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## The metabolic theory of ecology and algal bloom formation (Reply to comment by López-Urrutia)

The comment by López-Urrutia draws attention to the similarity between the temperature–growth rate relationships reported by Rose and Caron (2007) and the metabolic theory of ecology (MTE). Rose and Caron (2007) noted different responses of the maximal growth rates of heterotrophic and phototrophic protists to temperature that provide one potential explanation for massive phytoplankton blooms that characterize many polar ecosystems. López-Urrutia has noted that these relationships match quite well some predictions of the MTE, which provides a (potentially) unifying mechanistic theory of the interaction of body size, temperature, and stoichiometry (chemical composition) on biological structure and function at scales ranging from organisms to ecosystems (Brown et al. 2004).

We are in strong agreement with López-Urrutia on the heart of the matter: i.e., there is little doubt regarding the striking similarity between the relationships reported in Rose and Caron (2007) and the MTE vis-à-vis the differential effect of temperature on the metabolic processes of phototrophic and heterotrophic organisms. Moreover, we agree that our findings are consistent with the prediction of the MTE that metabolic rate provides an integrating concept linking the diverse activities among the individuals and species across broad scales of observation and measurement. The possibility that a single characteristic could have such a pivotal effect across such a diverse array of species and ecosystems is exciting in its simplicity. We also concur with the assertion of López-Urrutia that these relationships imply that unique and singular metabolic bottlenecks might result in the generalized (but different) responses to temperature observed for phytoplankton and heterotrophic microbes (a speculation offered by Rose and Caron 2007). The suggestion that a single characteristic can have such a far-ranging controlling influence on a huge diversity of organisms has its detractors, but it is nonetheless consistent with our analyses.

As a purely statistical tool, the MTE appears to have great utility for organizing our high-level understanding of these interactions and their outcomes. Questions remain that our data do not address, however, such as whether the MTE represents a truly mechanistic model that explains biological structure, or whether it constitutes a formalized representation of correlations derived from an examination of empirical data (i.e., is phenomenological). There presently does not seem to be general consensus on the mechanisms that give rise to allometric relationships (Cyr and Walker 2004). More importantly, as noted by López-Urrutia, the true challenge for the MTE will be the incorporation of resource availability into the theory. Our data do not provide a test or confirmation of this aspect of the MTE. The restriction of our analysis to the maximal growth rates of the microbial assemblages specifically eliminated all data that pertained to growth under resource limitation. In essence, our study does not include data pertaining to a primary facet

actively debated regarding the MTE, how to incorporate resource limitation (stoichiometry) and the multiplicity of resources that may be rate-limiting factors in nature. These factors are extremely important in controlling stocks and rates in real communities (Sterner 2004), but they are not addressed by our data set.

It is also important to note that the focus of our study and our conclusions does not relate to “time-averaged” processes or equilibrium conditions within an ecosystem. In fact, phytoplankton blooms are ephemeral in time and space. Specifically, we propose that the differential effect of low environmental temperature on the growth rates of heterotrophs and phototrophs can result in a temporal offset between production and grazing in extremely cold ecosystems, resulting in massive phytoplankton blooms. We make no claim that the primary production generated is not eventually consumed. Primary production may be consumed in a bloom situation in a relatively short time span as effectively and completely as it is in a warm climate, as the abundance of consumers increases and the algal bloom subsides (the former due to population growth, the latter due to waning nutrient or light availability and removal by an increasing number of consumers). Our analysis was performed specifically to understand the dynamic situation characterizing transient bloom phenomena and their prevalence in cold-water ecosystems. Thus, the extrapolation of our specific observations to the broader, more integrative nature of the MTE is unclear.

The relationships that we have presented are empirical observations that were of a type similar to those used to derive aspects of the MTE, so it would seem unusual if they did not agree with its predictions. As López-Urrutia has aptly pointed out, however, it extends those observations to an environment and to organisms that have not been the focus of the theory or the debate regarding its validity. These arguments have been primarily debated in terrestrial ecology.

Therefore, we agree with the claim that our analysis is in accordance with predictions of the MTE. However, our analyses did not provide a critical test of this theory, and therefore we do not make the claim that our data set constitutes strong support for applicability. At the same time, we do not discount the validity or potential significance of the MTE. As the review by Rose and Caron (2007) indicates, there exists a differential effect of temperature on phototrophic and heterotrophic protists, but that relationship plays itself out in nature together with several other factors that affect the growth rates of phototrophs and heterotrophs. If MTE can differentiate the direct effects of temperature from other confounding issues it may well provide some level of predictive capability for examining the effects of (for example) global climate change.

In summary, the findings of our analysis are consistent with the basic attributes of the MTE, but they address a

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decidedly less-controversial aspect of the theory. Whether these data can be used to support the greater, more far-reaching predictions of the MTE is not clear, and so the debate will probably continue over whether the MTE represents a phenomenological model expressing the behavior of communities, or a truly mechanistic model explaining the underlying basis for the observed correlations. Nevertheless, as noted at the end of the Comment, the dichotomy between ecological theory in aquatic and terrestrial ecology is unfortunate and unwanted, and we applaud the author for helping to bridge this sometimes-formidable gap.

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*References*

- BROWN, J. H., J. F. GILLOOLY, A. P. ALLEN, V. M. SAVAGE, AND G. B. WEST. 2004. Toward a metabolic theory of ecology. *Ecology* **85**: 1771–1789.
- CYR, H., AND S. C. WALKER. 2004. An illusion of mechanistic understanding. *Ecology* **85**: 1802–1804.
- ROSE, J. M., AND D. A. CARON. 2007. Does low temperature constrain the growth rates of heterotrophic protists? Evidence and implications for algal blooms in cold water. *Limnol. Oceanogr.* **52**: 886–895.
- STERNER, R. W. 2004. A one-resource “stoichiometry”? *Ecology*. **85**: 1813–1816.

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