



Impact of epilimnetic phosphorus supply and food web structure on phosphorus binding forms in settling material and sediments in a thermally stratified lake



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ABSTRACT

Knowledge about the contribution of food web structure and nutrient concentration in lakes to phosphorus (P) sedimentation and remobilisation at the sediment surface is still poor. Using four large enclosures placed in a eutrophic, thermally stratifying lake, we studied the effects of the structure of the planktonic food web (with and without planktivorous fish, $\pm F$ treatments) and nutrient concentration (with and without fertilisation, $\pm N$ treatments) on P sedimentation. We investigated the total P content and P binding forms in settling material (TP_{SM}) and of the uppermost 1 cm sediment layer (TP_{Sed}) during three consecutive stratification periods (2005–2007). Additionally, epilimnetic P (SRP_{Epi} , TP_{Epi}), chlorophyll *a* and biomass of total crustacean and *Daphnia* were measured. On a seasonal scale, *Daphnia* biomass tended to negatively influence chlorophyll *a*, sedimentation rate of total particulate matter and of P, but the latter two criteria did not differ significantly between treatments due to large fluctuations within each enclosure. The contents of TP_{SM} and loosely adsorbed P in settling material decreased in the following order: $-F/+N > +F/+N > -F/-N > +F/-N$, indicating greater effects of nutrient addition than of food web structure. In sediments, organically bound P was 9–23% higher in $-F$ variants compared to the corresponding $+F$ treatments, thus indicating an effect of food web structure. Furthermore, positive correlations between SRP_{Epi} , TP_{Epi} , TP_{SM} , TP_{Sed} , sediment reductant-soluble P and calcite bound P revealed an effect of the epilimnetic P concentration on P sedimentation and specific P binding forms. Compared to the composition of different P binding forms in the settling material, a considerable decrease of loosely adsorbed P (12–26%) and reductant-soluble P (14–21%), as well as an increase of organic P (14–26%) were observed in the uppermost 1 cm-layer of the sediments in all treatments. We conclude that both nutrient enrichment ($+N$) and food web structure ($-F$) enhance the P sedimentation and P content at the sediment surface. However, in addition to food web effects on organic P content in settling matter and sediments, factors like iron concentration and calcite precipitation might be of importance for P sedimentation and storage in sediments in complex systems such as lakes.

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Introduction

The control of the pelagic food web structure to support the development of large herbivorous zooplankton has been implemented to improve lake water quality for decades. The causes of successes and failures of this method in shallow and deep lakes have been discussed in numerous papers (e.g. Edmondson and Abella, 1988; Benndorf et al., 2002; Lathrop et al., 2002; Kasprzak et al., 2003, 2007; Hunt and Matveev, 2005; Søndergaard et al., 2007). It has been shown that in lakes both food web manipulation

and trophic state have direct and indirect effects on the sedimentation of nutrients, especially phosphorus (P) (e.g. Bloesch and Bürgi, 1989; Sarnelle, 1999; Houser et al., 2000; Pitsch et al., 2012). With respect to food web manipulation, considerable losses of P from the epilimnion may occur due to P incorporation into biomass (Lyche et al., 1996; Mazumder et al., 1990b; Pitsch et al., 2012), and further sedimentation of exuviae and dead individuals (Reinertsen et al., 1990) when the biomass of crustaceans, predominantly of daphnids, is high. With respect to P body incorporation, the specific P content is considerably higher in *Daphnia* species than in other crustaceans (Vrede et al., 1999) and phytoplankton (Behrendt, 1990). Thus sequestration in *Daphnia* biomass may lead to substantial reduction of P concentration in the water column. Additionally, further studies indicated that large, vertically migrating daphnids

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contribute to P export from the trophogenic zone by consuming P accumulated in the phytoplankton and subsequently excreting faecal particles, which sediment quickly (Bloesch and Bürgi, 1989; Dini et al., 1987; Pitsch et al., 2012). On the other hand, the success of biomanipulation in deep, thermally stratified lakes depends on P concentration and loading rate into the epilimnion during thermal stratification (Benndorf, 1987; Kasprzak et al., 2007; Scharf, 2008). Consequently, at high P availability in the trophogenic zone, phytoplankton production rates exceed zooplankton filtration capability and prevent the clear water period (Benndorf, 1987). These interactions in the pelagic food web affect sedimentation both quantitatively and qualitatively and have a significant impact on the vertical flux of P including various size fractions and binding forms of P (Bloesch and Bürgi, 1989; Mazumder et al., 1990a; Houser et al., 2000).

Enhanced P sedimentation by daphnids having a high specific and seasonally stable body P content should be reflected in lower P concentrations in epilimnetic water, and may affect the P binding forms in settling matter and also at the sediment surface. However, on its way through the hypolimnion to the sediment, P in settling matter underlies microbial and chemical transformation processes (Gächter and Mares, 1985; Hupfer et al., 1995; García-Ruiz et al., 2001; De Vicente et al., 2008). The nature and intensity of these transformation processes depends on the proportion of different P binding forms within the settling matter, the chemical conditions and the residence time of the settling particles in the ambient water column. The P amount and proportion of different P binding forms finally deposited at the sediment surface are of high importance for subsequent diagenetic processes and P retention in the sediments (Hupfer et al., 1995). Some studies indicated that mineralisation processes at the sediment surface and release of P into water depend on the quality of the settling matter (Dawidowicz et al., 2002; Lathrop et al., 2002). In fact, the proportions of loosely adsorbed, reductant-soluble, and organic bound P are often decisive factors for the internal P release from sediments (Boström, 1984; Hupfer et al., 1995; Rydin, 2000). Organically bound P is especially subject to microbial decomposition and its release therefore depends on the quality of settling matter (Ahlgren et al., 2006; Reitzel et al., 2007, 2012). For instance, Andersen and Jensen (1992) demonstrated that more P was released from seston consisting of cyanobacteria than from seston containing a mix of cyanobacteria, algae, and zooplankton. This suggests that seston merely composed by zooplankton is less degradable. Thus, relatively more P is removed from the epilimnion by sedimentation and can no longer be circulated within the short-circuited P cycle. Regarding the role of P losses from the epilimnion, attention has been paid to the export and transformation mechanisms of P as the consequence of food web structure (Benndorf et al., 2002; Kasprzak et al., 2007; Scharf, 2008). However, little is still known about transformation processes of P in thermally stratified lakes passing down from the epilimnion into the deep-water in response to food web manipulation. Only few studies have investigated the influence of manipulation of food web structure on processes in deeper parts of stratified lakes, such as shifts in hypolimnetic oxygen demand (Mazumder et al., 1990a; Schallenberg and Burns, 1999), methane accumulation (Rychła et al., 2012), and sediment P retention (Houser et al., 2000). Moreover, to the best of our knowledge, studies concerning the effects of food web structure on the quality and quantity of settling matter reaching the lake bottom, as well as on the P content and specific P binding forms at the uppermost layer of the sediment have not yet been published.

Therefore, the main objective of this study was to examine whether the structure of the planktonic food web and enhanced P concentrations in the epilimnion have a significant impact on (1) P content and proportion of different P binding forms in the settling material and on (2) P content and qualitative shifts in P binding

Table 1

Characteristics of Lake Dagow with relevant criteria for trophic status classification (TP, total phosphorus; TN, total nitrogen; Chl *a*, chlorophyll *a*; Secchi, water transparency). The values represent epilimnion samples (0–2.5 m) from the stratification period (June–August) of 1993–2007 (*n*, number of samples).

	TP (mg m ⁻³)	TN (mg m ⁻³)	Chl <i>a</i> (mg m ⁻³)	Secchi (m)
Mean	0.038	983	0.008	2.7
SD	0.013	190	0.003	1.0
Max	0.062	1375	0.017	5.3
Min	0.015	790	0.006	1.0
<i>n</i>	17	11	11	19
Trophic state	eu ^a	eu ^b	me-eu ^a	eu ^a

Trophic state classification according to:

^a OECD (1982).

^b Nürnberg (2001).

forms at the sediment surface at the end of the summer stagnation period. Controlled experiments were conducted in large enclosures (630 m³) in order to mimic real-lake conditions.

Materials and methods

Enclosures and experimental design

The effects of pelagic food web structure and nutrient enrichment on P sedimentation and retention in sediments were investigated in four large enclosures placed at the deepest site of the meso-eutrophic (Table 1), thermally stratifying Lake Dagow (53°08' N, 13°04' E; Brandenburg, Germany) during three consecutive summer stagnation periods (2005–2007). Each enclosure had a diameter of 10 m with plastic walls extending to the sediment surface at 8 m depth, thus enclosing a water volume of about 630 m³.

The enclosure experiments were carried out in a 2 × 2 factorial design, with manipulation of food web structure and nutrient concentration being the treatments. The food web structure was manipulated by adding (+F) or removing (–F) planktivorous fish. First, in all enclosures fish were removed using a set of gill nets with different mesh sizes. The nets were deployed until no more fish were caught. Next, in two enclosures (+F) fish biomass was set at 4 g fresh weight m⁻³. Juvenile *Perca fluviatilis*, *Rutilus rutilus*, and *Blicca bjoerkna* were sampled from Lake Dagow, immediately weighed, and released into the enclosures at equal biomass ratios.

In nutrient treatments, we considered that P was growth limiting for phytoplankton. Epilimnetic total phosphorus (TP_{Epi}) concentrations were established in the mesotrophic (14–45 mg m⁻³) and hypertrophic (>160 mg m⁻³) range (Vollenweider and Kerekes, 1982) in –N and +N treatments, respectively. To increase nutrient concentrations, we added phosphorus (KH₂PO₄) and nitrogen (NH₄NO₃) where necessary at an atomic TN:TP ratio of 13:1, which is optimal for freshwater phytoplankton growth (Klausmeier et al., 2004). The resulting TP_{Epi} concentrations in +N treatments at the beginning of each experiment amounted to approximately 700, 500 and 200 mg m⁻³ in 2005, 2006, and 2007 respectively, thus exceeding the TP_{Epi} values of –N treatments by a factor of 5–10.

The experiments were carried out during thermal stratification in 2005 (July–August, 5 weeks), 2006 (May–September, 18 weeks), 2007 (May–September, 16 weeks). In each year, four treatments (+F/–N, +F/+N, –F/–N, –F/+N) were tested without replicates because of the limited number of enclosures. In 2006 and 2007, before the experiments were started, the enclosures were moved to a new location in the lake to avoid “memory” effects from previous experiments and to obtain homogenous water and sediment properties in all enclosures. Consequently, we collected data from 12 independent experimental tubes recorded during three consecutive summer seasons. Thus we considered the obtained results

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