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A comparison of the Droop and the Monod models of nutrient limited growth applied to natural populations of phytoplankton

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Abstract. The extent of nutrient limitation of phytoplankton in eutrophic Plußsee was studied by enrichment bioassays and by analysing the cellular stoichiometry of monospecific fractions obtained by size fractionation and density–gradient separation. In this lake silicate and nitrogen, but not phosphorus, at times limit the reproductive rates of phytoplankton. The dependence of nutrient-limited reproductive rates on the cellular content of the limiting nutrient (cell quota) could well be described by the Droop model. Biomass specific minimal cell quotas of nitrogen ranged from 0·014 to 0·061 mol N mol^{-1} C, minimal cell quotas of silicon ranged from 0·055 to 0·127 mol Si mol^{-1} C. The cell quotas of the non-limiting nutrients usually increased with the cell quotas of the limiting nutrient. In contrast to the Droop model, the Monod model which relies on ambient concentrations of limiting nutrients was a much poorer predictor of growth rates.

Key-words: Cell quota, density–gradient separation, Droop model, enrichment bioassays, Monod model, nutrient limitation, phytoplankton, size separation

Introduction

Nutrient limitation of phytoplankton reproductive rates can either be described by the Monod equation or by the Droop equation. The first relates the reproductive rate (μ) to the dissolved concentration of the limiting nutrient (S), the latter relates μ to the intracellular concentration of the limiting nutrient ('cell quota', q). Field ecologists would prefer to use the Monod model because it directly relates a population level response (μ) to an easily measurable environmental parameter (S). However, the applicability of the Monod model is doubtful because luxury uptake of nutrients and storage for later growth may lead to a temporal uncoupling between reproductive rates and dissolved nutrient concentrations (Droop, 1973, 1983). The applicability of the Monod model is only warranted under steady state conditions as realized in chemostat cultures.

On the other hand, the applicability of the Droop equation is less restricted to steady state conditions but the cell quota of individual species cannot be measured easily under natural conditions. Normally seston consists of a mixture of many different phytoplankton species, protozoa, bacteria and detritus. Each component may have a different cellular stoichiometry. The restricted applicability of the Monod equation and the technical difficulties in measuring the independent variable of the Droop equation have been considered a major obstacle in predicting the extent of nutrient limitation of natural phytoplankton populations.

As a shortcut Goldman *et al.* (1979) replaced the actual reproductive rate of individual species by the quotient μ/μ_{max} ('relative reproductive rate'; μ_{rel}). Thus interspecific differences in the nutrient-saturated reproductive rate μ_{max} are cancelled out and only the assumption of uniformity in the normalized minimal cell quota (q_0; normalized to biomass) is required, to use the chemical composition of seston as an indicator of the nutritional status of phytoplankton. Goldman *et al.* (1979) took the widespread occurrence of a sestonic stoichiometry around the Redfield ratio (C:N:P = 106:16:1) as an indication of the absence of nitrogen and phosphorus limitation in the open, oligotrophic ocean. Harris (1986) extended this claim to all kinds of plankton habitats. Later C:N and C:P ratios clearly in excess of the Redfield ratio were found both in marine and freshwater sites (summarized in Sommer, 1990), thus making Harris' claim untenable. While rejecting the claim that growth is always saturated with nutrients, further research confirmed the usefulness of Goldman's methodological approach. The chemical composition of the entire seston in a shallow, hypertrophic lake (Sommer, 1989) and of seston size fractions (Sommer, 1988) could be matched to a weighted average of relative reproductive rates as predicted by the Droop equation.

However, this approach permits only a general test of the extent of nutrient limitation but it does not shed light on the performance of individual species. The coarse-grained size fractionation in Sommer (1988) with only five size fractions rarely yielded monospecific fractions. In a later study (Sommer, 1991) the combination of a finer size fractionation (10 fractions) and of density–gradient separation was used for the phytoplankton of mesotrophic Schöhsee (Northern Germany), where N, P and Si are potentially limiting nutrients. Droop kinetics of nutrient limitation could be established for 12 different species. In this study, the same approach is followed for the eutrophic Plußsee (Northern Germany), where only N and Si can be considered limiting. In addition to the Schöhsee study the cell quotas of non-limiting nutrients were also analysed and the potential of the Monod equation to predict reproductive rates was tested.

Materials and methods

Sampling, measurements and experiments

The study period extended from 13 February to 4 December 1989. Samples were taken at weekly intervals from the deepest point of Plußsee and restricted to the mixed surface layer. Samples for dissolved nutrient analyses and enrichment bioassays were taken at 1-m intervals and then mixed in equal proportions to give a mixed epilimnion sample. Samples for the analysis of the chemical composition of phytoplankton biomass were taken with plankton nets (10 and 20 μm mesh size) from the bottom of the mixed surface layer to the surface.

The entire phytoplankton and the size fractions were counted according to the standard Utermöhl technique. At least 400 individuals of each important species were counted, thus giving a counting precision of ±10% within 95% confidence limits. Cell volumes were estimated by microscopic measurements of at least 40 cells. Cell volumes were converted into cellular carbon according to Rocha & Duncan (1985). Dissolved nutrients (soluble reactive phosphorus, nitrate, nitrite, ammonium, silicate) were measured after filtration through 0·1-μm membrane filters according to standard techniques (Strickland & Parsons, 1972).

In order to obtain realistic estimates of the chemical composition of the different phytoplankton species the net samples had to be fixed prior to the separation procedure, otherwise losses of nutrients (especially P) from the particulate would be expected. Glutaraldehyde, formalin, and Lugol's iodine with acetate were found to be unsatisfactory, because the retention of P within the particulate phase was <30% over the duration of the separation procedure (maximally 6 h). Mercuric chloride had the highest retention (95–98%) but led to complications in the determination of particulate P. Unmodified Lugol's iodine gave a satisfactory P-retention (90–94%) and was chosen because of the disadvantages of mercuric chloride. Nitrogen and silicate were better retained in the particulate phase than phosphorus with any fixative.

Size separation of the net plankton was performed with net screens of 10, 20, 30, 40, 50, 65, 80, 100, 150, 250, and 500 μm mesh size. If this did not yield sufficiently monospecific fractions (>90% of cell volume by one species) fractions with low detritus content and already reduced species diversity were further separated in a CsCl density gradient from 1 to 1·45 g ml^{-1}. This separation was performed by sedimentation in a Brand Cell Sorting System CS 1001 (Brand, Wertheim, Germany). Occasionally it was not possible to obtain monospecific fractions, but two fractions with two dominant species in different proportions could be obtained. In this case cell quotas were calculated by solving two simultaneous equations with two unknown variables:

$$X_A = ([N/C]_1[1-f_{A2}] - [N/C]_2[1-f_{A1}])/(f_{A1}-f_{A2}) \quad \text{Equation 1}$$

where X_A is the N/C ratio in species A, $(N/C)_1$ and $(N/C)_2$ are the N/C ratios in fractions 1 and 2, respectively, and f_{A1} and f_{A2} are the fractions of particulate carbon contributed by species A in fractions 1 and 2, respectively. Similarly:

$$X_B = ([N/C]_2 f_{A1} - [N/C]_1 f_{A2})/(f_{A1}-f_{A2}) \quad \text{Equation 2}$$

where X_B is the N/C ratio in species B.

The fractions were divided into three aliquots for separation. The aliquots for particulate CN analysis (Carlo Erba Instruments) were filtered onto glass-fibre filters, the aliquots for opaline silicate analysis onto Nuclepore filters and the aliquots for particulate phosphorus analysis onto cellulose–nitrate filters. Cell quotas were expressed as carbon specific molar ratios (N/C, P/C, Si/C). If the algal C calculated from cell volumes was less than 80% of the chemically measured particulate carbon this was considered an unacceptable detrital contamination and data were not analysed further.

Samples for the enrichment bioassays consisted of unfractionated epilimnion water which was

filtered through a 250-μm mesh screen to remove larger zooplankton and then diluted 10-fold with filtered lake water. This suspension was distributed into nine Erlenmeyer flasks. Two of the flasks received no nutrient enrichment, three received one nutrient (Si, P, N), three received the pairwise combinations (Si + P, Si + N, P + N), and one received the triple enrichment. Nitrogen was added as ammonium nitrate. Therefore, no difference in the response between nitrate- and ammonium-preferring species was expected. The bottles were incubated at ambient temperatures, ambient L/D cycle, and at a photon flux density of $160\,\mu m^{-2}\,s^{-1}$ within the photosynthetically active spectrum (400–700 nm wavelength). This light intensity probably precludes light limitation and light inhibition for most phytoplankton species (Reynolds, 1984; Kohl & Nicklisch, 1988). Cell counts for reproductive rates were performed on days 0, 1 and 3. In the preparation of previous studies (Sommer, 1988, 1989) daily counts over 1 week had shown this to be the optimal time window because of a drop in growth rates after 3–5 days.

For the statistical test for limitation by a single nutrient all bottles enriched with the nutrient in question were considered as treatment, all bottles without this nutrient were considered as controls. This means four treatments *vs* five control bottles in the case of single-nutrient limitation. A nutrient was considered limiting if Tukey's non-parametric test showed a significant difference between controls and treatment at $P < 0{\cdot}05$. Double limitation would have been indicated by elevated growth rates in the bottles enriched by the two limiting nutrients and in the bottle with the triple enrichment. This means two treatments *vs* seven controls, for which no non-parametric test is available. However, contrary to a previous study in another lake (Sommer, 1989) the data never suggested double limitation.

Reproductive rates in the controls did not drop during the course of the experiments (no significant difference between the time intervals 0–1 and 1–3), indicating that enclosure effects did not artificially exaggerate nutrient limitation. If a nutrient was limiting, the full response of reproductive rates in the enriched bottles was either observed from the beginning (small algae) or in the time interval 1–3 days (large algae). Because of the magnitude of the nutrient additions (Si, 80 M NO_3^- and NH_4^+, 15 μM; P, 2 μM) reproductive rates in the enriched bottles were treated as estimates of the nutrient-saturated reproductive rate (μ_{max}). This assumption seemed justified by the fact that the enriched reproductive rates in the experiments with nutrient limitation were similar (difference $<0{\cdot}05\ day^{-1}$) to the reproductive rates in experiment without nutrient limitation under similar physical conditions.

Data analysis

All input data for the Droop and the Monod equations (reproductive rate, μ; nutrient-saturated reproductive rate, μ_{max}; dissolved nutrient concentration, S; cell quota, q) were obtained under variable physical conditions (temperature, day length). In order to fit the models to the data the assumption was made that only the maximal reproductive rates depend on physical conditions while the minimal cell quota of the Droop model (q_0) and the half-saturation constant of the Monod model (k_s) do not change with physical conditions. Under this assumption, replacing μ by μ_{rel} permits fitting of the two models to the available data.

The Monod equation relates the reproductive rate to the dissolved concentration of the limiting nutrient:

$$\mu = \mu_{max} \times S/(S + k_s) \qquad \text{Equation 3}$$

or, in its normalized form:

$$\mu_{rel} = S/(S + k_s) \qquad \text{Equation 4}$$

By taking μ from the controls of the enrichment bioassays and μ_{max} from the enriched cultures, k_s was estimated by non-linear regression (Statgraphics). The dependence of μ_{max} on temperature and day length was estimated by a multiple regression with stepwise variable selection (forward procedure, minimal F for accepting a variable in the model = 4) according to the model:

$$\mu_{max} = a \times DL^b \times t^c \qquad \text{Equation 5}$$

where DL is the day length (h) and t the temperature (°C).

The Droop equation relates the reproductive rate to the cell quota of the limiting nutrient:

$$\mu = \mu_{max}'(1 - q_0/q) \qquad \text{Equation 6}$$

where μ_{max}' is a theoretical maximal reproductive rate attainable only at infinite cell quotas. The realized nutrient-saturated reproductive rate (practically identical with the μ_{max} of equation 1) is attained at the saturating cell quota (q_{max}). If equation 4 is normalized in an analogous way to equation 2 μ_{rel}' becomes a linear function of $1/q$ or the C:limiting nutrient ratio:

$$\mu/\mu_{max}' = \mu_{rel}' = 1 - q_0/q \qquad \text{Equation 7}$$

If μ_{max} and μ_{max}' remain fairly proportional over the relevant range of physical conditions the linearity of this relationship is retained if μ_{rel}' is replaced by μ_{rel}:

$$\mu_{rel} = a - b/q = (1 - q_0/q)/(1 - q_0/q_{max}) \quad \text{Equation 8}$$

The minimal and the saturating cell quota can then be calculated from the slope and the intercept of the fitted regression of μ_{rel} on $1/q$:

$$q_0 = b/a \quad \text{Equation 9}$$

and

$$q_{max} = b/(a - 1) \quad \text{Equation 10}$$

The relationship of the cell quotas of the non-limiting nutrients to the nutritional status were analysed by an allometric regression according to the model:

$$q_{NL} = a \times q_L{}^b \quad \text{Equation 11}$$

where q_{NL} is the cell quota of the non-limiting nutrient and q_L the cell quota of the limiting nutrient. In the following the subscripts will be replaced by the chemical symbols of the elements in question.

Results

The phytoplankton biomass showed a seasonal pattern quite typical for eutrophic lakes (Sommer *et al.*, 1986). A biomass peak during spring was followed by a biomass minimum in May, the grazing-controlled 'clear-water phase'. The clear-water phase was then succeeded by an extended period of high algal biomass during summer (Fig. 1). The concentrations of dissolved nutrients exhibited the typical U-shaped seasonal pattern with high concentrations during winter and strong nutrient depletion during the vegetation period. There was a slight increase of ammonium and phosphate during the clear-water phase, but no such increase of silicate and nitrate concentrations. Phosphate can be exlcuded as a limiting factor for phytoplankton reproduction because dissolved reactive phosphorus concentrations were always >0·4 µM and N:P ratios in the dissolved phase were always <6; during the periods of nutrient depletion N:P ratios were usually <2.

The bioassays confirmed the absence of P-limitation. Significant silicate limitation was found in 14 cases. It only occurred in diatoms. One diatom species (the larger *Stephanodiscus* sp., 15 µm) was never nutrient limited. Significant nitrogen limitation was found in 44 cases. Nitrogen-limited species belonged to a variety of higher taxa (Cyanophyta, Chlorophyta, Dinophyta, Cryptophyta), but never to the diatoms. Four non-diatomceous algae were always nutrient saturated (*Chrysochromulina parva* Lackey, *Cryptomonas ovata* Ehrenberg, *Monoraphidium minutum* Komarkova-Legenerova, *Ankyra judayai* Fott). Contrary to other lakes in the region (Schöhsee – Sommer, 1988; Großer Binnensee – Sommer, 1989) no case of double limitation was found.

The temporal pattern of relative reproductivity rates agreed well with the temporal pattern of cell quotas of the limiting nutrients (Figs. 2 and 3). In all cases a satisfactory fit ($r^2 > 0·8$) of equation 8

Table 1. Minimal and maximal cell quotas (mol Si mol^{-1} C or mol N mol^{-1} C) of Plußsee phytoplankton species obtained by regression analysis according to equations 7 and 8.

Species	q_0	q_{max}	r^2	P	n
Silicon					
Stephanodiscus 6 µm	0·055	0·116	0·87	0·0067	6
Fragilaria crotonensis	0·126	0·766	0·96	0·0036	5
Asterionella formosa	0·127	0·816	0·91	0·0008	7
Nitrogen					
Phacotus lenticularis	0·014	0·161	0·91	0·0002	8
Anabaena flos-aquae	0·027	0·125	0·84	0·0810	4
Oocystis marssonii	0·029	0·246	0·94	<0·0001	11
Rhodomonas minuta	0·030	0·125	0·92	0·0006	6
Ceratium hirundinella	0·033	0·099	0·85	<0·0001	17
Peridinium spp.	0·036	0·146	0·97	0·0025	5
Sphaerocystis schroeteri	0·046	0·216	0·89	<0·0001	13
Pandorina morum	0·056	0·220	0·91	<0·0001	12
Chlamydomonas sp.	0·061	0·093	0·95	0·1471	3

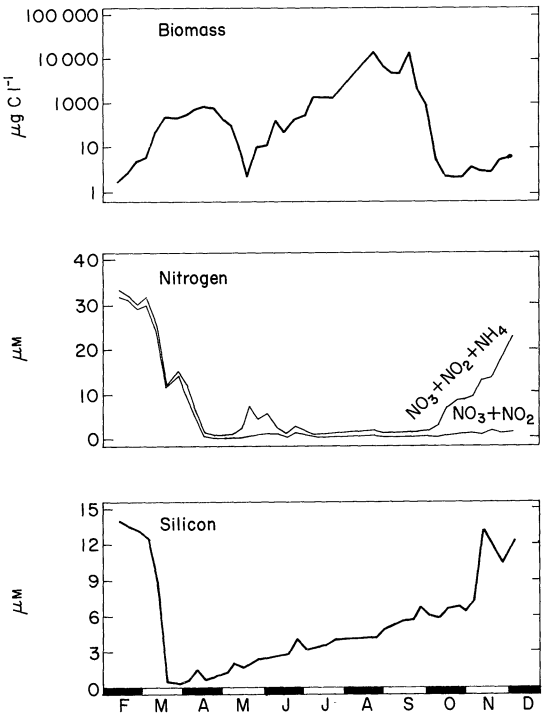

Fig. 1. Seasonal change of the phytoplankton biomass (µg C l^{-1}) and of the potentially limiting dissolved nutrients (nitrate + nitrite, ammonium, silicate; µM) in the epilimnion of Plußsee.

could be found (Table 1). The only two insignificant cases ($P > 0{\cdot}05$; *Anabaena flos-aquae* Brebisson, *Chlamydomonmas* sp.) are caused by too few degrees of freedom. Due to the scarcity of very strong N-limitation the q_0-estimates for nitrogen have to be regarded with some caution because they are based on a downward extrapolation from the real data.

Dissolved nutrient concentrations were a much poorer predictor of reproductive rates than cell quotas, with the exception of silicate limitation of *Asterionella formosa* Hassal and the small *Stephanodiscus* sp. (Fig. 4). In the case of N-limitation nitrate (including a small amount of nitrite), ammonium and dissolved inorganic nitrogen (DIN; $NO_3 + NO_2 + NH_4$) were tried as independent variables. The model giving the best fit is shown in Fig. 4. In all cases the coefficients of determination were much less than for the fits of the Droop model. In some cases (*Peridinium* sp.) the graphic representation of the data shows no resemblance to the shape of the Monod curve. In a number of cases with slightly better r^2 (*Rhodomonas minuta* Skuja, *Sphaerocystis schroeteri* Chodat, *Pandorina morum* Bory, *Ceratium hirundinella* Schrank) visual inspection of the plots indicates that high dissolved nutrient concentrations preclude nutrient limitation while at low nutrient concentrations anything may be possible from a μ_{rel} of c 0·3 to 1.

The multiple regression analysis according to equation 5 showed a significant dependence of the maximal reproductive rates of three species on both day length and temperature, of six species on day length alone, and of five species on temperature alone (Table 2). For two species no significant fit was obtained, because their maximal reproductive rates showed too weak a variation over the range of conditions tested. The analysis does not permit a final conclusion about the relative importance of temperature and day length effects for the species under study because short day/high temperature and long day/low temperature treatments were lacking. This is due to the unusually short hysteresis between day

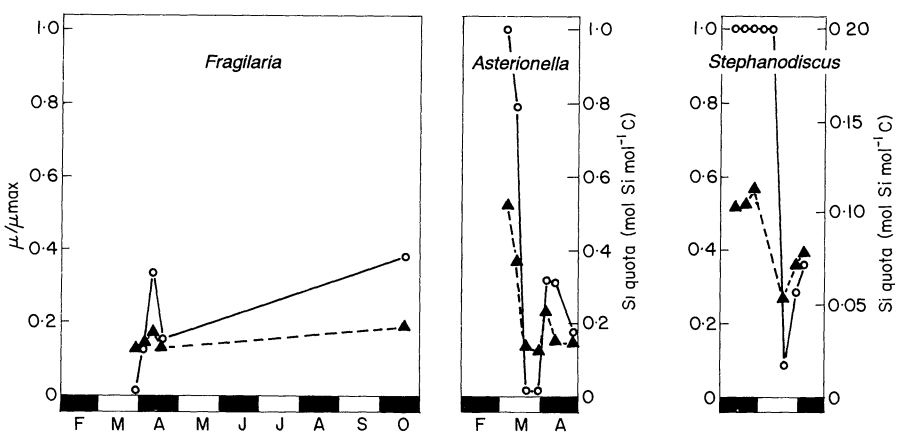

Fig. 2. Relative reproductive rates (μ/μ_{max}, open circles) and silicon cell quotas (mol Si mol^{-1} C, full triangles) of the Si-limited species (*Fragilaria crotonensis*, *Asterionella formosa*, the smaller *Stephanodiscus* sp.).

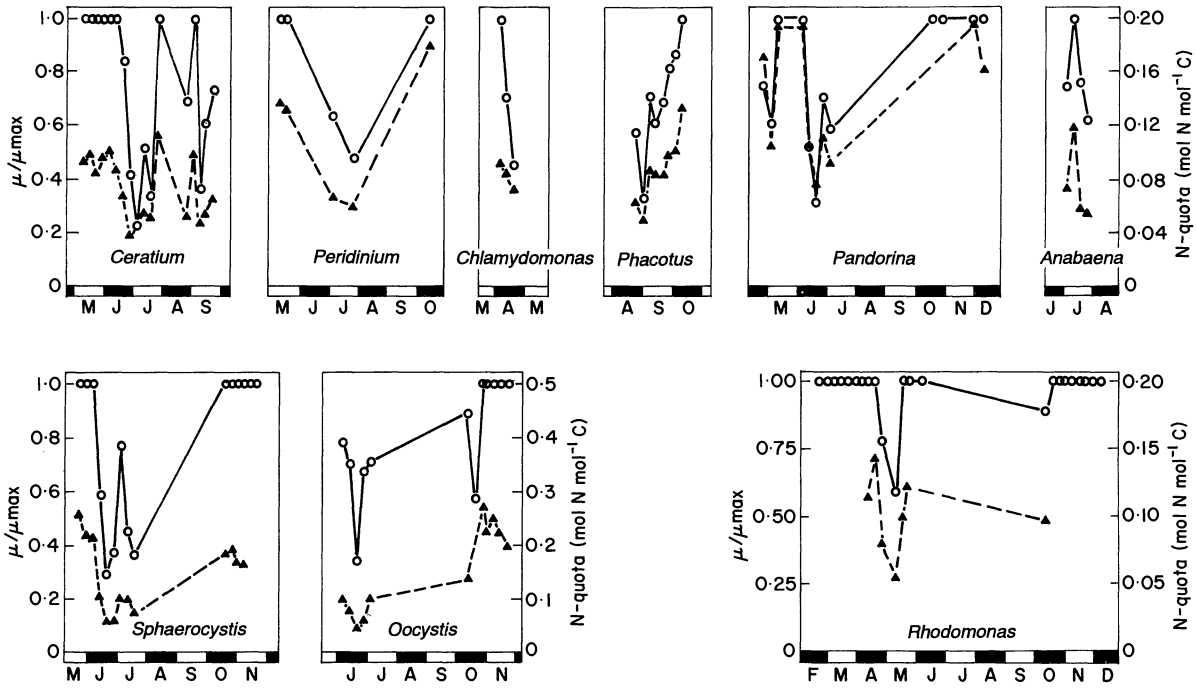

Fig. 3. Relative reproductive rates (μ/μ_{max}, open circles) and nitrogen cell quotas (mol N mol^{-1} C; full triangles) of the nitrogen-limited phytoplankton species (*Ceratium hirundinella*, *Peridinium* spp., *Chlamydomonas* sp., *Phacotus lenticularis*, *Pandorina morum*, *Sphaerocystis schroeteri*, *Oocystis marssonii*, *Anabaena flos-aquae*, *Rhodomonas minuta*).

length and water temperature in Plußsee 1989. A cross-correlation analysis between day length and water temperature revealed a time lag of only 3 weeks (r = 0·76) while without time lag the correlation coefficient still was 0·73.

The cell quotas of the non-limiting nutrients of nine species showed a significant ($P < 0·05$) relationship with the cell quota of the limiting nutrient (Table 3). In two cases (*Chlamydomonas* sp., *Anabaena flos-aquae*) this relationship was not significant, in one case (*Fragilaria crotonensis* Kitton) data of the cell quotas of the non-limiting nutrients were not available. For the majority of the nitrogen-limited species the relationship between the P-quota and the N-quota was nearly linear (exponent close to untiy), the most notable

Table 2. Dependence of the maximal reproductive rates (day^{-1}) on day length (h) and temperature (°C) according to the model $\mu_{max} = a \times DL^b \times t^c$ (equation 3). Standardized maximal reproductive rates (μ_{maxS}) were calculated for 14 h day length and 20 °C. If the data could not be fitted to the model, mean and standard deviation of the actual μ_{max} are given.

Species	μ_{maxS}	a	b	c	r^2	P
Monoraphidium minutum	2·09	0·0824		1·08	0·78	0·0053
Ankyra judayi	1·03	0·5845		0·19	0·85	0·0169
Rhodomonas minuta	0·95	0·0145	1·04	0·48	0·74	<0·0001
Stephanodiscus 6 μm	0·85	0·0026	2·20		0·70	0·0100
Pandorina morum	0·79	0·1089		0·66	0·65	0·0009
Sphaerocystis schr.	0·79	0·0475		0·94	0·73	<0·0001
Phacotus lenticularis	0·74	0·0419	1·09		0·91	0·0003
Chrysochromulina parva	0·74	0·0072	1·75		0·90	0·0518
Oocystis marssonii	0·72	0·0050		0·86	0·68	0·0006
Asterionella formosa	0·70	0·0049	1·88		0·77	0·0089
Fragilaria crotonensis	0·62 ± 0·02					
Cryptomonas ovata	0·60	0·0077	1·65		0·94	<0·0001
Stephanodiscus 15 μm	0·59	0·0033	1·97		0·72	0·0321
Anabaena flos-aquae	0·55 ± 0·02					
Peridinium spp.	0·31	0·0958	0·22	0·20	0·98	0·0093
Ceratium hirundinella	0·26	0·0295	0·83		0·76	<0·0001

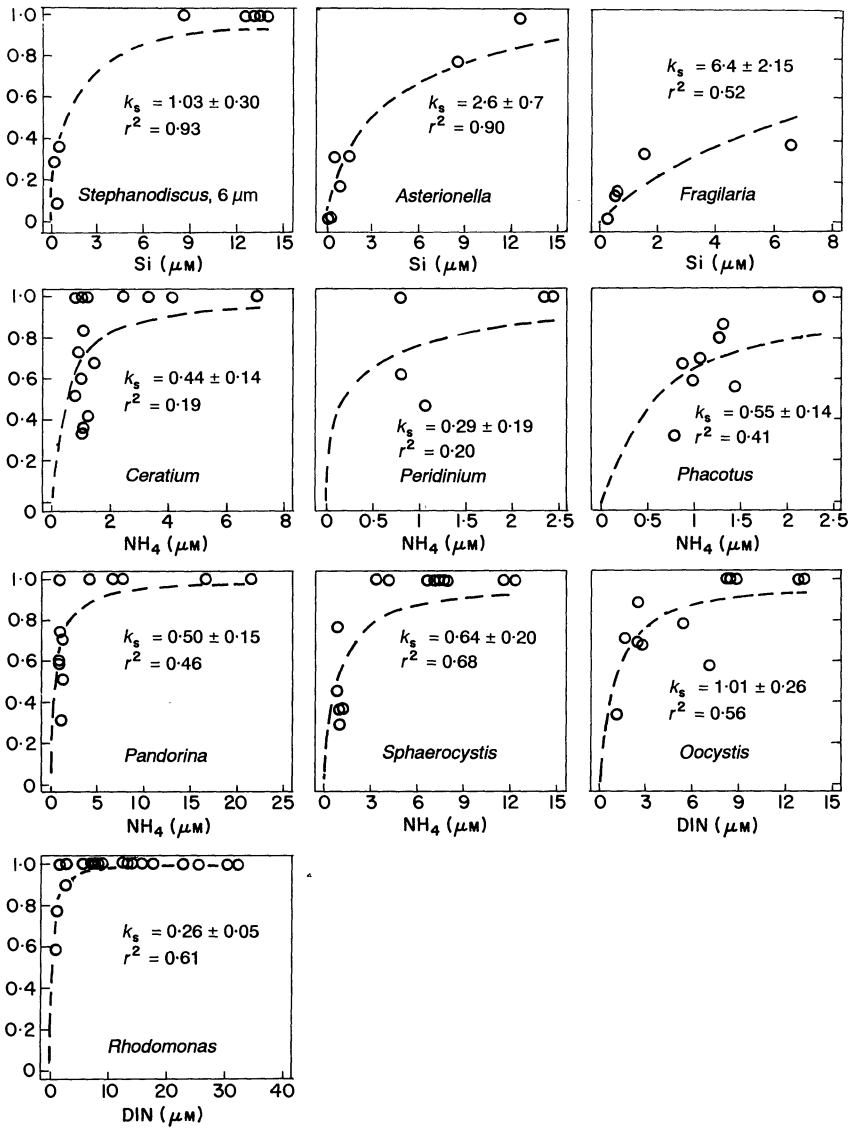

Fig. 4. Fits of the normalized Monod model to the relative reproductive rates of phytoplankton and the concentrations of dissolved nutrient in the epilimnion of Plußsee.

exception being the contrasting behaviour of the two dinoflagellates, *Ceratium hirundinella* (b = 1·45) and *Peridinium* sp. (b = 0·64). A similarly contrasting couple are the Si-limited diatoms *Stephanodiscus* (b = 1·22 for q_P and b = 1·30 for q_N) and *Asterionella formosa* (b = 0·50 for q_P and b = 0·46 for q_N).

Discussion

One of the central tenets in Harris' (1986) recent book is the alleged incompatibility between physiological models derived from phytoplankton cultures and the performance of natural populations. Among others, Harris criticizes the traditional concepts of nutrient limitation and their extension to modern competition theory (Tilman, 1982). Both work well in chemostat cultures but are said to fail in the field when the conditions of steady state are not fulfilled.

The traditional assumption of nutrient-limited phytoplankton growth during periods of nutrient depletion has been criticized during the last decade (Goldman *et al.*, 1979; Maestrini & Bonin, 1981; Harris, 1986). These and other authors have argued that low ambient concentrations of nutrients are insufficient evidence for nutrient limitation of reproductive rates. The main reason

Table 3. Dependence of the cell quota of the non-limiting nutrients on the cell quota of the limiting nutrient according to the regression model $q_{NL} = a \times q_L{}^b$ and stoichiometric ratio of the elements at q_0 and q_{max} of the limiting nutrient.

Species	a	$b \pm$ SE	r^2	Ratio at q_0	Ratio at q_{max}
q_P of N-limited algae				N:P	
Ceratium hirundinella	0·230	1·45 ± 0·26	0·68	20·2	12·3
Phacotus lenticularis	0·082	1·02 ± 0·11	0·94	13·3	12·6
Oocystis marssonii	0·070	1·01 ± 0·07	0·96	14·8	14·5
Pandorina morum	0·056	0·93 ± 0·11	0·87	14·6	16·1
Sphaerocystis schroeteri	0·046	0·81 ± 0·05	0·96	12·4	16·4
Rhodomonas minuta	0·050	0·77 ± 0·24	0·67	8·9	12·4
Peridinium sp.	0·031	0·64 ± 0·10	0·92	9·7	16·1
q_P of Si-limited algae				Si:P	
Stephanodiscus 6 µm	0·0133	1·22 ± 0·39	0·71	14·2	12·1
Asterionella formosa	0·013	0·50 ± 0·13	0·83	28	71
q_N of Si-limited algae				Si:N	
Stephanodiscus 6 µm	2·44	1·30 ± 0·13	0·96	0·98	0·78
Asterionella formosa	0·225	0·46 ± 0·13	0·80	1·46	4·0

for this was the rejection of the Monod model for temporally and spatially variable nutrient concentration. As has been frequently shown (summarized in Droop, 1983) cellular nutrient contents of nitrogen and phosphorus can be duplicated more rapidly than cellular biomass. This implies that those nutrients are stored beyond the actual demand for growth and can support higher reproductive rates than predicted from the Monod equation for some time after a decline in nutrient concentrations. Moreover, the Monod model failed occasionally in steady state chemostats (Caperon & Meyer, 1972) because the conventional analytical methods were not sensitive enough for sufficiently good estimates of the residual nutrient concentrations at low reproductive rates.

The results shown in Fig. 4 partially agree with the widespread dissatisfaction with the Monod model. The relatively better performance of this model in the case of silicate limitation can be explained in two ways. First, the silicate demands of diatoms as expressed by k_S are large compared to the analytical limit of detectability and the measured species of dissolved silicate is also the species which is utilized by diatoms. Second, silicate cannot be stored in significant amounts. Nitrogen lacks these advantages. First, the k_S values of the most efficient species are near the limit of detectability. Second, if a species uses nitrate and ammonium at the same time but with different efficiency neither a single ion nor DIN would be a valid independent variable in the Monod model. Third, nitrogen can be stored in excess of actual demands. The attempts to fit the Monod model to the nitrogen-limited cases are correspondingly poor, although not extremely bad. In an earlier study (Großer Binnensee – Sommer, 1989) better fits of N- and P-limited Monod-kinetics could be found. Those were mostly small, nanoplanktic algae (<30 µm) while here most algae (except *Phacotus lenticularis* Stein and *Oocystis marssonii* Lemmermann) belong to the net-plankton size spectrum (>30 µm). This difference suggests that storage might play a larger role in larger algae, as it has been shown for P-limited growth by Reynolds (1988).

In general, the criticizers of the Monod model accept the applicability of the Droop model. The approach by Goldman *et al.* (1979) to assess the nutrient status of phytoplankton by seston stoichiometry is a direct consequence of the Droop model. They used the 'Redfield ratio' (C:N:P = 106:16:1) as a cut-off point between nutrient limitation and maximal reproductive rates. Tett, Heaney & Droop (1985) showed that a cellular stoichiometry similar to the Redfield ratio can also be obtained by light limitation. Presumably, a similar effect can also be obtained by limiting nutrients other than N or P. Therefore, the Redfield ratio should not be used as an indicator of maximal reproductive rates but only as an indicator for the absence of P- or N-limitation. This restriction was implicit in Goldman's original paper, but it was omitted in Harris' (1986) extension of Goldman's claim to all kinds of aquatic habitats. Goldman's usage of the Redfield ratio as cut-off value between limitation and saturation was so far based only on

Table 4. Comparison of minimal (q_0 and saturating q_{max}) cell quotas of Si (mol Si mol^{-1} C) and N (mol N mol^{-1} C) in eutrophic Plußsee and mesotrophic Schöhsee.

	Plußsee		Schöhsee	
Species	q_0	q_{max}	q_0	q_{max}
Nitrogen				
Ceratium hirundinella	0·033	0·099	0·025	0·099
Peridinium sp.	0·036	0·146	0·036	0·131
Sphaerocystis schroeteri	0·046	0·216	0·041	0·265
Silicon				
Fragilaria crotonensis	0·126	0·766	0·142	0·394
Asterionella formosa	0·127	0·816	0·131	0·653

a few strains of marine algae. With respect to nitrogen limitation, the q_{max}-values obtained here permit an evaluation of the Redfield ratio-criterion for freshwater phytoplankton. The values of the saturated nitrogen quota in this study range from 0·093 to 0·246 mol N mol^{-1} C, with a mean of 0·159 and a standard deviation of 0·056. N/C quotient corresponding to the Redfield ratio is 0·151 mol N mol^{-1} C, which compares favourably with the mean of the values in this study. In a similar study in less eutrophic Schöhsee (Sommer, 1991) saturated nitrogen quotas ranged from 0·099 to 0·279, with a mean of 0·161 and a standard deviation of 0·076 mol N mol^{-1} C. This means that with respect to nitrogen limitation the Redfield ratio is a reasonably good criterion for average algae also in freshwaters, but not necessarily for all individual species. Morever, the N:P ratios at the transition point to nutrient saturation (at q_{max}) fall into a relatively narrow band between 12·3 and 16·4 (Table 3), which is again in agreement with the Redfield ratio.

A possible critique of the numerical values of q_0 and q_{max} could stem from the fact that the algae in the enriched bottles did not fully reach μ_{max}, especially if the reproductive rate *in situ* has been very low and the time lag for an adjustment of μ had been correspondingly long. However, the agreement between μ in the enriched bottles and μ in experiments without nutrient limitation but in similar physical conditions suggests that the bias in the estimate of μ must have been small. An underestimate of μ_{max} would have resulted in an overestimate of μ_{rel} and a proportional overestimate of the parameters a and b in equation 8. Since a appears in the denominator and b in the numerator of equations 9 and 10 this bias would tend to cancel out in the estimation of q_0 and q_{max}.

The physiological implications of the change of the cell quotas of non-limiting nutrients with the nutrient limitation can best be discussed for *Ceratium hirundinella* and *Peridinium* sp., because for these species P-limited Droop kinetics are available from nearby Schöhsee (Sommer, 1991). *Ceratium hirundinella* has a q_0 of 0·0011 P/C and a q_{max} of 0·008 P/C under P-limited conditions. Under N-limited conditions the regression in Table 3 predicts a P-quota 0·0016 P/C at q_0 of N and a P-quota of 0·008 P/C at q_{max} of N. This means that the P-quota behaves almost as if P was also a limiting nutrient and that there is no great luxury consumption of phosphorus at nitrogen-limited reproductive rates. *Peridinium*, on the other hand, has a q_0 of 0·00123 P/C and a q_{max} of 0·0086 P/C under P-limited conditions. Under N-limited conditions, the P-quota at q_0 of N is 0·0037 P/C and the P-quota at q_{max} of N is 0·009 P/C. This means that there is considerable luxury consumption of P under severely N-limited conditions.

The data set in this study has several species in common with the data set from Schöhsee (Table 4). With the exception of the q_{max} estimate for Si-limited *Fragilaria crotonensis* the parameter estimates agree well between the two lakes, i.e. identical species have almost identical properties in different lakes. Together with the generally good fit of the data to the model, this supports the usefulness of the Droop model even for field conditions and rejects an overly sceptical attitude towards the use of physiological models in field ecology.

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