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RESOURCE COMPETITION BETWEEN PLANKTONIC ALGAE: AN EXPERIMENTAL AND THEORETICAL APPROACH¹

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Abstract. The results of 76 long-term competition experiments between two species of freshwater algae (*Asterionella formosa* and *Cyclotella meneghiniana*) grown along a resource gradient agree with the predictions of two different models of resource competition. Both models are based on the functional resource-utilization response of each species to limiting resources. The Monod model and the Variable Internal Stores model of competition made similar predictions. *Asterionella* was observed to be competitively dominant when both species were phosphate limited; *Cyclotella* was dominant when both species were silicate limited; and both species stably coexisted when each species was growth-rate limited by a different resource. Almost 75% of the variance in the relative abundances of these two species along a natural silicate-phosphate gradient in Lake Michigan is explained by the Monod model.

Key words: Competition models; diatoms; functional response; Michaelis-Menten; Monod; phosphate; resource competition; resource gradient; resource utilization; silicate.

INTRODUCTION

Many recent theoretical studies of interspecific competition have dealt with the dependence of competition on the resource utilization abilities of each species. The models used in these studies may be classified as being of two types. One uses the classical Lotka-Volterra competition equations, estimating the coefficient of competition, α , from some measure of the resource utilization overlap between species (MacArthur 1969, 1970; Orrians and Horn 1969; May 1975). The other approach employs models which explicitly include the availability (concentration) of the resource and the functional dependence of growth of each species on the availability of the resource (Stewart and Levin 1973; Greeney et al. 1973; MacArthur 1972; O'Brien 1974; Petersen 1975; Taylor and Williams 1975; Tilman 1976). The work reported here is an experimental test of the latter type of mechanistic model. The results of 76 long-term competition experiments between two species of freshwater algae grown under controlled-culture laboratory conditions along a two-resource gradient are compared with the predictions of resource-utilization models of interspecific competition. This is a test of the utility of species-specific resource acquisition and utilization information in predicting the steady-state outcome of competition between two species potentially limited by two resources.

Asterionella formosa Hass. and *Cyclotella meneghiniana* Kutz., freshwater diatoms which are seasonally abundant in midlatitude, mesotrophic lakes (Kopczynska 1973; Stoermer and Kopczynska 1967), were the two species studied. The two potentially limiting resources for this study were phosphate

and silicate, the nutrients which most often limit algal growth in such lakes (Lund et al. 1963; Powers et al. 1972; Schelske and Stoermer 1971; Kilham 1971).

The nutrient kinetics of the clones of *Asterionella* and *Cyclotella* used in these competition experiments are reported elsewhere (Tilman and Kilham 1976). With this information on the ability of each species to acquire and utilize resources, two different models of resource competition are used to predict the steady-state outcome of interspecific competition for potentially limiting silicate and phosphate. The first model (Model I) is based on the Monod equations (Monod 1950; Herbert et al. 1956; Taylor and Williams 1975). The second model (Model II) is based on a variable internal stores model of growth (Droop 1974). Both competition models are founded on models of the functional acquisition and growth response of a single species to a single resource.

The experiments were designed to test how well such single species physiological information can predict the outcome of competition. To avoid variability in the outcome of competition that could be attributed to genetic changes in the populations (cf., Park et al. 1964), the same clone of each species was used throughout all the experiments. Both clones were bacteria-free isolates. Sterile technique was used throughout the experiments to eliminate the possible complication of bacterial competition for limiting resources. Competition experiments were allowed to proceed for between 30 to 40 days, to assure that the results observed were the steady-state outcome of interspecific competition. Two single-species culture controls were performed for all conditions at which competition experiments were performed, thus verifying that each species could exist by itself under all conditions tested. It was hoped that these precautions would minimize the variance in the outcome of the competition experiments, allowing a better test of the relationship between the resource utilization abilities of a species and its competitive abilities.

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The mathematical treatment of both models is a steady-state analysis, limited to those aspects that are relevant to the steady-state results of the competition experiments performed. The competition experiments were designed to determine the long-term outcome of interspecific competition under conditions in which each species, by itself, would be able to maintain a stable population. They were not designed for short-term dynamic analysis of competitive displacement. Thus the dynamic aspects of competitive displacement are not included in the analysis of the two models. The steady-state experimental results and theoretical predictions are compared with each other and with some observations on the relative abundances of *Asterionella* and *Cyclotella* along a natural gradient (in space and time) of phosphate and silicate in Lake Michigan.

MODEL I: MONOD MODEL OF RESOURCE COMPETITION

The Monod model of growth of a single species limited by a single resource was proposed by Monod (1950), and extensively developed and tested on single species cultures of bacteria (Herbert et al. 1956). The Michaelis-Menten model of enzyme kinetics has the same formulation as the Monod model. Dugdale (1967) proposed that the Michaelis-Menten model be used to describe nutrient use by marine phytoplankton, and O'Brien (1974) and Petersen (1975) proposed that it be used to describe nutrient competition between algae. Numerous other workers (Eppley and Thomas 1969; Guillard et al. 1973; Kilham 1975) have reported close agreement between experimental observations on a single species and the Monod or Michaelis-Menten equations. Although the Monod equation can be derived from enzyme kinetic theory, I consider it to be a simple equation that provides a reasonable approximation to the functional relation between growth rate and resource availability. For a continuous flow system, the equations for the i^{th} of n total species and for the j^{th} of m different resources are as follows:

$$dN_i/N_i dt = \min_{1 \leq j \leq m} [r_i S_j / (K_{ij} + S_j) - D] \quad (1)$$

$$dS_j/dt = D(S_0 - S_j) - \sum_{i=1}^n N_i r_i S_j / [(K_{ij} + S_j) Y_{ij}], \quad (2)$$

where

- r_i = maximal growth rate of species i
- K_{ij} = half saturation constant for species i limited by resource j (that is, the nutrient concentration at which it has half its maximal growth rate)
- Y_{ij} = yield of species i limited by resource j (number of cells produced per unit of resource j)
- N_i = number of cells of species i per unit volume
- S_j = concentration of resource j external to the cells
- S_0 = influent concentration of resource j

- D = steady-state growth rate (true dilution rate)
- n = number of species present
- m = number of potentially limiting resources.

Equation 1 states that the growth rate of a species will be completely determined by that one nutrient that is most limiting, of all those that are potentially limiting. This has been shown experimentally by Droop (1974) for a marine alga potentially limited by phosphate and vitamin B-12. The switching that occurs as a species changes from being growth-rate limited by one resource to being limited by another resource is not easily dealt with analytically. In this analysis, I employ a method that is suitable for steady-state conditions. Because the only cases of experimental interest are those in which each species can exist by itself, boundary condition peculiarities (such as washout of a species) are ignored.

For species i limited by resource j , Eqs. 1 and 2 provide the following steady-state relations (mathematical steady-state occurs when time derivatives are equal to zero)

$$N_{i(j)}^* = Y_{ij}(S_0 - S_j^*) \quad (3)$$

$$S_j^* = DK_{ij}/(r_i - D), \quad (4)$$

where

$N_{i(j)}^*$ = steady-state population size of species i when it *alone* is limited by resource j (This is comparable to the carrying capacity of environment j for species i)

S_j^* = steady-state external concentration of resource j when only species i is present.

The boundary between a species being growth-rate limited by resource 1 or by resource 2 is calculated by setting $N_{i(1)}^* = N_{i(2)}^*$. This provides an expression of the influent concentrations of resources 1 and 2 at which species i is equally limited by both resources at steady state (Eq. 5):

$$S_0 S_1 = S_1^* + (S_0 S_2 - S_2^*)(Y_{i2}/Y_{i1}). \quad (5)$$

The physiological constants in Table 1 were used to determine the boundary between phosphate and silicate limitation of *Asterionella*, for the concentrations of phosphate and silicate used in the experiments. This boundary (from Eq. 5) is shown in Fig. 1. For any silicate to phosphate ratios greater than 90 (to the left of the boundary), *Asterionella* should be phosphate limited. For $[S_i/P] < 90$ (to the right of the boundary), *Asterionella* should be silicate limited. The boundary between *Cyclotella* being phosphate or silicate limited was also determined from the kinetic parameters of Table 1. For $[S_i/P] > 6$ (to the left of the boundary), *Cyclotella* is phosphate limited. To the right of the boundary, for $[S_i/P] < 6$, *Cyclotella* is silicate limited (Fig. 1). The slight curvature in the boundaries comes from the dependence of S_1^* and S_2^* on dilution rate.

When several species are grown together, these

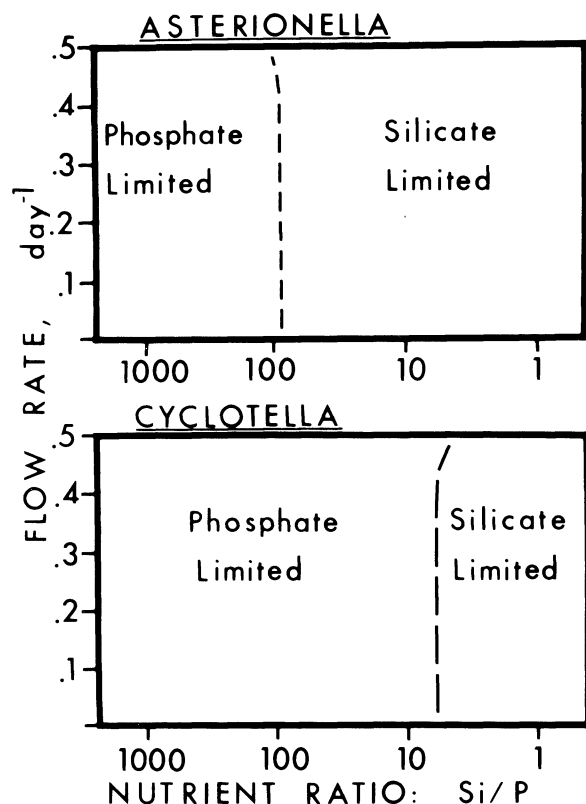


FIG. 1. The upper drawing shows the silicate to phosphate ratios for which *Asterionella* should be silicate or phosphate limited, as calculated using the physiological constants of Table 1 and Eq. 5. The lower drawing shows the same relationship for *Cyclotella*. The position of the curves reflects the resource gradient used.

boundaries should define, at steady state, the regions in which each species is limited by either silicate or phosphate. The boundaries for *Asterionella* and *Cyclotella* divide the nutrient ratio/flow rate plane into three regions (Fig. 2). For $[S_i/P] > 90$, both species should be phosphate limited. In the region to the right of the *Cyclotella* boundary ($[S_i/P] < 6$), both species should be silicate limited. In the region between the two boundaries, for $6 < [S_i/P] < 90$, both species should be limited by different resources: *Asterionella* by silicate and *Cyclotella* by phosphate.

Three cases of competition need be considered. For two species limited by the same nutrient, the species which is able to lower the external nutrient concentration the most will competitively displace all other species at steady state (Taylor and Williams 1975). From Eq. 4, species 1 will be competitively superior to species 2 when

$$K_{11}/(r_1 - D) < K_{21}/(r_2 - D). \quad (6)$$

Both species will be able to coexist stably only if $K_{11}/(r_1 - D) = K_{21}/(r_2 - D)$. For two species with the same maximal growth rates, the species with the lower half saturation constant for growth (K_{ij}) should be the

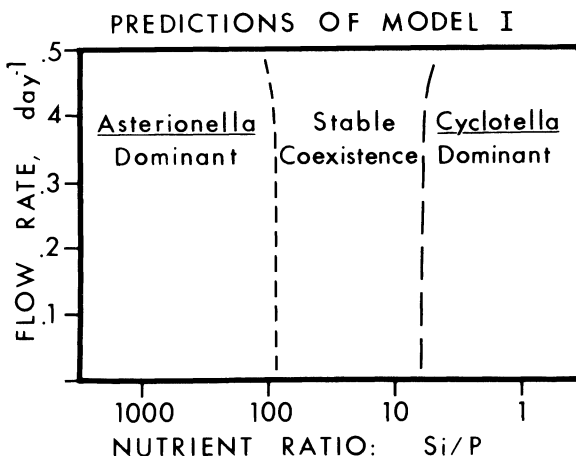


FIG. 2. The predictions of the Monod model of resource competition, made using the physiological constants of Table 1, are shown.

competitive dominant. Maximal growth rates of *Asterionella* and *Cyclotella* (Table 1) are not significantly different ($P \geq 0.95$). The lower half saturation constant of *Asterionella* ($0.02 \mu\text{M PO}_4$) compared to *Cyclotella* ($0.25 \mu\text{M PO}_4$) means that *Asterionella* should be competitively dominant over *Cyclotella* when both species are phosphate limited. When both species are silicate limited, the significantly lower ($P \geq 0.95$) half saturation constant for growth of *Cyclotella* ($1.44 \mu\text{M SiO}_2$) compared to *Asterionella* ($3.94 \mu\text{M SiO}_2$) indicates that *Cyclotella* should be the superior competitor. These predictions are shown in Fig. 2.

For the case in which species 1 is limited by resource 1 and species 2 is limited by resource 2, the steady-state solution for the system of equations represented by Eqs. 1 and 2 gives the following:

$$S_1^* = DK_{11}/(r_1 - D), \quad (7)$$

$$S_2^* = DK_{22}/(r_2 - D), \quad (8)$$

$$N_{1(1)}^* = N_1 + N_2 (Y_{11}/Y_{21}) \quad (9)$$

$$N_{2(2)}^* = N_2 + N_1 (Y_{22}/Y_{12}). \quad (10)$$

Equations 9 and 10 are directly analogous to the steady-state form of the Lotka-Volterra equations. Note that $N_{i(j)}^*$ is the "carrying capacity" of species i when it alone is limited by resource j (Eq. 3). Y_{11}/Y_{21} is directly analogous to alpha of the Lotka-Volterra equations at steady state; Y_{22}/Y_{12} is beta of the Lotka-Volterra equations. An analysis comparable to that used for the Lotka-Volterra equations at steady state shows that both species should coexist stably under the conditions defined by Eqs. 7, 8, 9 and 10 and by the parameters of Table 1. Coexistence of two species, when each species is limited by a different resource, has been demonstrated theoretically by Stewart and Levin (1973), Petersen (1975) and Taylor and Williams (1975).

Figure 2 summarizes the outcomes of competition predicted by Model I. In the region in which both

species are phosphate limited, it is predicted that *Asterionella* should be dominant. In the region in which both species are limited by different resources, coexistence is predicted. In the region in which both species are silicate limited, it is predicted that *Cyclotella* should be dominant.

MODEL II: VARIABLE INTERNAL STORES MODEL

The variable internal stores physiological model proposed by Droop (1974) to describe the response of a single species of algae to nutrient limitation was used in a modified form by Lehman et al. (1975) to model interspecific competition for resources. A simplified form of their equations is presented here. The model assumes that internal nutrient concentration (Q) determines growth rate and that internal nutrient concentrations are determined by the joint processes of nutrient uptake, assumed to follow a Michaelis-Menten process, and growth:

$$dN_i/N_i dt = \min_{1 \leq j \leq m} [r_i(1 - g_{ij}/Q_{ij}) - D], \quad (11)$$

$$dQ_{ij}/dt = V_{ij}(S_j/(S_j + k_{ij})) - r_i(Q_{ij} - g_{ij}), \quad (12)$$

$$dS_j/dt = D(S_0 - S_j) - \sum_{i=1, n} [N_i V_{ij}(S_j/(S_j + k_{ij}))], \quad (13)$$

where

- r_i = maximal growth rate of species i
- g_{ij} = minimal internal stores of resource j by species i ; i.e., internal nutrient concentration at which growth ceases. This is identical to k_Q of Droop (1974)
- V_{ij} = maximal rate of uptake of nutrient j by species i
- k_{ij} = half saturation constant for uptake of nutrient j by species i
- Q_{ij} = internal stores or "cell quotient"; amount of nutrient j internal to each cell of species i
- N_i = number of cells of species i per unit volume
- S_j = external concentration of resource j
- S_0 = influent concentration of resource j
- n = number of species
- m = number of resources.

Equation 11 includes the assumption that growth rate is determined solely by the internal nutrient concentration (Q_{ij}) which is lowest relative to the minimal internal stores for that nutrient (g_{ij}). This has been experimentally shown by Droop (1974).

The following relations hold at steady state:

$$N_{i(0)}^* = (S_0 - S_j)/Q_{ij}^* \quad (14)$$

$$Q_{ij}^* = g_{ij}r_i/(r_i - D) \quad (15)$$

$$S_j^* = r_i g_{ij} k_{ij} D / [V_{ij}(r_i - D) - r_i g_{ij} D]. \quad (16)$$

The boundary between a species being growth-rate limited at steady state by nutrient 1 or 2 is derived by setting $N_{i(1)}^* = N_{i(2)}^*$. This gives Eq. 17:

$$S_1^* = S_2^* + (S_0 - S_2^*)(g_{11}/g_{12}). \quad (17)$$

The predicted boundary between *Asterionella* being

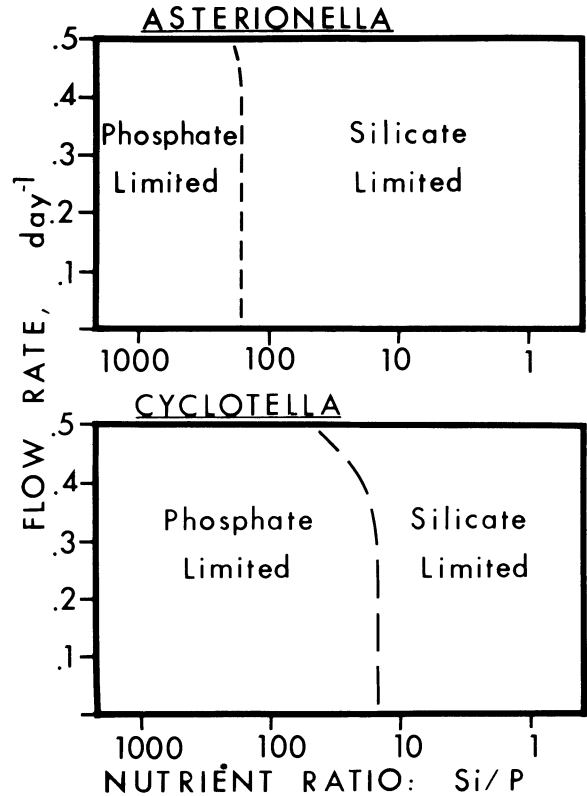


FIG. 3. The regions in which *Asterionella* should be silicate or phosphate limited, as predicted by Model II (Eq. 17) using the physiological constants of Table 2, are shown in the upper drawing. The lower drawing shows the same relationship for *Cyclotella*.

phosphate limited or silicate limited is shown in Fig. 3. This was calculated using Eq. 17 and the physiological constants of Table 2. The boundary is at $[Si/P]$ of ≈ 170 . For *Cyclotella*, the predicted boundary, calculated similarly, is at $[Si/P]$ of ≈ 15 (Fig. 3).

The variable internal stores model predicts that the nutrient ratio/flow rate plane will be divided into three regions: a region in which both species are phosphate limited, one in which each species is limited by a different nutrient, and one in which both species are silicate limited. According to Model II, two species limited by the same nutrient can only coexist if the steady-state nutrient concentrations caused by each species alone are equal. The species which causes the lower steady-state nutrient concentration will competitively displace all other species at steady state. Under limitation by resource j , species 1 will be dominant over species 2 if Eq. 18 holds:

$$r_1 g_{1j} k_{1j} D / [V_{1j}(r_1 - D) - r_1 g_{1j} D] < r_2 g_{2j} k_{2j} D / [V_{2j}(r_2 - D) - r_2 g_{2j} D]. \quad (18)$$

This can be approximated by Eq. 19 when D is much less than the washout rate:

$$r_1 g_{1j} k_{1j} D / [V_{1j}(r_1 - D)] < r_2 g_{2j} k_{2j} D / [V_{2j}(r_2 - D)]. \quad (19)$$

TABLE 1. Physiological constants needed for Model I (from Tilman and Kilham 1976). Maximal growth rates (r) of *Asterionella* and *Cyclotella* were not significantly different ($P \geq 0.95$). Yield (Y) is for cultures with 0.5r, to avoid bias from dependence of growth on internal stores. K is the half saturation constant

Species	Nutrient	K (μM)	r (doublings/day)	Y (cells/ μmole)
<i>Asterionella formosa</i>	PO_4	0.02	0.9	2.18×10^8
<i>Asterionella formosa</i>	SiO_2	3.94	1.1	2.51×10^6
<i>Cyclotella meneghiniana</i>	PO_4	0.25	0.8	2.59×10^7
<i>Cyclotella meneghiniana</i>	SiO_2	1.44	1.3	4.20×10^6

The physiological constants of Table 2 indicate that, for all flow rates and nutrient concentrations at which neither species would be washed out of a single species culture, *Asterionella* should be the superior competitor under phosphate limitation. Because there are not variance estimates for all the parameters of Table 2, a test for significant differences between the two sides of Eq. 18 is not possible. However, the two sides differ by a factor of four, which seems to be great enough to predict that *Asterionella* should be the superior competitor under phosphate limitation. When both species are silicate limited, Eq. 18 predicts that *Asterionella* should have a slight advantage over *Cyclotella*. However, the two sides of Eq. 18 differ by $< 15\%$. Because of the errors in estimating the parameters of Table 2 used in Eq. 18, I believe that this must be considered a prediction of no significant difference between the two species. It is unlikely that both species are identical, which is the condition needed for stable coexistence of both species when they are limited by the same resource. The "prediction" shown in Fig. 4 is that either *Asterionella* or *Cyclotella* should be the superior competitor when both species are silicate limited.

For species 1 limited by resource 1, and species 2 limited by resource 2, with no luxury consumption of a nonlimiting resource, the following equations hold at steady state:

$$\begin{aligned}
 S_1^* &= r_1 g_{11} k_{11} D / [V_{11}(r_1 - D) - r_1 g_{11} D]; \\
 S_2^* &= r_2 g_{22} k_{22} D / [V_{22}(r_2 - D) - r_2 g_{22} D]; \\
 Q_{11}^* &= g_{11} r_1 / (r_1 - D) \quad Q_{12}^* = Q_{11}^* (g_{12} / g_{11}) \\
 Q_{21}^* &= Q_{22}^* (g_{21} / g_{22}) \quad Q_{22}^* = g_{22} r_2 / (r_2 - D) \\
 N_{(1)}^* &= N_1 + (Q_{21}^* / Q_{11}^*) N_2 \\
 N_{(2)}^* &= N_2 + (Q_{12}^* / Q_{22}^*) N_1
 \end{aligned} \quad (20)$$

TABLE 2. Physiological constants needed for Model II (from Tilman and Kilham 1976). Symbols are: g = minimal internal stores of nutrient; r = maximal growth rate; K = half saturation constant; V = maximal rate of nutrient uptake (see text)

Species	Nu- trient	g ($\mu\text{M}/\text{cell}$)	r (ln/day)	K (μM)	V ($\mu\text{M} \cdot \text{cell}^{-1} \cdot \text{h}^{-1}$)
<i>Asterionella formosa</i>	PO_4	1.75×10^{-9}	0.7	2.8	9.85×10^{-9}
<i>Asterionella formosa</i>	SiO_2	2.96×10^{-7}	1.2	7.7	3.58×10^{-8}
<i>Cyclotella meneghiniana</i>	PO_4	1.07×10^{-8}	0.7	0.8	5.51×10^{-9}
<i>Cyclotella meneghiniana</i>	SiO_2	1.57×10^{-7}	1.2	7.5	1.51×10^{-8}

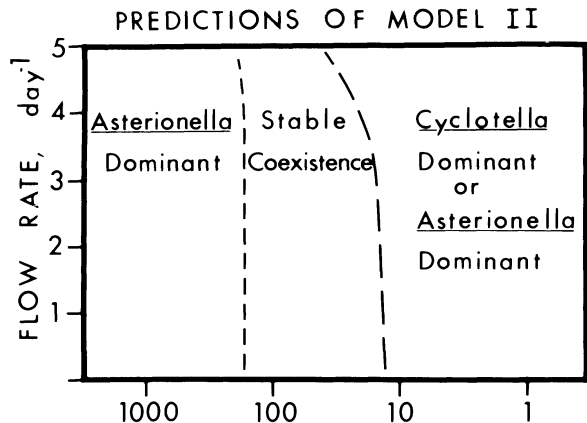


FIG. 4. The steady-state predictions of the variable internal stores model of competition, made using the physiological constants of Table 2, are shown.

These equations predict stable coexistence of two species if each is growth-rate limited by a different resource and each is a superior competitor for one of the two resources. These predictions are shown in Fig. 4.

The ability of these two models to predict the steady-state outcome of competition will be judged by three criteria. (1) The agreement between the predicted outcomes (dominance, coexistence) and those experimentally observed in the three general regions. (2) The agreement between the predicted placement of the boundaries and the observed placement. (3) The agreement between the predicted shape of the boundaries and the observed shape of the boundaries.

LONG-TERM COMPETITION EXPERIMENTS: MATERIALS AND METHODS

Asterionella formosa Hass. (clone FraAF) was isolated from Frains Lake, Michigan into axenic (bacteria-free) culture by S. S. Kilham. *Cyclotella meneghiniana* Kutz. (clone CyOh) was isolated from Lake Ohrid, Yugoslavia, by S. S. Kilham and obtained in axenic condition by V. McAlister. The general methods used for the competition experiments are described elsewhere (Titman 1976; Tilman and Kilham 1976). I will give the basic details.

A freshwater medium of double-distilled H_2O and inorganic salts and vitamins was used for all cultures ("WC" of Guillard and Lorenzen 1972). The concentrations of silicate and phosphate were varied so that silicate to phosphate ratios would range from $\approx 1,000$ to 1 (micromoles per micromoles). Concentrations of phosphate and silicate were never so low that steady-state populations of each species, grown singly, were not maintained at all nutrient ratios and flow rates tested. Influent phosphate concentrations ranged from $\approx 0.10 \mu\text{M}$ to $\approx 15 \mu\text{M}$. Influent silicate concentrations ranged from $\approx 100 \mu\text{M}$ to $\approx 9 \mu\text{M}$. Concentrations chosen were low enough that either silicate or

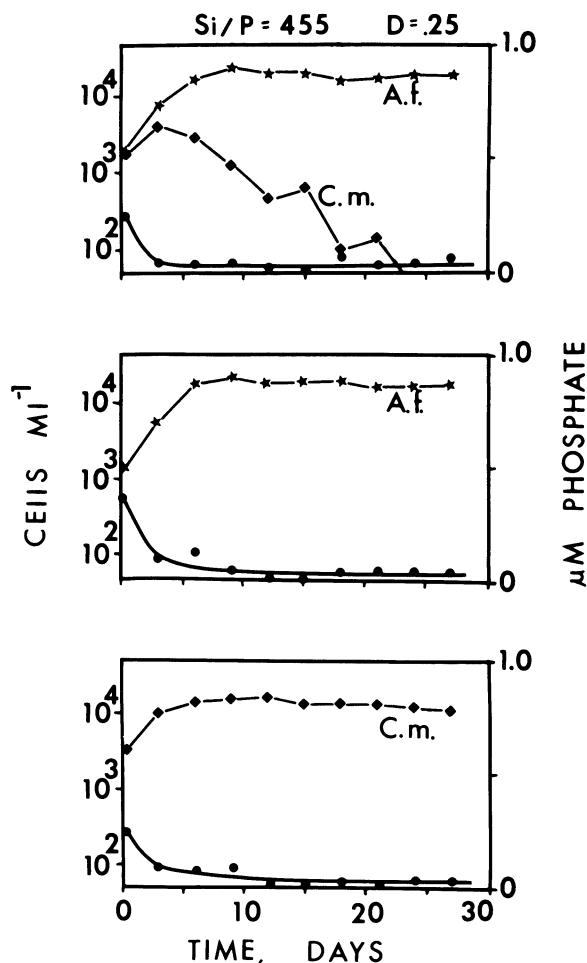


FIG. 5. Long-term semicontinuous growth experiments at $[Si/P]$ of 455 ($\mu M/\mu M$) and flow rate of 0.25/day. Upper graph: stars—*Asterionella* (A.f.), diamonds—*Cyclotella* (C.m.), and closed circles—phosphate concentration, throughout 27-day competition experiments. Middle graph: Number of *Asterionella* (A.f.) (stars) and phosphate concentrations (closed circles) throughout a 27-day experiment with only *Asterionella* present (control). Lower graph: Number of *Cyclotella* (C.m.) (diamonds) and phosphate concentration (closed circles) throughout a *Cyclotella* growth experiment (control).

phosphate should have been the growth-rate-limiting nutrient through all experiments.

Cultures were grown in a culture box at 20°C with $100 \mu\text{ein m}^{-2} \text{S}^{-1}$ illumination provided by "cool-white" fluorescent lights. All cell counts were done with a microscope using a Sedgwick-Rafter counting chamber, with samples preserved in Lugol's acetate solution (Guillard 1973). Cell counts and measurements of reactive extracellular phosphate and silicate were performed periodically. Phosphate and silicate were determined with the methods of Strickland and Parsons (1972), with absorbance read on a spectrophotometer with either 50- or 10-mm quartz cells. All samples were filtered through Millipore® filters which had been presoaked in double-distilled H_2O .

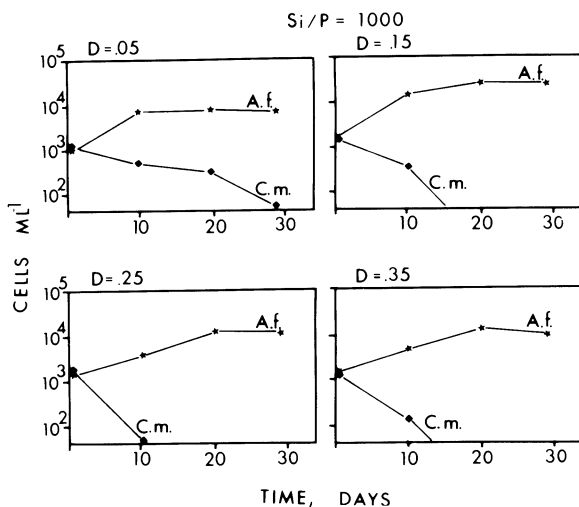


FIG. 6. Competition (two species) experiments for a silicate to phosphate ratio in the influent medium of 1,000, at four flow rates (D) (0.05, 0.15, 0.25, and 0.35/day). Symbols as in Fig. 5.

Long-term competition experiments were performed in flow-through (semicontinuous) culture. Cultures were started with each species in approximately equal abundance, generally at $\approx 1,000$ cells/ml. Inocula were grown in media low in phosphate and silicate for a week or more before being used. Cultures were diluted manually daily. The flow rate (f) is reported as the ratio of the volume removed per day to the total culture volume. This may be converted to the true steady-state growth rate by the conversion $D = \ln(1/(1-f))$. The flow rates generally used were 0.05, 0.15, 0.25, 0.35, and 0.50/day.

For each competition experiment at a particular silicate to phosphate ratio and flow rate, two single-species control cultures were also run. This was done both to gain physiological information (as in Table 2)

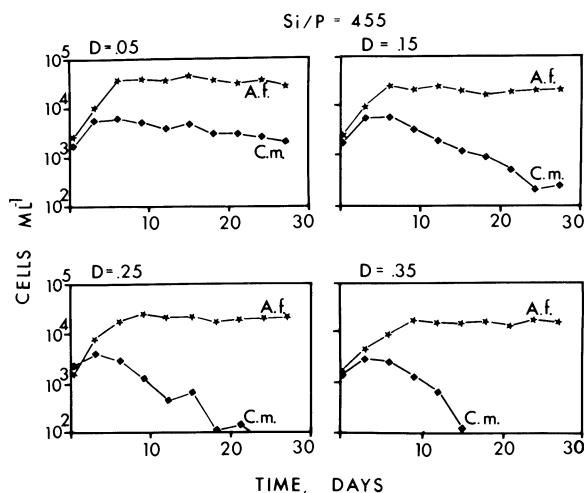


FIG. 7. Competition experiments for $[Si/P] = 455$ at flow rates of 0.05, 0.15, 0.25 and 0.35/day. Symbols as in Fig. 5.

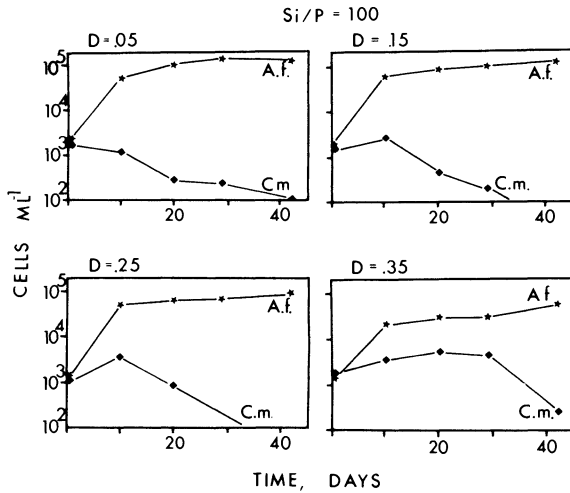


FIG. 8. Competition experiments for $[Si/P] = 100$ at four flow rates. Symbols as in Fig. 5.

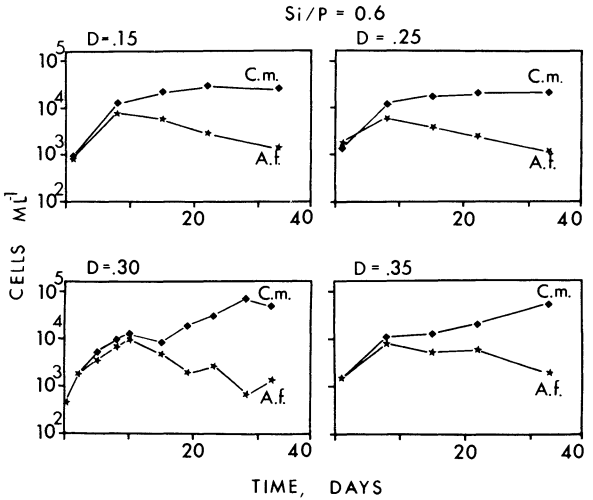


FIG. 10. Competition experiments for $[Si/P] = 0.6$ at flow rates of 0.15, 0.25, 0.30, 0.35/day. Symbols as in Fig. 5.

and to assure that each species was able to grow to a stable, steady-state population under all conditions tested. Any displacement of one species from a two species competition culture must be caused by interactions between the two species. The controls assure that the results observed are due to competition.

RESULTS

For the purposes of these experiments, a species was considered to be competitively dominant when it comprised 95% or more of the total number of cells in the culture. If neither species had reached dominance by the predetermined end of an experiment, the results were termed coexistence. Because of the arbitrary, but necessary, nature of this definition, the actual time course of competition is shown for numerous cases throughout the range of conditions tested.

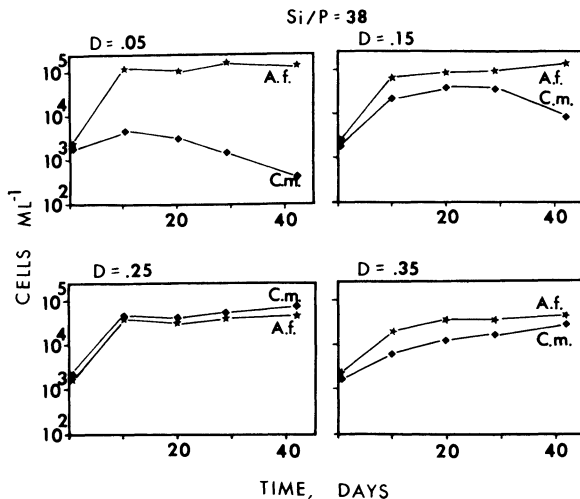


FIG. 9. Competition experiments for $[Si/P] = 38$ at four flow rates. Symbols as in Fig. 5.

Figure 5 shows the results of one competition experiment at $[Si/P] = 455$ and $f = 0.25$ /day, along with the two control (single-species) cultures. Phosphate concentrations are shown. Silicate concentrations were also periodically measured, but were never low enough to be limiting. A silicate to phosphate ratio of 455 is within the region for which both species are predicted by Model I and Model II to be phosphate limited. Both models predict that *Asterionella* should be the superior competitor. This was the case (Fig. 5). By day 24, no *Cyclotella* were observed in the 1 ml sample counted, but $> 10^4$ *Asterionella* were counted.

For $[Si/P] \geq 100$, *Asterionella* was dominant at all flow rates tested. Time series of competition for $[Si/P]$ of 1,000, 455, and 100 are shown in Figs. 6, 7 and 8. At $[Si/P]$ of 38, *Asterionella* was dominant at $f = 0.05$ /day in triplicate competition experiments and at $f = 0.5$ /day in two of three triplicates. Both species coexisted in the other triplicate experiments at intermediate flow rates for $[Si/P] = 38$. The time course of competition is shown in Fig. 9. At $[Si/P] = 0.6$, *Cyclotella* was dominant at all flow rates tested (Fig. 10).

The times to 99% dominance by *Asterionella* are shown in Fig. 11 for all cultures in which *Asterionella* became dominant. In general, it takes more time for *Asterionella* to become dominant the closer the silicate to phosphate ratio is to the observed boundary between dominance by *Asterionella* and coexistence of both species. Competitive displacement occurs more rapidly at higher flow rates, indicating the potential influence of mortality on the competitive process. There is a discontinuity in the trend of slower competitive displacement nearer the boundary of coexistence. This can be seen for the silicate to phosphate ratios < 100 , for which displacement is slightly faster than for ratios of 100. This trend was even more pronounced in the time to 95% and to 85% dominance. It should be

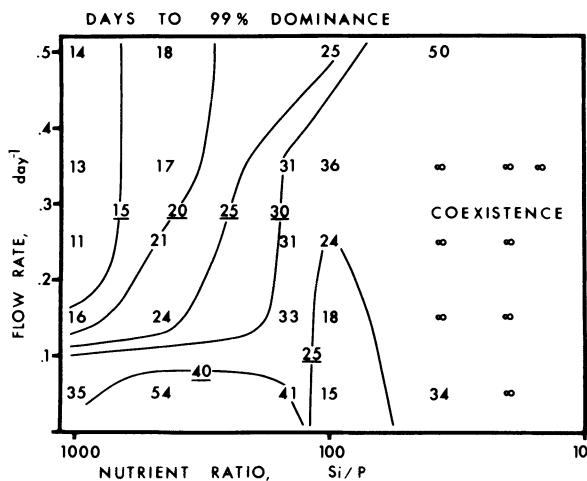


FIG. 11. The days to 99% dominance of *Asterionella* (by number of cells) over *Cyclotella* in cultures in which *Asterionella* became dominant. The times shown are the averages, rounded to integral days, computed by linear regression through log-transformed cell counts. The curves shown (with their labels underlined) are hand drawn.

noted that competitive exclusion to the level of 99% dominance is a fairly slow process, often requiring 25 to > 40 days, even at higher flow (turnover) rates.

The steady-state results of all 76 competition experiments between *Asterionella* and *Cyclotella* are shown in comparison with the predicted results (Figs. 12 and 13). Stars symbolize dominance by *Asterionella*; diamonds, dominance by *Cyclotella*; dots, coexistence of both species. The major trends observed in the competition experiments are: (a) A region at $[\text{Si}/\text{P}]$ generally greater than ≈ 80 , but with boundaries curving toward lower $[\text{Si}/\text{P}]$ at both high and low flow rates, in which *Asterionella* was dominant. (b) A region for $6 < [\text{Si}/\text{P}] < 80$ in which both species coexisted. (c) At region for $[\text{Si}/\text{P}]$ generally less than about 6 in which *Cyclotella* was dominant.

Tilman et al. (1976) have observed that *Asterionella* colonies exhibit morphometric changes in the number of cells per colony when they are limited by silicate and phosphate. The average number of cells per colony in *Asterionella* grown to steady state in flow-through cultures under silicate limitation decreased from > 20 cells/colony at low flow rates to 8.0 cells/colony at flow rates near the washout rate. Under phosphate limitation, a completely different trend was observed. The number of cells per colony in *Asterionella* increased from < 2 at low flow rates to 8 cells/colony as flow rate approached the maximal growth rate. At low to moderate flow rates, *Asterionella* never averaged > 6 cells/colony under phosphate limitation, nor < 8 cells/colony under silicate limitation.

For the competition experiments reported here, in the region in which *Asterionella* was observed to be dominant over *Cyclotella* (Fig. 12 or 13), no cultures

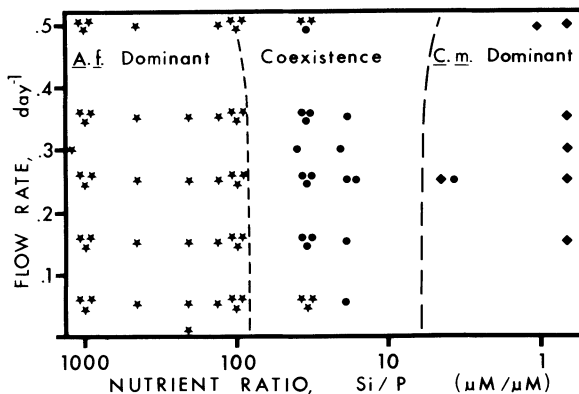


FIG. 12. The steady state results of all 76 long-term competition experiments are compared with the predictions of the Monod model (Model I). Stars represent cultures in which *Asterionella* (A.f.) was competitively dominant. Diamonds represent cultures in which *Cyclotella* (C.m.) was dominant. Closed circles represent stable coexistence of both species.

were observed at flow rates of $< 0.35/\text{day}$ to have > 8 cells/colony. Throughout this region, *Asterionella* averaged 5.7 cells/colony at flow rates from 0.15 to 0.40/day. This indicates that these *Asterionella* were phosphate limited. In the other competition cultures at these same flow rates (in which both species coexisted or *Cyclotella* was dominant), *Asterionella* averaged 8.9 cells/colony. These *Asterionella* were probably silicate limited. This provides some indirect evidence that *Asterionella* cells were phosphate limited in the region in which they were dominant over *Cyclotella* and silicate limited in the regions in which both species coexisted or *Cyclotella* was dominant.

DISCUSSION

The general agreement between the predictions of Models I and II and the observed experimental results indicates the potential power of resource-based theories of competition to predict the outcome of in-

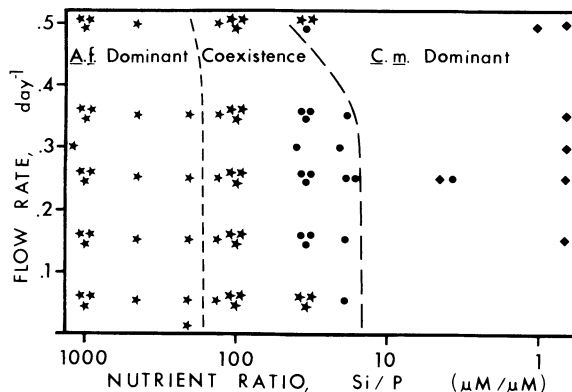


FIG. 13. The steady-state results of all 76 long-term competition experiments are compared with the predictions of Model II. Symbols are the same as for Fig. 12.

terspecific competition. The results also support a contention of mathematical models of competition: two species can coexist at steady state when each is limited by a different resource (Levins 1968; Stewart and Levin 1973; Petersen 1975; Taylor and Williams 1975).

Three criteria are used to judge the similarity of the experimental results and the predictions of Models I and II. The first is the agreement between the predicted outcomes of competition (dominance, coexistence) and the observed outcomes, independent of their quantitative placement. The Monod model (Model I) correctly predicted the steady-state outcomes in all three regions. The variable internal stores model (Model II) correctly predicted the outcome in two of the three regions (Fig. 13), with one region being "too close to call". The second criterion is the agreement between the quantitative placement of the predicted and observed boundaries. The predicted boundaries were determined using a complex algebraic function. Because variance estimates are not available on all the parameters used, it is difficult to determine if the boundaries predicted by each model differ significantly either from each other or from those observed. It is only possible to make qualitative comparisons. From Fig. 12, Model I seems to predict accurately the boundary between dominance by *Asterionella* and coexistence of both species. (Agreement of shape will be discussed later.) The other boundary, between coexistence and dominance by *Cyclotella*, is harder to judge, for lack of sufficient data points, but the predicted and observed outcomes seem in agreement. From Fig. 13, Model II seems to be a less accurate predictor of the boundary between dominance by *Asterionella* and coexistence of both species. For the number of data points there are to base a judgement on, it seems to be just as good a predictor as Model I of the other boundary. The remarkable agreement between the predictions of Model I and the observed results must be viewed with caution. The placement of the boundary depends on the ratio of yields (Y_{11}/Y_{12}). The yields used (Table 1) were obtained from steady-state single-species cultures at flow rates of half the maximal flow (growth) rate. This minimized the error caused by the increasing efficiency with which algae can utilize nutrients at low concentrations (viz. the variable internal stores model). If the classical estimate of yield had been used (Herbert et al. 1956), the boundary between *Asterionella* being limited by phosphate or silicate would have been at ≈ 150 . The third criterion is the agreement between the shape of the predicted and observed boundaries. As Figs. 12 and 13 show, neither model correctly predicted the observed curvature of the boundary between dominance by *Asterionella* and coexistence. The other boundary was not defined well enough for any comparison.

Of the models used, the Monod is the conceptually simpler. It requires fewer parameters and those

needed are more easily obtained. The steady-state comparisons of the two models indicate that the Monod model is apparently superior for one or two of the three criteria of judgement. This may be the case merely because of the increased experimental error necessitated by the greater number of parameters in Model II. Though more complex, a possible advantage of the variable internal stores model is its ability to easily include luxury consumption of resources (hoarding). Luxury consumption may not only affect the steady-state population densities of the two species and the dynamics of population growth, but also the outcome of competition. For instance, at low steady state growth rates under silicate limitation, *Asterionella* can store phosphate $80\times$ in excess of that needed at that growth rate. This luxury storage decreases with increasing growth rate (Tilman and Kilham 1976). Thus, at low flow rates in the region in which it is predicted that each species should coexist because *Asterionella* is silicate limited and *Cyclotella* is phosphate limited (Figs. 2 and 4), *Asterionella*, by its luxury consumption of phosphate, may lower the concentration of phosphate such that *Cyclotella* would be competitively displaced. Luxury consumption may thus be a factor causing curving of the boundaries describing the regions of Figs. 2 and 4. Further competition experiments will be needed to test the relative merits of these two models, and their variations, in describing both the steady-state and dynamic aspects of interspecific competition for resources.

Another possible criterion might have been to determine if each species were growth-rate limited by the predicted nutrient in the three observed regions of competitive dominance and coexistence. The morphometric changes in the number of cells per colony of *Asterionella* indicate that *Asterionella* was phosphate limited in the region in which it was dominant over *Cyclotella* and that it was silicate limited in the regions in which both species coexisted or *Cyclotella* was dominant. This agrees with the predictions of both Models I and II.

There are some observational data for Lake Michigan which indicate that competition for phosphate and silicate may be important in determining the distribution and relative abundance of *Asterionella* and *Cyclotella*. These are data from an intensive inshore sampling (Kopczynska 1973) and from transects across the lake (E. F. Stoermer, *personal communication*). In order to interpret these data in terms of the laboratory experiments performed, it is necessary to consider the difference between the silicate to phosphate ratios used up to this point, and those which are available from the Lake Michigan data. The silicate to phosphate ratios of Figs. 1 to 13 are ratios of the supply rates of these nutrients, but the data available for Lake Michigan are measurements of the concentrations of phosphate and silicate actually in the lake samples. Assuming that the measured concentrations are at or

near some steady-state values, the Monod model may be used to predict the outcome of competition. In theory, a species should be equally limited by external, steady-state concentrations of two resources when Eq. 21 holds:

$$[S_1]/[S_2] = K_1/K_2, \quad (21)$$

where S_1 and S_2 are the steady-state concentrations of resources 1 and 2 and K_1 and K_2 are the half-saturation constants for growth of this species limited by resources 1 and 2, respectively (Titman 1976). Using the half-saturation constants of Table 1, *Asterionella* should be dominant for ratios of external silicate to phosphate concentrations >200 ; *Cyclotella* should be dominant for ratios <5.7 ; and both species should coexist for ratios between 5.7 and 200. This prediction is shown across the top of Fig. 14. The relative abundance of *Cyclotella* along the observed silicate-phosphate gradient is also shown. As Fig. 14 shows, *Cyclotella* is very abundant relative to *Asterionella* at stations which have $[Si/P]$ less than about 10. These are generally near-shore stations. *Asterionella* is very abundant relative to *Cyclotella* at stations which have $[Si/P]$ greater than about 100. These are open lake stations. Coexistence (by the definition used previously) occurs, generally, for silicate to phosphate ratios between about 10 and 100. An analysis of variance on the combined data of Kopczynska (1973) and E. F. Stoermer (*personal communication*) revealed that 74.3% of the variance in the relative abundance of these two species can be explained by the Monod model of resource competition. Considering the non-steady-state nature of these samples, any agreement with a trend predicted from a laboratory study on two clones which were not isolated from Lake Michigan is especially encouraging. Many factors other than resource competition must influence the natural distribution of phytoplankton. Trophic interactions, spatial and temporal heterogeneity, and various physical factors must all play a part. However, the ability of the Monod model to explain over 70% of the observed variance in the natural distribution of these two species supports the view that resource competition is a major factor determining the distribution and abundance of species in nature.

Analysis of the two models of resource competition indicates that, at steady state, they are directly analogous to the steady-state form of the classical Lotka-Volterra equations of competition. This relationship is encouraging in that it demonstrates that resource-based models simplify to the classical equations at steady state. However, there is a danger in using resource-based models to estimate the parameters of the Lotka-Volterra equations. Resource-based models of competition are mechanistic, with the formulation of the model stating explicitly the mechanisms of competition in terms of the resource acquisition and utilization abilities of each species.

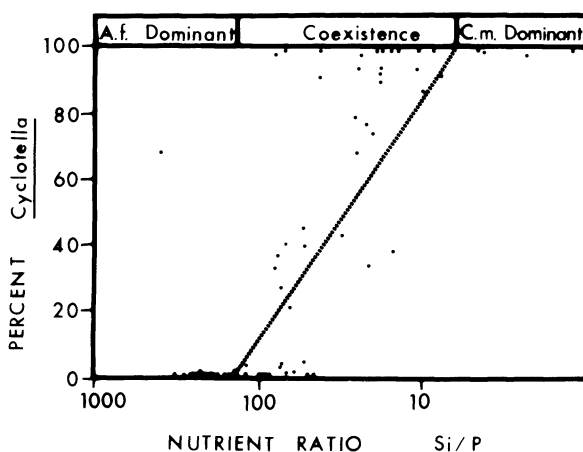


FIG. 14. The relative abundance of *Cyclotella* (C.m.) (compared to the total of *Cyclotella* and *Asterionella* [A.f.]) in samples from Lake Michigan plotted against ambient silicate to phosphate ratios in the same samples ($n = 78$). Over 70% of the observed variance in the relative abundance of these two species is explained by the steady state form of the Monod model. Notation at the top of the figure shows predicted outcomes of competition; the broken line shows the expected proportion of *Cyclotella* in the region of coexistence.

The Lotka-Volterra equations are purely descriptive and their parameters (alpha, beta, carrying capacities) are assumed to be constants. Resource-based models indicate that those parameters are only constant at steady state. For instance, the analog of alpha in the resource-based models varies with growth rate and past history, only being a constant at steady state. The steady-state estimate of alpha which can be obtained from resource-based models may only be used in the Lotka-Volterra equations at steady state. This use of an estimated alpha eliminates both the explicit statement of the mechanisms of resource competition and the ability to analyze competition under non-steady-state conditions. Moreover, use of resource models emphasizes the role of resources in determining competitive interactions and the need for information on the abilities of each species to acquire and use the potentially limiting resources. Although descriptive models of competition may be useful tools for understanding some aspects of community structure, mechanistic models may also be used for that purpose and are superior in that they may validly be used to analyze non-steady-state situations.

In conclusion, two currently used models of algal nutrient physiology seem able to make significant predictions about the nature of interspecific competition for resources. Both models are mechanistic. Both use the functional resource acquisition and/or utilization response of each species to potentially limiting resources to predict the outcome of interspecific competition for resources. Both models correctly predicted three regions of competition. The two regions in which each species should have been limited by the

same resource were dominated by a single species (Figs. 12 and 13). Both species coexisted, as predicted, in the region in which each species should have been limited by a different resource. The relative abundance of *Asterionella* and *Cyclotella* along a natural gradient of silicate and phosphate in Lake Michigan agrees with that predicted by these models. Over 70% of the observed variance in the distribution of these two species in Lake Michigan can be explained by the Monod model (Fig. 14). Although indirect, this supports the view that interspecific competition for resources may be important in structuring natural communities. These results demonstrate the power that resource-based theories of interspecific interaction may have in explaining the distribution and abundances of species in nature.

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