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Reply

Idiographic and nomothetic approaches to heterogeneity are complementary: Response to comments on "Evaluating the influences of temperature, primary production, and evolutionary history on bivalve growth rates"

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We thank Vermeij (2020) for his comments on Saulsbury et al. (2019), which provide an opportunity for us to clarify and expand on some points raised in the original paper. The goal of our study was to evaluate the degree to which relationships between environmental factors and growth rate observed in populations and species can be generalized across the entire bivalve clade. In our view, Vermeij's idiographic focus on specific examples complements rather than contradicts our nomothetic search for overarching patterns.

We highlight three points of apparent contention where we see no inherent contradiction between Vermeij's arguments and our findings.

1. Vermeij points out that the estimated dependence of growth on different factors (temperature, food supply, phylogenetic history) should be sensitive to sampling (Vermeij's point 4). Indeed, we recovered especially strong environment–growth relationships within a handful of families (Fig. S4, our study), with weak relationships

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being the more general pattern. This outcome suggests that broadening our study's scope would not qualitatively change our findings.

2. Although Vermeij objects to assuming that members of the same clade share physiological or ecological properties (his point 3), he also argues that taxonomic affiliation and environmental distribution are not independent of each other (his point 4). New species arise near their sisters, and environmental preferences may take a long time to evolve, so we might expect closely related species to live in similar environments. This is consistent with our finding that the range of sea-surface temperatures occupied tends to be conserved within clades (Saulsbury et al. 2019: Table 2; see also Roy et al. 2009), which is an important consideration when assessing the degree to which growth rates are also phylogenetically conserved. However, as noted in our paper, Vladimirova et al. (2003: Table 2) found that, even at standardized temperatures, major bivalve taxa showed different ranges of mass-specific metabolic rates.
3. We agree that it is useful to distinguish between environmental parameters that limit possible values of a response variable ("enabling factors") and those that instead influence the central tendency of that response variable ("determinants"), as Vermeij does in his points 1 and 2. These two kinds of agents yield distinctly different predictions: the former should influence both the mean and variance of growth rate, whereas the latter should influence only the mean. Vermeij appears to assume that environmental variables act as enabling factors ("At low temperatures, the difference between fast- and slow-growing bivalves or plants is smaller."), but this is precisely the question we evaluated in our study via linear and quantile regression. We do find evidence for a weakly wedge-shaped temperature–growth relationship that is consistent with temperature being a universal enabling factor: growth rates are both greater on average and slightly more variable at higher temperatures (Saulsbury et al. 2019: Fig. 3). If food supply were also a universal enabling factor for growth rate, we should be able to detect a wedge-shaped relationship between the two visually or with an analysis like quantile regression, but we do not. This finding does not conflict with the specific examples highlighted by Vermeij—there are without doubt instances in which productivity acts as an enabling factor on growth rate—but it does imply that these cases do not exemplify a more general trend.

This brings us to the primary difference between Vermeij's perspective and ours. Vermeij assumes that the causes of variation in growth rate cannot be extrapolated out to broad phylogenetic scales in a straightforward way. Rather than taking this as a given, we statistically evaluated this assumption. Our finding that there is significant phylogenetic signal in growth rates is thus entirely consistent with Vermeij's argument that there are important ecological and phylogenetic sources of heterogeneity. Yet Vermeij cites several examples that seem to imply that rapid growth is only possible at high temperatures or in highly productive areas. Whereas examining specific case studies can be a fruitful inductive strategy for formulating initial hypotheses, it is arguably less satisfying for testing hypotheses about broad-scale tendencies observed across many species. Given the great variation in the responses of growth rate to environmental factors documented in our analyses, case examples can be found to support almost any generalization. Our results are consistent with the assertion that rapid growth is possible only at high temperatures or in high-productivity areas for some species, but for this analysis we were interested in all species, not just some of them. Our broad-scale analyses suggest that across Bivalvia the effect of environment is not so pronounced: there is only a weak tendency for the spread of growth rates to increase with temperature, and rapidly growing bivalves are found in productive and unproductive waters alike (Saulsbury et al. 2019: Fig. 3).

More generally, we view Vermeij's natural-historical idiographic approach on the one hand and our nomothetic statistical approach on the other not as competing perspectives but as necessary complements of one another. As paleobiologists we are interested in how patterns across space in the modern fauna can provide insight into patterns through time in the fossil record. Because growth bands are commonly preserved in fossil bivalves, they may provide insights into both the metabolic physiology of ancient species and the environments in which they lived. Aquarium studies of bivalves and the whole body of metabolic theory indicate that at some level temperature does limit growth rate, so it is surprising that broad-scale differences in thermal regime correspond only weakly to differences in the central tendency and dispersion of growth rate at the broadest scale. Understanding the degree to which environment–growth rate relationships can be generalized requires both case studies of how specific modern populations respond to environmental variation and synoptic studies of how these responses vary across the entire clade.

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