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COMMENT

Why growth of nutrient-limited micro-organisms should have low-temperature sensitivity

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If molecular diffusion is the process that limits microbial growth at low substrate concentrations, one would expect low temperature dependence of nutrient-limited phytoplankton.

In both experimental and theoretical literature on microbial physiology, the relationship between a specific rate (μ) and the concentration of a substrate (S) limiting this process, is usually described by a hyperbolic function

$$\mu = \frac{\mu^{max} S}{K + S} \qquad (1)$$

where μ^{max} is the maximum rate and K is the substrate concentration corresponding to $\mu^{max}/2$, therefore usually termed the half-saturation constant. This relationship is traditionally referred to either as the Monod or the Michaelis–Menten function, terminologies originating from the scientific traditions of population growth [1] and biochemistry [2], respectively.

In a recent contribution [3], Marañón et al. use this hyperbolic formula to discuss their experimental finding that temperature sensitivity of metabolic rates in mineral nutrient-limited phytoplankton is much less than when grown under nutrient-replete conditions. They pointed out that this reduced temperature dependence of metabolic rates under nutrient limitation can be explained in terms of enzyme kinetics, because maximum reaction rates and half-saturation constants both increase with temperature.

Mathematically, this follows from Eq. (1): at high S ($S \gg K$), Eq. (1) reduces to $\mu_{S \to \infty} \approx \mu^{max}$, while at low S ($S \ll K$), it gives $\mu_{S \to 0} \approx \frac{\mu^{max}}{K} S$. If both μ and K correlate positively with temperature, it follows that temperature dependence of μ is less under mineral nutrient-limited

(low S) than under nutrient-replete (high S) conditions. Below, we extend their argument one step further and show that such low-temperature sensitivity at low S follows from microbial nutrient uptake theory. In short, this is because, at low S, growth rates of microbial organisms tend to become limited by nutrient transport processes outside the cell rather than by intracellular enzymatic processes (Pasciak and Gavis 1974, Aksnes and Egge 1993, [4–6]).

Since μ^{max} reflects enzymatic processes, it seems reasonable to expect a Q_{10} for μ^{max} comparable to that of enzymatic reactions. The theoretical arguments for a similar temperature sensitivity for K, seem, however, less obvious. In the Monod tradition, K is a purely empirical constant. In enzyme kinetics, it is derived using a model based on the formation of a substrate–enzyme complex [7]. In this model, K appears as the ratio between rate constants. From theoretical reasons, it is therefore not obvious that it should be equally sensitive to temperature as μ^{max}.

The hyperbolic relationship of Eq. (1) can, however, be parameterized in a mathematically equivalent way by substituting the half-saturation constant with the slope $\alpha = \mu^{max}/K$ at the origin

$$\mu = \frac{\alpha S}{1 + \frac{\alpha S}{\mu^{max}}} \qquad (2)$$

As S approaches 0, which corresponds to the nutrient-limited situation, this gives $\mu \approx \alpha S$. Although mathematically equivalent, this parameterization suggests an alternative interpretation of the mechanisms behind temperature sensitivity of microbial growth, where μ^{max} is the enzyme-dependent maximum growth rate as before, while α is determined by the physical processes of diffusion of nutrient molecules toward the cell ([8] and references therein). While μ^{max} is sensitive to temperature according to enzymatic processes inside the cell, α now depends on physical transport processes of mineral nutrients outside the cell, and is therefore expected to be much less sensitive to temperature [6]. With $K = \mu^{max}/\alpha$, and α insensitive to

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temperature, the temperature dependence of K will follow that of μ^{max}. Temperature effects on α have been considered by Jumars et al. [6] who concluded that diffusion-limited growth rates should have Q_{10} values of around 1.2–1.4. While mathematically equivalent to Marañón et al.'s arguments, the mechanistic interpretation becomes very different when diffusion-limited mineral nutrient uptake is considered.

Marañón et al. [3] conducted their experiments in nitrogen-limited chemostats. Growth rate and nitrogen uptake are then determined by the dilution rate D (=pump flow/culture volume) and consequently *not* affected by temperature since D is constant. A change in temperature with fixed D theoretically gives a new steady state with the new culture concentration S' that is needed to give the same growth rate $\mu' = \mu = D$ as before. The temperature independence of primary production and respiration found by Marañón et al. thus essentially means that the C:N stoichiometry of the organisms investigated is temperature-independent. If this is extrapolated to a nitrogen-limited photic zone, one could argue that the temperature sensitivity of primary production and respiration should follow that of the nitrogen uptake, and thus the low-temperature sensitivity originates from how molecular diffusion of mineral nutrients outside the cell is affected by temperature. As discussed by Jumars et al. [6], the simplest formulation that reasonably accurately indicates this temperature dependence is the Stokes–Einstein equation, which predicts much lower temperature sensitivity than for enzymatic processes. Under nutrient-replete conditions, rather than diffusion outside the cell, internal enzymatic processes become rate limiting. From this follows higher-temperature sensitivity than under nutrient limitation.

Larsen et al. [9] used a dynamic food web model, originally developed for mesocosms run at $17\,^{\circ}\mathrm{C}$ to interpret results from Arctic mesocosms run at $7\,^{\circ}\mathrm{C}$. They concluded that temperature correction of the rate parameters would be optimal with a Q_{10} of around 1.4. As this is within the range calculated by Jumars et al. [6], such low-temperature sensitivity of microbial food web dynamics is possible to explain in terms of diffusion-limited nutrient uptake, without the need for additional assumptions concerning adaptations in cell physiology and/or in community composition.

The trend in plankton models is to base their formulations on organism traits and the trade-off between these traits [8]. The important conceptual difference between the two mathematically equivalent formulations in Eqs. (1) and (2) illustrates the importance of deriving parameterizations that, in an accurate manner, represent the underlying processes. In this case, it highlights the importance of separating the temperature effects on physical and enzymatic processes.

Compliance with ethical standards

References

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