

Phytoplankton contribution to sestonic mass and elemental ratios in lakes: Implications for zooplankton nutrition

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Abstract

Phytoplankton carbon and particulate organic carbon (POC), nitrogen (PON), and phosphorus (POP) (POC : PON : POP) were analyzed in 109 temperate lakes covering a wide span in productivity and other key parameters. Seasonal means of total POC (four samples) ranged from 206 to 7160 $\mu\text{g C L}^{-1}$, with a grand mean of 960 $\mu\text{g C L}^{-1}$, whereas estimated phytoplankton C ranged 12 to 1,770 $\mu\text{g C L}^{-1}$, with a mean of 217 $\mu\text{g C L}^{-1}$. Sestonic C:P ratios ranged from 59 to 553 (atom:atom), with a mean of 207. The elemental contributions from phytoplankton and other sestonic compartments (mainly detritus) were analyzed with a simple regression model, in which autochthonous and allochthonous components were separated. Model-derived estimates for N:P ratios of phytoplankton and allochthonous seston compartments were nearly equal (15.4 ± 2.5 and 16.0 ± 2.0) and were not significantly different from the Redfield N:P ratio (16). The estimated C:P ratio of allochthonous detritus was 2.7 times higher than that for phytoplankton (123 ± 15), which again was not significantly different from the Redfield C:P ratio (106). Altogether, this indicates that sestonic components of autochthonous origin should be closer to Redfield proportions in eutrophic than in oligotrophic lakes. It also indicates that major contributions of allochthonous detrital C in oligotrophic lake seston may explain deviations from the Redfield ratio and calls for caution when interpreting elemental ratios in algae versus total seston. The regression model indicates that live phytoplankton cells rarely exceed 40% of total POC, yet it suggests that a major fraction of detritus is derived from autotrophs. This close link between live and dead cells could explain why total seston apparently carries the stoichiometric and biochemical footprints from the phytoplankton. Judged from algal biomass alone, *Daphnia* would face severe food limitation in a majority of lakes, while if we were to include total seston, *Daphnia* would be above threshold food levels in all lakes. Likewise, the effect of food quality limitation related to C:P ratios will turn out differently if total seston or only the phytoplankton fraction is considered.

During the past decade, it has become increasingly clear that not only food quantity in terms of carbon (C) mass of edible algae or quality in terms of digestibility or toxicity (Lampert 1977) but also the food quality in terms of specific content of key elements (Hessen 1992; Sterner 1993; DeMott et al. 1998) or biomolecules (Ahlgren et al. 1990; Müller-Navarra 1995) may be a main determinant of zooplankton growth. These aspects have been elaborated upon particularly for freshwater systems, but studies from a wide range of ecosystems indicate that food quality limitations may pose a general constraint on energy transfer in a variety of food webs (Elser et al. 2000a,b). In general, herbivores have higher C specific content of major nutrient elements like phosphorus (P) or nitrogen (N) when compared with their food (i.e., higher P:C or N:C ratios). Thus, following from the Liebig minimum principle, growth efficiency in terms of C may be governed by N or P in the food. The importance of N and P hinges on the fact that these elements are major constituents of amino acids and nucleic acids, respectively, and thus a deficiency in these elements may directly translate to reduced protein synthesis and growth. A strong mismatch in stoichiometry between herbivores and their food would intensify the quality constraint on the con-

sumer. Such an elemental deficiency could have strong bearings on pelagic community dynamics and energy flow (Andersen 1997). It will be most relevant for detritivores and herbivores and less relevant for carnivores, as reflected in the assimilation efficiencies that generally are low in detritivores, medium in herbivores, and high in carnivores (Sterner and Hessen 1994).

The actual elemental ratios offered to terrestrial grazers that feed on vascular plants and foliage may be measured with high accuracy, and grazers may adjust their distribution and food selection to balance their qualitative and quantitative demands (Van der Wal 1999). This may in fact invoke a selection for low quality (high C:N or C:P) in terrestrial plants to reduce the grazer fitness (Moran and Hamilton 1980). In contrast, most herbivorous zooplankton feed on a mixture of food sources of different origin (collectively labeled seston), and phytoplankton may in fact be a minor contributor to this seston pool. The fact that key grazers like *Daphnia* feed rather unselectively on seston within an appropriate size category (Hessen et al. 1990) does also suggest that selection for low quality would be less likely among phytoplankton, since this would invoke some type of group selection argument.

In all aquatic ecosystems, the grazer food chain based on autotrophic production will be supported by a detritus-based

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food chain utilizing dead organic matter either of autochthonous or allochthonous origin (Wetzel 1995). In many ecosystems, only a modest share of primary production will be directly grazed, leaving a major share for the detritus food chain (Wetzel 1995; Cebrian 1999). If a large proportion of seston retained on filters for elemental analysis is of nonalgal origin (detritus, bacteria, protozoans), this could yield contrasting interpretations of phytoplankton elemental ratios. Although marine seston in general approach the Redfield ratio (C:N:P atomic ratio of 106:16:1), lake seston typically show a major deviation from the Redfield ratio, with particularly high C:P ratios (Hecky et al. 1993; Elser and Hassett 1994; Sterner et al. 1997; Hessen and Faafeng 2000).

When searching for major patterns in elemental ratios of autotrophs, it may be of vital importance to know their share of the total seston pool. If the share is low, autotroph responses could be masked by other sestonic compartments. Also, food quality responses in zooplankton should be judged on this basis. Pelagic grazers such as *Daphnia*, which are the most likely candidates for direct P-limitation because of their high P demands (Andersen and Hessen 1991), will feed rather unselectively on a mixed diet of seston in the range of 0.5–50 μm (equivalent spherical diameter) (Burns 1968). This means that a large fraction of the diet may consist of items other than live phytoplankton cells. Also, for other zooplankton taxa, the major source of bodily C may be of detrital or bacterial origin (Hessen et al. 1990; Jones et al. 1997), and thus, food quality and food quantity responses in the zooplankton community may to a large extent be determined by nonalgal sestonic components. Since the threshold for food quality constraints in terms of P-limitation at low P:C ratios strongly depends on the assimilation efficiency for C relative to P and C assimilation efficiency tends to be low for detritus and bacteria (Sterner and Hessen 1994), a high fraction of nonalgal food could also affect predictions of zooplankton responses based on elemental ratios in crude seston. For some lakes, major proportions of particulate N and P may also be associated with allochthonous components like terrestrially derived humus.

In this study, the share of algal C, N, and P relative to total particulate fractions was assessed in a large number of Norwegian lakes, from which there exist data on both seston biomass and phytoplankton biovolume based on direct counts. This allows for a comparison of sestonic elemental ratios relative to those estimated for phytoplankton.

Material and methods

The data in this study are based on a survey of 109 lakes in southeastern Norway, sampled during daytime in May, June, July, and August of 1991 and 1992 (four samples per lake, a total of 436 analyses on all parameters). The dynamics and turnover of the total seston pool and its major composite fractions, detritus and phytoplankton, will be widely differing. Also, it is reasonable to expect consistent time lags between the live and dead components of seston. Thus, in order to avoid spurious effects of desynchronized pools, we used averaged data for each locality for the statistical analysis. Total phosphorus (TP), total nitrogen (TN), particulate

organic carbon (POC), chlorophyll *a*, color, as well as phyto- and zooplankton biomasses were analyzed from integrated samples over the trophogenic zone (two times Secchi depth, maximum 10–0 m, minimum 2–0 m).

Total P and N were analyzed with a Skalar san Plus Autoanalyzer after peroxodisulfate digestion. Chl *a* was measured spectrophotometrically after methanol extraction. Particulate P was estimated as the difference between the total P concentrations before and after filtering through a GF/F glass fiber filter. We wanted to include the total seston mass in our analysis; hence, no prescreening was performed to remove zooplankton. Particulate C and N were filtered on preignited (500°C, 2 h), acid-washed GF/F filters and combusted for analysis on a Carlo-Erba elemental analyzer (1106). Filtration volumes were dependent on the particle content of the water. Since the data set comprises only soft-water lakes (median Ca concentration of $<5 \text{ mg L}^{-1}$), any calcite contribution to particulate C was assumed to be negligible. Phytoplankton biomass was estimated using cell counts obtained by Utermöhl technique on Lugol-fixed samples, and cell volumes were estimated from measured cell dimensions and geometrical cell shape models. These microscopic counts also revealed that with exception of a few eutrophic localities, most of the particulate matter was well within a grazable size range for most *Daphnia* ($<10 \mu\text{m}$).

Zooplankton biomass (rotifers, copepods, and cladocera) was determined from a 10-liter pooled sample from the trophogenic zone (as for the parameters above) filtered on a 45- μm net. On a few occasions with highly turbid waters, a smaller volume (5–8 liters) was screened. A fixed mean weight was assumed for each of the various rotifer species as well as for the calanoid and cyclopoid nauplii. For all cladocerans and advanced stages of copepods, total length was measured either for each individual or based on a representative subsample (whenever there were >20 individuals of a species in a sample). Dry weights (DWs) of rotifers and nauplii, and length to DW conversions, were derived from Bottrell et al. (1976). Carbon was assumed to constitute 46% of DW (Andersen and Hessen 1991).

Historically, several researchers have reported nonlinear relationships between phytoplankton cell carbon and cell volume, which have been described by a power function $y = ax^b$, with $b < 1$. A nonlinear relationship should imply that one ought to first make the volume to C conversion for every taxon or cell size, before adding individual contributions, to get total phytoplankton carbon. More recently, Montagnes et al. (1994) concluded from a comprehensive study that the exponent b is most likely not significantly different from unity. If we accept their conclusion, this means that we can estimate phytoplankton C by direct proportionality to total biovolume, using their average conversion factor of $0.109 \mu\text{g C} (\mu\text{g WW}^{-1})$. Montagnes et al. (1994) also found consistent cell shrinkage under Lugol fixation. If we apply their average shrinking factor of 1.33, the conversion factor from biovolumes measured on fixed cells to cell carbon becomes $0.145 \mu\text{g C} (\mu\text{g WW}^{-1})$.

It should thus be noted that when we judge the fraction of live phytoplankton cell of total seston POC, this is based on microscopic counts and does not include dead cells. However, in the statistical treatments we analyzed this data set

under the basic assumption that suspended particulate matter can be decomposed into one part that is associated to phytoplankton and one that is not. The former component should be interpreted in more general terms than just the content of live phytoplankton cells; it also includes autochthonous detritus of algal origin and possibly also heterotrophic food web components (consumers, decomposers). For most lakes this heterotrophic component would be a small fraction of the total seston pool, and it would also be small compared with the biomass of live phytoplankton. Formally, we can write this as:

$$y = y_0 + b\nu \quad (1)$$

where y is the concentration of particulate organic C:N:P (i.e., $\mu\text{g L}^{-1}$ POX, with $X = \text{C, N, or P}$, as $\mu\text{g L}^{-1}$) and ν is phytoplankton biovolume (wet weight, as $\mu\text{g L}^{-1}$). The intercept y_0 is the overall background concentration of POX ($\mu\text{g L}^{-1}$) (i.e., the POC components not derived from phytoplankton [primarily allochthonous C]), whereas the slope b is the amount of POX associated to a unit phytoplankton biovolume ($\mu\text{g } \mu\text{g}^{-1}$). Since non-phytoplankton-related seston obviously will vary among individual lakes, the utility of Eq. 1 depends on the variability in the autochthonous seston component being so much larger than the allochthonous component that the latter can, for practical purposes, be approximated by a constant (y_0). It is thus important to note that the model considers two types of seston and detritus, one that is mainly allochthonous and one that is mainly of autochthonous origin. The latter component will increase proportionally with increasing production of autotrophs in the system.

When we can assume constant variance in measurements of y , estimation of y_0 and b obviously becomes a standard, unweighted least-squares problem; i.e., finding y_0 and b which minimize

$$\sum_i [y_i - (y_0 + b\nu_i)]^2. \quad (2)$$

If, on the other hand, the variance scales with the mean value (which is commonly found in practically all types of biological data), the standard least-squares solution will put unreasonably large weight on the data pairs with the largest ν values, in which case a least-squares procedure with non-uniform weights is more appropriate. Thus, instead of estimating y_0 and b by minimizing Eq. 2, we chose to minimize

$$\sum_i [\log(y_i) - \log(y_0 + b\nu_i)]^2. \quad (3)$$

This least-squares functional will apply strictly to cases with a lognormal error distribution but will probably also serve as a good approximation for heteroscedastic error distributions in general (i.e., distributions in which variance scales with the mean). The main difference between Eqs. 2 and 3 is that the latter is a nonlinear least-squares problem, so that we get the minor inconvenience of not being able to solve explicitly for the minimum solution. Equation 3 was minimized using a constrained optimization procedure from the Matlab Optimization Toolbox (The MathWorks). Confidence limits for parameters and confidence bands for fitted curves were constructed by a bootstrapping procedure (Efron and Tibshirani 1998).

Notice the qualitative difference between the present model (Eqs. 1 and 3) and a log-transformed power function model such as

$$\log(y) = \log(y_0) + b \log(\nu) \quad (4)$$

Although superficially similar, the power function model nevertheless gives a linear least-squares problem because it is linear in the parameters. More importantly, the parameters of the power function model will be in different units and have a different interpretation from those of Eq. 1.

Results

The lakes included in this survey covered a wide range of productivity. Seasonal mean total P ranged from 4 to almost 800 $\mu\text{g P L}^{-1}$, but a majority (54%) of the lakes measured $<15 \mu\text{g P L}^{-1}$. Correspondingly, chlorophyll ranged from 1.1 to 87 $\mu\text{g L}^{-1}$, but a majority (49%) of the lakes measured $<5 \mu\text{g L}^{-1}$. Seasonal means of total POC (four samples) ranged from 206 to 7,160 $\mu\text{g C L}^{-1}$, with a grand mean of 960 $\mu\text{g C L}^{-1}$. Estimated phytoplankton C ranged 12 to 1,770 $\mu\text{g C L}^{-1}$, with a mean of 217 $\mu\text{g C L}^{-1}$. Sestonic C:P ratios ranged from 59 to 553 (at:at), with a mean of 207. All these distributions were strongly skewed, with means more than two times higher than the medians. For zooplankton mass and color, the distribution was less skewed, with means of 86.5 ($\mu\text{g dry weight L}^{-1}$) and 25.5 (mg Pt L^{-1}), respectively. Summary statistics for major parameters is provided in Table 1.

When plotting phytoplankton biovolume against particulate C, N, and P on a logarithmic scale (Fig. 1A), we see a curvilinear relationship resembling Eq. 1. This is also reflected in the linear model 1, showing substantially better goodness of fit ($R^2 = 0.76$) than the more common power model (Eq. 4, $R^2 = 0.65$), even if they have the same number of parameters. As a test on the contribution of allochthonous matter and zooplankton in the total seston, we also tried bivariate models of the form $y = y_0 + ax + b\nu$. Regression models with either color (a proxy of allochthonous humus) or zooplankton biomass as the additional covariate (x) did not give any higher R^2 than was obtained using phytoplankton biovolume (ν) alone as explanatory variable. Although the estimate for a was in no case significantly different from zero ($P > 0.05$), the negative slope ($a = -0.095$) obtained with zooplankton as covariate might indicate that the grazing effect on total seston is perhaps higher than the actual zooplankton contribution to total POC. The mean zooplankton dry weight was nearly 87 $\mu\text{g L}^{-1}$, or 40 $\mu\text{g C L}^{-1}$, which is, on the average, 4.2% of total sestonic POC. The lack of any significant effect when using color as covariate might either be an indication that water color is not a good proxy for allochthonous POC or simply that the investigated lakes, which were all quite clear, spanned a limited range of color (maximum 103 mg Pt L^{-1} , mean 26 mg Pt L^{-1}).

When phytoplankton biovolume is low, seston will be dominated by allochthonous detritus and heterotrophic food web members (i.e., $y \approx y_0$ when $y_0 \gg b\nu$), whereas seston will be directly proportional to phytoplankton when their biovolume is high (i.e., $y \approx b\nu$ when $y_0 \ll b\nu$). The ratios of the fitted regression intercepts (y_0) can be interpreted as

Table 1. Summary statistics for major parameters of the sampled lakes. Total P, total phosphorus; Total N, total nitrogen; POP, particulate organic phosphorus; PON, particulate organic nitrogen; POC, particulate organic carbon; Chl *a*, chlorophyll *a*; PBV, phytoplankton volume or wet weight; ZDW, zooplankton (metazoans) dry weight; Color, visual color against the platinum standard. All concentrations as $\mu\text{g L}^{-1}$.

	N	Mean	0% Minimum	25% 1st Quartile	50% Median	75% 3rd Quartile	100% Maximum
Total P	109	30.1	4.0	7.3	13.3	24.1	798.0
Total N	109	678	139	279	476	929	3,536
POC	109	957	206	380	535	939	7,158
PON	109	118.6	10.0	28.0	47.0	136.1	907.0
POP	109	17.4	2.0	4.1	7.5	15.8	276.0
Chl <i>a</i>	109	10.4	1.1	2.6	5.3	11.4	86.6
PBV	107	1,496	85	242	722	1,586	12,192
ZDW	107	86.5	6.5	41.7	64.9	97.7	555.6
Color	109	25.5	3.5	13.0	21.9	30.7	102.6

the C:N:P ratios of the allochthonous detritus component (possibly including heterotrophs feeding directly on this component). Correspondingly, ratios of the regression slopes (*b*) can be interpreted as the C:N:P ratios of the autochthonous, phytoplankton-associated component (table inserted in Fig. 1). N:P ratios of regression slopes and intercepts

were nearly equal (15.4 ± 2.5 and 16.0 ± 2.0) and were not significantly different from the Redfield N:P ratio (16). The estimated C:P ratio of allochthonously derived seston component was 2.7 times higher than that for the autochthonous, phytoplankton-derived seston component (123 ± 15), which again was not significantly different from the Redfield C:P

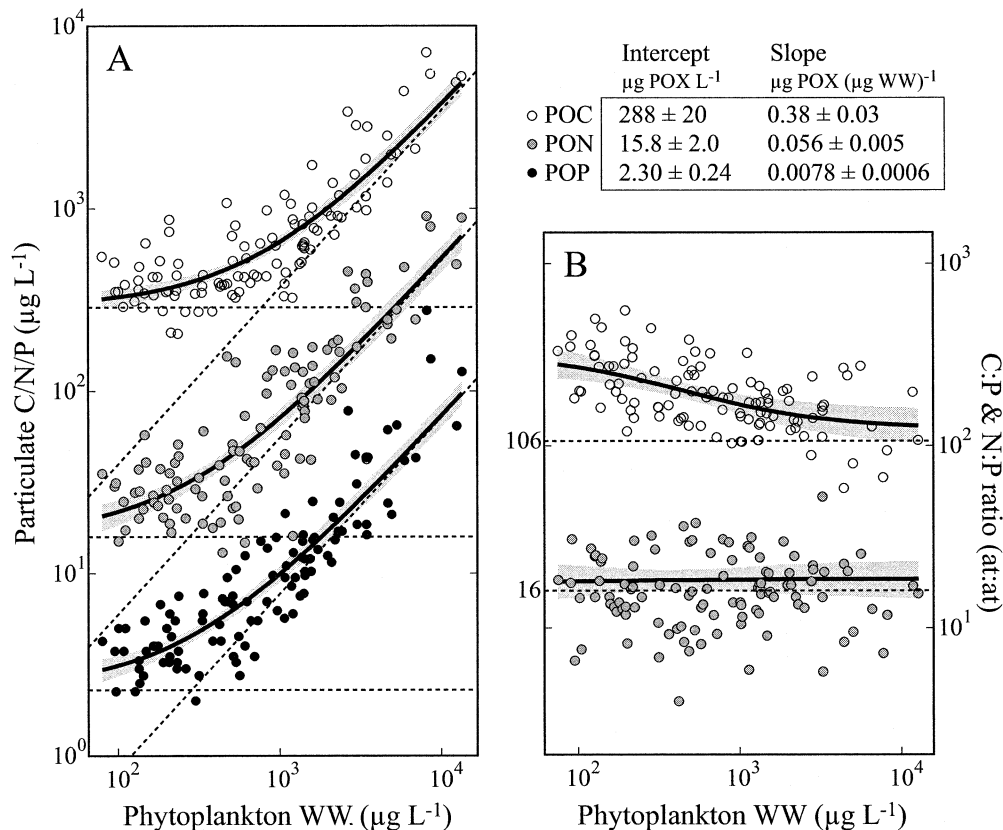


Fig. 1. A) Total particulate C (upper), N (middle), and P (lower) as related to phytoplankton biovolume (wet weight). Black lines: fitted regression models according to Eqs. 1 and 3. Gray areas: bootstrapped 95% confidence bands for the fitted curves. Dashed lines: asymptotes corresponding to model intercept (y_0) and slope (*b*). Fitted model parameters and bootstrapped standard deviations are inserted at upper right. See text for details on assumptions and regression analysis. B) C:P (upper) and C:N ratios (lower, both as atom:atom), as related to phytoplankton biovolume. Model curves and 95% confidence limits (black lines and gray shaded areas, as in panel A) are computed as pairwise ratios from the same bootstrap resamples as in panel A.

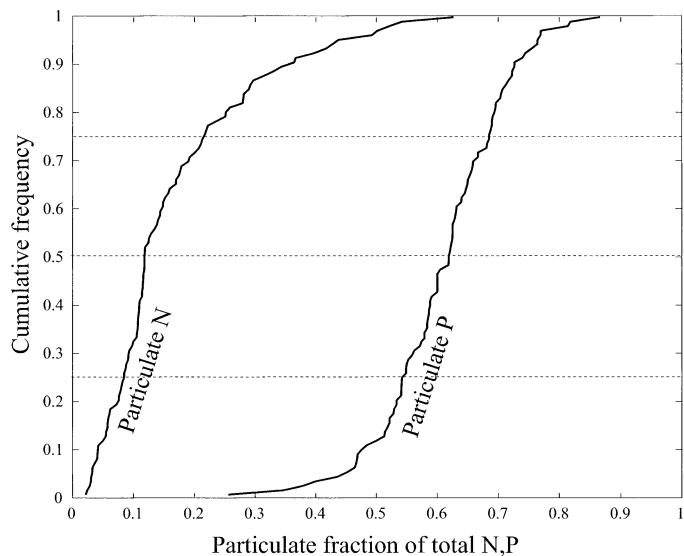


Fig. 2. Cumulative frequency plot of the fraction of particulate P of total P and that of particulate N of total N in the surveyed lakes.

ratio (106). This can also be illustrated by calculating the C:P and N:P ratios of individual, bootstrapped regression curves (Fig. 1B) to obtain the ensemble confidence band for the fitted model. The fitted model parameters imply decreasing C:P ratios with increasing phytoplankton biovolume (Fig. 1B), whereas N:P ratios appear uniform over the entire phytoplankton gradient.

On the average, slightly less than 60% of total P was in the particulate fraction (Fig. 2). Some of the nonparticulate fraction is probably material that passes through a glass fiber filter without being truly dissolved, such as small bacteria and constituents of broken cells. The share of particulate N to total N was no more than 12% (Fig. 2), strongly indicating the predominant P-limitation in these lakes. This also illustrates why ratios based on total N and total P may indeed be poor proxies for sestonic ratios.

The rather strong deviation in elemental ratios in various sestonic compartments will have strong bearings on any assessment of the potential for P-limitation in *Daphnia*. When considering total sestonic C:P ratios, a minority of lakes yield total C:P ratios below the Redfield ratio (Fig. 3), whereas, when considering phytoplankton alone, C:P ratios appear to be far closer to Redfield proportions. This point could also illustrate how different inferences of potential P-limitation in *Daphnia* may result, depending on the actual threshold value that is chosen. If applying a lower estimate for onset of P-limitation in *Daphnia* (C:P = 90; DeMott et al. 1998), most lakes should pose constraints on C-use efficiency for *Daphnia* as a result of P-limitation. On the contrary, only few lakes would have any risk of P-limitation if applying an upper bound for onset of P-limitation (C:P = 320; Urabe et al. 1997).

As mentioned above, we assume a linear relationship between cell volume (v) and cell carbon (x)—i.e., $x = cv$ with $c = 0.145 \mu\text{g C } (\mu\text{g WW})^{-1}$, according to Montagnes et al. (1994). If we substitute this relationship into Eq. 1 and re-

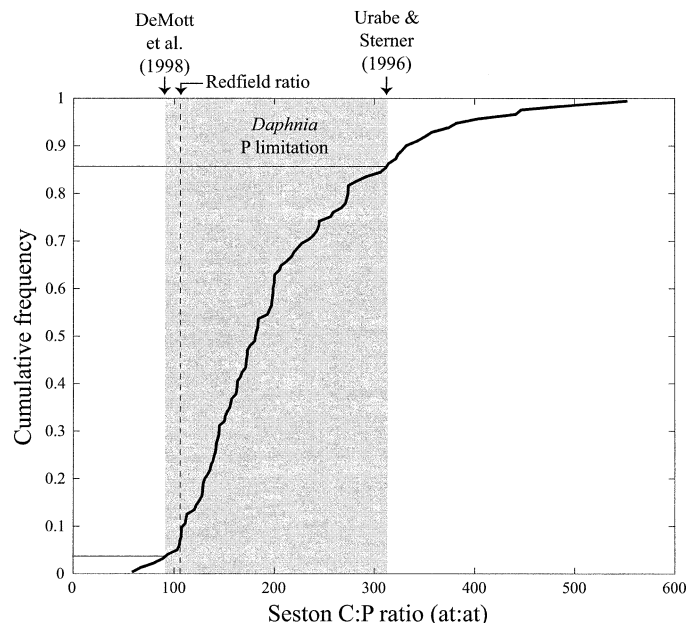


Fig. 3. Cumulative frequency of sestonic C:P (atom:atom) as related to potential thresholds for onset of P-limitation in *Daphnia* (shaded area).

express it in terms of the phytoplankton C fraction of total POC (x/y), we get that

$$\frac{x}{y} = \frac{c}{b} \left(1 - \frac{y_0}{y} \right). \quad (5)$$

Figure 4 shows the same bootstrap ensemble confidence band as in Fig. 1, but it is inverted and rescaled to match the observed phytoplankton fraction of POC as function of

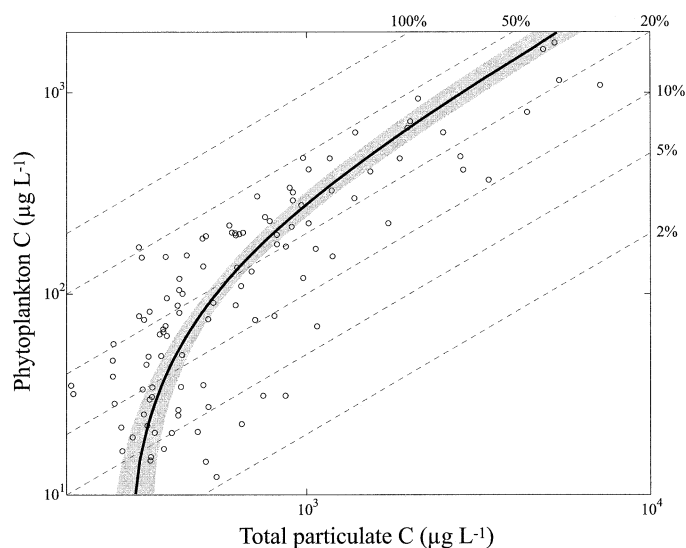


Fig. 4. Relationship between total particulate C and estimated phytoplankton C [calculated as $0.145 \mu\text{g C } (\mu\text{g WW})^{-1}$, see text for further explanation]. Dashed lines correspond to fixed percentages of 2% to 100% phytoplankton C of total seston C. Gray area depicts bootstrapped 95% confidence limits, as in Fig. 1.

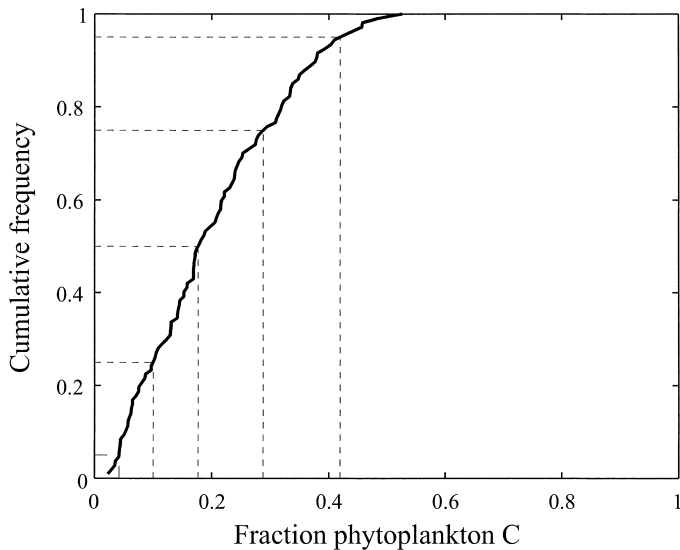


Fig. 5. Cumulative frequency of fraction of estimated phytoplankton C to total sestonic C.

total POC. Equation 4 has a singularity at $y = y_0$, so it will formally only be valid above this value (which means that it is more convenient to fit the parameters y_0 and b from Eq. 1 than from Eq. 4, even though they express the same relationship). More importantly, Eq. 4 implies that the asymptotic fraction phytoplankton C, approached when $y \gg y_0$, is given by $(c/b) = (0.145/0.373) = 39.3\%$. Even when total POC gets so large that the background level (y_0) becomes completely negligible, phytoplankton will constitute less than 40% of POC. Thus, it actually appears that total POC may be partitioned into three fractions, rather than two, as was originally assumed. Or, more precisely, this indicates that the phytoplankton-associated fraction may be split into a genuine phytoplankton biomass fraction and a non-phytoplankton material fraction (including detritus or higher trophic levels) that directly or indirectly originates from autochthonous primary production. This latter fraction may constitute $>50\%$ of POC in many lakes.

As shown by the cumulative frequency distribution (Fig. 5), virtually all lakes had a phytoplankton share of total seston of $<50\%$, and in fact more than half of them had $<20\%$. This has strong bearings on the assessment of food quantity limitation. Frequency distribution of particulate C based on total seston indicates food quantity (C) limitation to be of limited importance for *Daphnia*, as judged from the total seston data (Fig. 6). In fact, virtually no lakes had total seston C less than the assumed threshold for net positive growth in *Daphnia*. If considering estimated phytoplankton C only, however, *Daphnia* could face strong food limitation in a majority of lakes. This points to the important role of nonalgal seston as a food source for zooplankton.

The contribution of metazoan zooplankton itself to total seston is not trivial when judging food quantity (C) or food quality (C:P) based on total seston data. In some low-productivity lakes, zooplankton biomass did in fact exceed that of phytoplankton (although this could also involve underestimation of the picoplankton contribution to algal bio-

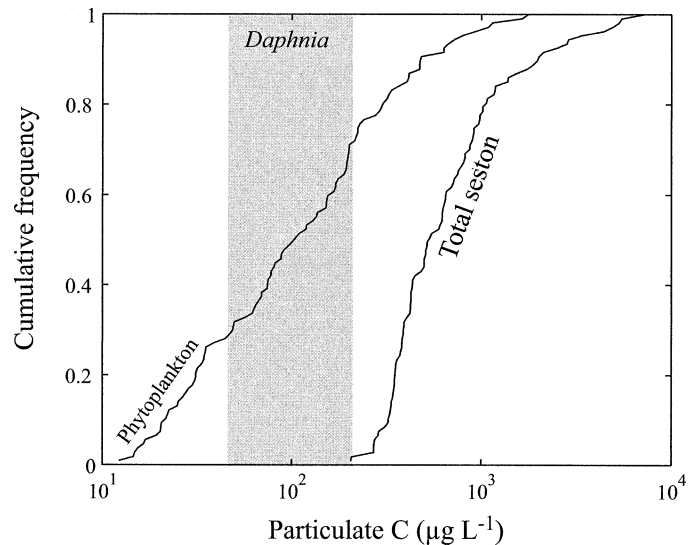


Fig. 6. Cumulative frequency of estimated phytoplankton C and seston C as related to predicted thresholds for net positive growth in *Daphnia* (shaded area).

mass). In general, zooplankton biomass was low compared with phytoplankton (Fig. 7), and it contributed, on the average, to less than 5% to total POC.

Discussion

There is no easy way to separate sestonic fractions, such as heterotrophic or autotrophic organisms and dead organic matter (detritus) of a mixed origin. The conventional way is to make some fractionated filtration and to assign major taxa or functional groups to specific size fractions. This may work satisfactorily in some localities, less so in others, and it does not account for the share of detritus that is distributed over all size categories. Changes in the seston pool are often rep-

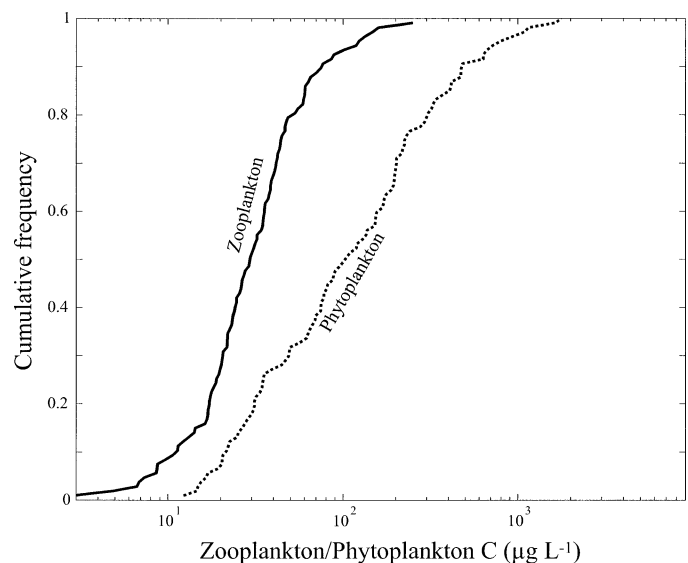


Fig. 7. Cumulative frequency of estimated phytoplankton C and zooplankton C.

resented to serve as a proxy for responses is the phytoplankton pool. Such assumptions critically hinge on the relative share of phytoplankton in the total seston pool. This share will show a strong interlake variability as well as seasonal shifts, but frequently phytoplankton make up a rather modest share of total seston.

A critical assumption is that manual estimates on phytoplankton volumes reflect true biomass. This may be particularly critical in oligotrophic systems with low biomasses and commonly small algal cells. The share of picophytoplankton in total phytoplankton biomass increases with decreased total algal mass. Based on a large compilation of freshwater data, picoplankton (defined as <3- μm size fraction) may exceed 20% at chlorophyll levels below 1 $\mu\text{g Chl } a \text{ L}^{-1}$ and 50% below 0.5 $\mu\text{g Chl } a \text{ L}^{-1}$ (Bell and Kalff 2001). Algal cells of <2 μm will not be properly accounted for by conventional Utermöhl technique and phase contrast microscopy. Although these smallest cells contribute comparatively less to the total volume than do larger cells, it must be expected that total phytoplankton biomass, and consequently, phytoplankton:seston ratios, are less reliable in the very oligotrophic end of the scale.

However, judging from the broad range of lakes included in our study, the rather modest share of algal cells in the seston pool appears to be a rather general phenomenon. When excluding samples with <10 $\mu\text{g Chl } a \text{ L}^{-1}$ (i.e., those in which the picoplankton biomass contribution may exceed 10%, according to Bell and Kalff [2001]), the average ratio of phytoplankton C to total sestonic POC will still be <35%. Jeppesen et al. (2000) revealed a strong gradient with an increase in suspended matter, with increasing lake P but with a decreasing share of detritus ranging from ~70% in the low-P lakes (<25 $\mu\text{g P L}^{-1}$) to 30% in the most eutrophic lakes. Conversely, the phytoplankton share of suspended matter rose from ~15% to somewhat 30% over the same gradient.

The major contribution of nonalgal C to the total pool of particulate C has several implications. When judging from phytoplankton biomass alone, food quantity limitation should be a common constraint to zooplankton growth. In fact, for nearly 40% of the lakes, estimated phytoplankton C fell below the estimated threshold for maintenance metabolism for *Daphnia* (~50 $\mu\text{g C L}^{-1}$) (Lampert 1977; Andersen 1997; Sterner 1997), and 90% of the lakes fell below an incipient limiting level of 400–500 $\mu\text{g C L}^{-1}$. This strongly contrasts with the interpretations based on total seston C, where apparently only a modest share of the lakes pose food quantity constraints for zooplankton (cf. Hessen and Faafeng 2000).

Our study supports the general conclusion from previous studies (Hecky et al. 1993; Elser and Hassett 1994; Brett et al. 2000) that freshwater seston normally exhibit C:P and C:N ratios higher than the Redfield ratio, and these ratio values are also higher than those measured in marine sites. This could indicate that the ratio between live phytoplankton cells and detritus is generally higher in lakes compared with marine systems, since detritus will be deprived of N and P relative to the biotic seston compartments. The decreased C:P ratio with increased phytoplankton mass is somewhat counterintuitive, since high phytoplankton biomass com-

monly is associated with low turnover rates and, thus, high C:P ratios. We believe this reflects a decreased relative share of allochthonous C when algal biomass is high. Since our data set includes few extremely eutrophic lakes, it could also be that seston C:P ratio actually increases again at even higher algal biomass levels.

A number of culture studies show typical C:P ratios in freshwater algae ranging from 80 under optimal conditions to >1,000 under strong P deficiency (Goldman et al. 1979; Rothhaupt 1995; Sterner et al. 1997; Hessen et al. 2002). This matches the reported range of sestonic ratios from lakes, yet the causality for this match is not evident when phytoplankton commonly make up less than 25% of seston mass, both in terms of C and P. Most likely a contribution from allochthonous organic matter, strongly deprived of N and P, may contribute to the high C:P ratio in some lakes.

Laboratory studies have indicated a C:P threshold of food of approximately 300, above which *Daphnia* faces direct P-limitation (i.e., where C-based growth efficiency will decrease [Sterner 1993; DeMott et al. 1998; Boersma 2000]). It is also convincingly demonstrated that a key determinant of C:P ratio in phytoplankton is the balance of light and nutrients (Urabe and Sterner 1996; Hessen et al. 2002), where high light and low P cause elevated C:P and vice versa. The same pattern is reflected in lakes, however (Sterner et al. 1997; Urabe et al. 2002), and the growth rate of *Daphnia* in these studies, yet facing a mixed sestonic diet, was closely correlated with sestonic C:P. The potential dependence of *Daphnia* growth rate and seston stoichiometry has been demonstrated in other studies as well (DeMott and Gulati 1999), yet the role of other food quality parameters, such as essential fatty acids, will add to this knowledge (cf. Brett et al. 2000; Boersma et al. 2001).

The reason for this strong effect of seston quality and quantity in spite of a modest contribution from live phytoplankton is not straightforward. It most likely reflects the strong link between a smaller but dynamic pool of living cells that fuel a larger and slower pool of detritus. Thus, even in lakes in which algal cells comprise a modest part of total seston, they may nevertheless be the source for most of the detritus, with their stoichiometric or biochemical footprints still being apparent. The overall contribution from bacteria, proto- and metazoans, and allochthonous matter may clearly be significant in some lakes, yet both this study as well as previous estimates (Hessen et al. 1992) indicate a modest contribution of metazoan C and P to the total seston pool, with an exception for ultraoligotrophic lakes. Also, the strong correlation between phytoplankton biomass and total particulate C in our data strongly supports the view of phytoplankton production as the major source of POC. The same holds for the observed close correlation between total P and total sestonic C. Thus, although seston in general may be a poor predictor of phytoplankton biomass and their elemental ratios, there seems to be a reversed causality (i.e., phytoplankton quantity and quality responses may have strong bearings on seston).

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