

COMMENT

Limnol. Oceanogr., 53(5), 2008, 2046–2047
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The metabolic theory of ecology and algal bloom formation

Rose and Caron (2007) have compiled a comprehensive data set of individual growth rates of planktonic protists in an attempt to answer a fundamental question in marine ecology: “Why are blooms of phytoplankton such common events in the ocean?”. They reach the interesting conclusion that, because the temperature dependence of the growth rate of heterotrophic protists is much stronger than that of autotrophic protists, the growth rates of algal grazers will be much lower than that of their prey when water temperatures are low. They conclude that this reduced predator growth will result in a lower grazing pressure, allowing frequent algal blooms to develop in polar regions. Most importantly, they speculate that this difference in the temperature dependence of heterotrophic and autotrophic growth might be due to their differing metabolic pathways. Here I try to link their results to the metabolic theory of ecology (MTE) (Brown et al. 2004), and I argue that the conclusion of Rose and Caron (2007) is very similar to one of the predictions of MTE.

MTE predicts a different temperature dependence for heterotrophic processes (mostly driven by adenosine triphosphate synthesis) and autotrophic rates (controlled by Rubisco carboxylation) (Allen et al. 2005). To describe the effects of temperature on metabolic processes, MTE uses the Van’t Hoff–Arrhenius equation (Arrhenius 1915), closely related to Boltzmann’s factor (Gillooly et al. 2001, 2002; Brown et al. 2004; Allen et al. 2005):

$$B = b_0 e^{-E/kT} \quad (1)$$

where B is the metabolic rate (with units of metabolite consumed or produced per unit time), b_0 is a normalization factor dependent on body size (with the same units as B), E is the average activation energy for metabolic processes (Gillooly et al. 2001), k is Boltzmann’s constant (8.62×10^{-5} eV K⁻¹) and T is the absolute temperature (in Kelvin). For heterotrophs, MTE predicts an activation energy of 0.65 eV, whereas for autotrophs the effective activation energy for photosynthetic reactions should be close to 0.32 eV (although Eq. 1 is just an approximation to a more complex equation; see Appendix 1 in Allen et al. [2005]). Rose and Caron (2007) use a simple exponential relationship between temperature in degrees Celsius (T_c) and growth rates, so the comparison between the slopes of 0.12, 0.10, and 0.13 that they obtain for heterotrophs (bacterivorous protists, herbivorous protists, and copepods) and the slope of 0.06 that they obtain for phototrophic protists to the activation energies predicted by MTE is not straightforward. Equation 1 can be expressed in degrees Celsius as (Gillooly et al. 2002):

$$B = B_0 e^{(E/kT_0^2)(T_c/[1+T_c/T_0])} \quad (2)$$

where B_0 is the metabolic rate at 0°C dependent on body size and T_0 is the absolute temperature at 0°C (i.e., 273 K). Because the term $1 + T_c/T_0$ is at most 1.15 for the temperature range considered by Rose and Caron (2007), Eqs. 1 and 2 can be approximated by (see Gillooly et al. 2002):

$$B \approx B_0 e^{(E/kT_0^2)T_c} \quad (3)$$

Equation 3 is indeed the equation used by Rose and Caron (2007). Accordingly, the slopes calculated by Rose and Caron (2007) are approximately E/kT_0^2 , with k and T_0 being constants. Hence, the slopes of 0.12, 0.10, and 0.13 for heterotrophs represent activation energies of 0.77, 0.64, and 0.84 eV respectively, very close to the activation energy for heterotrophic organisms of 0.65 eV predicted by MTE. On the other hand the slope of 0.06 for phototrophic protists represents an activation energy of 0.39 eV, very close to the activation energy of 0.32 eV predicted by MTE. In fact, these results are remarkably similar to those recently reported by Lopez-Urrutia et al. (2006) in a compilation of individual respiration rates of marine plankton. Lopez-Urrutia et al. (2006) obtained an activation energy of 0.56 eV for heterotrophic respiration (from bacteria to mesozooplankton) and an activation energy of 0.33 eV for the respiration of phototrophic plankton. Furthermore, Lopez-Urrutia et al. (2006) also compiled growth rates of phototrophic protists, as did Rose and Caron (2007), and obtained a similar activation energy of 0.29 eV. The main difference between the analysis of Lopez-Urrutia et al. (2006) and Rose and Caron (2007) is that the former used MTE to provide a full model of the combined effects of temperature and cell size on phytoplankton production, whereas Rose and Caron (2007) analyzed each effect separately.

Both studies when combined provide strong support for the application of MTE to marine planktonic ecosystems. The novelty of MTE is not to report the existence of body-size or temperature dependence of metabolic rate, which have been known for over a century. Even the differential temperature dependence of the rates of heterotrophic and autotrophic plankton was reported by Huntley and Boyd (1984), well ahead of the conception of MTE. The novelty of MTE is to attempt to give a theoretical explanation for these effects on the basis of the fractal structure of distribution networks and biochemical kinetics. This mechanistic basis of MTE is still under debate (see Allen and Gillooly 2007, O’Connor et al. 2007b, and references therein). But if it proves correct, MTE and its key proposition that metabolism drives higher-order ecological processes may provide a unifying theory for understanding of marine ecosystem function (Harris et al. 2006), enabling predictions under future climate scenarios

(Duarte 2007). The difference between a theoretically grounded prediction and an empirical relationship is quite crucial. A theoretical framework should help to distinguish between causal mechanisms and spurious relationships. This distinction is most important in the case of temperature, not only for the obvious implications in climate change modeling, but also because temperature usually covaries with other factors such as nutrient availability that are likely to have effects on plankton metabolism. For example, Lopez-Urrutia and Morán (2007) concluded, using MTE, that a previously reported relationship between heterotrophic bacterial growth efficiency and temperature is a noncausal relationship generated by the effects of resource availability on bacterial growth efficiency. Further, Lopez-Urrutia et al. (2006) report that the growth efficiency of phytoplankton is also independent of temperature because the activation energies for autotrophic respiration and production are similar. Furthermore, combining the results of Lopez-Urrutia et al. (2006) and Rose and Caron (2007) for heterotrophic protists and zooplankton, we can conclude that their growth efficiencies might also be independent of temperature because the activation energies for respiration and production are very similar.

The real challenge and potential of MTE is that it provides a framework to scale the effects of temperature, body size, and resources from the level of individual physiology to the ecology of populations, communities, and ecosystems (Brown et al. 2004). Applications of MTE scaling in marine ecosystems are rapidly emerging, from the analysis of the rates of development and dispersal of marine organisms (Hirst and Lopez-Urrutia 2006; Duarte 2007; O'Connor et al. 2007a) to the study of size spectra (San Martin et al. 2006) or the metabolic balance of planktonic communities (Lopez-Urrutia et al. 2006). The work of Rose and Caron (2007) suggests that MTE could be used to explain the dynamics of algal bloom formation. These results should encourage the testing and extension of MTE in marine ecosystems and foster the incorporation of resource limitation in the MTE framework (Finkel 2001; Lopez-Urrutia et al. 2006; Lopez-Urrutia and Morán 2007). If we aim to explain how the frequency of algal blooms varies with latitude or is modified by climate change, we need to incorporate resource availability into MTE, especially given that both nutrient concentration in the case of phytoplankton and algal biomass in the case of herbivorous zooplankton are highly correlated with latitude and temperature in marine ecosystems. But, if MTE is to be developed as a truly unifying theory of ecology, we should make these advances in concert with developments made in terrestrial systems.

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Received: 14 March 2007

Accepted: 13 September 2007

Amended: 16 November 2007

Acknowledgments

Funding was provided by a Ramon y Cajal grant and project PERPLAN from the Ministerio de Educación y Ciencia. X. A. G. Morán provided useful comments.