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Kiørboe, Thomas; Andersen, Ken Haste

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NUTRIENT AFFINITY, HALF SATURATION CONSTANTS, AND THE COST OF TOXIN PRODUCTION IN DINOFLAGELLATES

Thomas Kiørboe* (tk@aqua.dtu.dk) and Ken H. Andersen (kha@aqua.dtu.dk), Centre for Ocean Life, DTU-Aqua, DTU, DK-2800 Kgs. Lyngby, Denmark

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*Corresponding author: tk@aqua.dtu.dk; Phone: +45 4011 1884
Abstract: The two parameters of the Michaelis-Menten model, the maximum uptake rate and the half saturation constant, are not stochastically independent, and the half saturation constant not a measure of nutrient affinity, as commonly assumed. Failure to realize their interdependence and mechanistic interpretation may lead to the emergence of false trade-offs.
Trade-offs is at the root of diversity: competing species can co-exist because they excel in different traits that trade-off against one another. For example, competition and defense specialist may co-exist when predation prevents the superior competitor from monopolizing a limiting resource (Winter et al. 2010). Hence, a mechanistic understanding of the trade-offs between traits is key to understand and model biological communities (Tilman 1990). In a recent paper, Brandenburg et al. 2018 made a laudable attempt to experimentally quantify trade-offs between defensive and competitive traits in a toxic dinoflagellate. Several dinoflagellates produce toxins with grazer deterrent effects. The production of toxins is often induced by the presence of grazer cues (Selander et al. 2006, Xu and Kiørboe 2018), strongly suggesting that the defense is costly (Karban 2011). However, previous attempts have failed to experimentally measure any ‘cost’ of the defense, e.g., in terms of reduced growth (Selander et al. 2006, John et al. 2015). Hence, the study of Brandenburg and coworkers is most welcome. However, their analysis is based on a common misinterpretation of the half saturation constant and provides no clear evidence of nutrient uptake and defense trade-offs.

The authors describe measured nutrient uptake kinetics by the Michaelis-Menten model:

\[ V = V_{\text{max}} \frac{C}{K_{1/2} + C} \]  

where \( V \) is the nutrient uptake rate, \( V_{\text{max}} \) the maximum uptake rate, \( K_{1/2} \) the half saturation concentration, and \( C \) the nutrient concentration. From their experimental data they demonstrate positive relations between \( K_{1/2} \) and \( V_{\text{max}} \), and between \( K_{1/2} \) and cellular toxin content, as has been demonstrated earlier from between-species comparisons (Litchman et al. 2007, Edwards et al. 2012). Brandenburg et al. considers the half-saturation constant inversely proportional to the nutrient uptake affinity and argues that the relations represent trade-offs between traits, i.e., that faster maximum uptake rate and production of toxins are at the cost of a lower affinity and, hence,
reduced competitive ability. A similar claim (and finding) was made by Frangópulos et al. (2004).

However, there are two problems with this approach: (i) the two parameters are not stochastically independent of one another (Smith et al. 2014), and hence relations between them must be considered very carefully; and (ii) the half-saturation constant cannot be considered an inherent trait.

These two problems can be solved by a different parametrization of nutrient uptake:

\[ V = \frac{V_{\text{max}} \alpha c}{V_{\text{max}} + \alpha c} \]  

where \( \alpha \) is the nutrient affinity. Strictly speaking (1) and (2) are only valid descriptions of nutrient uptake kinetics if the cells are perfect absorbers (Fiksen et al. 2013). The two parameters, \( \alpha \) and \( V_{\text{max}} \), are now independent of one another in a statistical sense. Comparing (1) and (2) shows that \( K_{1/2} = \frac{V_{\text{max}}}{\alpha} \). Using this expression we can compute the affinity from data in Brandenburg et al. The relations between affinity and maximum uptake rate and between affinity and toxin content now vanishes (Fig. 1). The positive relation between \( V_{\text{max}} \) and \( K_{1/2} \) found by Brandenburg et al is expected because both affinity and maximum uptake rate increase with cell size, everything else being equal. The affinity is ultimately limited by the rate at which molecular diffusion transports nutrients to the cell. For a perfectly absorbing spherical cell this is \( 4\pi Dr \), where \( D \) is the diffusion coefficient and \( r \) the cell radius (Crank 1975). Hence, affinity scales with cell radius. Maximum uptake rate depends on the surface area and hence scales with radius squared. Thus, when comparing across differently sized species or strains, and in the absence of trade-offs, \( V_{\text{max}} \) is expected to increase with the square of \( K_{1/2} \). Given the scatter, the data of Brandenburg et al. are not inconsistent with this expectation, and there is thus no evidence of a trade-off.

The half saturation constant is not an organismal trait in a mechanistic sense, and it is not a measure of nutrient uptake efficiency. While it may be a useful diagnostic, half saturation constants are often
a source of confusion, as demonstrated here, and the Michaelis-Menten relation is insufficient when
one seeks mechanistic understanding. This has been pointed out repeatedly (Aksnes and Cao 2011,
Fiksen et al. 2013, Flynn et al. 2018), but the tradition persists. Brandenburg et al. further demonstrate negative relations between the maximum growth rate and
the specific contents of two (of 4) toxins produced by the algae and again consider this a
demonstration of a trade-off. However, these relations mainly hinges on differences between two
populations, from the Baltic and the Netherlands, respectively (Fig. 1 D,E), effectively reducing
sample size to $n = 2$, and so is difficult to generalize.

The difficulty of quantifying trade-offs applies to several other defense mechanisms (Pančić and
Kiørboe 2018). One reason may be that costs are significant only under resource limitation
(Meaden et al. 2015, Zhu et al. 2016, Chakraborty et al. 2018). The experiments of Brandenburg et
al. and those of others looking for costs of toxin production in dinoflagellates have not explored this
possibility.

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Fig. 1. Relations between estimates of $V_{max}$ (μmol N d$^{-1}$) and $\alpha$ (L d$^{-1}$) (A), between specific toxin contents (pg μm$^{-3}$) and $\alpha$ (B,C), and between specific toxin contents and growth rate (d$^{-1}$) (D, E) for two populations of the dinoflagellate *Alexandrium ostenfeldi*. PSP and CM are paralytic shellfish poison and cyclic imine toxins, respectively. In (A) the fitted line is $V_{max}=1.29 \times 10^{-5}+87 \times 10^{3}\alpha$ with the exponent of 2 fixed. The linear regressions (with confidence limits) in are: log $V_{max}=-2.71+0.40\alpha$. 
x Log α (A), $\alpha = 1.1 \times 10^{-5} - 2.6 \times 10^{-3}$ PSP (B), $\alpha = 6.9 \times 10^{-6} - 6.9 \times 10^{-6}$ CM (C), Growth rate = 0.35 – 135 x PSP for the Baltic population and Growth rate = 0.16 +7.4 x PSP for the Netherlands population (D), and Growth rate = 0.34 – 22.5 x CM for the Baltic population and Growth rate = 0.20 – 2.5 x CM for the Netherlands population. Data from Brandenburg et al. (2018).