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Re-oligotrophication by phosphorus reduction and effects on seston quality in lakes

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Abstract

We review published data of re-oligotrophication studies in different types of lakes and discuss whether re-oligotrophication by phosphorus reduction measures can affect seston quality in lakes due to an increase in C:P ratios of food for zooplankton. We analyze whether such an increase in elemental ratio may give rise to a stoichiometric constraint or bottleneck for regulation of phytoplankton by zooplankton and thus cause a decrease in trophic transfer efficiency.

Because seston C:P ratios of seston tend to decrease with increasing P concentration in lakes, i.e. by increasing eutrophication, the reverse may be true, i.e. the C:P ratio of the seston will increase when lakes become re-oligotrophicated by P reduction. This may imply lower food quality for P-demanding seston grazers, like *Daphnia*, which have both relatively low C:P ratios and are quite homeostatic with regard to C:P ratios. Consequently, the reduced grazer biomass may lead to lower grazing pressure on the phytoplankton and may result in lower trophic transfer efficiency. On the other hand, oligotrophication commonly leads to improved food quality in terms of composition of the phytoplankton community, e.g. increase of mixotrophs and reduced share of cyanobacteria. These two qualitative traits of seston (higher C:P ratios and change in phytoplankton composition) may thus work in opposite directions during re-oligotrophication.

Most investigated lakes – both deep and shallow – responded by improvement in underwater light climate due to reduction of P loadings. Several compensatory mechanisms prevented the occurrence of a stoichiometric bottleneck for top-down control. From a few documented cases of both deep and shallow lakes, where seston stoichiometry, the presence of *Daphnia* and the trophic transfer efficiency were concurrently measured during the process of re-oligotrophication, we may conclude that the anticipated increase in C:P ratios of the seston is not straightforward. It depends on lake-specific properties such as morphometry, water residence time, water temperature and trophic structure. A stoichiometric bottleneck is only likely to occur during summer in (1) the epilimnion of small deep and stratified lakes with a long water residence time and low mixing regime, and (2) shallow lakes with high C:P ratios caused by a relatively high detritus content of seston and/or grazing resistant algae, like colony forming cyanobacteria.

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Keywords: Zooplankton; Review; Top-down control; Stoichiometric bottleneck; Cyanobacteria; Nutrient reduction

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Introduction

Many lakes in NW Europe have suffered from increasing eutrophication over the past few decades because of anthropogenic increases in external nutrient loading (e.g. Gulati and Van Donk 2002). Eutrophication has caused major changes in the composition and quantity of phytoplankton, zooplankton and fish communities, and such changes are also likely to affect the overall food web structure and ecosystem stability (e.g. Jeppesen et al. 2000). The most obvious changes observed are in the phytoplankton community, where a transition from small, edible algae to larger and less edible algal forms and filamentous or toxic cyanobacteria, or both, become more frequent due to eutrophication. These latter algae and cyanobacteria are a poor food for most zooplankton species (e.g. Lampert 1977), resulting in reduced transfer efficiency to higher trophic levels (McCauley and Kalff 1981; Jeppesen et al. 2000; Jeppesen et al. 2003). This unutilized primary production, which sinks and accumulates at the bottom as ungrazed organic matter, is a major problem arising from eutrophication; the breakdown of this matter eventually leads to hypolimnetic oxygen depletion and internal P release from sediments especially in deep stratified lakes.

In the past, efforts have been made in many countries to improve the ecological quality of lakes by taking measures to reduce external nutrient loading, especially phosphorus (Sas, 1989), sometimes in combination with nitrogen reduction or additional restoration measures such as lake biomanipulation, or both (e.g. Benndorf 1990, 2005; Kornijow et al. 1990; Hansson et al. 1998; Mehner et al. 2002) or physicochemical methods (Cooke et al. 2005). We define the process to revert a lake by nutrient reduction, i.e. towards its original status before anthropogenic disturbance, as re-oligotrophication. Thus, the lake will respond to reduced nutrient loading by becoming oligotrophic (or at least less eutrophic) again in the course of time depending on the stringency of the measures to reduce nutrient loading (Anderson et al. 2005).

Most efforts to alleviate the detrimental and undesirable effects of eutrophication on aquatic systems address the problem of P reduction in the inflows. This has been demonstrated elegantly for Lake Washington by Edmondson (1994). Despite many cases of success in the reduction of nutrient loads of lakes in recent years, the expected corresponding reduction of phytoplankton abundances has often been delayed by many years (Jeppesen et al. 2005, 2007). Sometimes, lakes have been reported to be resistant in their response to loading reductions (e.g. Sas 1989; Van Liere and Gulati 1992; Istvanovics et al. 2007). Such a resilience to response will generally reflect insufficient reduction of nutrient inputs (both point and non-point sources), or increase in

nutrient inputs from the lake's sediment (e.g. Søndergaard et al. 1999). Recycling of P from the sediments (internal loading) becomes more important if the P in inflows (external loading) is reduced. Also a biological "P-pump" from very high standing crop of fish, notably cyprinids, can help to maintain lakes in an eutrophic state despite external reductions in nutrient loadings (Brabrand et al. 1990). Such internal loading may keep lakes in a eutrophic state for many years after the reduction of external loading (Sas 1989). Significant and sustained changes in the biological community and water transparency of shallow, temperate, freshwater lakes may not appear unless TP in the lake's pelagic zone is reduced to a level below 0.1 mg P l^{-1} (Jeppesen et al. 2000) or, for deep lakes, below 0.03 mg P l^{-1} (Sas 1989).

An important process during the oligotrophication event is the establishment of efficient, pelagic grazers like *Daphnia* that can control the algal biomass and can efficiently channel autotrophic production and biomass into higher trophic levels. Reduced seston quality can impair this grazing process however, since especially *Daphnia* may suffer nutritional constraints by P-limitation in lakes (Elser et al. 1998; Hessen et al. 2006). Since sestonic C:P ratios across lakes generally correlate negatively with total P (Hessen, 2006; Sterner et al. 2008), one could anticipate a reduced seston quality in a stoichiometric sense following removal of P. Primary producers such as algae are flexible in their stoichiometry and can vary widely in C:N:P ratios. For example, it is well known that differences in the supply of P to phytoplankton result in widely differing internal P cell quota (Andersen 1997). The relationship between phosphorus and C:P ratios in algae have been studied in both batch cultures and (semi)continuous cultures (Droop, 1974, 1975). In batch cultures, an initial pulse of P generally causes reduced cellular C:P in phytoplankton due to initial "luxury" uptake and storage of P, but growth by dilution of internal P quota eventually yields increased biomass by accumulation of C and hence elevated C:P. An improved stoichiometric quality of phytoplankton in response to added P is thus a transient response in batch cultures. In continuous cultures, a stable yield both in terms of mass and elemental ratios will occur, yet both biomass and C:P will depend on P concentrations, light levels and dilution rate. By varying light and P in the culture medium, atomic C:P ratios in freshwater chlorophytes can range from 80 (high P, low light) to >2000 (low P, high light) (Hessen et al. 2002). Several of such studies clearly support the mutual role of light and nutrients as determinants of phytoplankton C:P ratios (Urabe and Sterner 1996). Support for these results also comes from large-scale experiments with plankton towers (Sterner et al. 1998) and lake enclosures with shading and P-additions (Urabe et al. 2002; Elser et al. 2002). Such

culture and mesocosm-scale studies help to elucidate physiological mechanisms under controlled conditions, often with phytoplankton monocultures.

Zooplankton, on the other hand, particularly crustacean zooplankters tend to be homeostatic in their C:P ratios (Andersen and Hessen, 1991; Sterner, 1993) and have relatively much lower and much less variable molar C:P ratios than their seston food. The potentially large elemental imbalances between producers and consumers, as reflected on comparing C:P ratios, have implications for both the growth of the consumer and for nutrient recycling in food webs (Sterner and Hessen 1994; Elser and Urabe 1999). Zooplankton feeding on food with C:P ratios higher than their demands will thus have low growth efficiencies for C, which will eventually lead to low consumer growth rates and biomass. Consequently, the reduced grazer biomass will lead to lower grazing pressure on the phytoplankton.

Lower cellular P contents of algae (i.e. higher seston C:P ratios) do not only mean that algae contain less phosphorus (and thus less of P-rich compounds such as RNA, DNA and phospholipids), but are also associated with decreases in other components important for zooplankton growth and reproduction, such as the content of long-chained polyunsaturated (omega-3) fatty acids (Brett and Müller-Navarra 1997; Gulati and DeMott 1997).

In addition, P-starved algae may increase their cell size and form a thicker cell wall, probably owing to arrested cell division and accumulation of intracellular glycogen compounds (Van Donk et al. 1997). This makes these algal cells less digestible so that the cells pass undigested through the daphnid gut and are evacuated largely intact. Similar results have been obtained for feeding efficiency of a flagellate that was shown to depend on size, morphology and motility of its bacterial prey, which in turn is determined by mineral nutrient characteristics or food quality (the C:N:P ratio) of these bacterial prey (Shannon et al. 2007). In other words, P-deficient algae will be assimilated less suggesting that digestion resistance can be a factor in the food quality of P-deficient resources (Ferraro et al. 2007).

Finally, increased water transparency may in itself promote increased C:P since elevated photon flux density may increase photosynthetic rate and cause a disproportionately greater accumulation of C than P. This “light: nutrient ratio” effect increases with decreased P, and has been repeatedly demonstrated both in laboratory experiments and lakes (Urabe and Sterner, 1996; Sterner et al. 1997; Hessen et al. 2003; Diehl et al. 2005).

The seston C:P ratio can thus be used as a descriptor of seston quality as food quality for zooplankton, and a higher seston C:P ratios because of re-oligotrophication leading to poor zooplankton growth may thus form a “stoichiometric bottleneck” or a constraint for top-

down control of pelagic food webs in lakes. Therefore, if the C:P ratio of seston exceeds the “threshold elemental ratio” (TER) of certain zooplankton species, especially *Daphnia* spp., seston quality will be the cause of poor growth of these cladocerans. Most growth rate experiments suggest a TER for *Daphnia* to range between 200 and 300 (Sterner and Hessen, 1994; Vrede et al. 2002) although other studies suggest the TER to be as low as 100 (DeMott et al. 1998; Frost et al. 2006). Digestion-resistant algae may obscure the predicted effects of stoichiometry on grazers (DeMott and Tessier, 2002). At C:P ratios above TER, the overhead costs of feeding will increasingly inhibit zooplankton productivity, up to a critical elemental ratio (CER) where no more individual growth is possible and all the assimilated energy is consumed to offset energy requirements of feeding plus basal metabolism. Such limitations will concomitantly weaken the trophic transfer efficiency as well as the strength of trophic cascades in lakes. Several theoretical studies indicate the potentially far-reaching impacts of stoichiometric relations in food webs (e.g. Loladze et al. 2000; Grover 2003). Although field data on these phenomena are scarce, there are indications that such a bottleneck may indeed occur in natural systems (e.g. Elser et al. 1998).

In this paper, we discuss whether re-oligotrophication by phosphorus reduction can cause reduced seston quality in lakes due to an increase in C:P ratios of food for zooplankton and if such an increase in elemental ratio can give rise to a “stoichiometric bottleneck” as well as concomitantly weaken the strength of trophic cascades in lakes.

Seston C:P ratios versus P load

There is ample evidence suggesting that decreased C:P in algae or seston with increased P, also suggest increased C:P with reduced P load. Both batch and flow-through cultures and enclosures experiments provide strong evidence for such effects.

However, before drawing conclusions on the relevance of these laboratory experiments for oligotrophication processes in lakes, it is also necessary to find out if the results from experiments can be extrapolated to the field.

Observations in lakes

Large datasets suggest that across lakes, there is a strong tendency for increased C:P with decreasing ambient P (Hessen, 2006; Sterner et al. 2008) (Fig. 1). Unlike many culture situations, such correlations may not simply be attributed to changed stoichiometry in phytoplankton, since lake seston may be of heterogeneous origin, of which phytoplankton may form a

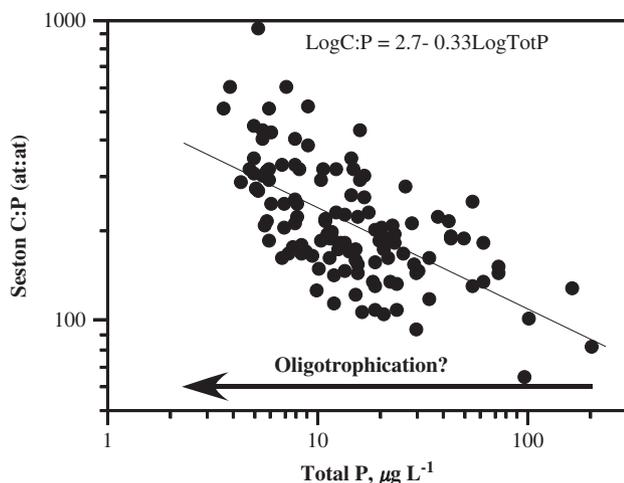


Fig. 1. Seasonal average of seston C:P over total P in 125 Norwegian lakes (modified from Hesse (2006)).

minor fraction. Lake seston (excluding zooplankton) often has C:P ratios that are both highly variable and highly dependent on the relative proportions of its main components: detritus and phytoplankton (Hesse et al. 2003). Several field studies have demonstrated that in oligotrophic lakes, C:P ratios of seston are commonly higher than TER (Hesse and Faafeng, 2000; Hecky et al. 1993; Elser et al. 2001). In many lakes, detritus is the dominant sestonic fraction (Gons et al. 1992; Hesse et al. 2003), and a high share of detritus is expected to increase the overall C:P ratio of the seston. In general, only a minor fraction of seston mass in lakes are composed of live phytoplankton cells, and estimated C:P ratio of seston was found to be 2.7 times higher than that for phytoplankton (Hesse et al. 2003). A higher rate of resuspension (i.e. shallow lakes) would generally increase the fraction of detritus in seston and hence increase the C:P ratio. Also, the phytoplankton community composition may have strong bearings for the share of detritus, since in systems dominated by inedible autotrophs, a greater share of algal biomass will decompose and be diverted through the detritus food chain.

Phytoplankton composition itself will also influence the seston C:P ratio in various ways (Quigg et al. 2003). Thus, seasonal dynamics of phytoplankton as well as the extent of detritus regeneration will affect the relative proportions of these two seston components and determine the seston C:P.

Seston C:P ratios in lakes can be influenced by many other biotic and abiotic factors (Hesse, 2006). Hecky et al. (1993) found that lakes with short residence time had lower C:P (average 330) than those that had longer residence time (C:P 416). Also, latitude affects the average C:P ratio, i.e. the ratios are higher for tropical and temperate lakes than for arctic and sub-arctic lakes. This latitudinal trend could reflect differences in

irradiation and temperature. More recent studies also suggest a decrease in seston C:P ratio at lower temperatures or at increasing latitude, or both (Elser et al. 2000; Woods et al. 2003). Temperature has been found to directly affect the elemental ratio of cells (e.g. Woods et al. 2003). More P in the cold-acclimated organisms may be due to a larger investment in ribosomes, which are the most P-rich organelles in cells (Sterner and Elser 2002). Thus, differences in biosynthetic capacities of the cells may affect seasonal stoichiometry of seston in lakes and contribute to low sestonic C:P ratios at low temperatures.

In spite of all these modifying aspects of lakes seston, irradiation and phosphorus levels can be reasonable predictors of seston C:P ratios. By calculating a ratio of light:P for a number of lakes by putting mixed-layer mean light in the numerator and total P concentration in the denominator, Sterner et al. (1997) were able to demonstrate that the light:P ratio was strongly correlated with the C:P ratio of seston. Mixing depth will strongly affect both biomass and elemental ratio of autotrophs, since there will be less light available at greater mixing depths (Huisman et al. 1999; Diehl et al. 2002; Diehl 2007; Berger et al. 2006). Data on mixing depth and light attenuation can be hard to achieve for a large number of lakes, but lake area may serve as a good proxy of mixing depth, and thus there is a causal link between elemental ratios and lake size (Sterner et al. 1997; Kunz and Diehl 2003).

Comparison across lakes may not necessarily serve as predictors on how individual lakes will react on reduced P loads. It should also be kept in mind that eutrophic lakes may have strong seasonal dynamics in seston biomass and seston stoichiometry. The stoichiometric response does also depend on phytoplankton community composition, zooplankton grazing and recycling and a suite of lake-specific properties that may be superimposed on the effects of seston C:P ratios. So, what can case studies on re-oligotrophication tell us about these issues?

Could re-oligotrophication cause a stoichiometric bottleneck?

Lake morphometry and renewal rate are critical not only for assessments on their vulnerability for P loads (Vollenweider and Kerekes 1980), but also for their recovery following reduced P loads. Many lakes showed an increase in transparency and decrease in chlorophyll levels in response to nutrient-loading reductions (Sas 1989; Jeppesen et al. 2005). An analysis of long time-series datasets from 35 European and North American lakes revealed that, despite a delay in recovery due to internal P loading, most of these lakes attained a new equilibrium with respect to total phosphorus after

<10–15 years (Jeppesen et al. 2005). This depended only marginally on water retention time and depth. Lakes with shorter retention time tended to recover faster despite their high TP concentrations when loadings were greatest. No clear effect of lake depth on recovery was detected. The latter corresponds well to earlier comparisons of lakes by Sas (1989) and Jeppesen et al. (1991).

One critical aspect of oligotrophication is top-down cascades in lakes mediated via reduced fish predation on large-bodied cladocerans, and thus increased grazing pressure on producers' biomass (Carpenter et al. 1996). The question is (1) if decreased P concentrations in restored lakes can cause a decline in seston nutrient status in general, and (2) if an increase in C:P ratio of seston, on which zooplankton feed, can lead to a "stoichiometric bottleneck" and thereby weaken the trophic cascades in lakes. Following the light:nutrient ratio hypothesis, one could also expect that increased water clarity and thus increased irradiance would cause decreased seston quality by increased C:P ratios.

Sturner et al. (1997, 1998) predicted an increasing decoupling of higher and lower trophic levels in lakes with seston C:P ratios >300. Elser and Hassett (1994) stated that C:P ratios exceeded even the most con-

servative thresholds in the majority of lakes they studied, and therefore P limitation of zooplankton growth may be ubiquitous in lakes. Some lake surveys (Hessen, 1992) have supported this theory, showing that the abundance of *Daphnia* is positively correlated with the concentration of particulate P in seston and negatively correlated with the seston C:P ratio (Hassett et al. 1997; Hessen, 2006).

Based on data from 276 lakes, Brett et al. (2000) observed that mean seston C:P ratios in 38% of the lakes exceeded a critical threshold of 300, above which C:P ratio, *Daphnia* production is often predicted to be limited by algal P content. Analysis of 91 observations revealed that critical threshold of C:P ratios for *Daphnia* ranged from 225 to 375.

Field tests of *Daphnia* P limitation, however, are few and often inconsistent with quantitative predictions of stoichiometric theory (Brett et al. 2000; DeMott and Tessier, 2002). DeMott and Gulati (1999) and DeMott et al. (2001a) reported that abundance of the smaller-bodied *Daphnia cucullata* in Loosdrecht lakes in the Netherlands is constrained by P limitation (Fig. 2). However, large-bodied *Daphnia* spp. appear to be excluded from these lakes due to poor edibility of food,

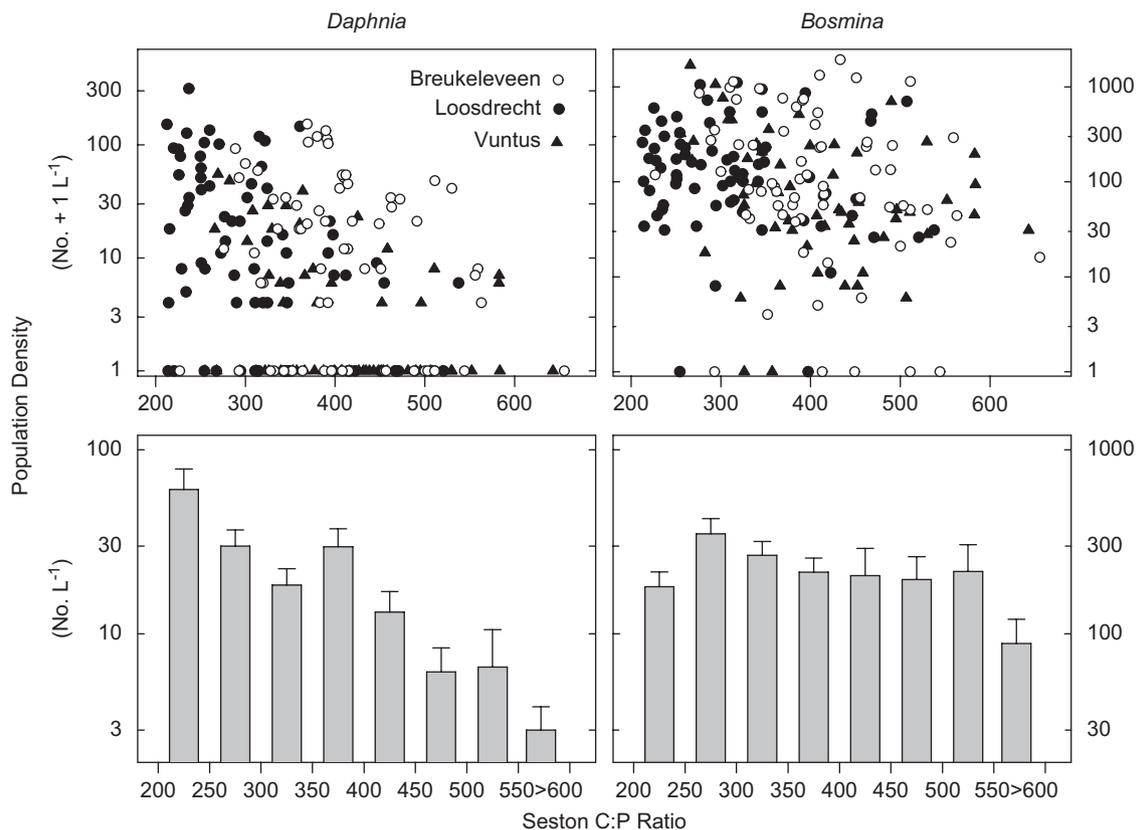


Fig. 2. Scatter plots of abundance of the zooplankters *Daphnia* and *Bosmina* and the seston C:P ratio in the same sample in each of the three Loosdrecht lakes: Breukeleveen, Loosdrecht and Vuntus (upper panels). Bars (lower panels) show mean abundance \pm 1 SE for intervals of 50 units in the seston C:P ratio. Bars are centered between the lower and upper limits of each 50-unit interval. Data from all three lakes are combined. Figure from DeMott and Gulati (1999, p. 1562, Fig. 4).

i.e. interfering filaments of cyanobacteria (DeMott et al. 2001a) rather than exclusively due to P limitation of the food. In such cases, both energy limitation (carbon) and food-quality limitation (phosphorus) may occur hand in hand, and may be thus inseparable.

In deep lakes, DeMott and Tessier (2002) found that resource C:P ratios were well above the threshold values for *Daphnia* P limitation, but intense grazing led to reduced resource digestibility and strong energy limitation. In shallow lakes, however, energy availability was relatively high, because of stronger predation of daphnids by fish and therefore their weaker grazing on seston, but here the resource C:P ratio remained near or below the threshold for P limitation in *Daphnia*. *Daphnia* growth rate assays with resources from shallow lakes gave growth rates that were twice as high as those for deep lakes. However, daphnids were dominant grazers in both lake types, particularly in the deep lakes that showed resource C:P ratios well above the threshold for *Daphnia* P limitation.

The above studies may raise questions as to when and where *Daphnia* will experience growth limitation after re-oligotrophication.

The variability in the seston C:P ratio after re-oligotrophication may depend on whether a lake behaves more like a continuous culture than a batch culture. In continuous cultures, ambient P always gives relatively low C:P due to a steady flux of P. In batch cultures, however, an initial pulse of P leads to low C:P due to initial storage of P, but growth by dilution of internal P stock eventually end with high C:P. Although most lakes will certainly tend to lie between these extremes, they may nevertheless be useful models. With regard to their P dynamics, deep lakes behave more like a batch culture. In temperate lakes, Hecky et al. (1993) observed the highest C:P ratios (>400) during summer in the epilimnion of small deep and stratified, oligotrophic lakes with a long residence time (>6 months). These small lakes are less frequently mixed than larger deep lakes, and phytoplankton may experience, therefore, high light conditions in the epilimnion. Also DeMott and Tessier (2002) and Brett et al. (2000) made similar observations.

Shallow lakes with their continuous P loading from the sediment may behave more like continuous cultures, especially after external P load reduction, so that the C:P ratios continue to be low. Examples of such lakes are some shallow Dutch and Danish lakes and the large shallow lake Balaton in Hungary (Jeppesen et al. 2007; Istvanovics et al. 2007). However, C:P values in eutrophic shallow lakes may be also high. Hecky et al. (1993) found that shallow tropical lakes, that do not stratify seasonally, have among the highest C:P ratios. This is related to the constant warm temperatures and constant illumination. Furthermore, high seston C:P ratios are also observed in some temperate eutrophic

shallow lakes where grazing resistant cyanobacteria and detritus form the major part of the seston (Gulati et al. 1991; DeMott et al. 2001b; Hessen et al. 2005).

Thus, the change in sestonic C:P ratios as consequence of reduced P-loads are not straightforward, and will depend on a number of lake-specific properties. A stoichiometric bottleneck for top-down control and a low trophic transfer efficiency are likely to occur during re-oligotrophication in the epilimnion of deep stratified lakes with a long water residence time and low mixing and in shallow lakes with high C:P ratios caused by higher detritus content of seston and/or grazing resistant algae. To investigate this hypothesis, we have summarized data on re-oligotrophicated lakes (see Table 1) and give more specific examples in the following paragraphs. There are, however, just a few documented lakes (Table 1) where during P reduction, the seston stoichiometry, the presence of *Daphnia* and the trophic transfer efficiency were concurrently measured. We also address the relative effects of decreased seston quality by elevated C:P ratios and improved seston quality by changes in community composition among the autotrophs.

Case studies

In the synthesis by Jeppesen et al. (2005) of 35 long-term lake re-oligotrophication studies, covering lakes ranging from shallow to deep, oligotrophic to hypertrophic before nutrient load reduction, subtropical to temperate, and lowland to upland, phytoplankton clearly responded to reduced nutrient loading, as mainly reflected in declining TP concentrations. Declines in phytoplankton biomass were, however, accompanied by shifts in community structure. In deep lakes, chrysophytes and dinophytes displayed greater importance at the expense of cyanobacteria. In shallow lakes, diatoms, cryptophytes and chrysophytes became more dominant, but cyanobacteria did not change significantly.

The observed declines in phytoplankton biomass and Chl *a* may have been further augmented by enhanced zooplankton grazing, as indicated by increases in the zooplankton: phytoplankton biomass ratio and declines in the Chl *a*:TP ratio. This effect was strongest in shallow lakes. This implies potentially higher rates of zooplankton grazing, which may be ascribed to the observed large changes in fish community structure and biomass with decreasing TP contribution. In 82% of the lakes for which data on fish are available, fish biomass declined with TP. The percentage of piscivores increased in 80% of those lakes and often a shift occurred towards dominance by fish species characteristic of less eutrophic waters.

Lake Constance, included in the synthesis by Jeppesen et al. (2005), is one of the few documented cases of deep

Table 1. Parameters of re-oligotrophicated lakes (+, increase; –, decrease; =, no change)

Lake	Average depth (m)	Maximum depth (m)	Surface area (km ²)	Average residence time (years)	Maximum annual TP (μg l ⁻¹)	Minimum annual TP (μg l ⁻¹)	Summer transparency	Initial seston C:P (eutrophic period)	Peak epilimnetic seston C:P (summer)	<i>Daphnia</i> biomass	Fish biomass	Summer stratification	Reference
Constance				98				98					Gächter and Bloesch (1985)
Constance	101	472	4.4	4.4	87	13	+					Yes	Jeppesen et al. (2005)
Constance	252	476			80	24		500					Hochstädter (2000); Gaedke et al. (2002)
Geneva (Leman)	153	309	12	12	43	17	-			+	=	Yes	Jeppesen et al. (2005)
Geneva (Leman)	152.1	309	11.4	11.4	90*	38*							Gerdeaux et al. (2006)
Gjersjøen	23	64	2.9	2.9	20	15				=		Yes	Lyche et al. (1990)
Loosdrecht	1.85	9.79	0.6	0.6	120	100	=					No	Van Liere et al. (1990)
Loosdrecht								247	488				DeMott and Gulati (1999)
Breukeleveen	1.45	1.79	0.4	0.4	200	110	+					No	Van Liere et al. (1990)
Breukeleveen								351	497	=	=	No	DeMott and Gulati (1999)
Vuntus	1.45	0.88	0.6	0.6	120	70	=						Van Liere et al. (1990)
Vuntus								333	500	=			DeMott and Gulati (1999)
Lucerne					117		+	100	320				Gächter and Bloesch (1985)
Lucerne	104	214	1	1	30*	2.2*						Yes	Gerdeaux et al. (2006)
Neuchâtel	64.2	152	8.2	8.2	60*	18*							Gerdeaux et al. (2006)
Superior	148.7	403	180.4	180.4	4.65			309				Yes	Gerdeaux et al. (2006)
Superior Walen	103	145	1.5	1.5	28*	2*	+	362					Guildford et al. (1994)
Walen								100	450			Yes	Hecky et al. (1993)
Washington		87.6							350				Gerdeaux et al. (2006)
Washington	32.9	65.2	2.38	2.38	61	14	+			+		Yes	Gächter and Bloesch (1985)
Zurich					80		+	100	400			Yes	Scheurell et al. (2002)
Zurich	51.7	136	1.4	1.4	117*	24*							Jeppesen et al. (2005)
Zurich													Gächter and Bloesch (1985)
Zurich													Gerdeaux et al. (2006)

*Soluble reactive phosphorus (SRP).

lakes, where during re-oligotrophication by P reduction, the seston stoichiometry has been documented (Hochstädter 2000; see Table 1). The sestonic C:P ratio increased significantly during two decades of re-oligotrophication, reflecting an enhanced phosphorus limitation of the plankton community in summer. The C:P ratio of phytoplankton showed the most pronounced seasonality with an increase from about 200 in spring to maximum values around 650 in summer. At the decline of the algal spring bloom, C:P ratios of 500 (0–8 m) and 470 (8–20 m) were found, which remained unchanged during the clear-water phase. Thereafter, C:P ratios extended further and reached average values of 690 (0–8 m) and 610 (8–20 m) from July to October. In December, phytoplankton C:P ratios dropped to 340 (0–8 m) and 280 (8–20 m). Similar trends are visible in the overall C:P ratios of the seston (Fig. 3).

Over a period of several years, the proportion of daphnids (*Daphnia hyalina* and *Daphnia galeata*, C:P 200) in zooplankton gradually went down from 80% to 60%, whereas the calanoid copepod *Eudiaptomus* sp. (C:P 400), gradually increased from 20% to 30% (Gaedke et al. 2002). Fig. 3 furthermore shows that the epilimnetic seston continuously has C:P ratios that exceed the $TER_{C:P}$ for *D. galeata*, whereas they exceed the $TER_{C:P}$ for *Eudiaptomus* only during summer and autumn.

Furthermore, during re-oligotrophication, a gradual shift was observed in phytoplankton composition of this lake. The relative importance of mixotrophic phytoplankton taxa has increased since the late 1980s, and the

mass development of dinoflagellates can be explained by their capability to migrate between the euphotic zone and deeper P-enriched water layers under suitable hydrological conditions (Gaedke 1998). Production of predominantly herbivorous plankton in Lake Constance was constrained by both P and C availability during summer and autumn. Models suggest during oligotrophication an increase in the proportion of P-rich protozoa in the zooplankton diet. These protozoa improved the food quality of algae and bacteria for the larger consumers not only by repackaging the algae and bacteria into larger food particles (Gaedke et al. 1996) but also by providing a more suitable chemical composition.

Similar trends have been observed during re-oligotrophication in other deep peri-alpine lakes, e.g. Lake Lucerne, Lake Walen and Lake Zürich (Table 1). In all these lakes, the phytoplankton species benefiting from oligotrophication included mixotrophic species and/or species indicative of oligo-mesotrophic conditions (Dokulil and Teubner 2005; Anneville et al. 2005). During re-oligotrophication of 11 peri-alpine lakes in Switzerland and France lakes (including Lake Constance), the fish communities that were dominated by cyprinids and perch in the eutrophic state, decreased in their total yield or remained nearly the same, while coregonids became dominant. Notably, when the TP was below $5 \mu\text{g l}^{-1}$, the total yield decreased rapidly, and fish production was low (Gerdeaux et al. 2006). Consequently, due to changes in the fish community, predation on zooplankton decreased, causing an increase

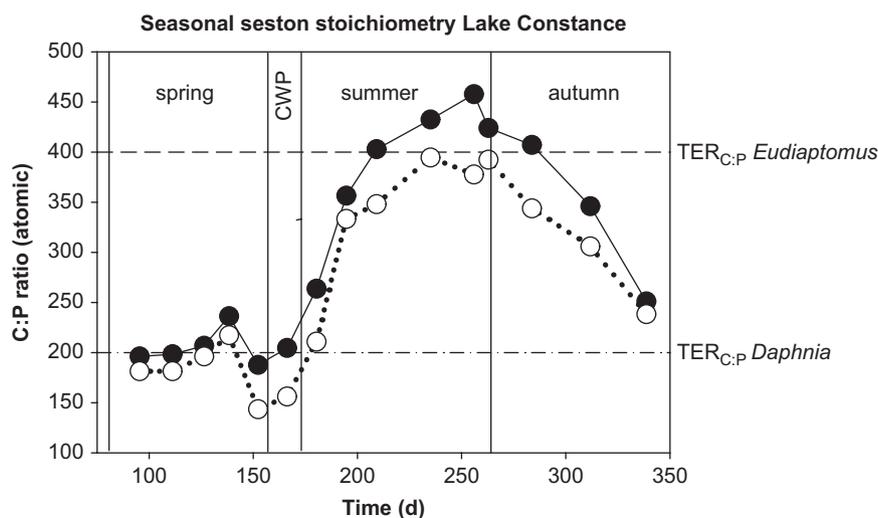


Fig. 3. Seasonal course of sestonic (molar) C:P ratios in Lake Constance in 1995, after Hochstädter (2000, p. 458, Fig. 4). Seston was sampled at 0–8 m (solid symbols, solid line) and 8–20 m (open symbols, dotted line). Vertical lines denote the transitions between the different seasons, and when the spring clear water phase (CWP) occurs. Dominant crustacean zooplankton species in Lake Constance are calanoid copepods of the genus *Eudiaptomus*, and the cladoceran *Daphnia galeata*. To indicate the transition between energy (C) and nutrient (P) limitation of these species, we have given the calculated threshold elemental ratios for carbon and phosphorus ($TER_{C:P}$: Frost et al. 2006). $TER_{C:P}$ have been given as horizontal lines for *Daphnia galeata* ($TER_{C:P}$ 200; dash-dotted line) and *Eudiaptomus gracilis* ($TER_{C:P}$ 400; dashed line) (Anderson and Hessen, 2005).

in zooplankton grazing on phytoplankton. Such top-down cascades will usually lead to an improvement in seston quality due to increased recycling of P that eventually reduces the seston C:P ratio. Clear stoichiometric bottlenecks may occur during re-oligotrophication of lakes that are already quite oligotrophic. Here, both phytoplankton quantity and quality may sometimes be insufficient to support zooplankton (Rellstab et al. 2007), which may also be a threat to higher trophic levels (Müller et al. 2007).

There are just a few documented cases of shallow eutrophic lakes where during P reduction, the seston stoichiometry, the presence of *Daphnia* and the trophic transfer efficiency were concurrently measured. The shallow Loosdrecht lakes in the Netherlands (Lake Loosdrecht, Lake Breukeleveen and Lake Vuntus) are among the best investigated lakes as far as the effects of reduction of external P loads are concerned (Gulati and Van Donk, 2002) (Table 1, Fig. 2). Cyanobacteria, other prokaryotes and detritus dominated the lake seston before restoration. Although after external P load reduction the C:P ratios of seston increased (Gulati et al. 1991, 1992), because of a decrease in particulate P, no change was observed in either phytoplankton or chlorophyll *a* levels, or underwater light climate. Cyanobacteria and detritus continued to dominate in these lakes. This is because cyanobacteria can withstand great variation in their P content and thus in their C:P ratios – for a unit weight of P, the cyanobacteria can yield relatively much more biomass and cause greater turbidity than, for example, green algae. The seston C:P ratios and *Daphnia* numbers were negatively correlated on the basis of 9-year data, not including those relating to Lake Breukeleveen. In the Loosdrecht and Vuntus lakes, the annual mean abundance of *D. cucullata* ranged from 104 to 0.7 ind l⁻¹ and mean seston C:P ratios varied from 250 to 500. In Lake Breukeleveen, the daphnid densities were relatively higher for a given seston C:P ratio, especially in the 2 years after the lake was subjected to biomanipulation (Van Donk et al. 1990).

The growth and abundance of native *D. cucullata* is reduced by P deficiency (DeMott et al. 2001a) in addition to its predation by bream, the dominant planktivore (Lammens et al. 1992), whereas larger *Daphnia* appear to be excluded by interfering filaments of cyanobacteria (DeMott et al. 2001a). That the high seston C:P ratios in the lakes constrained *Daphnia* abundance was confirmed later in laboratory studies using *in situ* lake seston (DeMott and Gulati, 1999; DeMott et al. 2001b). In contrast, the P requirements of *Bosmina* spp. and cyclopoid copepods appeared to be lower and there was no relationship with seston C:P ratios, which probably explained the relatively higher abundance in these lakes of these zooplankters (Fig. 2).

Pronounced seasonal shifts in seston C:P ratios in the Loosdrecht lakes are caused by a “growth by dilution”

in cyanobacteria that accumulate P in winter or in early spring when ambient concentration of P in lake water is high, thus exploiting these internal stores for C fixation and growth during late spring and summer when ambient P level is low (Hessen et al. 2005).

The example of the Loosdrecht lakes shows that bottom-up effect of high seston C:P ratios (lower algal quality and high detritus) may determine the structure in the rest of the food web of shallow lakes, even if fish predation pressure on zooplankton was reduced or was low.

Discussion

The negative correlation between P concentration and C:P across lakes does not necessarily imply that P reduction within a given lake causes increased sestonic C:P. Even in the case of increased C:P, this only becomes relevant if C:P exceeds the TER for P-limited growth of consumers. Many deep and shallow lakes have responded positively to reductions in phosphorus loading without exhibiting any symptoms of a stoichiometric constraint or bottleneck for top-down control and a decrease in trophic transfer efficiency (Jeppesen et al. 2005). Especially in shallow lakes, both fish community structure and biomass responded surprisingly fast to reduction in phosphorus loading (Jeppesen et al. 2005). The relative proportion of piscivores increased and the planktivorous fish biomass declined markedly, which may explain an increase in the body size of cladocerans and an increase in zooplankton to phytoplankton biomass ratio seen in many of these re-oligotrophicated lakes. This was particularly true in the shallow lakes where the risk of fish predation is relatively much higher. Consequently, the lower predation pressure on zooplankton by fish may compensate for the possible lower food (seston) quality in these lakes. Increased biomass of zooplankton, due to reduced fish stock, also in itself will improve seston quality by increase in recycling of phosphorus that reduces the seston C:P ratio.

In deep and shallow lakes, several other compensatory mechanisms might act as a buffer. Especially in deep oligotrophic lakes, when stratified, daphnids may survive by compensatory mechanisms. DeMott and Tessier (2002) found that *Daphnia* was the dominant grazer even in the deep lakes that had C:P seston ratios well above the threshold for *Daphnia* P limitation. This may be because, even in summer when seston C:P ratios in epilimnion are high, zooplankton that are mostly migratory, have access to seston with lower C:P ratios below the epilimnion. The daphnids can thus offset P shortages in surface seston phosphorus content by consuming a mixture of seston of varying phosphorus content from different depths in the lake during their

diel migration (e.g. Park et al. 2004; Schatz and McCauley, 2007).

Furthermore, a higher P concentration in the hypolimnion may favor the growth of motile mixotrophs in deep lakes: these mixotrophs may assimilate P in the hypolimnion and transport it to the epilimnion (e.g. Anneville et al. 2005; Katechakis et al. 2005; Kamjunke et al. 2007). The ability to use alternative production pathways indicates that the stoichiometric composition of mixotrophs might be less affected by alterations in nutrient supply than the stoichiometry of phototrophic specialists, which are confined to the epilimnion due to the availability of light. Also, potentially limiting nutrients, particularly P, are often an order of magnitude or even more concentrated in the biomass of food organisms of mixotrophs (bacteria and bacterial-sized particulate matter) than in the dissolved phase (e.g. Vadstein 2000). The C:P ratios of bacteria are relatively much lower (e.g. Makino et al. 2003). Heterotrophic nutrition might therefore entail low C:P ratios in mixotrophs, making them a nutrient-rich food source for herbivores. These results strongly imply that mixotrophs should be considered in the further development of ecological theories that incorporate stoichiometric effects on food web dynamics.

In the synthesis by Jeppesen et al. (2005) of re-oligotrophication studies in 35 lakes, declines in phytoplankton biomass were accompanied by shifts in community structure. In deep lakes, chrysophytes and dinophytes displayed greater importance at the expense of cyanobacteria. In shallow lakes, diatoms, cryptophytes and chrysophytes became more dominant, but cyanobacteria did not change significantly. The majority of the observations on growth of *Daphnia*-fed P-limited algae, however, were obtained from laboratory experiments using the chlorophyte *Scenedesmus* sp. This alga has been used in zooplankton production studies because it is easy to culture and has a moderately high food quality for daphnids (Brett et al. 2000). However, there is no *a priori* reason to assume that this alga, which is relatively rare in lakes (in terms of percent community biomass), is a general representative of all other algae that serve as zooplankton food in natural lakes. Different algal taxa have different C:P ratios and notably Chlorophyceae are characterized by higher variability in their C:P ratios than other classes (e.g. Andersen, 1997; Quigg et al. 2003).

Daphnids are key players for conversion of autotrophic production to higher trophic levels in lakes, and have proven important for successful biomanipulations in lakes. Hence, they deserve special attention as potential candidates for being confronted with stoichiometric constraints. Copepods may feed selectively on food particles with more suitable elemental contents to achieve a more balanced diet than is suggested by the bulk seston ratios; such a compensatory mechanism will

increase trophic transfer efficiency (Butler et al. 1989). Furthermore, copepod C:P ratios are generally higher than those of cladocera (e.g. Andersen and Hessen 1991), making them less prone to stoichiometric bottlenecks than daphnids. In many laboratory experiments, however, *Daphnia magna* or *Daphnia pulex* have been used as a model herbivore. These larger-bodied *Daphnia* species are very likely to be limited by the mineral P content of their diets, due to their relatively high P content and their strong homeostasis (Sterner and Hessen 1994). These species, however, rarely dominate in field situations as their body size makes them highly vulnerable to size-selective predation by zooplanktivorous fish. There are comparatively few studies that have examined the C:P hypothesis for other species. Yet, there are studies suggesting that other taxa also could be susceptible to elemental limitation by juvenile stages that have higher body P levels (Villar-Argaiz and Sterner 2002; Jones and Flynn 2005), while other species are more likely to suffer N limitation (e.g. the rotifer *Brachionus*, cf. Rothhaupt 1995; Jensen and Verschoor 2004). For extrapolating stoichiometric growth limitation found in the laboratory for *Daphnia* to other freshwater zooplankton or even to the trophic cascade in lakes, more research on zooplankton taxa other than *Daphnia* is needed.

Conclusions

Generalizations are difficult to make because there are only a few documented lakes where during P reduction, the seston stoichiometry, the presence of *Daphnia* and the trophic transfer efficiency were concurrently measured. Most investigated lakes – both deep and shallow – responded by improvement in underwater light climate due to reduction of P loadings. Several compensatory mechanisms prevented the occurrence of a stoichiometric bottleneck for top-down control. From the few well-documented cases of both deep and shallow lakes, we may conclude that the anticipated increase in C:P ratios of the seston is not straightforward. It depends on lake-specific properties like morphometry, water residence time, water temperature and trophic structure. We conclude that a stoichiometric bottleneck is only likely to occur during summer in (1) the epilimnion of small deep and stratified lakes with a long water residence time and low mixing regime; and (2) shallow lakes with high C:P ratios caused by higher detritus content of seston and grazing resistant algae, like colony forming cyanobacteria.

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