essary 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 β_1 and β_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 logarithmi-

cally 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.

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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 Großer Binnensee. 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

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

The coefficients symbolized by the greek letters cannot be recalculated, because six unknown variables cannot be calculated from three equations. This makes Prairie's test impossible if species are arrayed along more than one resource ratio gradient.

In Großer Binnensee three essential resources (N, P, light) were found to be limiting plus a couple of substitutable resources (NO_3^- , NH_4^+). Eleven of the thirteen species tested showed a significant response to more than one resource ratio in the multiple regression analysis presented in my table 1 (Sommer 1989). One of the two species, which responded to only one resource ratio showed no time lag: *Scenedesmus acuminatus*. My regression equation (Sommer 1989) was

$$Y = 0.82 + 0.096 \log(N:P) - 0.1 \log D - 0.34 \log t$$

$$(r^2 = 0.48; \quad P = 0.0003)$$

where Y is biomass *S. acuminatus*/total biomass, N is dissolved inorganic nitrogen (μM), P is soluble reactive phosphorus (μM), D is biomass of *Daphnia magna* (mg DW liter $^{-1}$), and t is temperature ($^{\circ}\text{C}$). If N and P are entered separately into the regression,

$$Y = 0.79 + 0.104 \log N - 0.117 \log P - 0.06 \log D - 0.41 \log t$$

$$(r^2 = 0.36; \quad P = 0.043).$$

This equation suggests that the relative importance of *S. acuminatus* really responds to the $N:P$ ratio, because the regression coefficients for the two separate resources are of similar magnitude and opposite signs, as required by Prairie.

In addition to this technical reply, I express doubt whether in the context of my article (Sommer 1989) a test of single resource effects vs. resource ratio effects would have been justified. This approach is certainly meaningful when in a trial-and-error manner all plausible independent variables are tested by regression analysis. The trial-and-error approach is consistent with the program of predictive limnology sensu Peters (1986), but it was not followed in the study under discussion, which was designed in the context of Tilman's (1982) competition theory. The analysis of phytoplankton competition comprised two steps. First, it

was tested physiologically (biomass stoichiometry and enrichment bioassays) whether resource competition occurred. Second, it was tested by the regression analysis under discussion whether relative species abundance patterns were consistent with the resource ratio hypothesis derived from Tilman's competition theory.

The verification of competition as such is independent of the results of the resource ratio analysis and rests entirely on the definition that exploitative competition consists in the depression of the competitor's reproductive rate by consumption of shared resources. Tilman's competition theory does not predict any abundance patterns for the incipient and transient stages of resource competition. The resource ratio hypothesis is a prediction for the final stage of competition under constant conditions only. As I stated on p. 1169 (Sommer 1989), the resource ratio analysis was performed to test whether competition had proceeded far enough toward this final equilibrium stage. In this case, the resource ratio hypothesis was expected to be a sufficient approximation of what actually occurred in the lake. Neither Tilman's competition theory nor any other competition theory permits one to derive the prediction that in such a situation relative species abundances should follow single resource concentrations. Therefore, I consider the single resource hypothesis an arbitrary, ad hoc hypothesis which does not need to be tested.

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