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Growth and form in modular animals: ideas on the size and arrangement of zooids

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Modular (colonial) invertebrates are mostly aquatic, sessile, active or passive suspension feeders. This paper proposes and discusses some generalizations concerning form that apparently are related to the sessile colonial mode of life. In contrast to the size of related unitary forms, the modules are small, maximizing feeding surface relative to metabolic mass and favouring production of a high energy surplus. Increasing colonial integration in ascidians and hydroids is associated with decreasing module size but in Bryozoa, with the lophophore as index, with some increase in size. The smallest lophophores are found in species with apparently primitive, near-linear branching. Among bryozoans with compact encrusting colonies, however, species with larger lophophores can outcompete abutting neighbours with smaller lophophores. Lophophore size may then be a compromise between energetic advantage and competitive disadvantage. Whereas internal filterers tend to have modules grouped to produce larger exhalant openings, favouring stronger discharge flow, in Bryozoa it appears advantageous to attain the maximum coverage of expanded lophophores. In Cheilostomata, lophophores are generally close packed, except at excurrent chimneys, and zooid size and shape are then directly linked to the dimensions of the lophophore. Bryozoa Cyclostomata, however, have evolved away from close-packed lophophores and quincuncial zooids towards fasciculated arrangements, possibly providing structural excurrent channels in a group that lacks the colonial coordination to maintain non-skeletal chimneys.

Variations in colony form are related to mode of growth, the disposition of modules to maximize filtration, and interactions with environmental factors. Increasing surface area leads to increased drag imposed by water movements. This may place constraints on growth and form, or may be exploited to augment filtration. Passive filterers often produce erect, branching, planar colonies oriented normal to directional currents. Bilaterally symmetrical, dish-shaped colonies with downstream zooids may occur in unidirectional flow. Erect bryozoan colonies more commonly are irregularly tufted or regularly branched in three dimensions, being then adapted to flows that vary in direction or velocity, or both.

INTRODUCTION

The modular invertebrates are those that form colonies of replicated units. The units arise, in the first instance, from a zygote but are thereafter effectively reproduced by non-sexual (mitotic) processes. Moreover, as formed, they remain in physical and physiological communication, thereby imparting to the colony some degree of individuality greater than that represented solely by an aggregation (clone) of otherwise comparable units. Such colonial invertebrates include many hydrozoan and anthozoan coelenterates, calyssozoans, bryozoans, pterobranchs, and some of the tunicates. Following Huxley (1851), the module of an

invertebrate colony is a definite entity, the zooid. Sponges generally function ecologically as colonies and arguably are constructed on a modular basis, but the modules comprise the oscula together with their aquiferous canals; unlike zooids, they are labile in form through time.

The useful concept of modular construction was introduced to biology by Harper (1977). Unlike zooids, modules are not exclusive to animals and provide a term equally applicable to an analogous organization in plants. Also, modules can be arbitrarily defined according to need or purpose. In animal colonies the primary modules are the zooids, but zooids themselves are often grouped in replicated patterns, variously 'systems' or 'cormidia' (Beklemishev 1969), which constitute modules of the second order. Further, colonies may replicate entire fronds, or divide into similar daughter colonies or 'cormomeres' (Oka & Usui 1944), these constituting modules of a third order.

Modularity and coloniality represent two viewpoints on the same phenomenon. 'Colony' in the modular sense is perhaps an unfortunate application of the word, for the Latin *colonia* was a settlement at a distance from the parent body, as in later human geographical colonies. It was applied in zoology first to the societies of Hymenoptera and communally nesting birds, and only in the late 19th century was it coined (Nicholson 1872) in what is here termed the modular sense. Haeckel (1866) had by then already appropriated 'cormus', from the Greek for a tree trunk, for a colonial body, but the word seems not to have found favour among English-speaking biologists, and persists mainly in the derivative cormidia. The meaning and applications of the term 'coloniality' have been considered recently by Rosen (1979) in a postscript introduction to a number of specialized contributions on that topic (Larwood & Rosen 1979).

Workers on colonial invertebrates were stimulated greatly by the appearance, first in German and then in English (1969), of Beklemishev's *Principles of comparative anatomy of invertebrates*. In this work Beklemishev identified certain universal trends which he associated with increased integration within colonies. His synthesis led to a reexamination of many of the major colonial taxa by specialists, resulting in some important publications on coloniality in sponges, Hydrozoa, corals, Octocorallia, Bryozoa, etc. (Mackie 1963; Boardman *et al.* 1973; Larwood & Rosen 1979). The increasing use of scuba as a research tool led contemporaneously to the discovery and study of animal communities in which sessile, colonial invertebrates dominated (Jackson 1977). These approaches converged with the introduction of the modularity concept and its development with reference to organization, genetic bases, evolutionary consequences, and community ecology (Chapman & Stebbing 1980; Chapman 1981; Jackson *et al.* 1985).

One of the most frequently remarked, though not invariable, characters of modular invertebrates is the small size of the modules (zooids) compared with their unitary relatives. The difference may be seen in such paired groupings as Scleractinia (corals) and Actiniaria (anemones), Bryozoa and Brachiopoda (lophophorates), and the 'simple' and 'compound' Ascidiacea. The reasons for small size, and the extent to which size varies within colonial taxa, however, have not been well explored. It might be expected that module size would further vary according to the manner of arrangement within colonies or with the degree of integration. Thus a superficial review of coral genera, exemplifying one of the more familiar modular taxa, suggested that massive forms budding by fission (intratentacular budding) often have large corallites. Many arborescent forms have much smaller corallites and, in many, greater integration implied by the ramose pattern and, in *Acropora*, differentiation of apical zooids. We have accordingly compiled some data and reviewed some of the literature dealing with three

other modular groups, Ascidiacea, thecate Hydroida and Bryozoa, to see whether the inverse correlation of size and colonial integration occurs elsewhere. In view of a possibly causal relation between integration and module size, and to avoid circular argument, some definition of integration seems necessary.

Beklemishev's trends that indicate increasing levels of integration are (i) the weakening individuality of zooids, (ii) the intensifying individuality of colonies, and (iii) the development of cormidia ('colonies within colonies'). The first two were exemplified by a number of usually parallel developments (Beklemishev 1969, p. 483). The concept of colonial integration in this way was attributed to Herbert Spencer. The source appears to be *First principles* (1862). Spencer perceived integration as the process of aggregating the diffuse into a whole, during either evolution (for example, of arthropods from annelids) or ontogeny. Among 'compound animals . . . integration is displayed not within the limits of an individual only but by the union of many individuals' (he cited salps and *Pyrosoma*). He commented on unifying features such as the colonial tunic in Botryllinae, the 'common system of nutrition' in Hydrozoa and corals, and noted what we now term somatic polymorphism in Siphonophora and their approximation to a 'single organism' (or 'superorganism' of Mackie (1963)).

The definition of integration in the *Shorter English dictionary* (edn 3, 1973) is: 'the making up of a whole by adding together or combining the separate parts or elements: a making whole or entire'. As applied to colonies, the degree of integration is usually inferred from comparative morphological series (see Boardman & Cheetham 1973; Cook 1979), although physiological criteria are applied when possible (see, for example, Mackie 1963; Ryland 1979). There seems to be no suggestion that change in size *per se* is associated with degree of integration. Indeed, as we show in this paper, the correlations with size are contradictory.

THE PHYSIOLOGICAL IMPLICATIONS OF MODULE SIZE

The significant biological manifestations of size are mass (or volume), W , proportional to the cube of the linear dimensions, and surface area, A , which varies as the square of the linear dimensions. Hence,

$$A \propto W^{\frac{2}{3}}.$$

The consequences of this relation are well-known in growth terms, and inevitably were introduced by D'Arcy Thompson (1942) very early in his treatise *On growth and form*. Obviously, if surface is proportional to the two thirds power of volume, the surface:volume ratio of an animal decreases as it grows. In many modular animals (but excepting corals with intratentacular budding and some ascidians) the module does not continue to grow through life. If modules were small to maximize their surface:volume ratio, evolution would favour budding methods which did not first involve increasing the size of the parent module. However, growth of colonies tends to be essentially two-dimensional, avoiding disproportionate increase in mass.

The pattern of growth in individual organisms (including modular forms: see, for example, Kaufmann (1981)) may be approximated by one or more descriptive models, which describe a flexed curve decaying to some asymptotic upper limit, for example, the von Bertalanffy, Gompertz, and logistic (Verhulst-Pearl) equations. The von Bertalanffy growth equation is descriptive and derivable empirically (Gulland 1983); but as formulated (von Bertalanffy 1957), following the idea of Pütter (1920), it had a physiological basis related to the acquisition

and utilization of energy, the former related to surface area and the latter to volume. Thus, the instantaneous rate of change in mass is given by the difference between surface-related anabolism and volume-related catabolism,

$$dW/dt = aW^b - kW^c,$$

where a and k are coefficients respectively of anabolism and catabolism, and the exponents $b = 0.67$ and $c = 1$ when growth is isometric.

The modular invertebrates discussed here are sedentary, usually sessile, and either suspension feeders *sensu stricto* or 'passive' suspension feeders, in both cases wholly dependent on a dilute food supply brought to them by water currents (Chapman & Stebbing 1980). Von Bertalanffy's b is therefore related to the surfaces available for particle capture. In passive feeders such as hydroids, antipatharians and gorgonians, the ability to capture particles will be directly proportional to the surface area opposed to the water flow; in true suspension feeders, whether unitary or modular, particle capture depends on the area of ciliated surface used to generate flow. Any ability to use dissolved organic matter (see, for example, Best 1985) would also be dependent on surface area. The exponent c is a function of processes occurring everywhere, and thus more nearly related to mass or volume.

Von Bertalanffy's equation can be shown as a pair of curves plotted against increasing mass (figure 11.19 in Jones 1976). One, representing energy utilization (or cost of living), based on mass to the power 1, would be linear; the other, representing the energy derived from food intake would be a decaying exponential based on $W^{0.67}$. The vertical distance between the two lines, energy surplus, E_s , decreases with increasing mass until the two lines intercept at W_∞ , the maximum attainable. In unitary organisms E_s has been termed the scope for growth (Warren & Davis 1966), where growth is both somatic and gametic. In the modular context, E_s expresses the energy available for gamete production within the zooid plus that transmitted to the extending, budding or regenerating zones of the colony.

If the exponent c departs from unity, the lower line will be curvilinear. In fish, b seems generally close to the theoretical 0.67 but c , from experiments on both mass loss and oxygen consumption, is nearer 0.7–0.8 than 1 (Zeuthen 1953; Jones 1976). Perhaps more obviously relevant are some figures for unitary suspension feeders, from Jørgensen (1975). In three bivalves, *Argopecten irradians*, *Mytilus edulis*, and *Cardium edule*, in which water transport is proportional to W^b , $b = 0.52, 0.60$ and 0.58 . For oxygen consumption, proportional to W^c , $c = 0.68$ (10 °C) or 0.87 (18 °C), 0.75 and 0.77 , respectively. The ratio b/c decreases with increasing body size, as does growth efficiency. Sebens (1982a) cites a number of other values of c in the range 0.84–1.05. Another appropriate data set refers to anemones, several of which are clonal though not colonial. Oxygen consumption varies considerably between the expanded state in water and the contracted state in air. A re-plot of data from Shick *et al.* (1979) provides an approximate value of 0.8 for c in *Anthopleura elegantissima*. This may be compared with the results of Sebens (1979), for three anemones, *A. elegantissima*, *A. xanthogrammica* and *M. senile*. For these, tentacle surface area increased as the 0.45, 0.71, and 0.73 power of mass, prey capture as the 0.60, 0.64, and 0.60 power, and metabolic costs derived from starvation as the 0.77, 0.98, and 0.80 power, respectively. Thus for a range of poikilotherms, values have been derived that evaluate b as 0.45–0.73 and c as 0.68–0.98. While different values, of course, have implications for particular energy budgets and life styles, none affects the generalization (for $b < c$) that small organisms generate proportionally the greatest energy surplus. It has, of course, been recognized

for some time that among filter feeders small species have the highest clearance rates (per unit dry mass) and that in bryozoan colonies it is zooid size and not colony size that is relevant (Bullivant 1968).

Sebens' (1979) simulations generated important conclusions, particularly that large size, for example, of solitary anemones, was optimal where prey were large and infrequent, and that a clone or colony of small, fixed-size modules was optimal where prey were small and frequent (the assumed pattern for modular coelenterate suspension feeders such as zoanthids and octocorals). Between these extremes, and optimal for intermediate prey size and frequency, are clones or colonies with modules of intermediate unit size (for example, fissile anemones). Presumably (Sebens 1982*a*), binary fission producing half-sized daughter modules is advantageous only if small prey are being used at that time and capture success does not suffer.

The general applicability of Sebens' (1979, 1982*a*) deductions seem clearly supported by the ascidian, hydroid and lophophorate data presented here. The unitary examples, by their very growth, are constantly reducing the relative area of their food-capturing surfaces, and therefore their energetic efficiency. Their specific growth rate therefore slows as size increases; or, the attainment of large size requires an allometric increase in the area of the collecting surface. Thus in Stolidobranchia, the ascidian suborder in which unitary form is most highly developed, a pleated branchial sac with four to eight folds per side has evolved, increasing the number of meshes. Concentric or spiral stigmata, which have evolved in both Phlebobranchia (Corellidae) and Stolidobranchia (Molgulidae), would not seem generally to increase the pore: filament ratio but maximize the length of the ciliated interface. Extreme examples are seen in *Corynascidia* in which the meshes have a spider's web appearance (Herdman 1882, plate 25) and in *Bostrychobranchus* in which they bulge as spiralled infundibula (Van Name 1945). (It should, however, be recorded that some solitary phlebobranchs with unmodified branchial sacs are large and some molgulids are small.) Comparably, in brachiopods, the evolution of spirolophes and plectolophes (Rudwick 1970) has facilitated lophophores bearing hundreds of filaments (that is, tentacles).

In contrast to the above examples, the modular Ascidiacea and lophophorates (Bryozoa) maintain small, determinate zooids; their growth strategy, as recognized by Sebens (1982*a*), is directed towards increasing the colonial surface area, whether encrusting or variously erect, so maximizing the number of modules. Thus volume does not increase to the detriment of relative collecting surface, and allometric adjustment is not necessary.

If it is accepted that having small modules confers energetic advantages on the colony, but that there are probably undetermined constraints on the lower limit, might increasing integration facilitate some depression of that limit? The following three sections examine three taxa for evidence that better colonial integration is accompanied by a decrease in module size.

MODULE SIZE AND DEGREE OF COLONIAL INTEGRATION IN TUNICATA ASCIDIACEA

The ancestor of present-day ascidians may have been solitary or loosely colonial (Millar 1966). Evolutionary pathways have led to the development of both complex unitary forms (for example, Molgulidae) and highly integrated modular genera (for example, Didemnidae among Aplousobranchia, Botryllinae among Stolidobranchia). Some of the usual criteria for degree of integration are not applicable: for example, there is no zooidal polymorphism among

ascidians, hence no cormidia, although there may be groupings of identical zooids as 'systems' and in some didemnids an apparently well regulated process of colonial fission (Ryland *et al.* 1984), an important adaptation to maintain high specific rates of growth. Moreover, although zooids are propagated by blastogenesis, the morphology of budding, the tissues involved, and the consequences to the parent zooid vary considerably (Berrill 1950; Millar 1966; Kott 1982).

Although these seemingly diverse methods of budding may have evolved separately, Millar (1966) argues a strong case for regarding the more complex methods of aplousobranch blastogenesis as derived from a primitive kind, in which the buds arise on a stolon incorporating an extension of the ventral blood vessel (*Clavelina*, *Perophora*). In Aplousobranchia a tissue known as epicardium becomes involved and the site of blastogenesis is moved from the stolon to the body. Diazonid and polyclinid budding is accomplished by strobilation of the abdomen, with the rest of the zooid often degenerating during the process. Didemnids generally have very flat, spreading colonies with minute zooids. Blastogenesis is clearly of a derived type with a pair of buds originating in the pyloric region; the parent zooid divides into thorax and abdomen, with the buds providing another abdomen or thorax as appropriate. The process can be continual and the zooids functional for most of the time.

Colonies occur in only one stolidobranch family, Styelidae, and whatever the ascidian ancestry it is difficult to envisage this as other than separately evolved. The method is termed pallial and involves outgrowth from the body wall incorporating ampullae of the test vessels. At first (Polyzoinae) this provides a method of cloning, for the short vascular stolons often degenerate as the daughter zooids develop (*Eusynstyela*), although they may form a continuous crust as in certain growth forms of *Distomus*. In the Botryllinae, however, the test vessels of developing buds merge with others to produce a truly colonial system.

The ascidian branchial sac consists basically of transverse rows of linear stigmata. In Phlebobranchia and Stolidobranchia inner longitudinal vessels are present, which effectively divide the stigmata into groups. It is impossible to use a standardized index of size of the branchial sac throughout the class, because taxonomic works usually state the number of transverse rows of stigmata for Aplousobranchia, while for the other two suborders they indicate the number of longitudinal vessels. In any case, use of a unidimensional index to describe the surface area of a three-dimensional structure will minimize differences. In figure 1 the number of rows or number of longitudinal vessels (mainly from Berrill (1950) and Millar (1970)) characterizing genera have been plotted according to whether the habit is solitary, colonial, or colonial with systems. The use of a logarithmic ordinate tends visually to conceal quite large differences, and the branchial sacs of unitary species are often an order of magnitude bigger, even in the single dimension.

The arrangement of zooids in systems around a common cloaca, instead of being irregularly disposed on stolons or a spreading base, is the most obvious indicator of the degree of integration. As shown in figure 1, particularly in stolidobranchs, the forms with systems (Botryllinae) have obviously smaller branchial sacs. Botryllines are the most highly integrated of all colonial ascidians, not merely through morphological systems but physiologically through the colonial vascular system. Budding and gonad maturation are in this way synchronized throughout the colony. The size reduction accompanying the evolution of systems is less marked in aplousobranchs unless there is a further breakdown within the category 'with systems'. In figure 1 polyclinids are distinguished from didemnids. It may be argued that the derived method of budding (though perhaps inextricably associated with reduction in size) is an advanced feature;

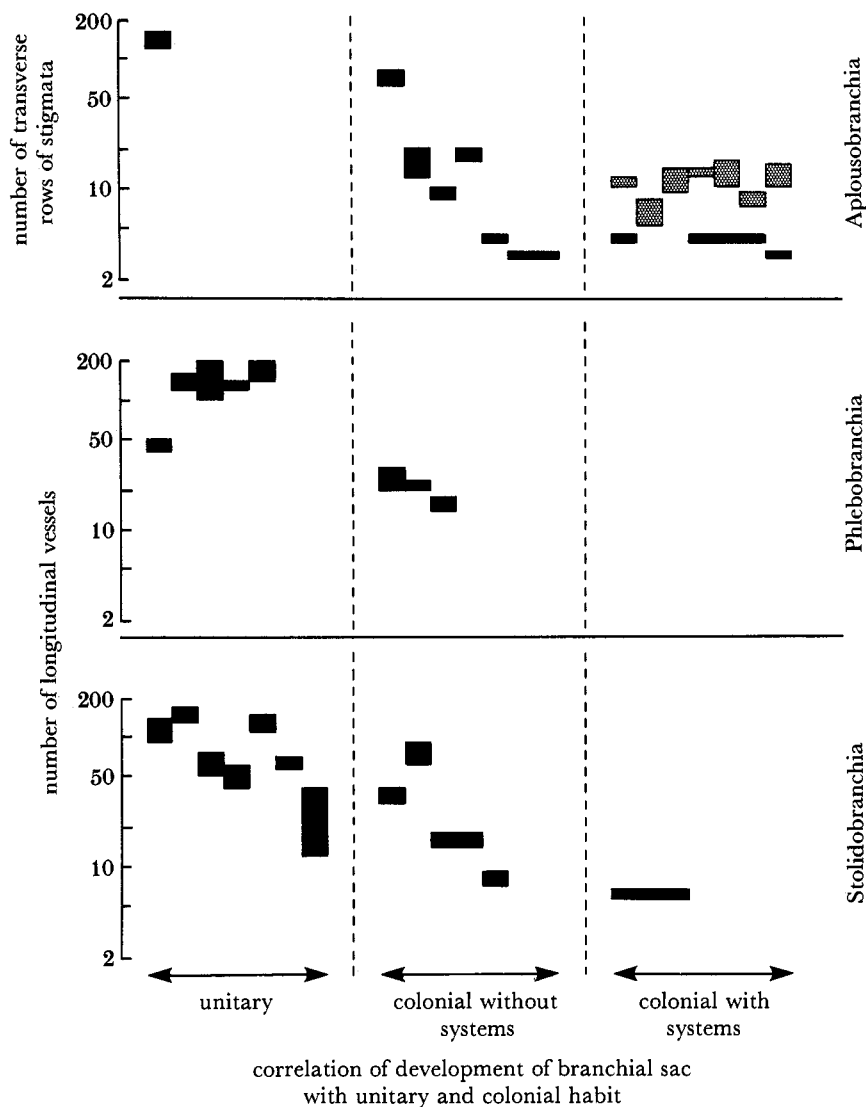


FIGURE 1. Correlation of the size of the branchial sac with habit in Ascidacea. The index of size in Aplousobranchia is the number of transverse rows of stigmata; in Phlebobranchia and Stolidobranchia it is the number of longitudinal vessels. Each column is based on one taxon, with measurements taken from the literature. In Aplousobranchia with systems, hatched columns represent polyclinid genera, black columns didemnid genera.

and that although the didemnid colony is characteristically a flat, spreading one (in Herbert Spencer's terms less integrated than the compact blobs of polyclinids), it is ecologically advantageous and in fact an advanced feature. Moreover, there is clearly colonial control over the regular fission and movement described in tropical didemnids (Ryland *et al.* 1984), although the mechanism is unknown. Overall we conclude that the ascidians provide a rather clear example of modular size decreasing as colonial integration increases. An important consequence of reduced zooid size, and possibly the chief advantage, is an accelerated rate of replication and colony growth.

MODULE SIZE AND DEGREE OF COLONIAL INTEGRATION
IN HYDROIDA THECATA

Naumov (1969) presented a table in which he correlated the number of rows of hydranths per branch with the degree of immersion of the hydrothecae in the colonial perisarc. He also indicated the degree of complexity of colonial ramification. This tabulation provides a suitable base for assessing the degree of colonial integration independently of zooid size. However, on grounds of level of polymorphism and the development of cormidia, the Plumulariidae (taken here as including aglaophenines) are arguably the best integrated thecate family. They do not display multiple rows of hydranths along the branches. Instead of Naumov's plotted correlation, therefore, type of hydrotheca was compared with branching pattern. A sample of 50 species in each of three groupings, namely Campanulinidae plus Campanulariidae plus Lafoeidae, Sertulariidae, and Plumulariidae, which together comprise a large proportion of all thecates, was taken from the literature (Naumov 1969; Millard 1975; Gibbons & Ryland 1986). Their hydrothecal and colonial characters are summarized in figure 2.

hydrothecae colony	pedicellate	sessile	under 50 % adnate or immersed	over 50 % adnate or immersed
monopodial growth point with ordered branching: pinnate, whorled, dichotomous or helicoid		▼ △	△□ △□ △□ △□ △□	△△△□□□■ △△△□□□■ △△△□□□■ △△△□□□■ △△△□□□■ △△△□□□■ △△△□□□■ △△△□□□■ △△△□□□■ △△△□□□■
monopodial growth point with single stem or irregularly arranged planar or arborescent branching	△	△	△△△□ △△△□ △△△□ △△△□ △△△□ △△△□ △△△□ △△△□ △△△□ △△△□	△△△□ △△△□ △△△□ △△△□ △△△□ △△△□ △△△□ △△△□ △△△□ △△△□
sympodial or monopodial with terminal hydranth: irregular branching with hydranths in single row	△○○ ▼○○ ▼○○ ▼○○ ▼○○ ▼○○ ▼○○ ▼○○ ▼○○ ▼○○	▼	▼	
stolonial	⊗○○▼ ⊗○○▼ ⊗○○▼ ⊗○○▼ ⊗○○ ⊗○○ ⊗○○ ⊗○○ ⊗○○ ⊗○○	⊗▼ ⊗▼		○ Campanulinidae and Campanulariidae ⊗ with medusa ▼ Lafoeidae △ Sertulariidae □ Plumulariidae ■ with phylactocarps or corbulac

FIGURE 2. Correlation of colony form and type of branching with the morphology of the hydrotheca in 150 species of Hydroida Thecata.

This diagrammatic tabulation shows clearly how simple colony forms and branching patterns are correlated both with pedicellate hydrothecae and the presence of a medusa: these are characteristic of campanulinids, campanulariids and lafoeids. Adnate or immersed hydrothecae are correlated with colonies that have monopodial growing points and ordered branching patterns: they are characteristic of sertulariids and plumulariids. However, the latter not only

are characterized by nematothecae and cormidia but, as indicated, frequently have special colonial reproductive structures (phylactocarps and corbulae). Taking all criteria together, this suggests an integrational series (Campanulinidae + Campanulariidae + Lafoeidae) < Sertulariidae < Plumulariidae. It is not suggested that the three families united by parentheses form a 'natural' group.

For assessing hydranth size, two indices seemed possible, neither entirely satisfactory. The

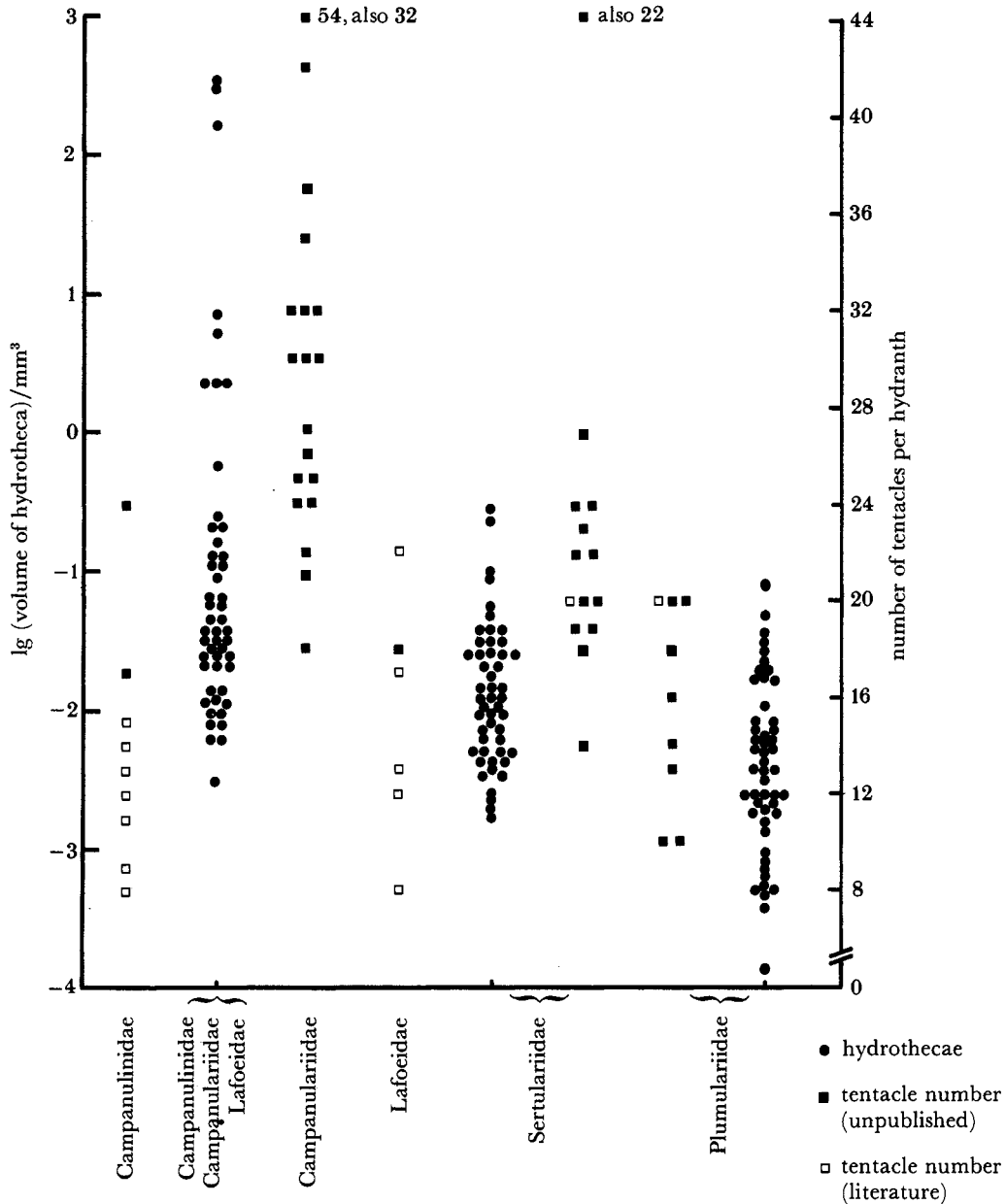


FIGURE 3. Indices of hydranth size in families of Hydroida Thecata. Solid circles (left ordinate) are estimates of hydrothecal volume based on published measurements for 150 species (as in figure 2). Squares (right ordinate) are mean tentacle numbers. Open squares represent numbers taken from the literature; solid squares are counts made by P. F. S. Cornelius or J. S. Ryland. Normally each species is represented by one point, but if two widely separated counts have been obtained for any nominal species, both are included.

first was an estimate, for the same 150 species, of mean hydrothecal volume, taken from published measurements and making appropriate allowances for geometry. One problem is that in certain thecates the hydranth does not fit into the hydrotheca. This particularly affects the Haleciidae, for which reason the family was excluded from the study, but it applies to some extent to the Plumulariidae. The second possibility was to use tentacle number. Unfortunately, contrary to the situation in Bryozoa, tentacle number is rarely included in taxonomic descriptions; when it is, the values may be inaccurate (P. F. S. Cornelius, personal communication) and, one suspects, sampling biased towards the lower end. This deficiency in the literature has been recognized by Cornelius (personal communication), who has been collecting data which have been made available and incorporated with our own into figure 3.

The results for hydrothecal volume appear unequivocal, the three ranges being well separated (Mann-Whitney *U*-test, $p \ll 0.01$). The very high values in the first group are attributable to a few species of *Bonneviella* (Bonneviellidae) also included. The tentacle counts appear more ambiguous. The three families in the first grouping have been separated and low numbers in the literature characterize Campanulinidae and Lafoeidae. For the Campanulariidae, Sertulariidae, and Plumulariidae, based mainly on original data, the distribution of numbers looks consistent with that of hydrothecal volumes. In *Aglaophenia*, one of the most advanced plumulariids, the number is always 10 (A. Svoboda, personal communication).

One other caution should be mentioned. The Plumulariidae are essentially a warm water, even tropical, family. A greater proportion of hydrothecal measurements was derived from Millard's (1975) southern African and Gibbons & Ryland's (1986) Fijian collections. It is well-known that the zooids in some colonial taxa are smaller in warm water; furthermore, water at 5 °C is 2.5 times as kinematically viscous as at 35 °C (Vogel 1981); a smaller hydranth in tropical waters, therefore, would not involve lower Reynolds numbers.

It is concluded that, with the possible exception of a few primitive forms, mean hydranth size in thecate hydroids does decrease as the level of integration increases. That this may incorporate a temperature-related effect in the Plumulariidae cannot be excluded.

MODULE SIZE AND DEGREE OF COLONIAL INTEGRATION IN BRYOZOA

In marine Bryozoa (freshwater Bryozoa are rather different and not treated here) the dimensions of the lophophore provide the indicator of size most appropriate for the present discussion. Several observers have counted the tentacles in expanded lophophores and tentacle number is well correlated with size in terms of bell diameter and height (Ryland 1975).

Tentacle number in marine Bryozoa ranges from 8 to nearly 40. Winston (1977) has reviewed feeding and her figure 2 summarizes the data on tentacle number for 212 species as histograms presented separately for five major taxa: orders Cyclostomata (class Stenolaemata), Ctenostomata Stolonifera, Ctenostomata Carnosa, Cheilostomata Anasca, and Cheilostomata Ascopora (all class Gymnolaemata). This breakdown to subordinal level precludes consideration of tentacle number in relation to states of integration within these major taxa, leaving us only zooid form and their degree of association. The most primitive zooid shape in these marine taxa, as in Phylactolaemata, appears to be cylindrical. This shape is preserved to the greatest extent in Cyclostomata and Ctenostomata Stolonifera, in the former often combined with crustose colonies but in the latter more commonly associated with spreading stolons or more compact mats of tall zooids. In these two taxa the lophophores are almost universally small,

commonly 8–10 tentacles and rarely exceeding 13. It seems reasonable to assume that this represents the primitive situation in marine bryozoans, and it is likely that eight tentacles represents the minimum from which an effective funnel can be constructed.

The carnose (commonly encrusting) Ctenostomata present a strikingly different range of numbers, with rather large lophophores of 14–25 tentacles predominating. The two cheilostome suborders display a wide range, with a rather flat mode of 11–16 in Anasca and 11–19 in Ascophora. The data pose a number of questions, some at present intractable; but we believe that there may be an explanation for the difference in size so dramatically apparent in these groups compared with Stolonifera. Many Carnosa and many Cheilostomata typically form compact encrusting colonies, which are rounded in outline, at least when young. Many such bryozoans live on substrata that become excessively crowded, with acute competition for space, with colonies being stopped or even overgrown by competitors (Gordon 1972; Stebbing 1973; Jackson 1977). There are no consistent winners in these communities (Stebbing 1973; Buss & Jackson 1979; Russ 1982; Rubin 1982).

An important contribution towards understanding mechanisms that might, in Bryozoa, be involved in determining the outcome of spatial encounters between species was made by Buss (1979a). He studied two anascan species, *Onychocella alula* (17 tentacles, funnel diameter 0.79 mm) and *Antropora tincta* (12 tentacles, 0.41 mm diameter). Buss was able to show that, at the interface between contiguous colonies of the two species, larger lophophores effectively interfered with the smaller, depriving them of food. This study has recently been developed by Best (1985), looking at the species inhabiting the *Fucus serratus* community earlier studied by Stebbing (1973). With carnosans *Flustrellidra hispida* (28–30 tentacles, funnel diameter 1.2 mm) and *Alcyonidium hirsutum* (17–18 tentacles, 0.77 mm diameter), the larger lophophores again overshadow the smaller. The capture of water by the marginal bells of *F. hispida* starves the immediately adjacent zooids of *A. hirsutum*, although there is enhanced feeding at a distance of four to five zooids from the edge, where the lophophores evidently benefit from the enhanced flow of water imperfectly cleared by *F. hispida*. These two investigations indicate that success in one kind of competition depends on having the larger lophophore. Clearly other factors are involved; for example, growth rate, in many cases, may be greater in species with smaller zooids (Buss 1979a). The angle at which opposing growing edges approach can be decisive (Rubin 1982), while longevity is another significant variable (Jackson & Winston 1981).

We consider that the stolonate life form is the more primitive in Ctenostomata, quick to colonize but less persistent (Buss 1979b; Jackson 1979): the guerilla strategy of Harper & Bell (1979). Small zooids are advantageous. Adopting an encrusting habit may confer greater permanence (the phalanx strategy of Harper & Bell). The most economical shape is circular, minimizing circumference to area, and ensuring that the front of the phalanx directly faces all potential competitors (see Rubin 1982). There are, we suggest, selective pressures favouring a larger lophophore, balancing energetic advantage against competitive success. It is interesting, in this context, to recall observations by Ryland (1975) on encrusting bryozoans in a rich habitat in New Zealand. The range of tentacle numbers over 43 species was 8–25. The mean was 13.9 and the coefficient of variation high (129%); for abundance, however, the mean tentacle number remained similar (14.6) but the coefficient of variation was dramatically reduced to 51%. The conclusion is that, in a competitive situation, species with either very small or very large lophophores are uncommon.

Competition directly involving the feeding apparatus does not occur in the major non-

bryozoan encrusters (sponges and modular ascidians), which instead rely on chemical defences (Jackson & Buss 1975; Buss 1976; Dyrinda 1985, this symposium). Allelochemicals, which are also found in bryozoans (Dyrinda 1986), are not confined to encrusting species since they are also used against predators and epizotes which equally attack erect species. Moreover, many other factors influence the success or failure of species in communities of bryozoans, ascidians and sponges. We have insufficient data to establish whether lophophores are smaller in well integrated erect bryozoans than in those of encrusting habit.

THE DISPOSITION OF ZOIDS IN COLONIES OF ENCRUSTING BRYOZOA

Of significance comparable to the size of modules is their disposition or arrangement in the colony. Zooids in suspension feeders may be organized with their filtering surfaces internal or external to the colony. Internal filterers, such as sponges and compound ascidians, may have their modules not evenly spaced but grouped around large exhalant openings, which facilitate enhanced filtration by passive means (Vogel 1974) and ensure that exhalant water is projected well clear of the inhalant apertures. External filterers may either be passive, as hydroids, Antipatharia and Octocorallia, or active, as Bryozoa and Calyssozoa. Passive filtration demands a colony organization, usually arborescent, that permits water to flow through it (and the integrational sequence we described above for hydroids clearly conforms to that). Active external filterers seem better adapted than passive filterers to exploit the encrusting form of growth, although, except when colonies are very small, excurrent pathways have to be provided (that is, the 'chimneys' of Bryozoa, see below). Other factors being equal it would seem necessary to arrange the zooids in such way as to maximize filtration area.

Assume, in marine Bryozoa, that lophophore funnel tops are circular in outline and essentially non-overlapping. If the zooids were square, of dimensions equal to the lophophore diameter, and in regular transverse rows, then the lophophores would be square-packed and each have an area 78.54% that of its zooid. If, on the other hand, the zooids were regular hexagons, zooids (and lophophores) would be in alternating rows, and each lophophore would cover 90.69% of its zooid (figure 179 in Thompson (1942)). Zooids with a regularly hexagonal frontal area are uncommon among living Bryozoa, and improbable among encrusting forms in which, to accommodate the retracted polypide, length typically exceeds width. Hexagonal (close) packing of lophophores can still be achieved with alternating (quincuncial), rectangular zooids, but only a limited number of shapes is possible. It can be shown that (J. P. Thorpe, personal communication) for a lophophore of top diameter D , the rectangle length l , and the width w , are given by

$$l = D[(n + 0.5)^2 + (\cos 30^\circ)^2]^{0.5}$$

$$w = (1.5 \tan 30^\circ)/l,$$

where $n = 0, 1, 2, \dots, \infty$.

Thus for a lophophore of unit top diameter the only probable zooid sizes are 1×0.866 , 1.732×0.5 and 2.165×0.4 units. Observation suggests that zooids of these dimensions (figure 4, centre, left and right, respectively) are characteristic of *Schizoporella unicornis* and most cheilostomes, *Membranipora membranacea* and several flustrines, and various cyclostomes, respectively. Elongate hexagons (figure 4), diamonds or linguiform shapes that pack contiguously can be regarded as rectangles having the same length and same mean width.

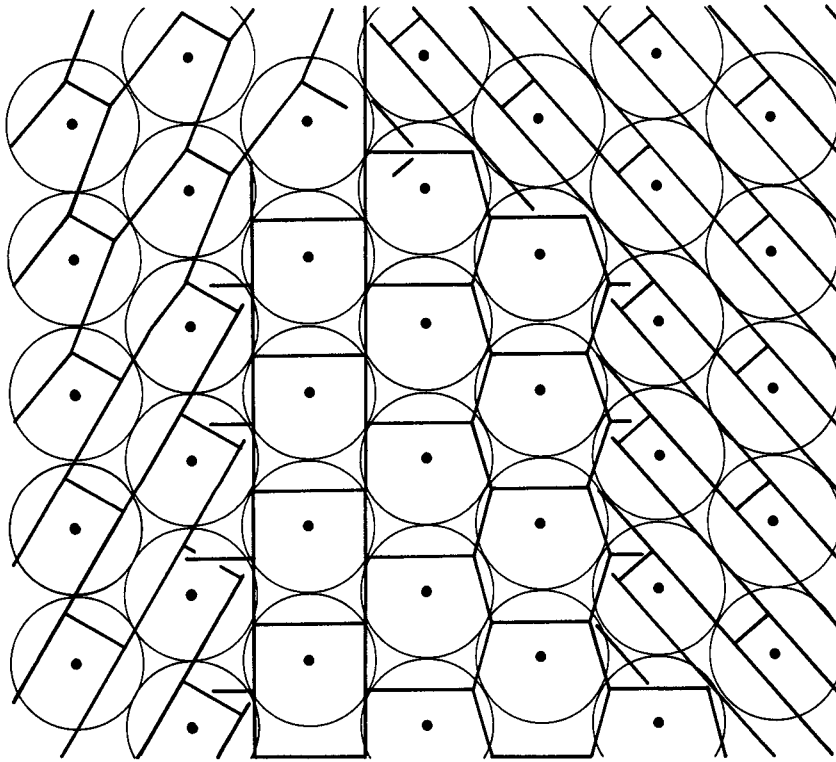


FIGURE 4. Possible zooid shapes in Bryozoa assuming close packing of lophophores. Circles represent the funnel top diameter of close-packed lophophores assuming no overlap. Solid dots indicate the mouth and also the centre of the orifice of the bearing zooid. Three basic zooid shapes (left, centre and right) have been fitted to the single size of lophophore: all shapes necessarily have the same area, 1.10 times greater than that of the lophophore, and are quincuncially arranged. The zooid outlines can be rectangles, hexagons or other shapes that pack contiguously and are reducible to a rectangle of the same length and same mean width. For a lophophore of unit diameter, the centre zooids have dimensions 1×0.87 , the zooids to the left 1.72×0.5 , and the zooids to the right 2.17×0.4 .

Only one data set suitable for testing these predictions has been published (Winston 1979). For 16 encrusting species approximating the first relationship, zooid width averages 0.6 times the length, rather than the predicted 0.87; and lophophore area averages 1.45 times the zooid area (1.32 times if *Celleporaria brunnea*, in which the factor is 3.58, is excluded). To provide a second data set, zooid dimensions have been measured in 21 encrusting cheilostome species from the reef flat at Leigh, New Zealand, source of the lophophore measurements earlier published (table 1 in Ryland 1975). Lophophore area averages 1.10 times zooid area if the whole sample is used, 0.97 times if restricted to the 13 species for which a full set of measurements was obtained (table 1). These ratios are moderately close to those derived from Winston's (1979) data, if the anomalous *C. brunnea* is excluded, and seem consistent with the degree of lophophore interdigitation which observation reveals. Zooid width averages about 0.6 times length, as in Winston, leading to the conclusion that lophophores must be imperfectly close-packed. Perhaps accommodation of the retracted lophophore requires zooids to be about 1.6 times long as wide; or, the average proportions are a function of the maximum zooid width which, in circular colonies, precedes bifurcation of a zooid row. In addition, the outline of lophophores in some species departs from circularity (Ryland 1975), in conformity with the slender proportions of zooids. Further investigation is required to elucidate the explanation.

TABLE 1. DIMENSIONS OF ZOOIDS AND LOPHOPHORES IN ENCRUSTING CHEILOSTOME BRYOZOA FROM THE REEF FLAT AT LEIGH, NORTH ISLAND OF NEW ZEALAND

(Lophophore diameters are from Ryland (1975); asterisked numbers are estimated from tentacle number (correlation in Ryland 1975). Zooid measurements \pm standard deviation are based on ten counts for each of five colonies unless a smaller number is indicated by the species name.)

	zooid average			lophophore	
	zooid length	width	zooid area	diameter	area
	μm	μm	mm^2	μm	mm^2
<i>Calloporina angustipora</i>	460 \pm 62	264 \pm 39	0.123	406	0.129
<i>Chaperia acanthina</i>	564 \pm 46	376 \pm 39	0.212	514	0.207
<i>C. cervicornis</i> (1)	474 \pm 25	304 \pm 32	0.144	586	0.270
<i>Crassimarginatella papulifera</i>	558 \pm 36	363 \pm 29	0.203	437	0.150
<i>Crepidacantha crenispina</i>	418 \pm 34	305 \pm 26	0.128	390	0.119
<i>Escharoides angela</i>	778 \pm 69	382 \pm 34	0.297	488	0.187
<i>E. excavata</i>	773 \pm 81	380 \pm 27	0.293	554	0.241
<i>Eurystomella foraminigera</i> (2)	572 \pm 72	268 \pm 22	0.142	530	0.221
<i>Exochella tricuspis</i>	390 \pm 42	196 \pm 17	0.077	350	0.096
<i>Fenestrulina thyreophora</i>	418 \pm 28	298 \pm 22	0.126	428	0.144
<i>Hippopodina adpressa</i>	520 \pm 73	269 \pm 26	0.141	442	0.153
<i>Hippothoa tongima</i> (= sp. C)	404 \pm 40	206 \pm 35	0.084	347*	0.094*
<i>Macropora grandis</i> (3)	1140 \pm 79	673 \pm 58	0.766	980	0.754
<i>Micropora mortenseni</i>	510 \pm 72	294 \pm 30	0.150	443	0.154
<i>Odontionella cyclops</i> (1)	592 \pm 65	302 \pm 18	0.179	595*	0.278*
<i>Osthimosia bicornis</i> (2)	392 \pm 50	228 \pm 12	0.089	431	0.146
<i>Retevirgula acuta</i> (3)	514 \pm 33	282 \pm 40	0.146	455	0.163
<i>Schizomavella immersa</i>	488 \pm 50	274 \pm 32	0.134	421	0.139
<i>Smittina torques</i>	512 \pm 60	230 \pm 34	0.120	393	0.121
<i>Steginoporella neozelanica</i>	857 \pm 78	548 \pm 42	0.471	842	0.557
<i>Umbonula bicuspis</i> (2)	666 \pm 88	293 \pm 52	0.196	631	0.313
overall mean (all species: $n = 21$)	569	321	0.201	470	0.221
(full data sets only: $n = 13$)	557	321	0.190	508	0.184

Much of the apparent variability in the appearance of the zooids of encrusting bryozoans, therefore, is related to size and is inseparable from the dimensions of the lophophore, though combined with variations on a small number of clearly defined basic rectangles. Square packing rarely occurs in cheilostomes: the presumed phenotype *Electra pilosa* f. *verticillata* (Ryland & Hayward 1977, figure 22), on filamentous algae, is one well-categorized exception. Among ctenostomes *Metalcyonidium gautieri* (Hayward 1985, figure 17), a minute erect form, has its zooids similarly in whorls. The Cyclostomata as a group, on the other hand, have definitely evolved away from hexagonally packed zooids. Why?

Harmelin (1976) described a number of evolutionary trends recognizable in three families of Tubuliporina (a suborder of Cyclostomata). In so far as these are colonial characters, he noted (i) a progression from uniserial (*Stomatopora*-like) to multiseriate growth: (ii) a tendency toward upright habit; and (iii) trends toward the grouping of zooids. In circular or lobate multiseriate colonies the most primitive arrangement of zooid erect portions (peristomes) seems to be quincuncial, such that the lophophores are close-packed. Especially in Tubuliporidae, however, this arrangement is superseded by the local fusion of peristomes to form short transverse rows, usually alternating to the left and right of the growth axis (Harmelin 1976, figure 1 and plate 1, figure 4; Hayward & Ryland 1985, figures 24, 26 and 31). In species that produce the largest colonies such connate rows may become multiseriate fascicles. The colonies in Diastoporidae develop a circular, rather than elongate, outline, and the connate

rows, when present, are radial. Significantly, this development is seen also in Lichenoporidae, a quite unrelated cyclostome family with circular colonies. Here, too, the final state, as in *Coronopora*, is with radial fascicles (Hayward & Ryland 1985, figure 47). Extensive colonies, as sometimes found in *Disporella hispida*, may be polycentric, with several mammillae bearing radiating lines of peristomes. When feeding, as shown by Cook (1977) and Winston (1978), excurrent water flows centripetally between the rows, and exits from the summit, which is devoid of zooids. The analogous circulation in tubuliporids would produce medial venting, though in taxa in which peristome height increases from the midline laterally (for example, *Nevianopora*), the circulation could well be reversed: observations here are needed.

Excurrent chimneys in cheilostomes may be associated with morphological features of the colony, as in *Celleporaria* (Winston 1978) and *Hippoporida* (Cook 1977; Ryland 1979), in which chimneys coincide with the summits of mammillae. This is also likely to be true in *Discoporella*, although unambiguous evidence is lacking (Winston 1978; Chimonides & Cook 1981). Extensive encrusting colonies of many other cheilostomes and carnosate ctenostomes display chimneys that are less obviously associated with skeletal morphology (Banta *et al.* 1974; Winston 1978; Cook 1979; Cook & Chimonides 1980; Lidgard 1981). Although some kind of heterozoid may here be involved, the formation of chimneys of any kind always seems to involve distinctive asymmetry (whether ontogenetic or behavioural) of the lophophore and a precise arrangement of zooids showing this asymmetry, implying some kind of coordination (Cook 1979). The extent of colonial feeding patterns in cheilostomes is positively correlated with the degree of integration inferred from their colonial morphology (McKinney 1984). Some at least of the species (or ones closely related to them) are known to have well developed colonial nervous systems (Lutaud 1977), although it is not known whether these are involved in coordination of this kind. The structure of interzooidal communication pores in cyclostomes (Nielsen & Pedersen 1979) seems poorly developed in comparison with cheilostomes (Banta 1969; Lutaud 1979a), and colonial nerves have not convincingly been demonstrated (Lutaud 1979b). It is therefore possible that, either on account of their incomplete protrusion (see below) or for reasons associated with poor coordination, cyclostome lophophores are unable to posture in the manner required to produce chimneys. Certainly we are unaware of reports of excurrent chimneys in cyclostomes having quincuncially arranged peristomes. An alternative possibility is that, since cyclostome lophophores do not project fully from the peristomes during feeding (Ryland 1975), there are direct hydrodynamic advantages to be gained from the replacement of quincuncial peristomes by connate or fasciculated rows.

Further investigation is again required.

FORM AND FUNCTION IN ERECT COLONIES

Jackson (1979) regarded the erect 'tree-like' growth form in colonial animals as a high-risk strategy owing to its dependence on a small attachment area. However, an erect growth form has two clear advantages: it permits partial escape from the competition among encrusters (see, for example, Sebens 1982b), and it allows greater exploitation of the water column for suspension feeding. The rate of flow in the water column is reduced by friction with the substratum; encrusters inhabit a boundary layer sheltered from mainstream flow, but the taller an erect colony becomes, the more it projects into mainstream flow and the greater the range of flow rates that it experiences (Okamura 1984, 1985).

The ambient water flow has important influences on the form and function of erect colonies. There are two main effects of flow. Of primary importance to suspension-feeding organisms is the delivery of food by flowing water. Second, flow imposes drag forces on erect colonies. These two effects are closely connected because the mechanisms of food particle deposition on to the feeding surfaces depend on the pattern of water flow (Rubenstein & Koehl 1977; LaBarbera 1984) which, in turn, depends on the orientation and other properties of the colony. In this section we describe the influences of water flow on orientation, growth forms and feeding mechanisms, concentrating mainly on non-coralline, passive suspension feeding coelenterates such as hydroids, octocorals and antipatharians (those octocorals and scleractinians which derive nutrition from symbiotic zooxanthellae are excluded because the requirements of photosynthesis impose conflicting influences on colony and module form and function). The discussion leads us to an environmental interpretation of the inverse correlation described above (figures 2 and 3) between the degree of integration and module size.

Feeding efficiency, drag and planar orientation

The efficiency of particle capture in biological systems is best seen in relation to metabolic cost rather than just to clearance of a filtered volume. If metabolic cost is constant over time, t , and directly proportional to mass of living tissue, m , the efficiency can be expressed as $Pt^{-1}m^{-1}$, where P is the number of trapped particles of diameter d . Clearly the efficiency will vary with the characteristics of the filter, being more efficient at some particle diameters than at others (LaBarbera 1984; Okamura 1985), and with the rate at which particles are delivered to the filter. In passive suspension feeders the particle delivery rate is proportional to, but not the same as, the flow rate in the environment since the filter resists the flow (Vogel 1981).

Erect growth forms contend with both environmental and structural constraints on their efficiency. A measure of the extent to which the surface area is exposed to water flow is the drag, in this case pressure drag (Vogel 1981). In directional currents such as those produced by wave surge or tidal flow, growth forms are often planar, pinnate or fan-shaped, with the plane normal to the flow (see Riedl (1971) for review). This orientation maximizes drag by exposing the maximum surface area to the maximum volume of flowing water. Experimental evidence that this orientation also maximizes particle capture was provided by Levesee (1976). Factors that increase drag in normally oriented planar colonies include increasing flow rate and increasing surface (that is, number and length of branches). To retain a perpendicular orientation with increasing drag, skeletal strengthening is required.

Flat planar colonies are unusual among erect Bryozoa, perhaps because active filtration reduces the dependence on orientation normal to the water flow or because they are more adapted to situations subject to turbulence or multidirectional flow. In *Petralia*, however, rigid fenestrate fans are supported by clustered rhizoids arising from the lower zooids. The frond may be flat or concave, with the zooids opening only on the concave face (cf. discussion below). *Petralia* is found in conditions of moderate current. *Adeona* also has rigid, fenestrate colonies, but the fans are bilaminar and supported by a stout, transversely corrugated, flexible stem. Non-fenestrate bilaminar pedunculate fans occur in *Celleporaria* and *Parmularia*. Observations on the ecology and responses to flow of these bryozoans would be useful.

Colony flexibility

Most erect non-coralline colonies are flexible. Increasing drag therefore causes bending, the extent depending on the balance of drag and skeletal properties. Bending moderates the increased drag since it reduces the surface exposed to mainstream flow. Reduction of drag by bending has evident importance in extreme environments since it is better to bend than to break. The stems of some shallow-water gorgonians are shaped to facilitate bending in response to the risk of detachment by storm waves (Wainwright & Koehl 1976). In other gorgonians (Muzik & Wainwright 1977) and in some antipatharians from deeper water (Warner 1981) the stems are shaped to resist bending, probably in response to a reduced risk of excessive water movement.

Avoidance of breakage is not, however, the only function of flexibility. In the pinnate hydroid *Abietenaria* the detachment strength of normal flexible colonies is sufficient to resist the drag imposed by impossibly high flow rates (up to 150 m s^{-1}) (Harvell & LaBarbera 1985). Even artificially stiffened colonies were not detached by flows of up to 5 m s^{-1} . Harvell & LaBarbera (1985) measured flow rates adjacent to the polyps of *Abietenaria* over a range of experimental mainstream velocities. They found that the range of actual velocities experienced in normal flexible colonies was less than in artificially stiffened colonies, because the normal colonies bent out of the faster mainstream flows. They suggested that the function of the flexibility of this hydroid was the maintenance of a particular flow régime around the polyps which was optimal for feeding.

Mechanisms of passive filtration

As well as bending the entire colony, increased flow may bend the filtering elements, for example, the polyps and their tentacles (Riedl & Forstner 1968; Patterson 1984). According to LaBarbera (1984), the sizes of the filtering elements of most passive suspension feeders are such that under environmental flow rates they operate at a low Reynolds number (Re) in conditions of laminar flow; the drag that they experience is therefore mostly skin friction (Vogel 1981). Biological filtration at the small-scale level of the filtering elements has been discussed by Rubenstein & Koehl (1977) and LaBarbera (1984). Their analyses show that 'sieving' (capturing only particles that are larger than the spaces between the filtering elements) is less important than 'aerosol filtration' (capturing smaller particles in addition), and that the commonest aerosol mechanism of particle capture by erect passive suspension feeders is the direct interception of particles by filtering fibres (for example, tentacles) oriented perpendicular to the flow. Direct observation and close-up underwater photography have confirmed that the tentacles of planar hydroids are usually oriented normal to the flow (Warner 1977). In conditions of laminar flow, far less water is intercepted by a tentacle bent parallel to the current than by one normal to it. Unless the particles are independently motile (motile particle deposition: Rubenstein & Koehl (1977)), the number intercepted and therefore captured is similarly reduced. Erect passive suspension feeders which feed in fast currents therefore benefit from any modification that limits the bending of their filtering elements. Reduction in tentacle length is a simple and evident example, and is also a normal consequence of a reduction in zooid size.

Adhesion and downstream capture

An essential assumption of aerosol filtration theory is that particles adhere to the filter on contact (Rubenstein & Koehl 1977; LaBarbera 1984). In coelenterates, capture and adhesion is achieved through cnidae or mucous secretions. Forces that oppose adhesion include intrinsic mobility of the captured particle (for example, live zooplankton) and skin frictional drag where the particle projects from the surface of the filtering element. Drag increases with particle size and increasing water velocity, leading to loss of adhesion and reducing particle capture efficiency at increased current speeds, especially for larger particles. Riedl & Forstner (1968) pointed out that gorgonian polyps projecting laterally are bent by faster currents into an environment behind the supporting skeleton in which current speed is reduced and turbulent eddies are present. They suggested that adhesion of particles to tentacles (that is, particle capture) is more effective in slowly moving eddies than in faster mainstream flow. Thus bending of polyps into downstream eddies compensates for the loss of a perpendicular orientation and increases the range of environmental current speeds over which feeding is possible. The effect of the bending of these polyps is therefore analogous to that of the bending of the whole colony of the hydroid *Abietenaria* mentioned above.

Eddies are present on the downstream sides of colonies because, although the filtering elements operate at low Re in largely laminar flow (LaBarbera 1984), the entire colony operates at high Re and is subject to pressure drag (Wainwright & Koehl 1976; Vogel 1981). The presence of downstream eddies in antipatharians at environmental current speeds has been confirmed by direct observation (Warner 1977, 1981). Lasker (1981) observed greater capture rates by downstream polyps of the gorgonian *Bryarium* in a flow tank; the food particles (*Artemia* cysts) were detached from upstream polyps by the current and were made available to downstream polyps by the eddies. A similar result was obtained in an arborescent bryozoan by Okamura (1984), who found that in slow currents upstream zooids captured more particles, but that in fast currents zooids in the central regions of the bushy colonies achieved greater feeding success. In flow tank experiments with the octocoral *Alcyonium siderum* (short cylindrical growth forms), Patterson (1984) found that in slow smooth flow (2.5 cm s^{-1}) upstream polyps caught more food particles, but in fast smooth flow (19 cm s^{-1}) downstream polyps caught more. In 'rough' (containing turbulence) flow however, there was no upstream-downstream asymmetry in catch rate over a range of current velocities.

Downstream orientation in planar colonies

Since in faster flow downstream zooids often achieve greater feeding success than upstream zooids, it is advantageous to colonies inhabiting environments with fast ambient flow to place most or all of their zooids on the downstream sides of their skeletal supports.

However, the directional currents to which planar suspension feeders are exposed are often oscillating, that is, produced by waves or tides. Since these modular organisms are mainly sessile on hard substrata, downstream placement is not always feasible. Apart from the bending of polyps described by Riedl & Forstner (1968), two other possibilities exist: living in unidirectional currents, or reorientation when the current changes.

Mainly unidirectional flow can occur at sites exposed to oceanic currents, or where local conditions cause a preponderance of tidal or wave-driven water to go in one direction. In coral ecosystems water flow may be unidirectional and incursive across the reef, with abundant

hydroids appropriately oriented in the flow channels; outflow takes place through passes between the reefs (Penn 1983; Dilly & Ryland 1985; Gibbons & Ryland 1986). Unidirectional currents are also experienced by species which grow epizoically on flexible substrata (Warner 1977; Hughes 1980). Observations of planar organisms in mainly unidirectional currents have revealed examples with downstream placement of modules. Bilaterally symmetrical pinnate hydroids such as *Aglaophenia*, *Plumularia* and *Thecocarpus* are shallowly V-shaped in cross-section and the more streamlined dorsal side of each pinnate fan faces the current. The hydranths arise on the ventral side and face downstream (Svoboda 1976; Warner 1977; Hughes 1980). Svoboda (1976) placed colonies of *Aglaophenia picardi* in a flow tank oriented so that the pinnate fans were parallel to the current; he found that these fans were resorbed and new fans grown which reinstated the normal orientation with the dorsal sides facing the current. In gorgonians, downstream placement of polyps was observed by Muzik & Wainwright (1977) in fan-shaped colonies of *Melithaea* growing in channels through a coral reef. Most species of fan-shaped antipatharians studied by Warner (1977, 1981) showed downstream placement of polyps in mainly unidirectional flow resulting from an oceanic current.

Passive reorientation occurs when colonies can twist or bend so that the same aspect of the filtering surface is presented to the current, whatever its direction. Hydroids such as *Hydrallmania*, which support several bilaterally symmetrical pinnate fans projecting at right angles from a central flexible hydrocaulus, passively reorient by bending. The current always strikes the dorsal aspects of the fans and the hydranths face ventrally downstream (Warner 1977). Single bilaterally symmetrical pinnate hydroid fans also reorient to some extent by twisting. In two species of *Aglaophenia*, *A. harpago* (Svoboda 1973, personal communication) and *A. pluma* (N. G. Cartwright, personal communication), a hinge formed by an oblique constriction at the base of the fan appears to facilitate twisting. Hinge joints of this type are a characteristic feature at the base of the unbranched stems of various sertularian genera (for example, *Dynamena*, *Sertularia*: Millard (1975)). Bilaterally symmetrical pennatulids also orient with their polyps facing downstream; they reorient, probably actively, when the current changes (Magnus 1966; Svoboda 1976).

Dish-shaped planar colonies

A further refinement of colony morphology is possible in unidirectional currents. In a flat planar colony subject to pressure drag, approaching streamlines diverge and spill past the edges at angles of less than 90°. Recurving the edges of the colony into a dish-shape, to achieve an orientation normal to the streamlines, increases particle capture, as was demonstrated empirically by Warner (1977). The effect is due to the greater amount of water intercepted, and is necessarily associated with an increase in pressure drag. It can be predicted that the recurvature to achieve a normal orientation to divergent streamlines is proportional to the resistance to flow of the colony (that is, the branching density) and to the rate of flow. Antipatharians and gorgonians growing in unidirectional currents form parabolic dishes with the concave side facing the current (Muzik & Wainwright 1977; Warner 1977, 1981), and in bilaterally symmetrical pinnate hydroids the hydrocaulus and hydrocladia are often recurved dorsally, into the current (Warner 1977). Dish-shaped orientations also occur in unitary passive suspension feeders such as stalked crinoids and basket stars (Meyer 1982; Warner 1982).

Non-planar colonies

In contrast to planar morphology is the bushy or arborescent growth form, found in representatives of colonial coelenterates, sponges and bryozoans. Within this growth form are various grades of integration from the irregular branching of many campanularian hydroids to the ordered spirals of some species of *Sertularia* and *Bugula*. These bushy forms are adapted to environments in which water movement is multidirectional or turbulent (Riedl 1971; Warner 1977). In such environments normally planar species have been found to adopt bushy growth forms (Velimirov 1973). Planar colonies in multidirectional flow are not optimally oriented for maximum feeding success, and in addition they experience twisting stresses (Wainwright & Dylan 1969) which increases the risk of breakage. A bushy morphology avoids twisting and is equally well oriented to the flow whatever the current direction. (In bushy gorgonians and branching scleractinians, which contain zooxanthellae, the growth form is adapted to harvest light as well as to capture suspended particles.)

Colony form in the active suspension-feeding Bryozoa involves great hydrodynamic complexity, in part because planar branch morphologies may become organized during growth into spirals and other non-planar shapes (McKinney 1981; Cheetham & Hayek 1983). Branches are generally narrow, whether joined by bridges or not, to permit water to flow between them. Such forms may be rigidly calcified (Cheetham & Thomsen 1981) and dependent for strength on thickening towards the base of the branches and colony; others achieve flexibility either by the lightness of the calcification (*Bugula*, *Caberea*, *Euthyrisella*, *Flustra*) or by having non-calcified joints separating rigid internodes (*Cellaria*, *Crisia*, *Margaretta*, *Scrupocellaria*). Both rigid and flexible frondose colonies may be bilaminar but in those with unilaminar, non-cylindrical branches, the lophophores are, with few exceptions, directed inwards, as in the spiralling *Bugula* and most scroll-like reteporids. Cheetham & Hayek (1983) have shown that adherence to a restricted range of branching angles and link lengths (distances between successive bifurcations) minimizes branch interference in late growth stages, providing space for protruded lophophores to function. Such non-planar colony morphologies are adapted not only to multidirectional flow situations but to variable velocities, which will favour lophophores situated in different regions of the colony, over a range of ambient flow régimes (Okamura 1984).

Module size and colony integration

Two points in the foregoing discussion bear on the question of module size in passive suspension feeders. First, smaller polyps with shorter tentacles are less easily bent into a parallel (unfavourable) orientation to the current. Second, smaller food particles are less easily detached from the tentacles by the current. Thus in faster currents it is expected that polyps should be small and should feed on small particles. This conclusion extends those of Sebens (1979) by including the effects of flow on the filter structure and on adhesion. A further extension can be made by considering the nature of food particles. Live zooplankton forms an important part of the diet of all passive suspension-feeding coelenterates (Lewis 1978, 1982; Warner 1981; Sebens & Koehl 1984) and live zooplankters are motile particles. The incidence of motile particle deposition as a mechanism of aerosol filtration increases with decreasing current speed at the expense of direct interception (Rubenstein & Koehl 1977). With decreasing flow the delivery rate of all particles decreases, but the delivery rate of larger zooplankters decreases least because of their motility; it therefore becomes advantageous at reduced current speed to concentrate on the capture of larger zooplankters, using larger polyps.

A final extension of this argument involves colony form. If motile particle deposition is important at lower current speeds, a planar colony form is less important since particles can move between streamlines; colonies therefore become more bushy as current speed decreases. It is also the case that multidirectional flow, the condition associated with bushy growth forms, is rarely encountered in exposed locations (except in the special conditions directly beneath breaking waves); it is more usually observed as turbulence behind some sheltering topographical feature (Warner & Woodley 1975; Meyer 1979; see discussion by Patterson 1984). Thus, combining the arguments presented here, it is expected that in slow, multidirectional-flow colonies should be bushy and polyps large. In faster, directional-flow colonies should be planar and polyps small. The two ends of the spectrum of integration of colony form in hydroids (figure 2) therefore partly represent, on the one hand a disordered response to the disordered nature of large motile particles and slow turbulent flow, and on the other hand an ordered response to the ordered nature of fast directional flow. It is noteworthy that Meyer (1979) came to the same conclusion with respect to a series of crinoid species inhabiting a coral reef. In these unitary passive suspension feeders the filtering modules are the tube feet, and the arms and pinnules may be held in either bushy or planar array (Meyer 1982).

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