


Comment

Bivalve growth and the invisible hand of heterogeneity

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Abstract.—A recent study by Saulsbury and colleagues assessed factors influencing growth coefficients in bivalves. Like many macroevolutionary studies that cover a wide range of taxa and environments, this study fails to account for important heterogeneity among taxa and among environments. Rankings of factors depend on the range of values sampled, patterns of allocation of energy to various competing functions, and whether taxa in any given clade are uniform in their growth coefficients. Heterogeneity is universal and must be taken into account in large-scale analyses.

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Introduction

Which factors are most important in accounting for variations in the growth coefficients of bivalves? This is the question posed in a recent paper by Saulsbury et al. (2019). These authors conducted a series of analyses in which they consider temperature, primary productivity, and taxonomic (or phylogenetic) affiliation as factors that might independently affect (some would incorrectly say “drive”) bivalve growth as calculated from growth coefficients. They conclude that, although environmental factors are predominant at the species level, taxonomic affiliation emerges as the most important factor for the analysis as a whole. These results generally contradicted expectations: growth coefficients should generally be greater at higher temperatures and in settings of high primary productivity (i.e., food availability). I shall argue below that these expectations apply only within species and not necessarily among species and that the analyses conducted by Saulsbury and colleagues are compromised by ignoring ecologically and phylogenetically important sources of heterogeneity.

1. Temperature. Just because some species will grow rapidly at tropical temperatures, in part because metabolically unencumbered processes obey some version of the Q10 rule,

(Broell et al. 2017), co-occurring species will not all have similar patterns of growth, as well demonstrated by experimental studies with four large South African mussels (Erkom Schurink et al. 1993). The Californian mussel *Mytilus californianus* exhibits growth rates that vary by a factor of nine depending on the shore level at which individuals grow, even though individuals at all shore levels are exposed to a generally similar thermal regime (Connor and Robles 2015). Likewise in a tropical forest, lianas can grow as much as a meter in length per day, whereas trees—including shaded saplings and especially species with dense wood—on average grow much more slowly, at most a few millimeters per day (Vermeij 2010; Pasquini et al. 2015).

At low temperatures, the difference between fast- and slow-growing bivalves or plants is smaller, so that the effect of temperature on comparisons of growth coefficients among and within species will be smaller. Crucially, temperature is an enabling factor, not a determining one (Vermeij 2013). This applies not only to growth, but also to all other biological processes that are temperature dependent and to all situations in which co-occurring species vary in their sensitivity to the thermal environment.

2. Productivity. The same arguments apply to productivity. Like temperature, productivity

is an enabling factor (Vermeij 2013). High productivity can promote rapid growth, but species with low metabolic rates, low competitive status, or limited access to a rich food supply are not in a position to take advantage of productive waters. The large difference in growth rate between high-shore and low-shore mussels referred to above (see also Seed 1968) reflects a difference in access to food, because high-shore individuals have less time to feed. Individuals at all shore levels are exposed to waters with a similar concentration of phytoplankton. As the study of the four South African mussels discussed above shows, co-occurring species have different growth rates according to how they allocate metabolic resources to defense (shell thickness) as compared with growth in size.

3. Taxonomic affiliation. A problematic assumption that afflicts many macroevolutionary analyses is that all members of a clade share particular ecological or physiological properties. Such an assumption might be justified, or at any rate not lead to serious misinterpretation, when small compact clades are considered, but at a larger phylogenetic scale of inclusion, it is likely to be violated, as the chance that members of subclades enter new environments or new ecological positions where enabling factors differ and where patterns of allocation deviate from the norm increases. Even within bivalve families there are differences of one to two orders of magnitude in body mass and growth rate, and species occupy environments ranging from plankton-poor deep waters and reef environments to eutrophic estuaries. In the Cardiidae, for example, growth rates in the Arctic *Serripes groenlandicus* are about one-hundredth those in the tropical photosymbiotic members of the genus *Tridacna* (Beckvar 1981; Gerasimova et al. 2019; Mohammed et al. 2019).
4. Sampling. A ranking of factors affecting phenotypes like growth coefficients depends critically on the range of circumstances and taxa sampled. A different sampling scheme would almost certainly yield a different ranking and therefore a different interpretation of and rationalization for the results.

Furthermore, taxonomic affiliation is not likely to be independent of environmental factors: clades that do well in the tropics or in areas of high productivity are by nature likely to have intrinsically high growth coefficients, or at least the potential for such high coefficients. Such artifacts can be partially resolved by examining phenotypes of species in different clades that are exposed to a similar environment of enabling factors.

Discussion

Although the points raised here apply to one particular study, many recent studies conducted at large ecological and phylogenetic scales suffer from the same problems. They do not account for heterogeneity arising from ecological differences among co-occurring taxa; they fail to account for heterogeneity within clades; and they confuse enabling factors with determinative agencies. In short, just because growth can be rapid does not mean that it will be; and just because some species can take advantage of what appear to be favorable conditions does not mean that others will too. Heterogeneity and variation are intrinsic to the world in which we live. Analyses that do not account for these factors, or ignore them altogether, will be inevitably compromised and problematic.

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