A comment on "Nutrient status and nutrient competition of phytoplankton in a shallow, hypertrophic lake" (Sommer)

Sommer (1989) reported the results of a field study in which he tested some predictions derived from resource competition theory (sensu Tilman 1982), namely that the competitive performance of various species of phytoplankton can be ordered along some resource ratio gradient. Although Sommer (1989) found significant correlations between the success of a species within the phytoplankton and some resources ratio gradient that are consistent with his original hypothesis, the method he used to analyze the data is inappropriate. The inadequacy stems from its inability to distinguish between a resource ratio effect and a direct resource effect. I maintain that while resource ratios may be important in regulating species abundance in natural phytoplankton populations, alternate hypotheses inconsistent with the resource ratio hypothesis may also explain Sommer's results.

The inadequacy of the approach is essentially statistical and can be demonstrated by considering the different ways by which a significant correlation between the species' performance and a resource ratio (log-transformed as by Sommer 1989) can arise. As an example, consider the following simple model:

\[ Y = \alpha + \beta \log(A:B) + \epsilon \]  

(1)

where \( Y \) is some index of the dominance of this algal species in the phytoplankton, \( A \) and \( B \) are two different essential resources (e.g. the concentration of two nutrients), \( \alpha \) and \( \beta \) are regression coefficients, and \( \epsilon \) is a stochastic error term. The regression slope (\( \beta \)) can be statistically significant \((H_0: \beta = 0)\) for at least four different reasons, only two of which are consistent with the resource ratio hypothesis: first, resource \( A \) has a significant effect on \( Y \) but \( B \) does not; second, resource \( B \) has a significant effect on \( Y \) but \( A \) does not; third, the ratio \( A:B \), as a ratio, has an effect on \( Y \)(i.e. the effect occurs independent of the absolute magnitudes of \( A \) and \( B \)); and fourth, a combination of resource ratio effects and direct resource effects. Only the last two cases involve an effect of the ratio per se. The first two are direct resource effects. The magnitude of a correlation between \( Y \) and \( \log(A:B) \) when, in fact, only \( A \) influences \( Y \) will depend essentially on the relative magnitude of the variances of \( A \) and \( B \). Thus, the occurrence of a significant correlation between a variable of interest \( Y \) and a ratio can not only falsely attribute the effect to the ratio but can, in some cases, even obscure a direct resource effect when expressed as a ratio. Briefly, in no way does it constitute a proper test of the hypothesis at stake, namely that it is the ratio that is important in determining the value of \( Y \). Nor does it refute it. The hypothesis that a ratio \( A:B \) influences \( Y \), say positively, corresponds to two distinct but necessary subhypotheses: if \( B \) is held constant, increasing \( A \) corresponds to an increase in \( Y \); and when \( A \) is held constant, increasing \( B \) results in decreasing \( Y \). It is these two hypotheses that need to be tested. Except in an experimental setting where resources \( A \) and \( B \) can be manipulated at will, the two hypotheses can be difficult to test. However, the logarithmic transformation of the ratio in Sommer's analysis makes it easier to test the ratio effect hypothesis even in an observational study. The logarithm of a ratio \([\log(A:B)]\) is equal to the difference between the two logarithms \([\log(A) - \log(B)]\), so the ratio can be decomposed and the statistical significance of its components tested separately in a multiple regression model such as

\[ Y = \alpha + \beta_1 \log(A) + \beta_2 \log(B) + \epsilon. \]  

(2)

The coefficient \( \beta_1 \) corresponds to the influence of \( \log(A) \) once the influence of \( \log(B) \) on \( Y \) has been taken into account, and \( \beta_2 \) the converse. The two coefficients therefore correspond to the two subhypotheses nec-
Comment

necessary to imply the influence of the ratio. A purely ratio-dependent effect (i.e. independent of the absolute values of $A$ and $B$) would require that both regression coefficients $\beta_1$ and $\beta_2$ be statistically significant and of equal magnitude but opposite sign. Statistically significant coefficients but of differing magnitudes would correspond to a mixture of ratio and direct effects. When only one coefficient is significant, this would clearly imply that the influence cannot be attributed to a ratio effect but rather to a direct resource effect.

It should be noted that, in Sommer's case as well as in other instances where variables are regressed against the logarithms of composite variables (ratios or products only), it is advisable to always decompose them into their components so as to optimize the potential predictive power of the model. Decomposing ratios and products into their primary variables can increase the fit of the model. Although restricted to logarithmically transformed variables, this decomposition procedure would allow us, in the present case, to tease apart the real ratio effects from the direct resource effects. Although it may well be that the trends found by Sommer are real as stated, it will be necessary to perform the necessary multiple regression analyses before conclusions regarding resource competition in phytoplankton species can be agreed upon.

Yves T. Prairie

Département des Sciences Biologiques
Université du Québec à Montréal
P.O. Box 8888, Station “A”
Montréal, Québec H3C 3P8

References


Resource ratios or absolute concentrations:
A reply to the comment by Prairie

In his comment Prairie (1990) suggests that I should have tested not only resource ratios but also absolute resource concentrations as independent variables to explain the relative importance of phytoplankton species in Großes Wemmerssee. My reply consists of two components, a technical one and more substantive one.

First, the technical reply: Prairie is right that the logarithm of a ratio between two resources $[\log(A : B)]$ is equal to the difference between the logarithms of the two resources $[\log A - \log B]$. In principle, the multiple regression model suggested in his equation 2 can serve to distinguish between resource ratio effects and simple resource effects. However, this procedure does not work if more than two resources and one resource ratio gradient must be considered.

Let us modify his equations 1 and 2 for three resources:

$$Y = \alpha + \beta \log(A : B) + \gamma \log(B : C) + \delta \log(A : C) + \epsilon.$$  

Decomposed into simple resource concentrations this model becomes

$$Y = \alpha + \beta_1 \log A + \beta_2 \log B + \gamma_1 \log B + \gamma_2 \log C + \delta_1 \log A + \delta_2 \log C + \epsilon.$$  

A multiple regression analysis of $Y$ on the logarithm of the simple resources would yield the equation

$$Y = a + b \log A + c \log B + d \log C.$$  

By definition

$$b = \beta_1 + \delta_1; c = \beta_2 + \gamma_1; d = \gamma_2 + \delta_2.$$