

Metabolic Implications of Modularity: Studies on the Respiration and Growth of *Electra pilosa*

D. J. Hughes and R. N. Hughes

Phil. Trans. R. Soc. Lond. B 1986 **313**, 23-29

doi: 10.1098/rstb.1986.0023

References

Article cited in:

<http://rstb.royalsocietypublishing.org/content/313/1159/23#related-urls>

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

Metabolic implications of modularity: studies on the respiration and growth of *Electra pilosa*

BY D. J. HUGHES AND R. N. HUGHES

School of Animal Biology, University College of North Wales, Bangor, Gwynedd LL57 2UW, U.K.

The mass-specific respiration rate of *Electra pilosa* is independent of colony size and therefore there is no allometric metabolic constraint on colonial growth rate (modular iteration). Budding, however, is confined to peripheral zooids and so the amount of meristem per unit area of colony declines as the colony grows. Hence the rate of zooid production per individual is a decreasing function of colony size. *E. pilosa* partly compensates for this, first by increasing the budding rate of peripheral zooids as the colony grows and second by expanding the peripheral meristem into lobes.

Among colonial invertebrates, a modular construction frees colonies from metabolic allometry and if modules retain their capacity for replication these may accumulate exponentially until restrained by extrinsic factors. Encrusting forms with strictly two-dimensional growth, however, are constrained by the peripheral location of the budding zone. This may be alleviated by faster budding, perhaps as a result of nutritional subsidies as the colony grows, and by departure from a circular shape.

INTRODUCTION

The negative allometric relationship between metabolic rate and body mass is a fundamental property of most organisms that increase in size volumetrically (Hemmingsen 1961). As a rule, therefore, larger organisms metabolize more slowly than smaller ones and this might be expected to influence their growth and reproductive rates. Mass-specific metabolic rate has an allometric exponent of about -0.25 over the several orders of magnitude in body mass covered by interspecific comparisons and whereas intraspecific values may differ significantly from the norm, the exponent is always negative. Organisms expanding volumetrically, therefore, are destined to grow progressively more slowly once beyond the embryonic or juvenile stages (Bertalanffy 1960).

Modular colonial organisms such as hydroids, corals and bryozoans present an exception. As a result of fission or budding, genetically identical modules are added to the colony, increasing its biomass. Each module (polyp or zooid) is probably of a size optimizing its functional capacities. Consequently the variance of modular size within a colony is likely to be small: among Caribbean corals, for example, the coefficient of variation for polyp diameter within colonies is usually less than 10% (Lehman & Porter 1973); bryozoans may adjust the number of tentacles on the lophophore in response to microenvironmental conditions (Thorpe *et al.* 1986) but this represents only a slight variation on zooidal biomass. Yet by modular iteration, the colonial organism can increase its total biomass far beyond the constraints operating on the modules themselves (Hughes & Cancino 1985).

Many colonial benthic invertebrates live on ephemeral substrata or in situations of intense competition for space (Connell 1973; Ryland 1976, 1981; Buss 1979; Jackson 1979), so mechanisms avoiding constraints on the rate of modular iteration could be selectively

advantageous. It is of interest to know, therefore, whether modular metabolic rate is an allometric function of colonial biomass, following the trend of most non-modular organisms, or whether it is independent of colonial biomass, without constraint on growth rate. To investigate these questions, the respiration rate and the rate of zooidal accumulation were measured in different sized colonies of the encrusting cheilostome bryozoan *Electra pilosa* (L.), a modular colonial animal with monomorphic zooids (Ryland & Hayward 1977) which normally buds only distally and distolaterally, producing on plane surfaces a simple two-dimensional structure (proximal and proximolateral buds can occur following lesion of the colony).

MATERIALS AND METHODS

Larvae of *Electra pilosa* were allowed to settle naturally on glass microscope slides held in a Perspex rack suspended in the Menai Straits. Superfluous colonies and other fouling organisms were periodically scraped away. Colonies brought into the laboratory, from January to July, 1984, were acclimatized to 15 °C over two days and the encrusted slides cleaned of small fouling organisms and detritus. To measure colonial respiration rate, a circular Perspex chamber, 5 mm deep, was fitted round the downward-facing colony and sealed to the microscope slide with silicone grease (figure 1). Chambers of different diameters were used for different sized colonies,

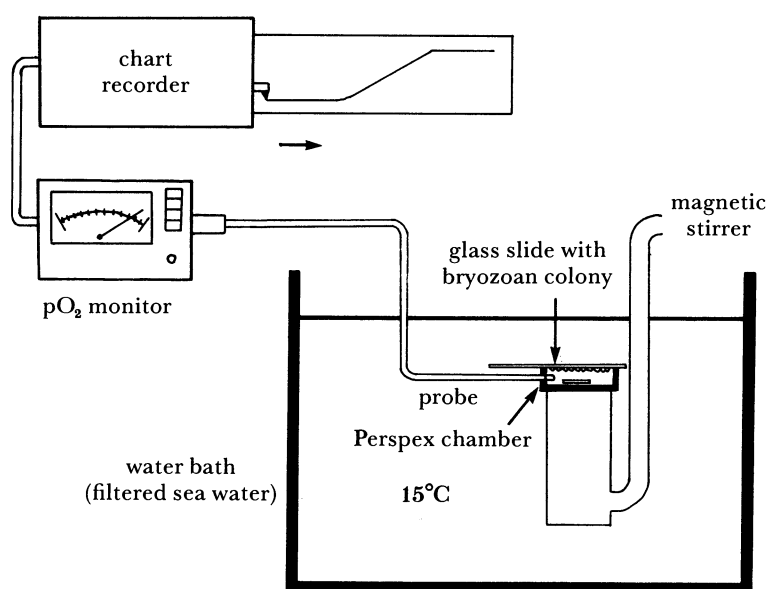


FIGURE 1. Diagram showing the apparatus used in the respirometry experiments.

keeping the working volume to a minimum in all cases. Circulation within the chamber was achieved with a magnetic stirrer and the oxygen tension of the initially saturated, filtered seawater was monitored with a Searle oxygen electrode, passing through a 2 mm hole in the wall of the chamber, and connected via a pO₂ monitor to a chart recorder. As a control, the procedure was repeated after moving the respiration chamber to an area of the slide adjacent to the colony. The colony was subsequently scraped from the slide, dried at 60 °C for 24 h, weighed, ashed at 500 °C for 6 h and reweighed.

To measure colonial growth rates during June 1983, 76 colonies on microscope slides were individually placed in a chamber of recirculating, cooled seawater, mounted on the stage of a Wild dissecting microscope (Cancino 1983) and drawn by using a camera lucida. The colonies were redrawn after replacement in the sea for 14 days. Above a size of 1000 zooids, only the perimeter of each colony was measured, the total number of zooids being predicted from a regression of zooid number on colony area (figure 3*a*). Perimeters and areas were measured from the drawings by using a microcomputer with digitizer.

RESULTS

Respiration

Colonies of *Electra pilosa* consumed oxygen more slowly as it was depleted from the water, but at oxygen tensions above 90% saturation colonies consumed $1.77 (\pm 1.40 \text{ s.d.}) \times 10^{-3} \mu\text{l O}_2$ per zooid per hour. By comparison, Mangum & Schopf (1967) reported the consumption of $4.5 \times 10^{-4} \mu\text{l O}_2$ per zooid per hour for *Bugula turrita* (Desor) at 20 °C and constant oxygen tension.

The regression of \ln (mass-specific respiration rate) on \ln (colonial biomass) was not statistically significant (figure 2), giving no grounds for refuting the hypothesis that modular respiration rate is independent of colony size.

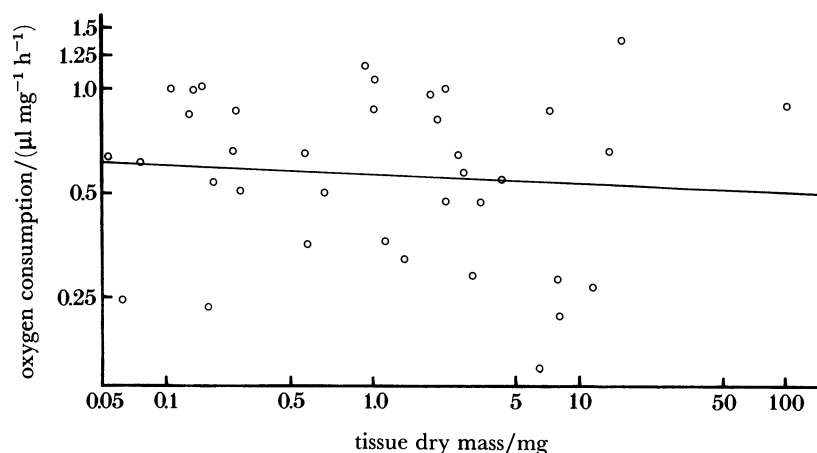


FIGURE 2. Mass-specific rate of oxygen consumption of colonies of *Electra pilosa* plotted as functions of colonial ash-free dry mass. Regression equation fitted to data: $y = -0.030x - 0.574$, standard error of coefficient = 0.008.

Growth

The total number of zooids (figure 3*a*) and total biomass (figure 3*b*) were linear functions of colonial area, the mean biomass per zooid remaining at $3.70 (\pm 1.79 \text{ s.d.}) \mu\text{g}$ throughout all stages of colonial growth. The rate of zooid production per zooid was a decreasing function of colony size (figure 4*a*), whereas the rate of zooid production per unit of colonial perimeter was an increasing function of colony size (figure 4*b*). Since only peripheral zooids undergo budding, it was inferred that their budding rate increased as colony size increased.

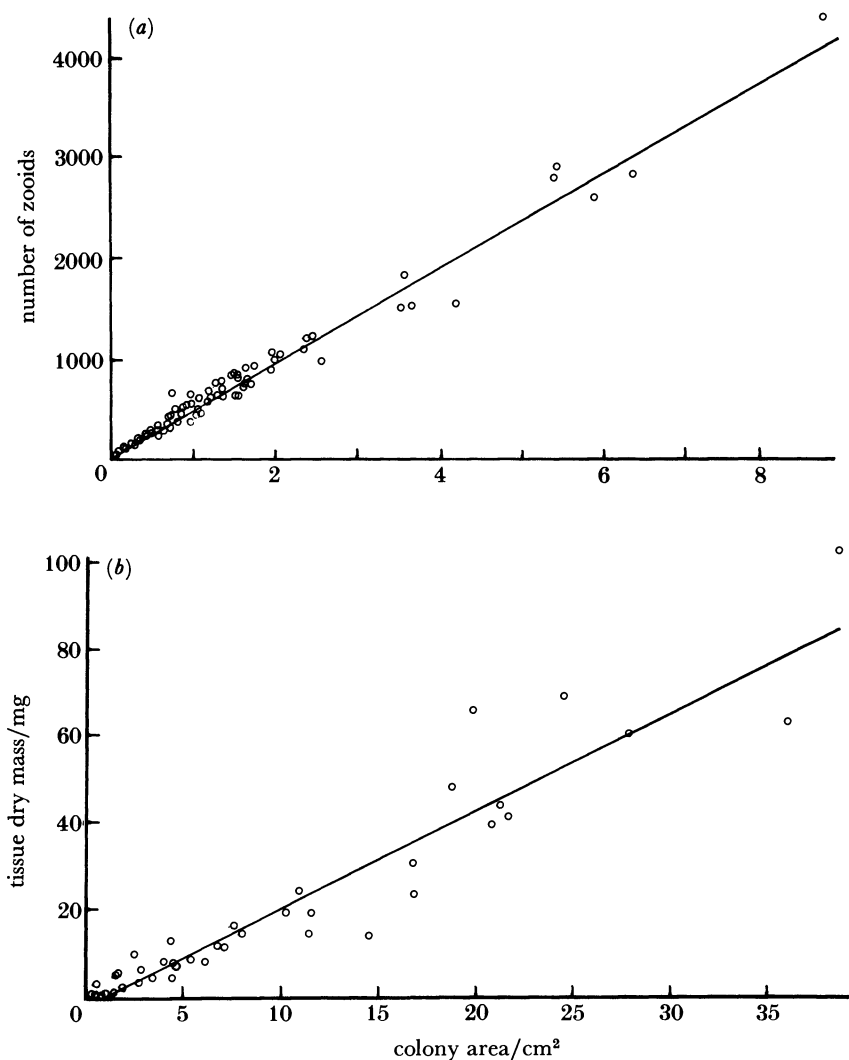


FIGURE 3. (a) Number of zooids per colony plotted as a function of colony area. Regression equation fitted to data: $y = 472x + 13.7$, standard error of coefficient = 5.5. (b) Ash-free dry mass of colony plotted as a function of colony area. Regression equation fitted to data: $y = 2.22x - 1.85$, standard error of coefficient = 0.014.

DISCUSSION

Respiration

The isometric relation between colonial respiration rate and biomass of *Electra pilosa* suggests that compartmentalization into modules avoids the metabolic allometry normally associated with volumetric somatic growth. Intra- and interspecific metabolic isometry is also found among small metazoans of up to about 1 mg wet mass, whereas in protozoans and larger metazoans metabolism is usually allometric (Hemmingsen 1961; Zeuthen 1970). Metabolic rate might be determined by the aggregative surface area of cells and organelles (Hemmingsen 1961; Zeuthen 1970; Peters 1983). Among unicellular organisms this surface area is confined by limits to the development of organelles, but the cellular construction of small metazoans increases their total surface area of membranes sufficiently to compensate for the decreasing ratio of

RESPIRATION AND GROWTH OF *E. PILOSA*

27

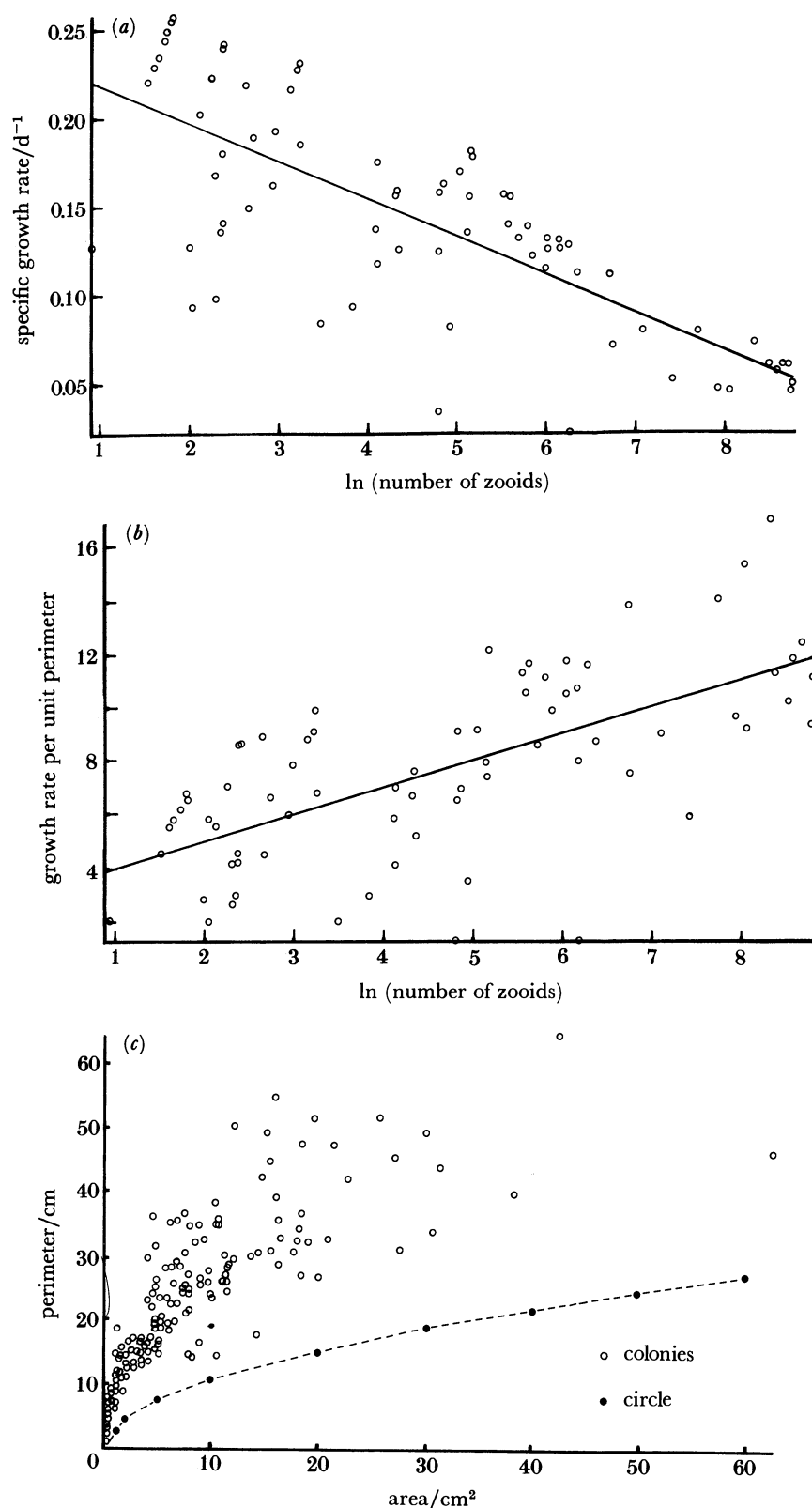


FIGURE 4(a) Specific growth rate (instantaneous rate of zooid production per individual, calculated as $(\ln n_2 - \ln n_1)/14$, where n_1 = number of zooids at start, n_2 = number after 14 days) plotted as a function of \ln (colony size) (where size is expressed as the geometric mean of the initial and final number of zooids present in the colony). (b) Finite growth rate per unit of perimeter (calculated as $(n_2 - n_1)/14\sqrt{p_1 p_2}$, where p_1 = length of perimeter at start, p_2 = length after 14 days) plotted as a function of \ln (colony size). (c) Length of colonial perimeter plotted as a function of colony area.

somatic surface area to volume. With increases in biomass beyond about 1 mg, the degree of compensation declines and the allometric metabolic relationship is resumed. Metabolic allometry is preserved even in slices of tissue taken from *Littorina littorea* (L.) of different sizes but is obliterated by homogenizing these tissues (Newell & Pye 1971), partly, although not unequivocally, corroborating the surface area hypothesis.

The parallel between the small metazoans and modular colonial animals is striking; whereas the former maintain a high ratio of surface area to volume by somatic division into cells, the latter do it by division into polyps or zooids. The exposed surfaces of each zooid are apparently sufficient to maintain adequate gaseous exchange by diffusion (Ryland 1967).

Of course, the lack of allometry does not imply that modules are metabolically independent of one another; gymnolaemate bryozoan zooids are cytologically interconnected (Ryland 1979), and the translocation of metabolites has been demonstrated in *Membranipora membranacea* (L.) (Best & Thorpe 1985). Such metabolic interactions allow the nourishment of specialized, non-feeding zooids and, in certain cheilostomes, the electrophysiological coordination of zooids (Ryland 1979).

Growth

Despite the isometric relation between metabolic rate and biomass in *Electra pilosa*, the specific rate of zooidal budding declines as colonies grow. A constant specific rate of budding would cause an exponential increase in the number of zooids throughout colonial growth. However, the specific growth rate will remain constant only if there is no constraint on the number of successive multiplications that each module can undergo. *Electra pilosa* does not satisfy this requirement, since after establishment of the ancestrula, growth quickly changes from a linear to a two-dimensional pattern, producing, on an unlimited plane substratum, an approximately circular colony in which only the peripheral zooids have room to bud. This constraint also applies to other bryozoan species in which exponential growth has been reported, for example *Plumatella repens* (Bushnell 1966), in which each zooid has only a limited number of budding sites. For an encrusting, two-dimensional colony, therefore, the number of zooids will increase as a quadratic function (Kaufmann 1970; Wass & Vail 1978) and the number of peripheral zooids as a linear function of time.

Electra pilosa, however, shows two properties that partly compensate for the constraint on budding imposed by two-dimensional growth. First, peripheral zooids, although remaining constant in size (figure 3*a, b*), bud faster as the colony grows (figure 4*b*), perhaps being subsidized by metabolites translocated from the non-replicating zooids accumulating within. Second, the periphery becomes expanded into lobes, increasing the perimeter, and hence the number of replicating zooids. The colony perimeter rapidly becomes about twice that of a circle of the same area, and remains so throughout later growth (figure 4*c*). Frontal budding is potentially another method by which the constraints set by two-dimensional growth can be avoided, but in species such as *Celleporella hyalina* (L.) this is usually concerned with the production of non-replicating sexual zooids, and growth remains essentially two-dimensional (Cancino 1983).

In conclusion, a modular construction frees colonies from the influence of metabolic allometry, with the result that the specific rate of modular iteration need not decline with increasing colonial biomass. If all modules retain their capacity for replication they may accumulate exponentially until influenced by external constraints such as resource depletion,

competition, architectural instability or environmental change. This, however, is only possible with three-dimensional growth, as occurs in some branching hydroids and bryozoans or in mound-forming massive corals. Two-dimensional colonial growth restricts replication to the peripheral modules, but the development of a non-circular perimeter and nourishment of peripheral modules by translocation allow modular accumulation to exceed the quadratic function of time appropriate for a circular colony expanding at a constant rate.

We thank Dr J. Davenport and Mr A. Woolmington for providing the advice and equipment necessary for the respirometry.

REFERENCES

- Bertalanffy, L. von 1960 Principles and theory of growth. In *Aspects of normal and malignant growth* (ed. W. W. Nowinski), pp. 137–259. Amsterdam: Elsevier.
- Best, M. A. & Thorpe, J. P. 1985 Autoradiographic study of feeding and the colonial transport of metabolites in the marine bryozoan *Membranipora membranacea*. *Mar. Biol.* **84**, 295–300.
- Bushnell, J. H. 1966 Environmental relations of Michigan Ectoprocta, and dynamics of natural populations of *Plumatella repens*. *Ecol. Monogr.* **36**, 95–123.
- Buss, L. W. 1979 Bryozoan overgrowth interaction: the interdependence of competition for space and food. *Nature, Lond.* **281**, 475–477.
- Cancino, J. M. 1983 *Demography of animal modular colonies*. Ph.D. thesis, University of Wales.
- Connell, J. H. 1973 Population ecology of reef building corals. In *Biology and geology of coral reefs, vol. II, biol. 1.* (ed. O. A. Jones & R. Endean), pp. 205–245. New York: Academic Press.
- Hemmingsen, A. M. 1960 Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Rep. Steno Meml Hosp. Nordisk Insulin Lab.* **9**, 1–110.
- Hughes, R. N. & Cancino, J. M. 1985 An ecological overview of cloning in Metazoa. In *Population biology and evolution of clonal organisms* (ed. J. B. C. Jackson, L. W. Buss & R. E. Cook), pp. 153–186. New Haven: Yale University Press.
- Jackson, J. B. C. 1979 Overgrowth competition between encrusting cheilostome ectoprocts in a Jamaican cryptic reef environment. *J. anim. Ecol.* **48**, 805–823.
- Kaufmann, K. W. 1970 A model for predicting the influence of colony morphology on reproductive potential in the Phylum Ectoprocta. *Biol. Bull.* **139**, 426.
- Lehman, J. T. & Porter, J. W. 1973 Chemical activation of feeding in the Caribbean reef-building coral *Montastrea cavernosa*. *Biol. Bull.* **145**, 140–149.
- Mangum, C. P. & Schopf, T. J. M. 1967 Is an ectoproct possible? *Nature, Lond.* **213**, 264–266.
- Newell, R. C. & Pye, V. I. 1971 Quantitative aspects of the relationship between metabolism and temperature in the winkle *Littorina littorea* (L.). *Comp. Biochem. Physiol.* **38B**, 635–650.
- Peters, R. H. 1983 *The ecological implications of body size*. Cambridge University Press.
- Ryland, J. S. 1967 Polyzoa. *Oceanogr. Mar. Biol. Ann. Rev.* **5**, 343–369.
- Ryland, J. S. 1976 Physiology and ecology of marine bryozoans. *Adv. Mar. Biol.* **14**, 285–443.
- Ryland, J. S. 1979 Structural and physiological aspects of coloniality in Bryozoa. In *Biology and systematics of colonial organisms* (ed. G. Larwood & B. R. Rosen), pp. 211–242. London and New York: Academic Press.
- Ryland, J. S. 1981 Colonies, growth and reproduction. In *Recent and fossil bryozoa* (ed. G. P. Larwood & C. Nielsen), pp. 221–226. Fredensborg: Olsen & Olsen.
- Ryland, J. S. & Hayward, P. J. 1977 *British anascan bryozoan: Cheilostomata: Anasca. Synopses of the British fauna no. 10* (ed. D. M. Kermack). London, New York and San Francisco: Academic Press.
- Thorpe, J. P., Clarke, D. R. K. & Best, M. A. 1985 Natural variation in tentacle number in marine bryozoans and the possible effects of intraspecific and interspecific ecological competition for food. In *Bryozoa: Ordovician to Recent. Proc. Sixth int. Conf. int. Bryozool. Ass.* (ed. C. Nielsen & G. P. Larwood). Fredensborg: Olsen & Olsen.
- Wass, R. E. & Vail, L. L. 1978 Encrusting bryozoa exhibit linear growth. *Search* **9**, 42–44.
- Zeuthen, E. 1970 Rate of living as related to body size in organisms. *Pol. Arch. Hydrobiol.* **17**, 21–30.