Nutrient affinity, half-saturation constants and the cost of toxin production in dinoflagellates

Kjørboe, Thomas; Andersen, Ken Haste

Published in:
Ecology Letters

Link to article, DOI:
[10.1111/ele.13208](https://doi.org/10.1111/ele.13208)

Publication date:
2019

Document Version
Peer reviewed version

[Link back to DTU Orbit](#)

Citation (APA):
Kjørboe, T., & Andersen, K. H. (2019). Nutrient affinity, half-saturation constants and the cost of toxin production in dinoflagellates. *Ecology Letters*, 22(3), 558-560. <https://doi.org/10.1111/ele.13208>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

**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

Authorship statement: TK and KHA performed the analyses and wrote the manuscript

Data accessibility statement: Not relevant

Number of words in abstract (50) and main text (807), number of cited references (19), number
figures (1)

Running title: Nutrient affinity and defense costs

Keywords: Trade-off, defense, nutrient affinity

Type of article: Technical Comment

*Corresponding author: tk@aqua.dtu.dk; Phone: +45 4011 1884

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

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:

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

where V is the nutrient uptake rate, $V_{\max}$ 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 $V_{\max}$, 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:

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

where α 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, α and $V_{\max}$, are now independent of one another in a statistical sense. Comparing (1) and (2) shows that $K_{1/2} = V_{\max} / \alpha$. 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 $V_{\max}$ 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, $V_{\max}$ 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

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.

83 References

- 84 Aksnes, D. L., and F. J. Cao. 2011. Inherent and apparent traits in microbial nutrient uptake. *Marine*
 85 *Ecology Progress Series* 440:41–51.
- 86 Brandenburg, K. M., S. Wohlrab, U. John, A. Kremp, J. Jerney, B. Krock, and D. B. Van de Waal.
 87 2018. Intraspecific trait variation and trade-offs within and across populations of a toxic
 88 dinoflagellate. *Ecology Letters* 21:1561–1571.
- 89 Chakraborty, S., M. Pančić, K. H. Andersen, and T. Kiørboe. 2018. The cost of toxin production in
 90 phytoplankton: the case of PST producing dinoflagellates. *The ISME Journal*.
- 91 Crank, J. 1975. *The mathematics of diffusion*. 2nd edition. Clarendon Press, Oxford.

- 92 Edwards, K. F., M. K. Thomas, C. A. Klausmeier, and E. Litchman. 2012. Allometric scaling and
 93 taxonomic variation in nutrient utilization traits and maximum growth rate of phytoplankton.
 94 *Limnology and Oceanography* 57:554–566.
- 95 Fiksen, Ø., M. J. Follows, and D. L. Aksnes. 2013. Trait-based models of nutrient uptake in
 96 microbes extend the Michaelis-Menten framework. *Limnology and Oceanography* 58:193–
 97 202.
- 98 Flynn, K. J., C. Lindemann, D. Kirchman, and E. Laws. 2018. Effects of growth rate , cell size,
 99 motion , and elemental stoichiometry on nutrient transport kinetics. *Plos Computational*
 100 *Biology*:1–30.
- 101 Frangópulos, M., C. Guisande, E. DeBlas, and I. Maneiro. 2004. Toxin production and competitive
 102 abilities under phosphorus limitation of *Alexandrium* species. *Harmful Algae* 3:131–139.
- 103 John, U., U. Tillmann, J. Hulskotter, T. J. Alpermann, S. Wohlrab, and D. B. Van de Waal. 2015.
 104 Intraspecific facilitation by allelochemical mediated grazing protection within a toxigenic
 105 dinoflagellate population. *Proceedings of the Royal Society B: Biological Sciences*
 106 282:20141268–20141268.
- 107 Karban, R. 2011. The ecology and evolution of induced resistance against herbivores. *Functional*
 108 *Ecology* 25:339–347.
- 109 Litchman, E., C. A. Klausmeier, O. M. Schofield, and P. G. Falkowski. 2007. The role of functional
 110 traits and trade-offs in structuring phytoplankton communities: Scaling from cellular to
 111 ecosystem level. *Ecology Letters* 10:1170–1181.
- 112 Meaden, S., K. Paszkiewicz, and B. Koskella. 2015. The cost of phage resistance in a plant
 113 pathogenic bacterium is context-dependent. *Evolution* 69:1321–1328.

- 114 Pančić, M., and T. Kiørboe. 2018. Phytoplankton defence mechanisms: traits and trade-offs.
115 Biological Reviews 93:1269–1303.
- 116 Selander, E., P. Thor, G. Toth, and H. Pavia. 2006. Copepods induce paralytic shellfish toxin
117 production in marine dinoflagellates. Proceedings of the Royal Society B: Biological Sciences
118 273:1673–1680.
- 119 Smith, S. L., A. Merico, K. W. Wirtz, and M. Pahlow. 2014. Leaving misleading legacies behind in
120 plankton ecosystem modelling. Journal of Plankton Research 36:613–620.
- 121 Tilman, D. 1990. Constraints and Tradeoffs: Toward a Predictive Theory of Competition and
122 Succession. Oikos 58:3–15.
- 123 Winter, C., T. Bouvier, M. G. Weinbauer, and T. F. Thingstad. 2010. Trade-Offs between
124 Competition and Defense Specialists among Unicellular Planktonic Organisms: the “Killing
125 the Winner” Hypothesis Revisited. Microbiology and Molecular Biology Reviews 74:42–57.
- 126 Xu, J., and T. Kiørboe. 2018. Toxic dinoflagellates produce true grazer deterrents. Ecology 0:1–10.
- 127 Zhu, X., J. Wang, Q. Chen, G. Chen, Y. Huang, and Z. Yang. 2016. Costs and trade-offs of grazer-
128 induced defenses in *Scenedesmus* under deficient resource. Scientific Reports 6:1–10.

129

130

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).