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Review article.

Symbiosis, Size and Celerity

JOHN A. RAVEN
Division of Environmental and Applied Biology, University of Dundee at SCRI, Invergowrie, Dundee DD2 5DA, UK, Email. j.a.raven@dundee.ac.uk

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Abstract

Description of the way in which metabolic and growth rates scale with the size of organisms, and the search for mechanisms which determine these relationships, is an important aspect of the growing field of macroecology. Symbiosis is not specifically addressed in most of the published investigations of these allometric relationships, despite the near ubiquity of symbioses and the possibility that studies of allometry can give insights into nature of symbioses and *vice versa*. Using chemo-organotrophic organisms in symbiosis with microscopic photobionts as an example, the literature was analyzed for data sets that could be used in allometric analyses. Few such data sets were found. It is argued that further such data sets, perhaps obtained as part of research programmes whose primary aim is not to investigate allometry, would be helpful in determining if symbioses follow similar allometric relations to the (putatively) non-symbiotic organism for which data are available, and would illuminate discussions on the applicability of optimality principle to symbioses.

Keywords: Allometry, macroecology, modular organisation, scaling, specific growth rate, unitary organism

1. Introduction

Macroecology is a rapidly growing area of ecology, and indeed of organismal biology. McGill (2003) defines macroecology as the search for large-scale

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patterns, and the subsequent search for the mechanisms underlying these patterns. McGill (2003) cites the power-low species area relationship, the hollow curve distribution of species abundance, and the skewed-lognormal distribution of body size as three examples of macroecological patterns. To these can be added the 3/2 thinning 'law' for plants, with some applications to animals (Begon et al., 1996).

A fifth example of macroecology is the scaling of metabolic and growth rates to the size of organisms (West et al., 1997; Brown and West, 2000; Enquist et al., 2003; White and Seymour, 2003). The scaling of specific growth rate (μ) with cell/body size (M) is the large scale pattern, of the form given in equation (1):

$$\mu = a.M^b \quad (1)$$

where μ is the specific growth rate (s^{-1}), M is the cell/body size (mass or volume) and a and b are variables (Brown and West, 2000). The mechanistic basis for this relationship is still a matter of debate (West et al., 1997; Brown and West, 2000; Enquist et al., 2002; Enquist et al., 2003; White and Seymour, 2003). It is this fifth example that is considered here in the context of symbiosis.

Little seems to have been published on the scaling of metabolic and growth rates with the size of symbiotic associations, and allometry in general is not commonly mentioned; exceptions are Griffiths and Klumpp (1996) and Wilkinson and Douglas (1998). Considering the influence of symbiosis in macroecology poses difficulties in addition to the usual problems in both of the stages, i.e. searching for patterns, and then searching for the reasons for the patterns, of macroecology (McGill, 2003). One problem comes from the ubiquity of symbiosis, so it can be difficult to find comparable, e.g. without phylogenetic bias (Harvey, 1996), examples which have, and which lack, symbionts. It is known that the largest bivalves (tridacnids: Barnes, 1980) and foraminifera (Lee and Hallock, 1987; Lee, 1988; cf. Pawlowski et al., 2003) are symbiotic with photosynthetic microalgae rather than relying on their plesiomorphic phagotrophy.

Analyses of size scaling of growth and photosynthetic rates of phototrophs do not normally emphasize symbiotic systems (Duarte et al., 1995; Enriquez et al., 1996; Nielsen et al., 1996). Communities in which the dominant primary producers are the photobionts of animal hosts, e.g. coral reefs, have similar maximum chlorophyll contents per unit projected area as do other shallow-water marine benthic communities (Raven, 1984). However, coral-dominated reefs generally have lower rates of gross photosynthesis on a projected area basis than do reefs which are mainly, or entirely, based on macroalgae as primary producers (Gattuso et al., 1998).

It is important that the kind of symbioses that are chosen for the analysis, at

least initially, have a clearly quantifiable symbiont with a clearly defined role. The example that is used here is that of microalgae or cyanobacteria in symbiosis with non-photosynthetic organisms. Such symbiosis converts a saprotroph (e.g. ascomycete) or a phagotroph (e.g. a ciliate or a cnidarian) into a phototroph. Specifically, the two examples examined are symbiotic ciliates, since these are more readily analysed than are more ecologically significant symbioses such as symbiotic cnidarians and ascomycetes (i.e. lichens).

The use of equation (1) requires that growth is exponential and. In the present context, that closely related symbiotic and non-symbiotic organisms are compared. This is experimentally most readily achieved in unitary rather than modular organisms, and the two examples examined later in this paper are symbiotic ciliates, although even then the comparison of symbiotic with symbiotic cells only involved the same host species in one case.

Such comparisons are even less readily achieved for other photosynthetic symbioses. In the case of lichens, growth has frequently been measured as specific (relative) growth rate (e.g. Proctor, 1977; Hooker, 1980; Hill, 1981; Procotor, 1983; Armstrong and Smith, 1987; Armstrong, 1991, 1992; Armstrong and Smith, 1996; Cooper et al., 2001; Sundberg et al., 2001; Murtagh et al., 2002; Armstrong, 2003; Myvanin et al., 2003). However, it is not easy to find comparable data for related non-symbiotic ascomycetes growing under similar conditions., so that the lichen specific growth rate and organism size data cannot be employed in equation (1) to compare symbiotic and non-symbiotic taxa. Thus, the excellent quantitative data on the ecophysiology of lichens (e.g. Collins and Farrar, 1978; Budel and Scheidegger, 1996; Palmqvist, 2000; Palmqvist et al., 2002) is of little use in relation to the use to which we would wish to put equation (1). For cnidaria, while specific growth rate data are available for solitary hydroids (*Hydra*, sea anemones) in symbiotic and non-symbiotic forms, most colonial hydroids are non-symbiotic and most colonial corals and symbiotic, again complicating analysis of specific growth rate (Barnes, 1980).

2. Macroecological Questions and Symbioses

The search for large scale patterns in ecology, and the attempts to find the mechanism underlying such patterns, predate the term macroecology, but the word is a useful focus for research in this general area (McGill, 2003). The focus of this paper is on the relation of size to growth rate of asymbiotic and symbiotic heterotrophic host organisms associated with microalgal photobionts. Here two considerations relating to equation (1) are involved.

The first consideration is one of the 'big ideas' in macroecology, i.e. that of the allometry of metabolic and growth rate with organism size. The null

hypothesis here is that the exponent b in equation (1), i.e. the slope of the line relating the specific growth (or metabolic) rate to the $\log_{10}$ of the body mass, is the same in the symbiotic and in the asymbiotic state. This question does not seem to have been raised for what are generally thought of as mutualistic symbioses such as most lichens, coelenterates and ciliates. However, it is implicit in the analysis of Morand and Harvey (2000) the allometry of growth rate and body size for mammals in relation to the extent of parasitism, i.e. an antagonist symbiosis.

A problem with testing the 'big ideas' is that of defining the mathematical relationship, and of then defining the rejection criteria (McGill, 2003): when are the data deemed not to fit? This is still a live issue; White and Seymour (2003) claim that the exponent b in equation (1) for mammals is –0.33 rather than the more widely accepted –0.25.

For algae there are data sets which seem to show a range of values for the exponent b in equation (1), almost all equal to or less than the 'benchmark' –0.25, especially when the data sets used for particular analyses are phylogenetically circumscribed (Banse, 1982; Reynolds, 1984; Raven, 1986, 1993, 1995, 1998; Chisholm, 1992). However, it is important to bear in mind that size does not generally account for the majority of the variation of the growth rate even within a phylogenetically circumscribed data set (Reynolds, 1984; Chisholm, 1992).

Nevertheless, it is worth considering the question of the value of the exponent b in equation (1) for asymbiotic and symbiotic ciliates.

The second consideration of the allometric relationships of growth rate and organism size is that of the value of a in equation (1). Again referring to data on growth rate as a function of size among microalgae, Banse (1982) showed that a was significantly lower for dinoflagellates than for diatoms, so that, for a given cell size, dinoflagellates grow less rapidly than diatoms.

The reason for the differences in the value of a between diatoms and photosynthetic dinoflagellates are not entirely clear, although arguments based on the smaller fraction of the non-vacuolar biomass of dinoflagellates which is occupied by chloroplasts than is the case for diatoms (Raven, 1984; Tang, 1996). Essentially the argument here is that the ratio of plastids to 'non-photosynthetic' apparatus in the cell in diatoms is closer to the ratio that permits the maximum rate of photolithotrophic growth, based on a cost-benefit analysis of the allocation of resources to plastids and to the rest of the non-vacuolar part of the cell (Raven, 1984; Tang, 1996). The argument about ratio of photosynthetic to non-photosynthetic machinery used in this comparison of diatoms and dinoflagellates is clearly relevant to considerations of symbiosis. Sud (1968) shows a range of ratios of photobiont (green microalga) to ciliate volume in photosynthetic symbioses of plastids. Cases of variation of a in equation (1) within a class (Chrysophyceae *sensu lato*) of 'algae' which reflect

trophic level are discussed by Raven (1995). The cases involve a comparison of photosynthetically growing chrysophytes (which may or may not have the potential for phagotrophy and saprotrophy) with mixotrophic chrysophytes (phagotrophic organisms which can photosynthesise) growing phagotrophically with or without light and with non-photosynthetic phagotrophs. There is little variation in cell size among these three trophic categories, so the order of specific growth rates, i.e. lowest in photolithotrophs, intermediate in mixotrophs, and highest in phagotrophs, is not biased by differences in size among trophic categories as well as not being phylogenetically biased (Raven, 1995). The small size variation within the three trophic categories means that estimation of a from regression of specific growth rate on the log of cell size is not possible, and the implied differences in a come from the cluster of specific growth rates for the three trophic groups.

As to the mechanism(s) underlying these differences, an optimal allocation model (Rosen, 1967; Shuter, 1979; for an application to symbiosis see Hyvarinen et al., 2003) was proposed by Raven (1995), based on the fraction of the biomass allocated to the resource acquisition processes that present the 'heterotrophic' part of the organism with the materials needed for growth and maintenance, i.e. organic C and N, P, K, Fe and other inorganic nutrients. Optimal allocation between the resource acquisition and the resource use machinery occurs when the rate of supply of resources to the heterotrophic machinery is equal to that at which they can be used for growth in the average environment in which the organism is growing. This average environment comprises temperature, flux of photosynthetically active radiation (PAR) and concentration of inorganic C and other nutrient elements for photolithotrophs, and particulate or soluble organic C and other nutrients in the case of the phagotrophs and saprotrophs. The quantity of photosynthetic machinery required, under optimal external resource supply conditions, is much higher than that of the phagotrophic and especially, the saprotrophic cells. This means that more of the resources gained by the photolithotrophic cell must be used in producing more photosynthetic machinery than is the case for the phagotrophic and saprotrophic cells. Per unit mass in the cell, a smaller fraction is devoted to the heterotrophic machinery, so that few catalysts per unit mass are available for the growth processes. Accordingly, growth is slower for the photolithotrophs than for the phagotrophs or the saprotrophs. The mixotrophs, with significant investment in the photosynthetic apparatus, are intermediate.

The assumption of optimal allocation implies that all cells of a certain size and trophic mode should have similar specific growth rates under optimal conditions at a given temperature. We have already seen that this is not the case when photolithotrophically growing cells are compared across taxa, e.g. diatoms grow faster than do dinoflagellates of a given size (Banse, 1982), and suggested that allocation of resources between the photosynthetic and he

heterotrophic components of the cells is less close to optimal than is the case for the diatoms.

At all events, Chisholm (1992) made a very pertinent point that the value of a (inter-clade variations in growth rate at a given cell size) is more important than b (the determinant of the variation of specific growth rate with size) for phytoplankton.

It is also possible that the degree of optimality of allocation within a clade with different trophic modes may differ among different trophic modes. This would mean that, for a given size of cells, the specific growth rates for photolithotrophs, mixotrophs and chemoautotrophs may not have the same relative values as in chrysophytes. Banse (1982) comments on this for dinoflagellates (see also Raven, 1984; Tang, 1996). In extending this analysis to symbiotic systems, the study of the fraction of the biomass occupied by photobionts (Sud, 1968) should be extended to a consideration of the photobiont which is occupied by the photosynthetic apparatus (see Raven, 1984). This is more readily achieved for eukaryotis photobionts, where the photosynthetic machinery compartmented in chloroplasts, than for prokaryotic (i.e. cyanobacterial) symbionts. Such analyses would allow a more accurate allocation of biomass to the photosynthetic and to the heterotrophic structural and catalytic machinery in the symbioses.

3. What Data Are Available?

Banse (1982; his Fig. 1C) has compiled data on growth rate as a function of cell size for chemoorganotrophic flagellates. Banse (1982) notes that the data are more disposed than is usual for such data, and that the variability may reflect sub-optimal nutrition for the slower-growing organisms.

With such variability it may seem unlikely that significant effects of photosynthetic symbioses can be discerned. Be that as it may, two data sets will be examined. The one that concerns symbiosis *sensu stricto* involves symbiotic and bleached strains of *Paramecium bursaria* (Karakashian, 1963). The data (Table 2 of Karakashian, 1963) show that the growth rate of the two strains have equal light-independent specific growth rates when grown phagotrophically at saturating prey (bacteria) concentrations. The specific growth rates measured at 25°C are 1.23–1.32 d^{-1}; normalised to 20°C (assuming a Q_{10} of 2) the rates are 0.95–1.01 d^{-1}. From the host cell volume of $2.62.10^5$ μm^3 for *Paramecum bursaria* (Sud, 1968) the growth rate is very close to the line drawn through the data for ciliate specific growth as a function of cell volume (Banse, 1982). To the extent that conclusions can be drawn from the dispersed data for chemoorganotrophic growth (Banse, 1982), the maximum specific growth rate or *Paramecium bursaria* with or without photobionts is

unexceptional. Sud (1968) showed that 25% of the cell volume of *Paramecium bursaria* is occupied by the photobiont *Chlorella*. Assuming that this is the same fraction of the cell occupied by the photobiont in the strain of *Paramecium bursaria* used by Karakashian (1963), the growth rate data suggest that the loss (to the machinery of chemo-organotrophic growth) of 25% to cell volume has no impact on growth rate. This suggests that the optimal allocation (Rosen, 1997) assumption made earlier does not apply. If optimal allocation occurred in the symbiotic strain then the specific growth rate should be 33% higher in the non-symbiotic strain, noting that the symbionts are non-functional in achieving the maximum specific growth rate saturated by bacteria, the phagotrophic substrate.

When the phagotrophic substrate is limiting the growth rate of *Paramecium bursaria* the role of the photobionts becomes clear. Growth with sufficient light occurs even in the absence of bacteria in the symbiotic strain, while the non-symbiotic strain dies (Karakashian, 1963).

The other ciliate examined may not show symbiosis *sensu stricto*, but rather seems to show kleptoplasty. *Mesodinium rubrum* (=*Myrionecta rubra*) is a marine planktonic ciliate which invariably contains cryptophycean chloroplasts and mitochondria, but apparently lacks cryptophycean nuclei (Gustafson et al., 2000). Despite the absence of a cytostome, the *Mesodinium* cells can ingest cryptophytes and use their plastids in photosynthesis. It appears that continued ingestion of cryptophytes is needed to maintain the plastid population, a reasonable finding in the context of the absence of cryptophyte nuclei from the 'symbiosis' and the need for algal nuclei in supplying more than 90% of the proteins in the plastids are nuclear-encoded (Rumpho et al., 2000).

Growth rates of *Mesodinium rubrum* from Sutton Harbour (Plymouth Sound) is 0.680 d^{-1} at 15.8°C, or ~1.0 d^{-1} at 20°C, assuming a Q_{10} of 2 (Leakey et al., 1994). This may be a slight underestimate as a result of the impact of small grazers and parasites (large grazers were eliminated). The *Mesodinium rubrum* cells had a mean volume of 7.10^{-13} μm^3 so that the predicted growth rate (Banse, 1982) of just above 2.1 d^{-1} is just over twice the minimum estimate of Leakey et al. (1994).

Before concluding that the kleptoplastidic photosynthesis of *Mesodinium rubrum* is related to it having a lower rate than predicted for chemoorganotrophic ciliates (Banse, 1982) it must be realised that non-photosynthetic (phagotrophic) ciliates growing in the same environment as *Mesodinium rubrum* also only grow at about half the rate predicted from the Banse (1982) relationship. Once more we are confronted by the question of the value of b in equation (1) in relation to the assumption of optimal allocation. Since the specific growth rate of *Mesodinium* is less than that of other ciliates of a similar size, the optimal allocation assumption cannot be used to account

for the relatively low specific reaction rate of *Mesodinium* unless the fraction of the biomass occupied by the kleptoplastids is somehow unavailable for heterotrophic reactions in the absence of kleptoplastids.

The arguments on resource allocation for kleptoplastids are rather different for those for photobionts comprising whole algal cells. Unless there has been transfer of cryptophyte genes to the ciliate nucleus, the savings in the resource costs of replacing damaged nuclear-encoded proteins in the plastids must be set against the cost in resource acquisition of the gradual loss of function of the kleptoplastids unless more algal cells are acquired with further resource costs in feeding. For the ciliates with algal cells as photobionts the symbiosis has resource costs of maintaining both photobiont and ciliate, with corresponding decreased resource costs of acquisition of more photobionts to replace those that are time-expired and no decrement in resource acquisition from less than adequate maintenance of the photobiont. We do not yet know enough about the relative costs involved in these two sets of 'symbioses' to know the relative costs, and their impact on the specific growth rate.

4. Conclusions

The available data on ciliates with or without photosynthetic symbionts (whole algal cells, or plastids from algae) are not sufficient to show whether a in equation (1) is the same for symbiotic (growing with at least some of their organic carbon supplied by photosynthesis) and non-symbiotic ciliates, i.e. whether the specific growth rate values with size in the same way for symbiotic and no-symbiotic hosts. The data are also insufficient to show whether symbiotic (growing with at least some of their organic carbon supplied by photosynthesis) and non-symbiotic ciliates have similar values for b in equation (1), i.e. whether the specific growth rate for a given size of host cell is the same with and without functioning photosynthetic symbionts. Even with more relevant information, i.e. data on a range of sizes of ciliates growing with and without photosynthetic symbionts in the light and in the dark, the question about b in equation (1) might not be solved if the specific growth rate was not close to the maximum for that trophic mode, so that it is difficult to see if the criteria for optimal allocation were met in the absence of independent data on allocation to, for example, 'defence' components in the symbiotic and non-symbiotic cilates.

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