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

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19 **Abstract:** The two parameters of the Michaelis-Menten model, the maximum uptake rate and the
20 half saturation constant, are not stochastically independent, and the half saturation constant not a
21 measure of nutrient affinity, as commonly assumed. Failure to realize their interdependence and
22 mechanistic interpretation may lead to the emergence of false trade-offs.

23

24 Trade-offs is at the root of diversity: competing species can co-exist because they excel in different
25 traits that trade-off against one another. For example, competition and defense specialist may co-
26 exist when predation prevents the superior competitor from monopolizing a limiting resource
27 (Winter et al. 2010). Hence, a mechanistic understanding of the trade-offs between traits is key to
28 understand and model biological communities (Tilman 1990). In a recent paper, Brandenburg et al.
29 (2018) made a laudable attempt to experimentally quantify trade-offs between defensive and
30 competitive traits in a toxic dinoflagellate. Several dinoflagellates produce toxins with grazer
31 deterrent effects. The production of toxins is often induced by the presence of grazer cues (Selander
32 et al. 2006, Xu and Kiørboe 2018), strongly suggesting that the defense is costly (Karban 2011).
33 However, previous attempts have failed to experimentally measure any ‘cost’ of the defense, e.g., in
34 terms of reduced growth (Selander et al. 2006, John et al. 2015). Hence, the study of Brandenburg
35 and coworkers is most welcome. However, their analysis is based on a common misinterpretation of
36 the half saturation constant and provides no clear evidence of nutrient uptake and defense trade-
37 offs.

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

39
$$V = V_{\max} \frac{C}{K_{1/2} + C} \quad (1)$$

40 where V is the nutrient uptake rate, V_{\max} the maximum uptake rate, $K_{1/2}$ the half saturation
41 concentration, and C the nutrient concentration. From their experimental data they demonstrate
42 positive relations between $K_{1/2}$ and V_{\max} , and between $K_{1/2}$ and cellular toxin content, as has been
43 demonstrated earlier from between-species comparisons (Litchman et al. 2007, Edwards et al.
44 2012). Brandenburg *et al.* considers the half-saturation constant inversely proportional to the
45 nutrient uptake affinity and argues that the relations represent trade-offs between traits, i.e., that
46 faster maximum uptake rate and production of toxins are at the cost of a lower affinity and, hence,

47 reduced competitive ability. A similar claim (and finding) was made by Frangópulos *et al.* (2004).
 48 However, there are two problems with this approach: (i) the two parameters are not stochastically
 49 independent of one another (Smith *et al.* 2014), and hence relations between them must be
 50 considered very carefully; and (ii) the half-saturation constant cannot be considered an inherent
 51 trait.

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

53
$$V = V_{\max} \frac{\alpha C}{V_{\max} + \alpha C} \quad (2)$$

54 where α is the nutrient affinity. Strictly speaking (1) and (2) are only valid descriptions of nutrient
 55 uptake kinetics if the cells are perfect absorbers (Fiksen *et al.* 2013). The two parameters, α and
 56 V_{\max} , are now independent of one another in a statistical sense. Comparing (1) and (2) shows that
 57 $K_{1/2} = V_{\max} / \alpha$. Using this expression we can compute the affinity from data in Brandenburg *et al.*
 58 The relations between affinity and maximum uptake rate and between affinity and toxin content
 59 now vanishes (Fig. 1). The positive relation between V_{\max} and $K_{1/2}$ found by Brandenburg *et al.* is
 60 expected because both affinity and maximum uptake rate increase with cell size, everything else
 61 being equal. The affinity is ultimately limited by the rate at which molecular diffusion transports
 62 nutrients to the cell. For a perfectly absorbing spherical cell this is $4\pi Dr$, where D is the diffusion
 63 coefficient and r the cell radius (Crank 1975). Hence, affinity scales with cell radius. Maximum
 64 uptake rate depends on the surface area and hence scales with radius squared. Thus, when
 65 comparing across differently sized species or strains, and in the absence of trade-offs, V_{\max} is
 66 expected to increase with the square of $K_{1/2}$. Given the scatter, the data of Brandenburg *et al.* are not
 67 inconsistent with this expectation, and there is thus no evidence of a trade-off.

68 The half saturation constant is not an organismal trait in a mechanistic sense, and it is not a measure
 69 of nutrient uptake efficiency. While it may be a useful diagnostic, half saturation constants are often

70 a source of confusion, as demonstrated here, and the Michaelis-Menten relation is insufficient when
71 one seeks mechanistic understanding. This has been pointed out repeatedly (Aksnes and Cao 2011,
72 Fiksen et al. 2013, Flynn et al. 2018), but the tradition persists.

73 Brandenburg et al. further demonstrate negative relations between the maximum growth rate and
74 the specific contents of two (of 4) toxins produced by the algae and again consider this a
75 demonstration of a trade-off. However, these relations mainly hinges on differences between two
76 populations, from the Baltic and the Netherlands, respectively (Fig. 1 D,E), effectively reducing
77 sample size to $n = 2$, and so is difficult to generalize.

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

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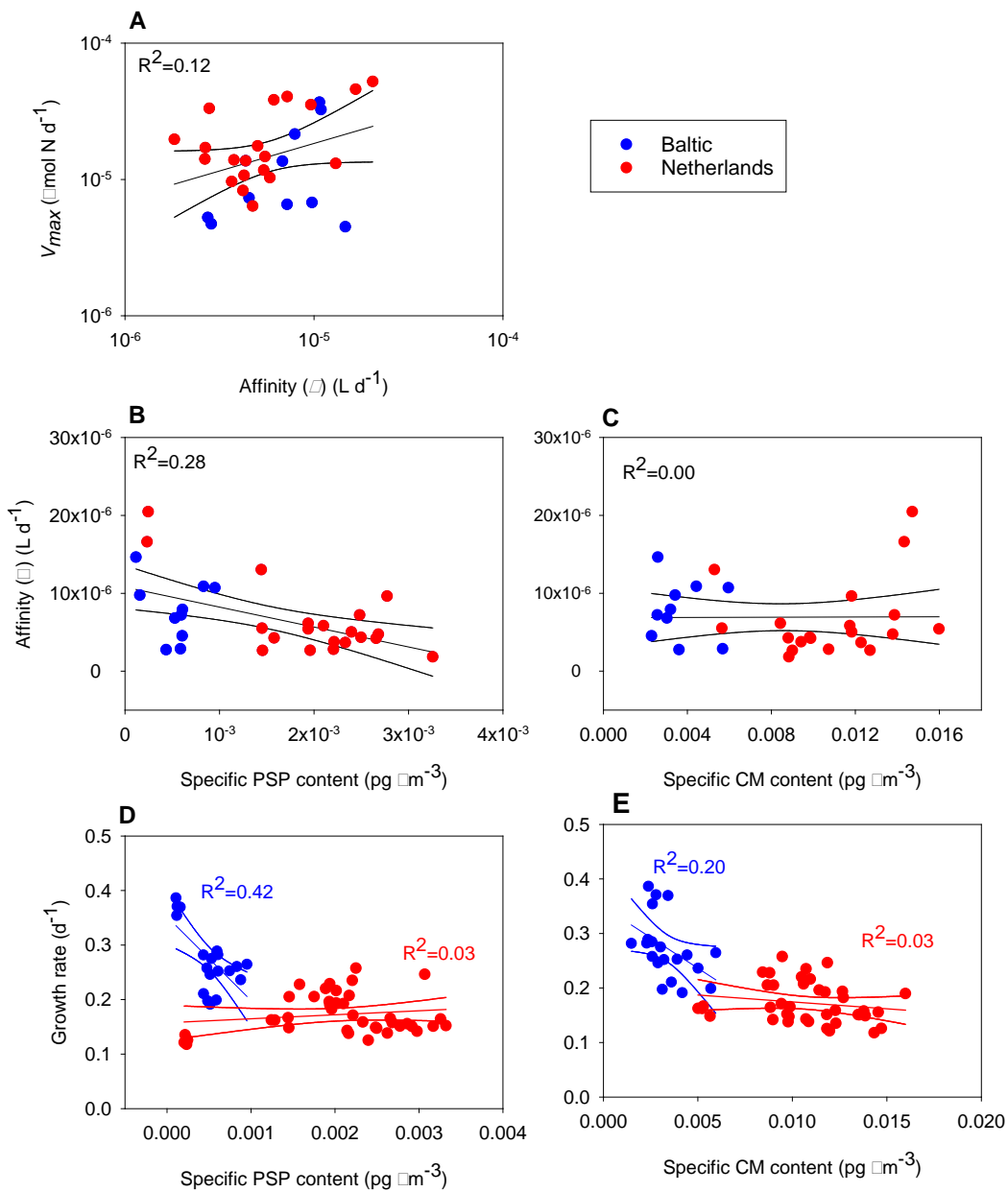
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131 Figures



132

133 Fig. 1. Relations between estimates of V_{max} ($\mu\text{mol N d}^{-1}$) and α (L d^{-1}) (A), between specific toxin
 134 contents ($\text{pg } \mu\text{m}^{-3}$) and α (B,C), and between specific toxin contents and growth rate (d^{-1}) (D, E) for
 135 two populations of the dinoflagellate *Alexandrium ostenfeldi*. PSP and CM are paralytic shellfish
 136 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
 137 the exponent of 2 fixed. The linear regressions (with confidence limits) in are: $\log V_{max} = -2.71 + 0.40$

138 $\times \text{Log } \alpha$ (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 =
139 $0.35 - 135 \times \text{PSP}$ for the Baltic population and Growth rate = $0.16 + 7.4 \times \text{PSP}$ for the Netherlands
140 population (D), and Growth rate = $0.34 - 22.5 \times \text{CM}$ for the Baltic population and Growth rate =
141 $0.20 - 2.5 \times \text{CM}$ for the Netherlands population. Data from Brandenburg et al. (2018).