The scientific basis of eutrophication management: reconciling basic physiology and empirical biomass models

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ABSTRACT

This article compares the results of empirical biomass-phosphorus relationships with basic physiological knowledge from algal cultures. First, a brief recapitulation of the physiological models of nutrient limitation will be given. Droop's variable internal stores model ("cell quota-model") is used as a basis for comparison with the P-chlorophyll-relationship of the OECD-model. Under moderate or strong P-limitation of algal growth rates (low cell-quotas of P) there is an order-of-magnitude discrepancy between the biomass predictions of both models. But even at minimal P-limitation (high cell-quotas of P) a much higher algal biomass would be predicted from the Droop-model than from the OECD-model. In the following section, a case will be made for the inclusion of heterotrophic plankton (bacterioplankton and zooplankton) into the considerations of biomass trends in eutrophication. It will be shown that allowance for P-trapping by heterotrophs can resolve the discrepancy between the Droop- and the OECD-model. Empirical relationships between phytoplankton and heterotroph biomass show that phytoplankton phosphorus is usually much less than half of the phosphorus incorporated into biotic particles.

In the final section, the impact of biomanipulation on the partitioning of phosphorus between different components of the plankton will be discussed. Special emphasis will be given to side effect of biomanipulation on the microbial loop. It will be hypothesized that success and failure of biomanipulation are unpredictable because of their sensitivity to minute differences in initial conditions and external disturbances.

Key words: eutrophication, plankton, nutrient-limitation, biomass, biomanipulation

1. INTRODUCTION

Cultural eutrophication is a chain of events, beginning with increased release of nutrients into the environment and ending with algal nuisance

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blooms in lakes. In his comparative study about lake resoration, Sas (1989) has distinguished two subsystems. Subsystem I contains all mechanisms which are important in translating nutrient emissions in the catchment into nutrient concentrations in lakes (loading, sedimentation, release from sediments, export etc.). Subsystem II contains the biotic response to inlake nutrient concentrations (algal growth and biomass, nuisance blooms). Here, I will concentrate on the pelagic components of subsystem II. I will also omit the meanwhile historical debate about the role of phosphorus relative to other biogenic elements. This case has been settled mainly by the correlational approach of Vollenweider and his coworkers (Vollenweider & Kerekes 1982) and by the lake experiments of Schindler (1987).

The starting point of my study are some seeming discrepancies between the physiology of P-limitation and empirical models for biomass prediction. These discreapancies will be resolved by making allowance for the P-content of planktonic heterotrophs, which have been neglected too much in traditional eutrophication research. The importance of P-partitioning between algae and heterotrophs will lead to an evaluation of the conceptual basis of biomanipulation. Finally, I will offer some explanations why success and failure of biomanipulation might be unpredictable.

2. THE PHYSIOLOGY OF NUTRIENT LIMITATION

The term nutrient limitation has been used rather loosely in the literature. Phytoplankton physiologists usually refer to the limitation of physiological rates, namely nutrient uptake rates. Population ecologists are interested in the limitation of growth rates and ecosystems ecologists are more interested in the limitation of the attainable biomass or production.

Apparently only the latter perspective seems important as a scientific basis for eutrophication management. The relevant question is "How much biomass can be built from a given pool of a limiting nutrient". If this question can be answered without considering the lower hierarchical levels (physiological, population ecological) then those lower levels might be safely ignored. A constant conversion factor ("yield-coefficient") between the mass of incorporated nutrient and total biomass would be a sufficient justification to ignore phytoplankton physiology. Unfortunately, there is no such constant conversion factor, especially not for phosphorus whose content in biomass is notoriously variable.

The simplest complete model of nutrient limitation is Morel's (1987) elaboration of Droop's (1973) "variable internal stores model" (Fig. 1). The first step in this model is the limitation of specific nutrient uptake rates (v) by dissolved concentrations (S) of the limiting nutrient:

$$v = \frac{v_{max} \cdot S}{S + k_m} \qquad (1)$$

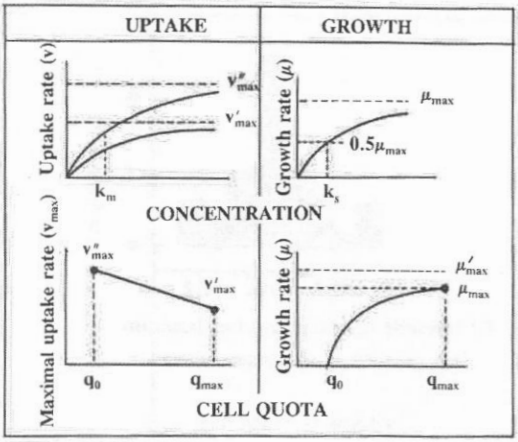

Fig. 1. The variable internal stores model of nutrient limitation. Upper left: equation (1) (upper left), eq. (2) (lower left); eq. (4) (upper right); eq. (4) (lower right).

where k_m is a species-specific constant (half-saturation constant of uptake) defined by the concentration at which uptake rates are half of the possible maximum.

Contrary to Dugdale's (1967) simplification, v_{max} (the maximal uptake rate) is no constant. It is a variable depending on the nutritional state of the organism in question. At the same external concentration, hungry cells have higher uptake rates than satiated cells. This negative feedback between uptake rates and the nutritional state can most simply be modelled by a negative linear dependence of v_{max} on the intracellular nutrient pool ("cell quota"; q). The upper boundary of v_{max}

(v''_{max}) is reached at the minimal cell quota (q_0), the lower boundary of v_{max} is reached at the maximal cell quota (q_{max}):

$$v_{max} = v''_{max} - (v''_{max} - v'_{max}) \frac{q - q_0}{q_{max} - q_0} \qquad (2)$$

The cell quota is a dynamic result from increase by uptake and dilution by biomass growth and cell divisions. Its relationship to reproductive rates (μ) is described by a saturating function:

$$\mu = \mu'_{max} (1 - \frac{q_0}{q}) \qquad (3)$$

The maximal reproductive rate (μ'_{max}) in eq. (3) is a hypothetical one

which would only be reached at an infinite cell quota. The real maximal reproductive rate (μ_{max}) can be calculated by substituting the maximal cell quota (q_{max}) for q in eq. (3).

Only under constant nutrient concentrations can the three components of the variable internal stores model be condensed into an equation relating the reproductive rate to dissolved concentrations (Monod-model):

$$\mu = \frac{\mu_{max} \cdot S}{S + k_s} \tag{4}$$

where k_s is the half-saturation constant of growth. Constant nutrient concentrations are an extreme exception in nature. Therefore, the Monod-model is usually not applicable. Equation (3), however, can be well used to describe the behaviour of natural populations (Sommer 1991 a, b).

3. THE NUTRIENT-BIOMASS CONVERSION

Equation (3) can be used to convert the amount of incorporated limiting nutrient into biomass if the cell-quota is normalized to cell mass or cell carbon (e.g., P/C). Then the yield-coefficient (Y) is the inverse of the cell quota.

A prediction of total phytoplankton biomass would be possible if biomass specific q_0 and q_{max}-values are sufficiently uniform between species. A survey of the literature yielded a log-normal distribution of biomass specific minimal P-quotas (Fig. 2) with a geometric mean of 0.00148 atoms P/atoms C and a coefficient of variation of 55% (summarized in Sommer 1991b).

The maximal cell quotas are more uniformly distributed around 0.01 atoms P/ atom C. This q_{max}-value is near the "Redfield-ratio" which is a generally acknowledged indicator of nutrient sufficiency (Goldman *et al.* 1979).

The mean values for minimal and maximal cell quotas mean, that average phytoplankton will incorporate *ca* 675 atoms C per atom incorported P under extreme P-deficiency and *ca* 100 atoms C per atom P under P-sufficiency. Thus, the potential to build biomass (B') from a given amount of incorporated nutrient (S_{inc}) depends on reproductive rates:

$$B' = S_{inc} \frac{1 - \mu / \mu'_{max}}{q_0} \tag{5}$$

Two extreme scenarios can be conceived:

q_0-scenario: If phytoplankton suffer no mortality from grazing (no grazer present or phytoplankton totally resistant) they will grow until all of the available nutrient is exploited and until their internal stores are exhausted. Then their cell quota is at q_0 and reproductive rate are zero. The available phos-

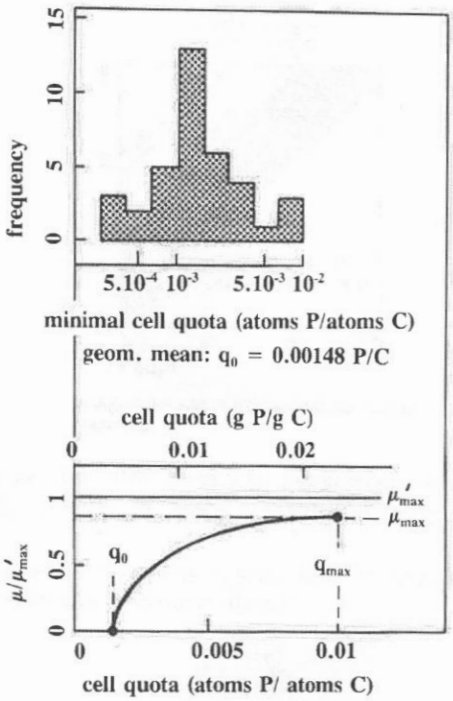

Fig. 2. Upper panel: Distribution of minimal cell-quotas of phosphorus among freshwater phytoplankton; lower panel: standardized form (m replaced by μ/μ'_{max}) of cell-quota dependent growth kinetic of average phytoplankton.

phorus is maximally used for biomass build-up and no turnover of phytoplankton biomass takes place. In other words, low turnover means high biomass.

q_{max}-scenario: The other extreme is a situation where phytoplankton have to reproduce at maximal rates in order to balance high mortality by grazing. The cell quotas will be maximal and a minimal biomass will be built per unit incorporated nutrient. In other words, high turnover means low biomass.

4. COMPARISON WITH THE OECD-MODEL

First step: phytoplankton only. In order to compare the biomass prediction of eq. (5) with the OECD-models (Vollenweider & Kerekes 1982) conversions have to be made (Tab. 1), because biomass is given as chlorophyll in the

Tab. 1. Conversions of biomass components.

	stoichiometry (atom/atom)	mass (g/g)
Phytoplankton		
Chlorophyll:C		0.02
P:C at q_0	0.00148	0.00382
P:C at $0.5m_{max}$	0.00258	0.00666
P:C at q_{max}	0.01	0.0258
Bacterioplankton		
C:cell		20 fg/cell
P:C	0.02	0.0517
Zooplankton		
P:C	0.01	0.0258
C:dry weight		0.45

OECD-model. The regression model for the full data set relating annual mean chlorophyll (*Chl*; in mass units) to annual mean total phosphorus in a lake (P_{tot}; in mass units) is:

$$Chl = 0.28\ P_{tot}^{0.96} \quad (6)$$

The regression is highly significant, but the 95% confidence limits for the dependent variable span one order of magnitude. The relationship is nearly linear (exponent 0.96), therefore a direct comparison with the potential biomass predicted by eq. (5) is possible. Using the conversions in table 1 and assuming that all phosphorus is trapped in algae the extreme cases are:

For the zero-turnover scenario (at q_0):

$$Chl = 5.2\ P_{tot} \quad (7)$$

For the maximal turnover scenario (at q_{max}):

$$Chl = 0.78\ P_{tot} \quad (8)$$

The prediction of eq. (7) is nearly one order of magnitude above the upper 95% C.L. of the OECD-model; the prediction of eq. (8) roughly coincides with the upper 95% C.L. (Figs 3-4). This means, that mean phytoplankton biomass in real lakes is practically always lower than the potential biomass. The discrepancy is nearly one order of magnitude.

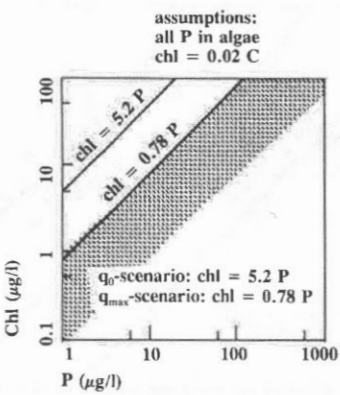

Fig. 3. Comparison of the OECD-model for annual mean chlorophyll with the phytoplankton-only predictions for minimal and maximal cell quotas.

The discrepancy is not resolved by using the OECD-regression for annual maximal chlorophyll (Chl_{max}) concentrations:

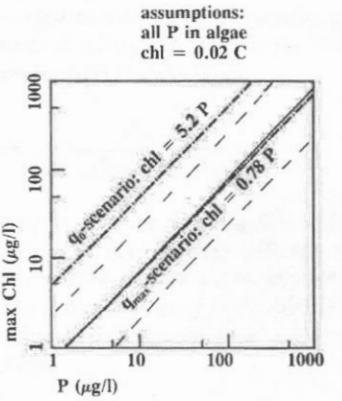

Fig. 4. Comparison of the OECD-model for maximal chlorophyll with the phytoplankton-only predictions for minimal and maximal cell quotas.

The discrepancy is not resolved by using the OECD-regression for annual maximal chlorophyll (Chl_{max}) concentrations:

$$Chl_{max} = 0.64\ P_{tot}^{1.05} \quad (9)$$

Equation (9) is remarkably close to eq. (8), but this similarity is rather coincidental. It would imply for average lakes that P would not be limiting for growth rates even during the annual maximum of biomass. It cannot be conceived how a nutrient could set a limit to biomass without limiting growth rates. Two alternative remains:

1) The correlations in the OECD- and similar models arises from the fact that P is not limiting but correlated with some other limiting resource, e.g. N or a trace element. The former hypothesis can be ruled out because chlorophyll-N-correlations are generally worse than chlorophyll-P-correlations. The latter hypothesis has not been tested so far.

2) It is wrong to assume that phytoplankton biomass is the only important fraction of particulate P. In the following I will show that P in heterotroph biomass can indeed be a substantial fraction of particulate and total P.

Second step: phytoplankton and bacteria. Bacteria are known to compete successfully for P with most species of algae (Bratbak & Thingstad 1985). Before the discovery of the "microbial loop" their biomass has been usually underestimated. Meanwhile it became clear that bacterial biomass contributes significantly to plankton biomass. Especially when phytoplankton biomass is low (in oligotrophic lakes and during phytoplankton minima in eutrophic lakes) bacterial biomass might be even higher than phytoplankton biomass. A survey by Simon *et al.* (1992) reveiled a weak but significant correlation between bacterial biomass (B_{bact}; mg C l^{-1}) and phytoplankton biomass (P_{phyt}; mg l^{-1}, only limnetic data):

$$B_{bact} = 24.5\ B_{phyt}^{0.22} \quad (10)$$

The scatter is very wide (Fig. 5), permitting a wide variation of B_{bact}:B_{phyt}-ratios at each biomass level. The low exponent implies that this ratio declines with biomass. This regression model cannot be compared directly with OECD-type models. Equation (10) is based on many individual samples from rather few different lakes whereas OECD-type models are based on annual or seasonal averages or annual maxima from many differnt lakes.

If bacteria contribute significantly to total plankton biomass they must take a significant share of the total phosphorus. Bacterial cell quotas of P are usually higher than algal ones. If they are C-limited, as they usually are in hab-

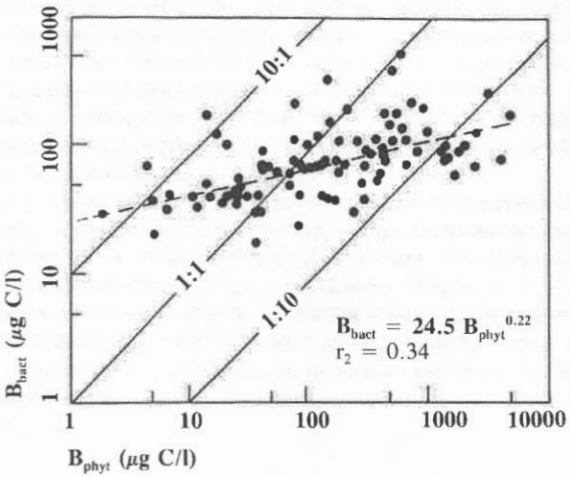

Fig. 5. Relationship between bacterial biomass and phytoplankton biomass for lakes (data from Simon *et al.* 1992).

itats with low organic pollution, their P-quota will be relatively constant and maximal. For the further calculations I assume a constant q_{bact} of 0.02 atoms P/atoms C (Jürgens & Güde 1990).

Assuming that all P is incorporated into bacteria and phytoplankton, phytoplankton biomass depends as follows on the bacterial P-quota, on the biomass ratio B_{bact}:B_{phyt} and on the algal P-quota (q_{phyt}):

$$B_{phyt} = \frac{P_{tot}}{q_{bact}(B_{bact} : B_{phyt}) - q_{phyt}} \qquad (11)$$

The consequences of eq. (11) for the chlorophyll:P-ratio are shown in figures 6 and 7. A biomass ratio of *ca* 0.4 is already sufficient to place the Chl:P-ratio of the q_0-scenario within the 95%-confidence interval of the OECD-model (Fig. 6). The central tendency of the OECD-model (Fig. 7) is approached at biomass ratios <1 by phytoplankton which is not or only very weakly P-limited (μ/μ_{max}>0.9).

Third step: phytoplankton, bacteria and zooplankton. Similar to bacteria zooplankton has also been more or less neglected by classic eutrophication research. According to their higher position in the trophic chain it was justifiably assumed that the flux of matter and energy through zooplankton must be much smaller than the flux through phytoplankton. However, the smallness of

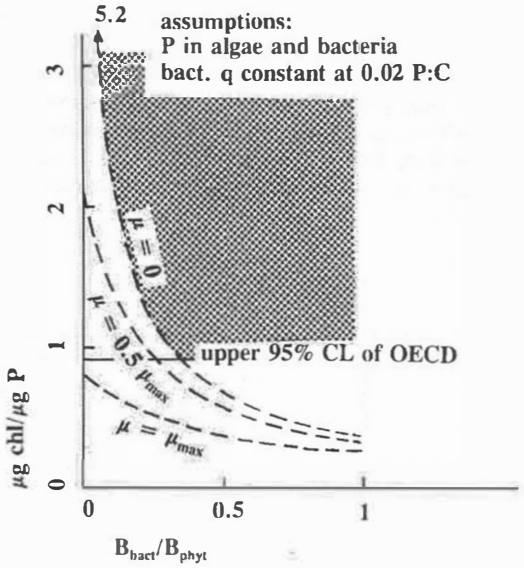

Fig. 6. Chlorophyll:P-quotients if all P is assumed to be incorporated into bacteria and phytoplankton for different nutritional states of phytoplankton and different bacteria:phytoplankton biomass ratios.

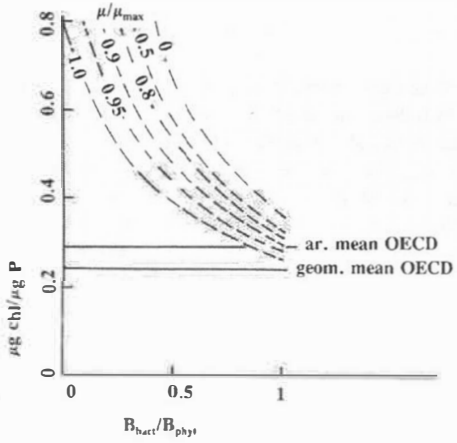

Fig. 7. Chlorophyll:P quotients if all P is assumed to be incorporated into bacteria and phytoplankton; only shown for low values of Chl:P.

the flux is counterbalanced by the longer residence times of substances in the compartment zooplankton. The longer residence time makes it possible, that zooplankton biomass can be within the same order of magnitude as phytoplankton biomass. In Lake Constance, for example, annual mean values of total zooplankton biomass are nearly twice (1.84-fold) as high as annual means of phytoplankton biomass (Geller *et al.* 1991). About 90% of zooplankton biomass in this lake consists of metazoa and 10% of protozoa.

Contrary to phytoplankton, metazoan zooplankton have a relatively stable stoichiometry, variation arising not from physiological change but from interspecific differences (Andersen & Hessen 1991; Hessen 1990; Hessen & Lyche 1992). The P-quota of cladocerans is *ca* 0.012 atoms P/atoms C, the P-quota of copepodes is *ca* 0.005 atoms P/atoms C. For the following calculations I use a zooplankton P-quota (q_{zoo}) of 0.01, which implies a biomass dominance of cladocerans. Assuming that phytoplankton, bacteria and zooplankton divide the entire phosphorus pool among themselves phytoplankton biomass can be calculated as:

$$B_{phyt} = \frac{P_{tot}}{q_{bact}\,(B_{bact} : B_{phyt}) + q_{zoo}\,(B_{zoo} : B_{phyt}) + q_{phyt}} \qquad (12)$$

The consequences of different algal cell quotas and $B_{zoo}:B_{phyt}$-ratios are shown for three diffrent levels of $B_{bact}:B_{phyt}$-ratios (Fig. 8). Good compatibility with the OECD-model results for reasonable biomass ratios. The importance of the nutritional state of phytoplankton diminishes with increasing contribution of heterotrophs to plankton biomass.

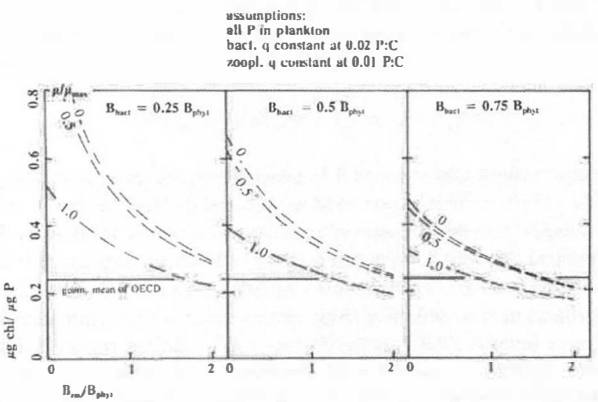

Fig. 8. Chlorophyll:P ratios if all P is assumed to be incorporated into bacteria, zoo- and phytoplankton. Dependence on phytoplankton:zooplankton-ratios shown for three different bacteria:phytoplankton ratios and three different nutritional states of algae.

The diminishing importance of the phytoplankton cell quota becomes strongly apparent if C:P-ratios in the entire plankton are considered (Fig. 9). This might resolve a hotly debated misunderstanding in plankton ecology. Goldman *et al.* (1979) found that the C:N:P-ratio in the marine seston was rather stable near the "Redfield-ratio" (106:16:1 by atoms). They concluded that phytoplankton should not be nutrient limited. In fact, the stabilty of seston stoichiometry could well be due to the stability of the stoichiometry of heterotrophs while no conclusion for the phytoplankton can be derived from seston stoichiometry.

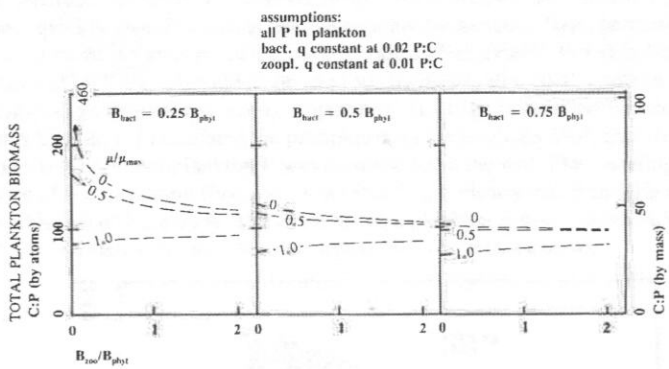

Fig. 9. Atomic C:P-ratios in the entire plankton biomass in the depnedence of the zooplankton:phytoplankton ratio for three different bacteria:phytoplankton ratios and three different nutritional states of algae.

Strong upward deviations from the Redfield-ratio and from the central tendency of the OECD-model are only expected when phytoplankton has an unusually high share of total plankton biomass and becomes strongly nutrient limited. This would be easiest the case during blooms of large, inedible phytoplankton species, particularly Cyanobacteria and large dinoflagellates. They could impede the growth of zooplankton (Gliwicz & Siedlar 1980). The lack of grazing would reduce nutrient recycling and reinforce nutrient limitation. In fact, the highest C:P-ratio in the particulate matter (750:1 by atoms) have been measured during the *Ceratium hirundinella*-bloom in Esthwaite Water (Heaney *et al.* 1987).

It is evidendent from the above calculations that the bacteria-phytoplankton- and the zooplankton-phytoplankton-ratio have strong impact on the possible phytoplankton biomass at a given level of inlake phosphorus. Bacteria are mainly important because of the high amount of P trapped per unit biomass and zooplankton because of their grazing pressure of phytoplankton.

Grazing is not only a removal of algal biomass, it also improves the nutritional status of the remaining algae and, thereby, reduces the amount of biomass built per unit incorporated phosphorus.

5. EMPIRICAL PHOSPHORUS-HETEROTROPH-RELATIONSHIPS AND THEIRIMPLICATIONS FOR PHOSPHORUS-CHLOROPHYLL-RELATIONSHIPS

Unfortunately, heterotrophs have been neglected during most large-scale eutrophication projects, especially during the OECD-project. Thereofore, empirical relationships between heterotroph biomass and lake trophic status are based on a much narrower data base than the OECD-model. Not only is the number of included lakes much smaller, they are also distributed over a much narrower section of the trophic state gradient. Because of compatibility with the OECD-model only relationships based on annual averages are usable for the following considerations. This excludes for instance the bacteria:phytoplankton-relationship by Simon *et al.* (1992; see eq. (10)).

Bird and Kalff (1984) published a regression model for bacterial numbers (N_{bact}) on total P based on 12 lakes. I have converted their equation to a biomass model (B_{bact} in mg l^{-1}) by assuming a mean bacterial biomass of 20 fg C.-$cell^{-1}$ (Lee & Fuhrman 1987).

$$N_{bact} = 0.9.10^6 P_{tot}^{0.66}; B_{bact} = 18P_{tot}^{0.66} \quad (13)$$

A 12-lake regression model for zooplankton biomass (Pace 1986) needed only a minor and less controversial transformation. The original biomass measure was dry weight, which was converted by assuming a carbon content of 45%.

$$DWT_{ZOO} = 38P_{tot}^{0.64}; B_{zoo} = 17.1\ P_{tot}^{0.64} \quad (14)$$

Up to now, only the partitioning of P between planktonic organisms has been taken into account. It has not yet been considered, that only a part of the total P is used for plankton biomass. The equilibrium concentration of dissolved P demanded for uptake (eq. (1)) and growth (eq. (2)) is usually negligible relative to P_{tot} For many phytoplankton species it is <1 mg P l^{-1} under low to moderate turnover rates. However, nutrient limitation is normally restricted to relatively short periods of the year (Sommer 1988). Annual averages of P-utilization by plankton include periods, when shortage of light prevents further growth or when growth of algae and bacteria has not yet caught up with P-availability. Figure 4.2. in Vollenweider and Kerekes (1982) shows that on average more P remains in the dissolved phase the more eutrophic lakes are. The regression of soluble reactive phosphorus (SRP) on P based on their data

yields:

$$SRP = 0.069\ P_{tot}^{1.40} \quad (15)$$

Assuming dissolved, unreactive P and mineral, particulate P negligible, the difference P_{tot}-SRP would be the amount of P bound to biotic paricles. This amounts to *ca* 87% of P_{tot} at a Ptot level of 5 mg l^{-1}, *ca* 67% at 50 mg l^{-1}, and *ca* 17% at 500 mg l^{-1}.

Biotic particles consist mainly of phyto-, zoo-, and bacterioplankton and of detritus. The latter will contain little P only, because after death organic mass quickly loses P which is taken up mainly by bacteria. Thus, particulate P measured in "detrital particles" will be mainly bacterial P. For simplicity, I assume that P will be divided among four fractions only: SRP, bacteria, zooplankton, phytoplankton. Using equations (13), (14), (15) and the transformations in table 1, I calculated the phosphorus in the fractions SRP, bacteria and zooplankton. Phytoplankton P was assumed to be the rest. The resulting diagram of P-partitioning (Fig. 10) shows that P_{phyt} is clearly less than 50% of P_{tot} at all levels of P-richness. The share of phytoplankton is maximal at *ca* 50 mg l^{-1} and becomes very small both in oligotrophic and eutrophic lakes.

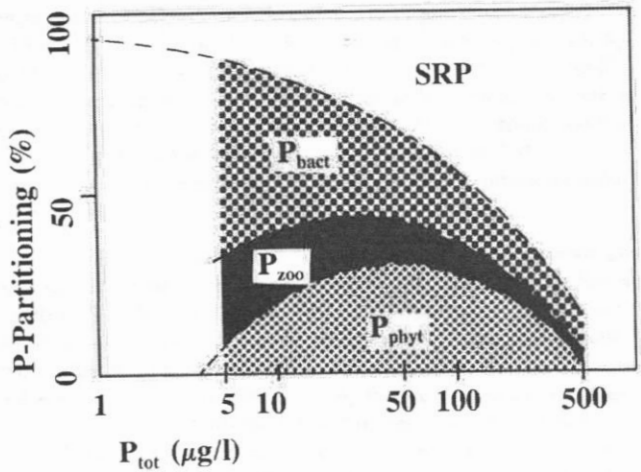

Fig. 10. Partitioning of P between SRP, bacteria, zooplankton and phytoplankton in dependence of total P; calculated from eq. (13), (14) and (15).

The extent of non-linearity in figure 10 might be questioned, however. Equation (13) and (14)' are based on lakes from *ca* 5 to 100 mg l^{-1}, as opposed to a range of *ca* 5 to 500 mg l^{-1} in the OECD-data set. The high share of the

hetreotrophs at the lower end of the gradient and the high share of SRP at the higher end of the range seem unrealistic. They predict negative values for phytoplankton, if extrapolated beyond the original range of data. It seems plausible that extending the range of original data would flatten out the curves in figure 10 and 11.

The chlorophyll:P curves in figure 11 were constructed by taking the P-share of phytoplankton from figure 10 and the P-quotas and the chlorophyll:C-transformation from table 1. Except for their strong non-linearity they are well compatible with the OECD-model. In conclusion, P-partitioning explains most of the seeming discrepancy between physiological P-demands of phytoplankton (eq. (3)) and the empirical OECD-model (eq. (6)).

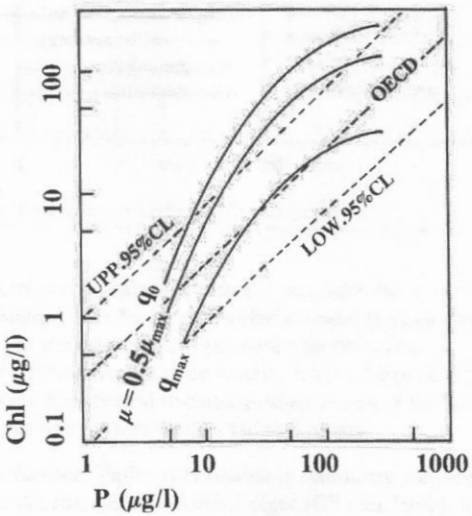

Fig. 11. Chlorophyll:P_{tot}-relationship calculated from P-partitioning in figure 10 for three different nutritional states of phytoplankton; comparison with the OECD-model for annual mean chlorophyll.

6. A NEW PERSPECTIVE OF BIOMANIPULATION: NEGLECTED SIDE EFFECTS IN THE MICROBIAL LOOP

The partitioning of P calculated for figure 10 is derived from double-logarithmic relationships with wide confidence limits. Such wide confidence limits are usual for all kinds of empirical eutrophication models. By necessity, a strong degree of variability in the partitioning of P has to be expected at all levels of P_{tot} There is no empirical evidence and no *a priori* reason to consider

one particular value as equilibrium value.

Biomanipulation (Shapiro & Wright 1984) by removal or reduction of zooplanktivorous fish may be considered a direct attempt to influence the partioning of P between the functional components of plankton. The idealized causal chain of pelagic biomanipulation consists of three steps:

1) a decrease in fish pressure increases the biomass and the mean individual size of herbivorous zooplankton;
2) more and larger zooplankton exert a stronger grazing pressure on phytoplankton. Larger zooplankton have a broader size spectrum of edible algae;
3) more grazing on a broader spectrum of algae leads to a lower density and biomass of phytoplankton.

Steps 2) and 3) lead to a shift from P_{phyt} to P_{zoo} and SRP. The remaining phytoplankton experience a higher *per capita* income of phosphorus. In order to withstand grazing they have to grow fast and need high cell quotas. Because of the high cell quotas a only a small biomass is built per unit P_{phyt}.

The practical experience with biomanipulation has been mixed. The anticipated change in zooplankton has been successful in the majority of cases, while the anticipated change in phytoplankton took place less frequently (Benndorf 1990). This lead to the bottom up:top down-hypothesis by McQueen *et al.* (1989) which assumes that predation effects ("top-down") diminish while cascading downwards the trophic pyramid while resource effects ("bottom-up") diminish while propagating upwards. As a result, there is an apparent lack of correlation at the phytoplankton:zooplankton link.

In the following I want to explore several problems and undesired side-effects of biomanipulation:

Bacterivory by herbivorous zooplankton. If herbivorous zooplankton graze on bacteria this might redistribute nutrients from bacteria to algae and thus lower the P_{bact}:P_{phyt} ratio. Thus, bacterivory might be an undesired side-effect of biomanipulation. It has not yet been addressed in biomanipulation studies, therefore any consideration is rather speculative.

The food spectrum of filter feeders is mainly limited by particle size (Geller & Müller 1980; Geller & Gophen 1984; Sterner 1989, and references herein; Fig. 12). A number of filter feeders are highly efficient bacteria feeders, among them some small Cladocerans (e.g., *Chydorus sphaericus*) but also large ones, such as *Daphnia magna* (Geller & Müller 1980). The small Cladocerans have low upper size limits of their food spectrum (<10 mm), therefore they cannot control even medium sized algae and their effect would be most strongly opposed to the goals of biomanipulation.

Large *Daphnia* spp, however, ingest also larger particles (up to 30-50 mm) and can exert efficient control over medium sized algae too. They also

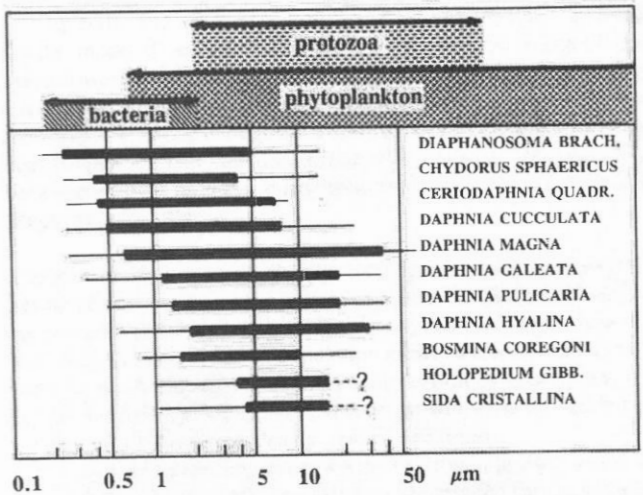

Fig. 12. Size spectra of food particles for freshwater cladocerans.

feed on a wide spectrum of protozoa which are otherwise the most important bacteria feeders. Bacterivory by large *Daphnia* would thus be partially or totally compensated by the supression of protozoan bacterivores.

Well functioning biomanipulation usually favors large filter feeders. Therefore, bacterivory is expected to cause problems only if for some of the reasons discussed below large filter feeders fail to develop.

Inedibility of phytoplankton. Failures of biomanipulation are frequently associated with the mass development of inedible algae (Gliwicz 1990). Inedibility even for *Daphnia magna* can result from size (large dinoflagellates, colonial cyanobacteria), resistance against digestion (gelatinous green algae and cyanobacteria), and toxicity (some strains of cyanobacteria). Large, colonial diatoms are also poorly edible for many filter feeders (e.g., *Asterionella formosa*) or nearly inedible for most (e.g., *Fragilaria crotonensis*) but they cause no problem for biomanipulation. After stratification they tend to exhaust dissolved silicate in the epilimnion and sink out thereafter.

As soon as inedible, non-diatom algae are present several positive feedback loops tend to reinforce bloom development. Filter feeders suppress their edible competitors and redistribute phosphorus from the "undergrowth" of pico- and nanoplankton to the inedible algae. Vertical motility by flagella (dinoflagellates) and gas-vesicles (cyanobacteria) enables them to utilize nutrient pools in deeper strata and pump nutrients upwards into the epilimnion.

Their motility also protects them against sinking losses. The high resistance against losses permits growth until complete exhaustion of external and internal nutrient pools. Blooms of inedible algae are the closest approximation to the q_0-phytoplankton-only-scenario discussed above.

Inhibition of herbivory by inedible algae. Filter feeders clean their food grove by postabdominal rejection movements if undesired algae enter their filtration apparatus. This rejection movements cost energy and time and reduce the overall filtration rate and growth rate of filter feeders. Larger cladocerans are more strongly inhibited than small ones (Gliwicz & Siedlar 1980; Gliwicz 1990, and references herein), because the smaller filter feeders less frequently get inhibiting particles into their food grove. This inhibition might shift the competitive balance from large filter feeders to small ones. Interestingly, the inhibition effect leads to the same changes in zooplankton communities as fish predation.

If the small filter feeders favored by inhibiting algae are also efficient bacteria feeders a further positive feed-back is switched on. The shortage of nanoplankton during dominance periods of large algae is expected to favor picoplankton feeders.

The question of predictability. There is little doubt that blooms of inedible algae can resist against the intervention of biomanipulation. It is less well understood why such blooms sometimes devleop and sometimes not. Both from a theoretical and from a practical point of view it would be desirable to increase the predictability of the success of biomanipulation. Benndorf (1990) tried to find regularities along the trophic state gradient and hypothesized that biomanipulation would be more successfull in less eutrophic lakes. He even coined the term "biomanipulation-efficiency threshold of the phosphorous loading". So far the data base is too small to finally test his hypothesis.

Here, I present an alternative hypothesis: The success of biomanipulation is unpredictable because the unsucessfull state (high B_{phyt}:P_{tot}-ratio) is stabilized by several positive feed-back loops whose functioning depend on unpredictable or poorly predictable factors:

- external (physical) disturbance;
- idiosyncrasies in the recruitment patterns of local populations;
- minute differences in initial conditions and timing.

Disturbance. Inedible, bloom-forming phytoplankton species grow slowly and need long time to establish blooms. The establishment of blooms depends on the continuity of appropriate physical conditions (Reynolds 1987, 1990, 1993). The majority of them (*Ceratium, Microcystis, Anabaena, Aphanizomenon*) develop best under continued stratification, some others (*Planktothrix* and *Limnothrix* = foremrly called *Oscillatoria*) depend on continued mixing. Some *Planktotrhix* spp (*P. rubescens, P. agardhii* var. *isothrix*) may retreat to the metalimnion during summer stratification.

Episodic mixing during summer stratification has several effects including the import of new nutrients into the euphotic zone, changes of the light climate, lowering of the pH, and the dilution of algal densities. Both permit intermittent growth pulses of small, fast-growing and well-edible phytoplankton species. If strong enough such disturbances may break several of the feedback loops stabilizing the dominance of large algae. Intermittent mixing has been successfully used as a mangement tool in order to break nuisance blooms (Reynolds *et al.* 1984).

Recruitment idiosyncrasies. Before reaching the size of inedibility colonial and filamentous algae have to grow up from unicells. In the cases of nostocalean cyanobacteria (*Anabaena, Aphanizomenon*) there are specialized "overwintering" cells (akinets, cysts). If population growth starts from unicells, small colonies or small propagules a timely intervention by grazing may prevent the development of a bloom. If zooplankton growth starts too late too many algal colonies might have exceeded the critical size limits.

There are cases, however, where the annual growth of nuisance algae does not start from small size. *Microcystis*-populations in some lakes overwinter as colonies on the sediment surface from where the recolonize the water column during spring or early summer (Reynolds *et al.* 1981). If they are sufficiently large during recolonization intervention by grazing would fail to prevent a mass development.

Initial conditions and timing. Except for *Planktothrix rubescens*, lakes spring blooms of phytoplankton usually start with edible nanoplanktonic algae or diatoms (Reynolds 1980; Sommer *et al.* 1986). The nanoplankton bloom is a good food base for the beginnig growth of herbivorous zooplankton which eventually reaches filtration rates higher than algal production rates. This imbalance leads to a mid-season minimum of phytoplankton biomass ("clear-water-phase"; Lampert 1978, 1988, and references herein). A few weeks later, zooplankton mortality mainly by juvenile fish and the advent of inedible and inhibiting algae terminate the clear-water-phase. Biomanipulation by fish removal or reduction aims at reducing the mortality of herbivores and thereby prolonging the clear-water phase over the entire summer period.

To achieve that goal, it is critically important that strong herbivore populations build up before the advent of interfering algae and before the algal spring becomes seriously nutrient limited. The former is evident from the preciding considerations, the latter needs some explanation.

Recently plankton ecologists discovered that herbivorous zooplankton can be P-limited in the presence of sufficient food in terms of carbon and energy (Andersen & Hessen 1991; Hessen 1990; Urabe & Watanabe 1992). Sommer (1992) permitted the well edible phytoplankton species *Scenedesmus acutus* to grow until equilibrium at different degrees of P-limitation in chemostats. Then *Daphnia galeata* was added to the cultures. At algal cell quotas

<0.00102 atoms P/atoms C *Daphnia* could not grow at all and algal biomass remained high. At slightly higher cell-quotas (>0.00113) there was initially very slow growth of *Daphnia*. The slightly increasing grazing pressure improved the nutritional state of the algae (q increasing) which permitted zooplankton reproduction to become faster. The positive dependence of algal cell-quotas on grazing pressure acted as a positive feed-back loop which finally led to high zooplankton densities and low algal biomass (Fig. 13).

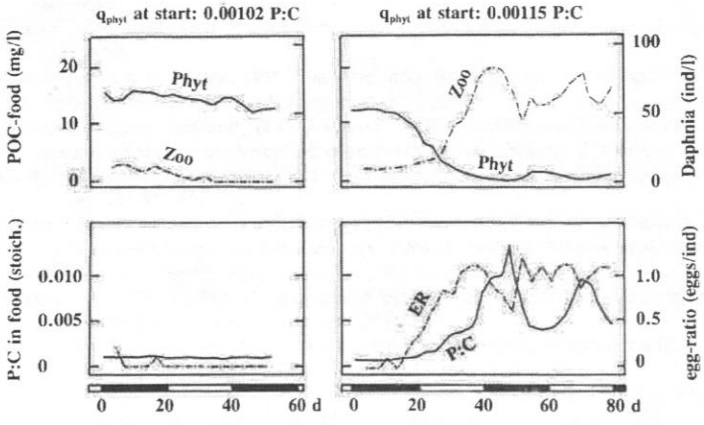

Fig. 13. Development of phytoplankton-zooplankton interactions in dependence of the initial cell quota of phytoplankton. Left: initial P-quota of food alga (*Scenedesmus acutus*) at 0.00102 P:C by atoms; right: initial P-quota of food alga at 0.00115 P:C by atoms; upper panel: biomass of *Scenedesmus* in mg C l^{-1} and density of *Daphnia galeata* (in ind l^{-1}); lower panel: stoichiometric P:C ratio in food, egg-ratio of *Daphnia*.

The important point is that very minute differences in the initial conditions (cell-quota of phytoplankton) led to a qualitatively different system behaviour. During the build-up phase of an algal bloom such a small decrease in cell quotas may be a question of one day or even less. Admittedly, as low cell-quotas as in my experiments are very rare in nature. But in combination with beginning interference by large algae and slight mortality of zooplankton the cell-quota threshold of edible algae can increase substantially.

There are many factors which can increase the time lag between the phytoplankton and the zooplankton spring bloom. Unusually good whether condition may cause an earlier than usual start of algal growth. Mortality of overwintering propagules, disease and parasitism or predation by invertebrate predators may delay the growth of zooplankton.

Biomanipulation-failure as a cusp-catastrophy. In conclusion, I reformulate my hypothesis. The failure of biomanipulation is a cusp-catastrophe *sensu* Thom (1957). The successful and the unsuccessful state of biomanipulation (Fig. 14) are both reinforced by a number of positive feed-back loops. Whether the pelagic system develops into one or the other state depends on minute differences. This differences include:

- the intensity and frequency of external disturbances;
- the timing of phytoplankton spring growth;
- the timing and the strength of nutrient shortage of food-algae;
- the timing of the growth of interfering algae;
- the timing of zooplankton growth;

Near the breakpoint decisive differences can be smaller than the resolution of conventional methods. Then, success and failure of biomanipulation become unpredictable.

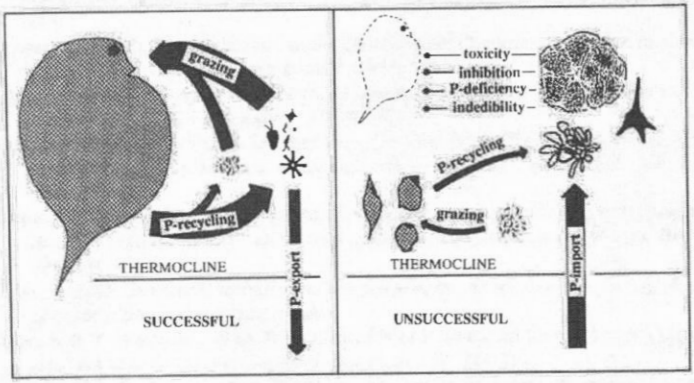

Fig. 14. Idealized representation of the successful and the unsuccessful state of biomanipulation.

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