0.0	10.9	11.7	9.3	8.8	10.8	6.9	8.5	5.2	6.8	7.6	0.0	0.0	0.0
CEcb	0.0	2.8	0.0	4.0	6.0	6.3	6.1	6.1	6.9	6.1	6.1	7.1	7.0	7.1	8.3	9.2
CEub	6.0	5.4	0.0	5.9	5.5	7.0	5.6	5.4	5.4	5.3	6.8	6.9	6.3	6.0	8.4	6.4
CEbb	6.9	6.2	0.0	8.2	8.6	7.0	7.9	6.1	6.2	6.2	4.8	5.6	5.8	3.7	5.7	6.2
CEfs	5.7	3.6	0.0	9.1	8.5	7.2	9.9	6.8	5.7	8.1	4.6	6.1	6.2	4.1	2.1	5.0
RAcb	10.0	7.8	7.4	6.6	6.7	7.2	6.0	5.5	5.8	5.9	5.6	5.2	5.5	5.7	5.7	5.8
RAub	5.7	10.7	12.8	5.7	7.7	8.7	7.7	0.0	6.5	5.6	5.1	5.4	6.4	7.2	7.0	3.3
RAzo	12.0	10.5	15.0	5.2	5.1	7.0	6.9	5.4	5.6	5.7	4.7	4.9	5.3	6.0	5.6	6.3
RRes	0.0	0.0	0.0	3.5	0.0	8.9	0.0	9.2	7.8	6.2	9.7	7.8	9.5	6.4	8.4	5.2
RRbr	0.0	4.1	0.0	6.5	8.8	5.2	3.0	8.7	6.9	7.1	6.8	6.2	6.4	4.7	7.4	7.6
RRbs	6.0	3.2	11.6	5.6	7.5	4.6	5.8	4.9	6.4	5.6	7.0	5.1	4.3	9.1	8.3	7.5
RRfs	10.5	4.4	0.0	8.3	7.8	8.3	11.0	6.6	6.1	7.6	6.2	5.6	6.8	3.8	0.0	0.0
RRcd	0.0	9.0	0.0	0.0	6.4	3.3	4.3	4.8	6.1	3.3	6.0	8.3	6.3	9.9	10.9	14.3
FLmd	13.8	14.1	25.3	4.5	0.0	2.2	0.0	6.7	7.3	6.5	5.8	8.2	7.2	9.3	3.7	0.0

Characterization of Regions

Regions (groups from cluster analysis) can be characterized based on their physiographic location and the substrate lithology of sample localities (Fig. 6; James et al.,

Locality

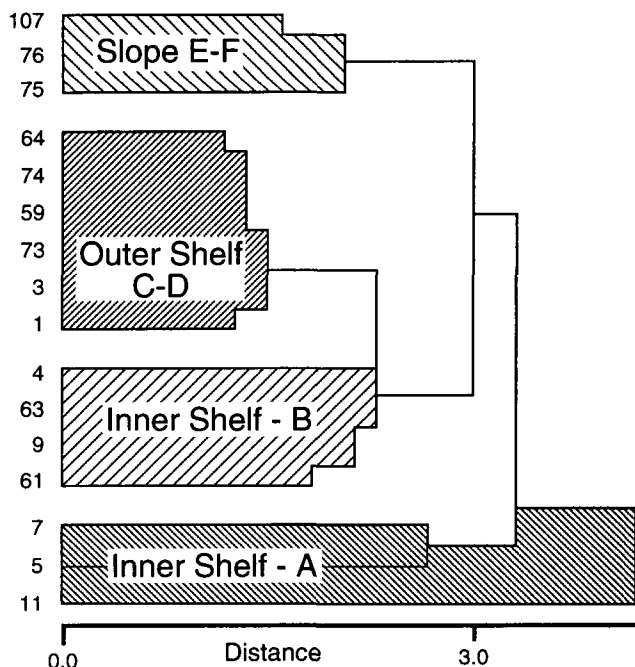


FIGURE 5—Dendrogram from cluster analysis of 16 sample localities from the Lacepede Shelf, based on the distribution of 17 growth forms (Appendix 2) using combined indexed abundance and species richness data, scaled to account for within growth form and within locality distributions (Table 5). Clustered groups correspond to the natural physiographic distribution of the sample localities: Inner Shelf-A (clastic dominated), 5, 7, 11; Inner Shelf-B (carbonate dominated), 4, 9, 61, 63; Outer Shelf 1, 3, 59, 64, 73, 74; and Slope, 75, 76, 107.

1992) *Inner Shelf A*—loose quartz and relict carbonate sand substrate associated with deposition from the River Murray, water depth 40 to 70 m (Fig. 6); *Inner Shelf B*—mixed relict carbonate and sub-recent bryozoan, mollusc, foraminiferal calcarenite, water depth 40 to 80 m (Fig. 6); *Outer Shelf*—robust bryozoan sand and bivalve-coral gravel, water depth 80 to 180 m (Fig. 6); *Slope*—bryozoan mud, water depth 160 to 450 m (Fig. 6).

Data from Table 5 are summarized by grouping sample localities into their physiographic regions (Table 6). This is done by averaging all growth-form values from one region (e.g., Cemented Unilaminar solid substrate, CUss-Inner Shelf-A A5, A7, A1, $(2.8 + 5.3 + 19.1)/3 = 9.1$).

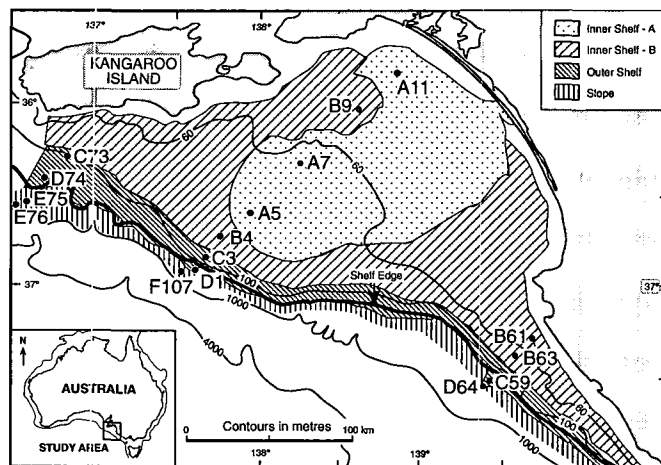


FIGURE 6—Physiographic provinces for the Lacepede Shelf, southern Australia (Inner Shelf, Outer Shelf and Slope) corresponding to four groups recognized in cluster analysis of bryozoan growth forms from the region (cf., Fig. 5). Letters A-F on sample localities correspond to six bryozoan assemblages based on the distribution of 88 bryozoan species (Hageman et al., 1995).

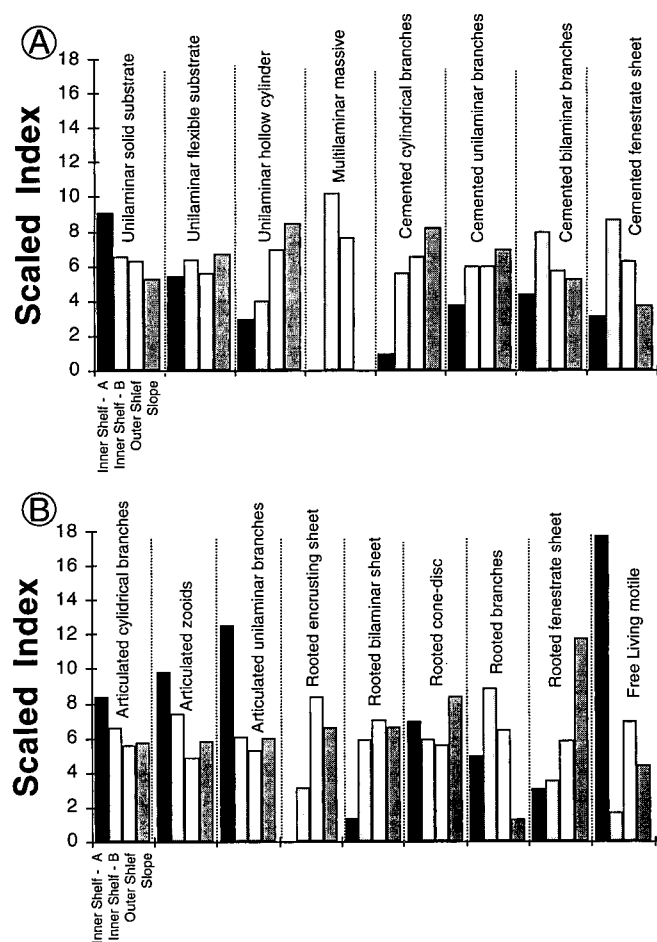


FIGURE 7—Relative importance of Lapepe bryozoan growth forms based on their physiographic distribution (Figs. 5, 6). Growth-form data are scaled to account for within and among growth-form distributions and combined specimen abundance and species richness data (Table 6). The larger the value, the greater the correlation between growth form and physiographic region.

Survey Data

Once a single, combined data set, such as either Table 5 or 6 has been developed, one can examine it in a number of ways. Figure 7 is designed for optimal viewing of changes within growth forms among physiographic provinces. Trends within provinces (among growth forms), although present in Figure 7, are more easily viewed when plotted by single physiographic province (Fig. 8).

Because abundance and species richness data and within locality and growth-form data are combined, distributions between two localities (physiographic provinces/facies) can be compared directly. For example, if growth-form values from the Slope are subtracted from those of the Inner Shelf-A (Fig. 8A, D; Table 6), the resultant histogram (sorted) highlights differences between the two (Fig. 9).

DISCUSSION OF EMPIRICAL STUDY

Components of the most striking trends can be summarized in order to develop viable predictive models:

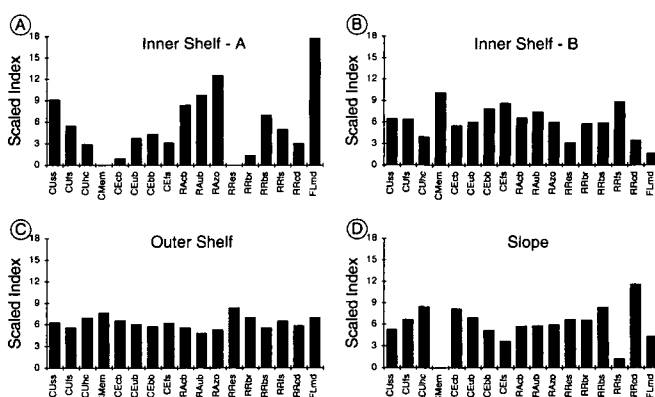


FIGURE 8—Relative importance among Lapepe growth forms at four physiographic provinces, based on combined abundance and species richness and indexed for with growth form and locality data (Table 6). All bryozoan growth forms are of approximately equal importance on the Outer Shelf (C). Both specimen abundance and species richness among all growth forms is greater on the Outer Shelf (C), than it is on the Inner Shelf (A, B) or Slope (D). Although growth-form variety and relative importance are generally lower on the Inner Shelf (A, B) than on the Outer Shelf (C), certain growth forms are more important on the Inner Shelf and different forms are important on the Slope (D). See Figure 1 for abbreviations.

- (1) There is an overall increase in homogeneity of growth-form importance from Inner to Outer Shelf (cf. Fig. 8A, B, C).
- (2) Inner Shelf-A is distinguished by lower species richness among all growth forms (Fig. 8A), with a notable dominance of the following growth forms—Free Living motile discs (FLmd), Rooted Articulated zooids (RAzo), Rooted Articulated unilaminar branches (RAub), Rooted Articulated cylindrical branches (RAcb), Cemented Unilaminar solid substrate (CUss), and Rooted Rigid bilaminar sheets (RRbs). These forms characterize the Inner Shelf, but are *not* exclusive to the province.

TABLE 6—Growth-form importance based on regional distributions. Columns represent the average value for a growth form from all localities representing the specified region (Table 5, Fig. 5). Abbreviations from Figure 1.

Form	In-shelf-A	In-shelf-B	Outer shelf	Slope	Shelf A - slope
CUss	9.1	6.5	6.3	5.3	3.8
CUfs	5.4	6.4	5.6	6.7	-1.3
CUhc	3.0	4.0	6.9	8.5	-5.5
CMem	0.0	10.2	7.6	0.0	0.0
CEcb	0.9	5.6	6.6	8.2	-7.3
CEub	3.8	6.0	6.0	6.9	-3.1
CEbb	4.4	7.9	5.7	5.2	-0.8
CEfs	3.1	8.7	6.3	3.7	-0.6
RAcb	8.4	6.6	5.6	5.8	2.6
RAub	9.8	7.4	4.8	5.8	4.0
RAzo	12.5	6.0	5.3	6.0	6.5
RRes	0.0	3.1	8.4	6.6	-6.6
RRbr	1.4	5.9	7.0	6.6	-5.2
RRbs	7.0	5.9	5.5	8.3	-1.3
RRfs	5.0	8.9	6.5	1.3	3.7
RRcd	3.0	3.5	5.8	11.7	-8.7
FLmd	17.7	1.7	7.0	4.3	13.4

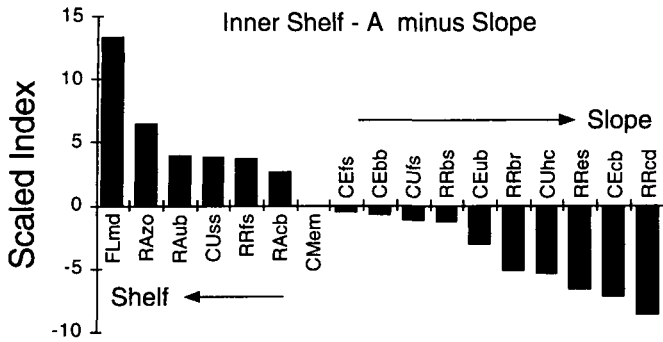


FIGURE 9—Slope values subtracted from Inner Shelf-A values (Table 6). Positive values (left) indicate growth forms are more characteristic of, but not exclusive to, Inner Shelf. Negative values (right) indicate growth forms that are more characteristic of, but not exclusive to, the Slope. See Figure 1 for abbreviations.

- (3) The Outer Shelf is characterized by a relatively equal (and high) importance of growth forms (Fig. 8C). Only one growth form, Rooted Rigid encrusting sheet (RRes), is of significance particularly on the Outer Shelf (Figs. 7B, 8C). These are unilaminar sheets that have rootlets on the reverse sides that allow for epizoic attachment on sponges, hydroids, worm tubes, and other rooted bryozoans.
- (4) The relative importance of growth forms on the Inner Shelf-B (Fig. 8B) lies somewhere between the lower species richness, specialized abundance of the Inner Shelf-A and the higher species richness and overall moderate abundance on the Outer Shelf.
- (5) The Slope (Fig. 8D) is distinguished by a notable dominance of Rooted Rigid cones-discs (RRcd), Cemented Unilaminar hollow cylinder (CUhc), Cemented Erect cylindrical branches (CEcb), and Rooted Robust bilaminar sheets (RRbs). These forms characterize, but are *not* exclusive to, the Slope.

Based on these simple observations, a non-specialist should be able to characterize a suite of samples from a single locality of unknown environmental setting, compare them to the distributions characterized in Figures 8 and 9 and predict whether the unknown locality was collected from Inner Shelf-A, Inner Shelf-B, Outer Shelf, or Slope. More specific details about ecological controlling parameters would require a comprehensive analysis of the fauna.

SUMMARY

- (1) Bryozoans play an important ecological role in many modern marine settings. Bryozoans have a rich fossil record and in certain settings their skeletons have contributed significantly to modern and ancient sediments. Their important ecological role, combined with the fact that colonial growth forms are often correlated with environmental conditions in which the organism grew, means that colonial growth forms can be used as paleoenvironmental indicators.
- (2) Growth-form analysis can be used in detailed studies to characterize regions (environmentally), or used as predictive tools applied to unknown samples from re-

lated settings. Although specific ecological controls over growth-form distributions are not always established, general trends and interpretations are nonetheless valid.

- (3) Growth-form analyses can be qualitative or quantitative. Quantitative methods have proven viable, but methodological problems exist. Methods are proposed here to incorporate changes within growth forms and within localities into a single analysis, and to combine information about growth-form abundance and species richness within growth forms.
- (4) Growth-form distributions should be established independently from causal factors and then, later, compared to all available ecological controlling parameters and later to broader environmental factors (Table 1). This allows for greatest predictive utility of the model.
- (5) A standardized method of growth-form analysis is suggested, which additionally considers methods of data acquisition, scaling, analysis, and interpretation. Methods for combining abundance and species richness data and distributions within growth forms and with localities into a single data set have proven viable. An empirical example is provided using data from the Lacepede Shelf of South Australia and the suggested standardized methodology.
- (6) Although this paper presents many problems encountered in these studies, the outlook for application of bryozoan colonial growth forms to paleoenvironmental analyses remains optimistic. Problems raised here are all testable; their resolution will allow bryozoan colonial growth forms to achieve their full potential as paleoenvironmental indicators.

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- Moyano, 1979
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- Gordon, 1987
- Moissette, 1988, 1989, 1993
- Moissette and Saint Martin, 1995
- Bianchi et al., 1988, 1991
- Blondel et al., 1990
- Poluzzi et al. 1991
- Zágorsek, 1993
- Paleozoic*
- Perry and Horowitz, 1963
- Cuffey, 1967
- McKinney, 1972
- Kelley and Horowitz, 1987
- Bancroft et al., 1988
- Sedimentology*
- Hyden, 1979
- Hancock, 1980
- Leask, 1980
- Nelson et al., 1982
- Keane, 1986
- Nelson et al., 1988
- Quine and Bosence, 1991
- James et al., 1992
- Bone and James, 1993
- James and Bone, 1994

APPENDIX 2

Bryozoan growth forms (Table 1) and member species observed from the Lapede Shelf (Fig. 6). Data are used in the empirical example employed in this study (Tables 4, 5, 6, and Figs. 7, 8, 9).

- Cemented Unilaminar solid substrate (CUss) *Anarthropora monodon*, *Chiastosella daedala*, *Hippomenella bituberosa*, *Lichenopora* sp., *Microporella diademata*, *Parasmittina* sp., *Schizomavella* sp. A, *Smittoidea calceolus*, *Smittoidea formosa*.
- Cemented Unilaminar flexible substrate (CUfs) *Arachnopusia monoceros*, *Hiantopora radificera*, *Hiantopora ferox*.
- Cemented Unilaminar hollow cylindrical (CUhc) *Labioporella* sp. A, *Schizoporella acuminata*, *Schizoporella cecilii*, *Schizoporella phymatopora*.
- Cemented Multilaminar encrusting massive (CMem) *Celleporaria columnaris*, *Celleporid* sp. A, *Celleporid* sp. B, *Celleporina tota*.
- Cemented Erect cylindrical branches (CEcb) *Celleporina munita*, *Entalophora regularis*, *Entalophora* sp. B, *Entalophora* sp. C, *Entalophora* sp. E, *Entalophora* sp. F, *Galeopsis longirostris*, *Galeopsis porcellanicus*.
- Cemented Erect unilaminar branches (CEub) *Hornera robusta*, *Idmidronea* sp. A, *Idmidronea* sp. B, *Mesonea radians*, *Nevianipora* sp., *Reteporella* sp. A, *Reteporellina* sp. A, *Reteporellina* sp. B, *Triphyllozoon* sp. A.
- Cemented Erect bilaminar branches (CEbb) *Adeonellopsis yarraensis*, *Adeonellopsis sulcata*, *Caleschara denticulata*.
- Cemented Erect fenestrate sheet (CEfs) *Hornera foliacea*, *Iodictyum phoenicea*, *Phidolopora avicularis*, *Sertella* sp. A, *Sertella* sp. B.
- Rooted Articulated cylindrical branches (RAcb).
- Cellaria bicornis*, *Cellaria rigida*, *Cellaria sigillarioides*, *Cellaria tenuirostris*, *Crisia acropora*, *Margaretta barbata*, *Quadriscutella papillata*.
- Rooted Articulated unilaminar branches (RAub) *Caberea glabra*, *Caberea grandis*, *Canda arachnoides*.

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APPENDIX 1

Partial list of bryozoan growth-form studies.

Cenozoic and Mesozoic

- Brown, 1952
- Gautier, 1962
- Cheetham, 1963, 1971
- Lagaaij and Gautier, 1965
- Labracherie and Prud'Homme, 1966
- Cook, 1968, 1981
- Askren, 1968

Rooted Articulated zooids (RAzo) *Bicrisia biciliata*, *Bicrisia edwardsiana*, *Bicrisia edwardsiana*., *Calpidium ornatum*, *Cornuticella cornuta*, *Emma triangula*, *Orthoscuticella* sp., *Pterocella scutella*, *Scuticella plagiostoma*.

Rooted Rigid encrusting sheet (RRes) *Mucropetraliella* sp., *Sinupetraliella* sp. B, *Sinupetraliella* sp. A.

Rooted Rigid branches (RRbr) *Porina gracilis*.

Rooted Rigid bilaminar sheets (RRbs).

Bipora flabellaris, *Corbulipora oriparma*, *Flabellopora umbonata*,

Melicerita angustiloba, *Parmularia reniformis*., *Steginoporella fornicina*.

Rooted Rigid fenestrate sheets (RRfs) *Adeona grisea*, *Petralia undata*.

Rooted Rigid cone-disc (RRcd) *Conescharrellina biarmata*, *Conescharrellina* sp. A, *Conescharrellina angulopora*, *Conescharrellina* sp. B, *Conescharrellina* sp. C, *Sphaeropora* sp. B, *Sphaeropora* sp. A, *Sphaeropora fossa*.

Free Living motile discs (FLmd) *Otionella australis*, *Selenaria* sp. A, *Selenaria bimorphocella*, *Selenaria* sp. C, *Selenaria* sp. B.

