

## Assessing P status and trophic level of two lakes by speciation of particulate phosphorus forms

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### ABSTRACT

Seasonal variability of dissolved and particulate P forms was investigated in two lakes in Mecklenburg-Western Pomerania (North-East Germany): the polymictic Lake Bützow and the dimictic Lake Dudinghausen. Both lakes had a different trophic status according to the classic parameter total phosphorus, chlorophyll-a as well as phytoplankton biomass and composition. The aim of the study was to test P compounds and P fractions for characterization of the nutrient status of the phytoplankton, especially Polyphosphates and Phospholipids. The field study shows, that these intracellular reserve compounds in algae can not reflect the different nutrient status of the phytoplankton in the two lakes and is therefore not a more sensitive scale to indicate phosphorus limitation of plankton communities.

Key words: lake, eutrophication, phosphorus fraction, polyphosphate, phospholipid, phytoplankton biomass and composition

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### 1. INTRODUCTION

Over the last decades, eutrophication of freshwater systems has been promoted by phosphorus, whose sources and bioavailability have dominated primary production (Reynolds & Davies 2001). P availability and P cycles in freshwater were determined by P input and transformation in the pelagic subsystem and by processes at the sediment-water interface.

Phosphorus transport from the water column to the sediment is either particulate or particle associated (Tartari & Biasci 1997). Release from the sediment takes place in dissolved or particulate form. Benthic-pelagic coupling fuels primary production and nutrient availability in the water column of the euphotic zone in lakes.

Relevant publications (Fitzgerald & Nelson 1966; Rhee 1973; Lean 1984) have demonstrated that conventional monitoring data of dissolved nutrients does not provide a sensitive indicator of the duration or degree of nutrient status and limitation in lakes. Phytoplankton is also capable of assimilating P from the particulate organic fraction (Cembella *et al.* 1984) and dissolved organic phosphorus (Cotner & Wetzel 1992). Algae grown under resource limitation exhibit considerable variation in their biochemical composition, depending on the type of limiting nutrient and degree of limitation (Shifrin & Chisholm 1981; Kilham *et al.* 1997). Accordingly, seston stoichiometry has been proposed as an indicator for limiting nutrients (Sommer 1989; Urabe 1993). The variability of the C:N:P ratio in marine microalgae was described (Banse 1974a; Geider & La Roche 2002) for the interpretation of nutrient deficiency

of microalgae in aquatic systems. Especially in shallow lakes with abundant resuspended particles, the nutrient stoichiometry cannot characterize limitation conditions.

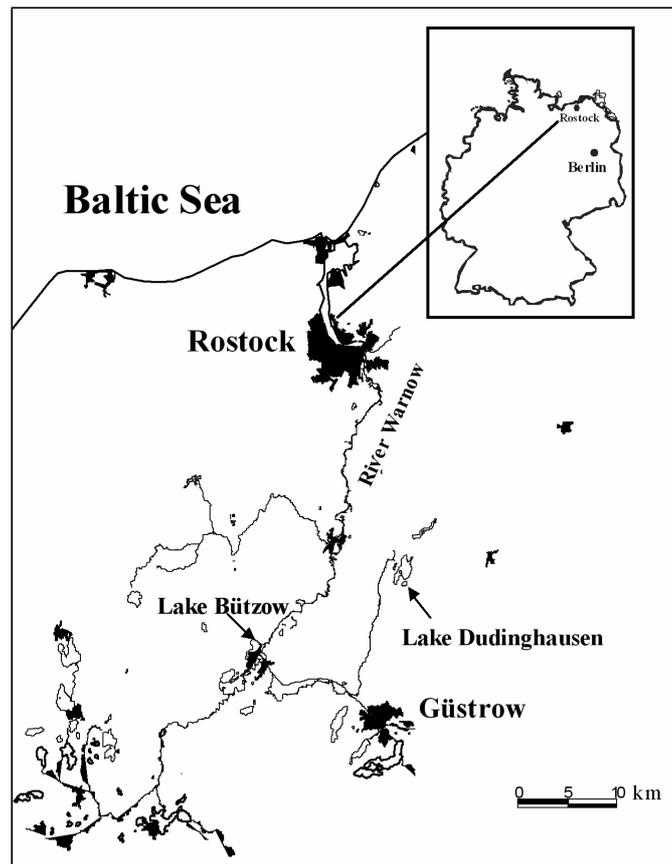
Phosphorus can be stored as polyphosphate granules; these serve as an energy and phosphate reserve (Kornberg 1995) and have been detected in eubacteria, fungi, algae, protozoans and in various tissues of plants and animals (Kulaev & Vagabov 1983). These granules only accumulate under a sufficient P supply. Polyphosphate granules in algal cells have therefore been used to indicate high phosphorus loads in the water body (Schelske & Sicko-Goad 1990) and to reconstruct the trophic development of lakes based on sediment analyses (Kenney *et al.* 2001).

This field study was designed to investigate the seasonal variation of different forms of phosphorus in two lakes with different mixis and eutrophic status. Besides the dissolved and total phosphorus concentration, P-binding forms, polyphosphates and phospholipids as reserve compounds were analysed to characterise the P status of phytoplankton communities. The hypothesis was that internal P compounds - especially polyphosphates and phospholipids - are a sensitive indicator of P status of phytoplankton communities and helpful for lake monitoring and lake management by restoration projects.

### 2. METHODS

#### 2.1. Study site

Lake Bützow and Lake Dudinghausen are located in Mecklenburg-Western Pomerania (North-East Germany), approximately 40 km southwest and south of



**Fig. 1.** Geographic location of Lake Bützow and Lake Dudinghausen in Northern Germany.

**Tab. 1.** Morphometric and limnological characteristics of both lakes.

	Lake Bützow	Lake Dudinghausen
Morphometric parameter		
Surface area in ha	98.1	18.8
Volume [m <sup>3</sup> ]	1.02 106	1.29 106
Mean depth [m]	1.0	6.9
Maximum depth [m]	2.2	15.2
Mixis	polymictic	dimictic
Physico-chemical parameter		
O <sub>2</sub> saturation [%] (water surface)	59 - 161	63 - 129
Secchi disk depth [m]	0.3-0.7	0.6-3.6
pH (water surface)	8.0 - 9.4	7.9 - 8.8
Trophic classification 1995/1996	eutrophic	mesotrophic

Rostock (Fig. 1). The main morphometric and limnological parameters of both lakes are presented in table 1. Lake Bützow is classified as eutrophic, Lake Dudinghausen as mesotrophic according to the German standard (Lawa 1998) and the OECD (1982) criteria. Both represent two typical lake types in North-East Germany: shallow lake with a polymictic circulation and deeper lake with a dimictic thermal stratification. Lake Bützow is a shallow lake situated on a tributary of the Warnow River (Selig *et al.* 2002). Sixty percent of the catchment area from the Warnow River is intensively used by agriculture and the nutrient input from the catchments area is high: an average of 4430 t of N

and 90 t of P annually (Behrendt 1996). Separate data for the Lake Bützow no exist. In contrast Lake Dudinghausen has a thermal stratification and anoxic hypolimnion during the summer (Selig *et al.* 2004). The catchments area is small (<16 km<sup>2</sup>) and the most input of nutrients comes from the groundwater (Dressler *et al.* 2006).

## 2.2. Sampling

Water temperature, pH and dissolved oxygen were measured in the surface water (0.5 m) in the shallow Lake Bützow and in 0.5 m, 1 m and then in 1 m steps down to the bottom in the dimictic Lake Dudinghausen

with the multiprobe Torphil 406 (Remember eG, Germany). Nutrient concentrations and phytoplankton counts were determined in the same steps in both lakes, but only presented here for the surface water (0.5 m) for the direct comparison of both lakes. Results of the vertical distribution of nutrients and plankton in Lake Dudinghausen were described in Selig *et al.* (2004) separately. Samples were kept at 4 °C in the dark and analysed within the next 3-5 h.

### 2.3. Nutrient analysis

Soluble reactive phosphorus (SRP) was analysed after membrane filtration (0.45 µm) by applying the molybdenum blue method in a flow-through system at 660 nm according to Malcom-Lawes and Koon (1990). Total phosphorus (TP) was analysed from the unfiltered sample as SRP after acid hydrolysis under UV irradiation and determined after the molybdenum blue method according to Nakamura *et al.* (1980). Benson *et al.* (1996) compared this flow injection method and found a good agreement to the conventional batch digestion method.

Aliquots of water samples were filtered (Whatman GF/F) and the filter subsequently dried (at 60 °C for 24 h) to determine particulate matter. Particulate organic carbon (POC) and particulate nitrogen (PN) were analysed with a C/N Analyser vario EL after Verardo *et al.* (1990). Particulate phosphorus (PP) was determined as the HCl-soluble residues after heating at 500 °C (Andersen 1976). The authors described a high reproducibility of this ignition method with the conventional perchloric acid method. HCl-soluble particulate iron (PFe) was measured in the extract after Stookey (1970).

### 2.4. Chlorophyll-a and phytoplankton analysis

Chlorophyll-*a* (Chl-*a*) was extracted in ethanol according to DEV (1985). 500 to 1000 ml of the sample was glass fibre filtered. The filter was rubbed and put into boiled ethanol. After 20 h in darkness the suspension was centrifugated. At first the supernatant was measured at 663 and 750 nm. For differentiation of degradation compounds of Chl-*a* (phaeophytine-*a*) it follows an acidification (0.1 M HCl) and a replication of the measurement at 663 and 750 nm. Phytoplankton biomass was analysed according to Utermöhl (1958). Abundant species were counted to 100 units at least. The biovolume of dominant species was determined by measuring the dimensions of 10 counting units and calculating to the closest geometrical figure (Edler 1979). Biovolume was transformed into fresh-weight biomass based on a mean density of 1 g cm<sup>-3</sup>.

### 2.5. Sequential P extraction and special P analysis

The extraction method of Psenner *et al.* (1984) was used to analyse the different forms of phosphorus in particulate matter. The extractants were applied in the following sequence: H<sub>2</sub>O (distilled water, 20 min), 0.11

M BD (bicarbonate dithionite, 30 min), 1 M NaOH (16 h), 0.5 M HCl (16 h). The extractants were separated from the residues by centrifugation at 4000 g for 20 min. The soluble reactive phosphorus (SRP) was analysed in each extractant. Total phosphorus (TP) was determined as SRP in the extractant after acid hydrolysis under UV irradiation. The non-reactive phosphorus (NRP) is the difference between TP and SRP. Fractions were defined as follows: H<sub>2</sub>O-TP as available phosphorus, BD-SRP extract as reductant soluble phosphorus, NaOH-SRP as sorptive bound phosphorus, NaOH-NRP as organic bound phosphorus and HCl-SRP as carbonate bound phosphorus. SRP and TP were analysed no later than 6 h after extraction, after the sample was neutralized. Blanks and references were prepared by extracting filters without samples.

For determination of polyphosphate (polyP), the samples were extracted with 2N KOH containing 30 mg EDTA ml<sup>-1</sup> according to Feuillade *et al.* (1995). The <sup>31</sup>P-NMR spectra were recorded on a Bruker ARX-300 spectrometer (12.5 MHz, 3000-4000 scans) described by Selig *et al.* (2002). Phospholipids (Plipid) were extracted in chloroform/methanol after the method of Findlay *et al.* (1989) modified for suspended matter. Plipid was determined after decomposition (K<sub>2</sub>HSO<sub>4</sub>) and neutralisation as soluble reactive phosphorus (SRP) with the molybdenum blue method followed the description of nutrient analysis.

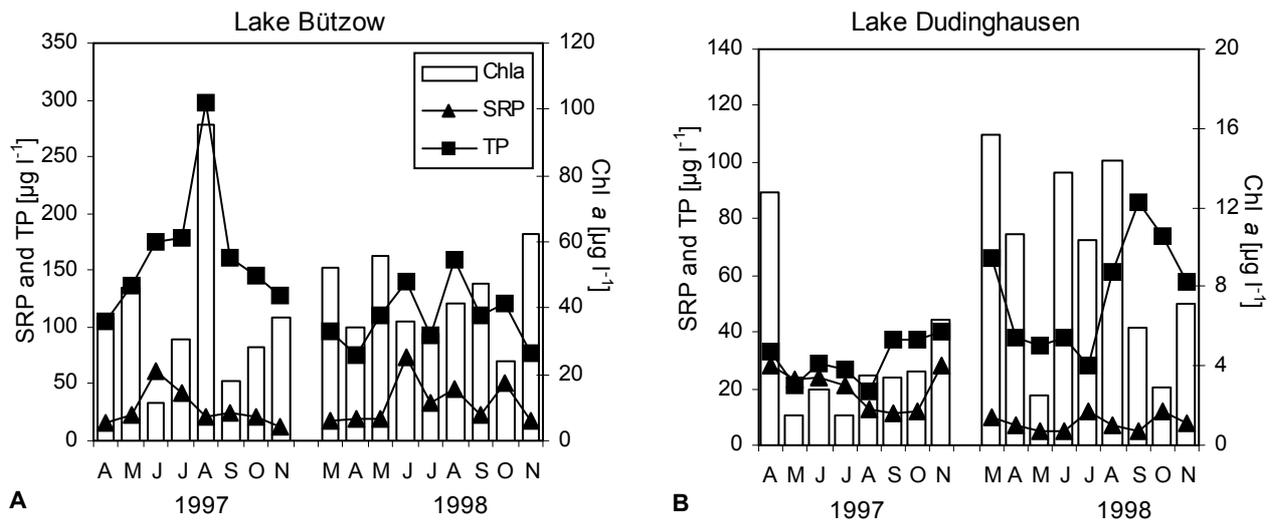
## 3. RESULTS

### 3.1. TP, SRP and Chl *a* analysis

TP concentration in the surface water layer was lower in Lake Dudinghausen (19-68 µg l<sup>-1</sup>) than in Lake Bützow (93-298 µg l<sup>-1</sup>, Fig. 2). In the former, the highest values were recorded in spring and autumn, whereas in the latter the values were higher in summer. The SRP concentration was 5-28 µg l<sup>-1</sup> in Lake Dudinghausen and 13-74 µg l<sup>-1</sup> in Lake Bützow. The Chl-*a* concentration, which was measurable throughout the year, was under 16 µg l<sup>-1</sup> in Lake Dudinghausen, with maximum concentration in spring and summer. In Lake Bützow, Chl-*a* varied between 10 and 90 µg l<sup>-1</sup>.

### 3.2. CNP analysis

The POC, PN, PP and PFe concentrations were lower in Lake Dudinghausen (Tab. 2). The ratio between the particulate nutrients shows a different picture: the POC/PN ratio was generally higher in Lake Dudinghausen, whereas the PFe/PP ratio was consistently higher in Lake Bützow. Neither lake showed clearly higher POC/PP and PN/PP values. In summer – during thermic stratification – the ratios were higher in Lake Dudinghausen. A high correlation was found between PP and PFe in both lakes (and also between POC and PP in Lake Dudinghausen, Tab. 3).



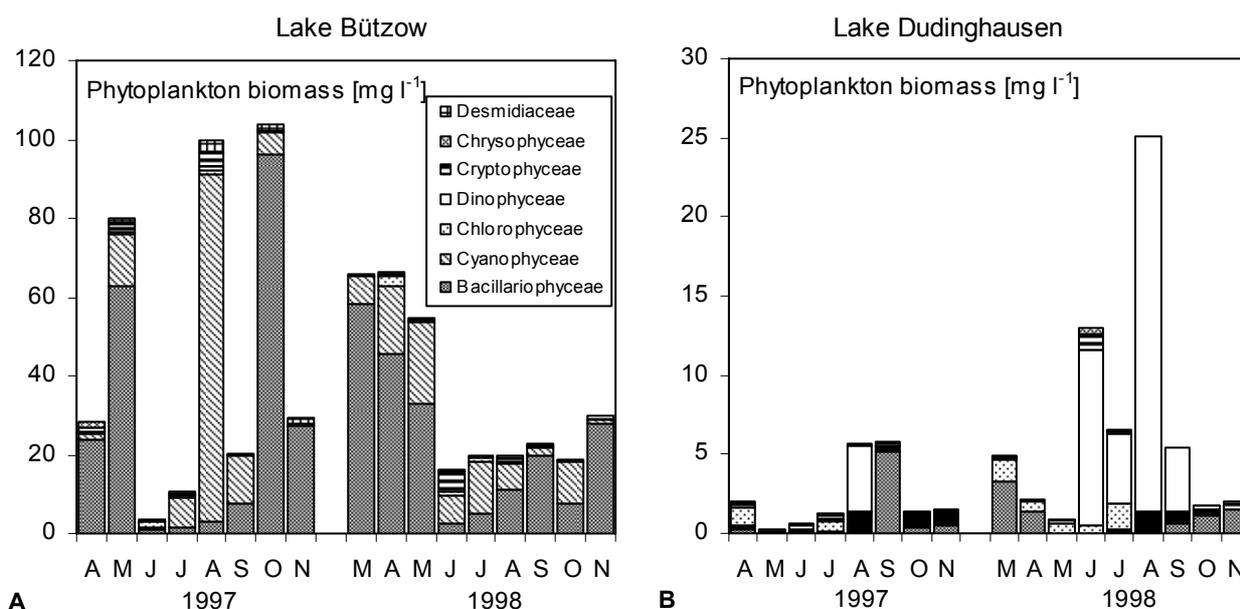
**Fig. 2.** SRP, TP and Chl-a concentration in 1997 and 1998 in Lake Bützow (A) and Lake Dudinghausen (B).

**Tab. 2.** Concentration of POC, PN, PP and PFe in both lakes and the molar ratio (μmol:μmol) of these particulate nutrients during 1998.

	POC [mg l <sup>-1</sup> ]	PN [mg l <sup>-1</sup> ]	PP [mg l <sup>-1</sup> ]	PFe [mg l <sup>-1</sup> ]	POC/PN molar	POC/PP molar	PN/PP molar	PFe/PP molar
<b>Lake Bützow</b>								
March	4.2	0.7	0.051	0.066	7.2	213.9	29.7	0.72
April	4.2	0.7	0.048	0.067	6.7	227.1	34.1	0.77
May	4.8	1.0	0.112	0.101	5.6	110.9	20.0	0.51
June	3.2	0.7	0.087	0.128	5.3	102.8	19.4	0.81
July	3.6	0.7	0.074	0.073	6.4	126.7	19.7	0.55
August	3.0	0.6	0.067	0.052	5.8	115.3	19.9	0.43
September	3.6	0.7	0.054	0.067	6.0	173.3	29.0	0.69
October	1.9	0.4	0.039	0.097	5.8	127.5	22.1	1.37
November	2.9	0.6	0.041	0.074	5.8	182.1	31.6	1.00
<b>Lake Dudinghausen</b>								
March	1.7	0.2	0.022	0.006	9.0	203.1	22.5	0.15
April	1.8	0.3	0.038	0.046	8.0	123.5	15.5	0.69
May	0.6	0.1	0.010	0.002	6.6	149.4	22.8	0.11
June	1.6	0.2	0.013	0.005	7.8	310.5	39.9	0.21
July	2.2	0.3	0.026	0.012	7.9	212.3	26.8	0.25
August	1.9	0.2	0.019	0.007	12.6	259.5	20.7	0.21
September	1.5	0.2	0.014	0.006	9.4	276.2	29.4	0.23
October	0.7	0.1	0.013	0.008	6.6	132.0	20.0	0.33
November	0.8	0.1	0.011	0.009	6.7	174.0	25.9	0.44

**Tab. 3.** Correlation coefficients (Pearson coefficient as  $r^2$ ,  $\alpha = 0.05$ ) for particulate nutrients, phytoplankton biomass (PB), Chl- $\alpha$ , Plipid and the dominant P-fraction; bold figures show the coefficients above 0.4.

		POC	PP	PFe	PB	Chl- $\alpha$	P-Lipid	BD-SRP	NaOH-NRP	NaOH-SRP	$\Sigma$ SRP	$\Sigma$ NRP
Lake Bützow	POC	-----	0.04	0.09	<0.01	<0.01	0.02	0.03	0.15	0.04	0.19	0.13
Lake Dudinghausen		<b>0.46</b>	0.09	0.28	<b>0.61</b>	0.09	0.07	0.01	<0.01	<0.01	0.23	
Lake Bützow	PP	-----	0.25	<0.01	0.02	0.01	0.12	0.44	0.3	<b>0.49</b>	0.15	
Lake Dudinghausen		<b>0.73</b>	<0.01	0.20	0.01	0.06	0.15	<0.01	0.05	0.31		
Lake Bützow	PFe	-----	0.05	<0.01	0.03	<0.01	<b>0.65</b>	0.31	0.35	<b>0.44</b>	0.27	
Lake Dudinghausen		0.05	0.02	0.08	0.29	0.22	0.02	0.02	0.02	0.08		
Lake Bützow	PB	-----	0.13	<b>0.67</b>	<0.01	0.11	0.27	0.19	0.03	<0.01	<0.01	
Lake Dudinghausen		0.38	0.06	0.03	0.02	<0.01	<0.01	<0.01	<0.01	<0.01		
Lake Bützow	Chl- $\alpha$	-----	<0.01	<0.01	0.05	0.02	0.01	0.02	0.01	0.02		
Lake Dudinghausen		<0.01	0.05	0.15	0.01	<0.01	<0.01	<0.01	<0.01			
Lake Bützow	P-Lipid	-----	<0.01	0.15	0.16	0.18	<0.01	<0.01	<0.01			
Lake Dudinghausen		0.16	0.04	0.30	0.04	0.18						
Lake Bützow	BD-SRP	-----	0.22	<b>0.49</b>	0.31	<b>0.77</b>	<0.01	<0.01				
Lake Dudinghausen		0.03	0.07	0.29	0.06							
Lake Bützow	NaOH-NRP	-----	<b>0.44</b>	<b>0.59</b>	0.07	0.07	0.07					
Lake Dudinghausen		0.31	0.04	0.04								
Lake Bützow	NaOH-SRP	-----	<b>0.59</b>	0.07	0.07	0.07						
Lake Dudinghausen		<b>0.83</b>	0.13									
Lake Bützow	$\Sigma$ SRP	-----	0.24	0.24								
Lake Dudinghausen		0.09										
Lake Bützow	$\Sigma$ NRP	-----	0.09	0.09								
Lake Dudinghausen		0.09										

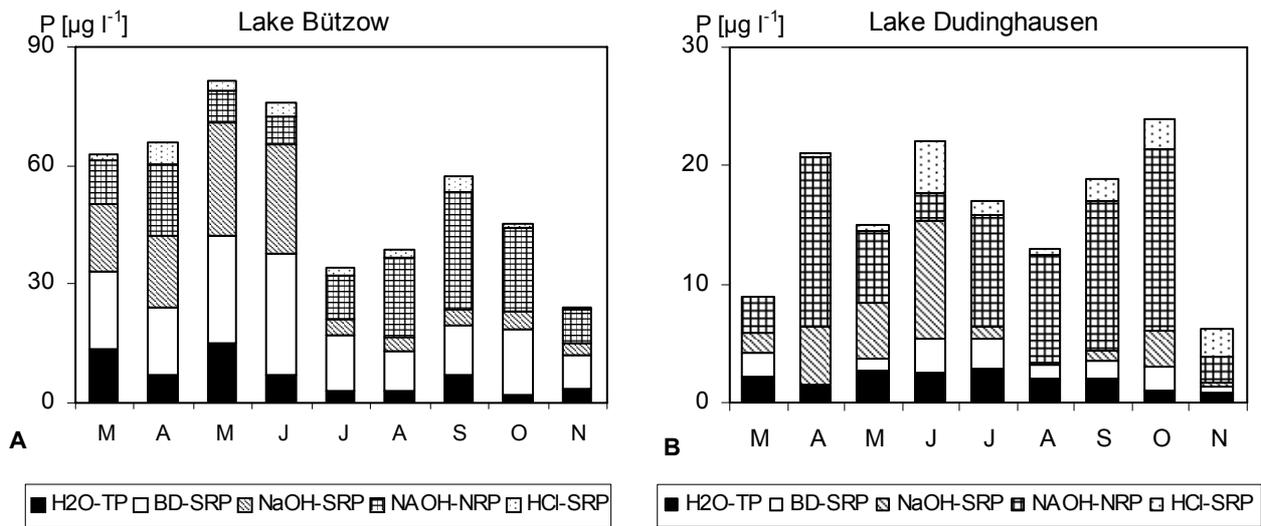
**Fig. 3.** Seasonal variability of phytoplankton dominance in Lake Bützow (A) and Lake Dudinghausen (B) in 1997 and 1998.

### 3.3. Plankton communities

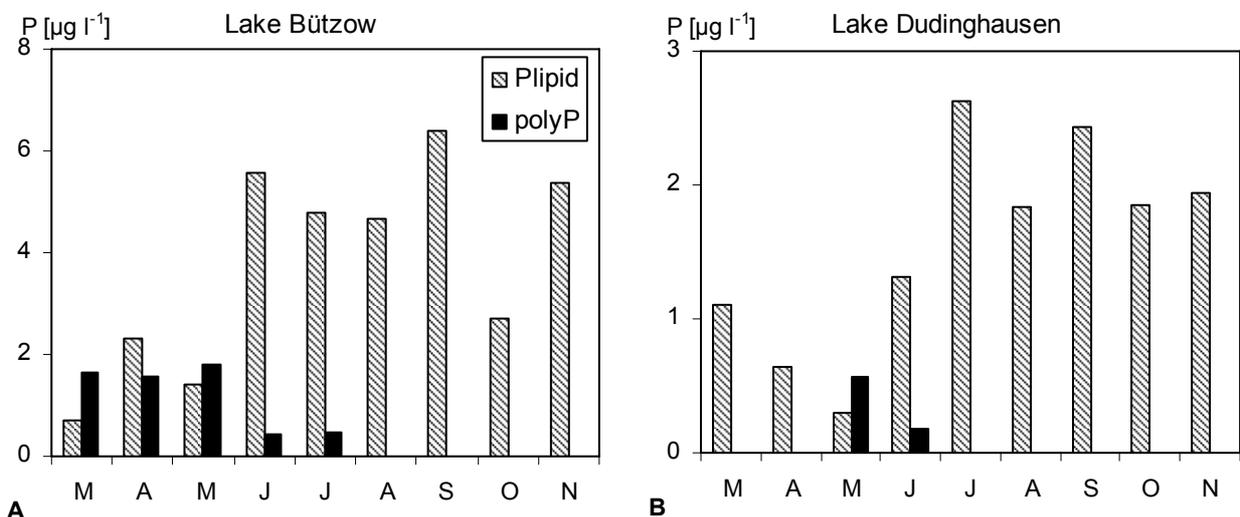
The highest phytoplankton biomass ( $109 \text{ mg l}^{-1}$ ) was found in Lake Bützow, with a high variability. The values were higher than in the surface layer in Lake Dudinghausen (1 to  $25 \text{ mg l}^{-1}$ , Fig. 3). In Lake Bützow the seasonal variation was very different in both investigation years: in 1997 biomass peaked in summer,

in 1998 in spring. In both years the dominances changed between Bacillariophyceae (spring and autumn) and Cyanobacteria (summer).

In Lake Dudinghausen a summer phytoplankton biomass peak was typical for both years, yet with different values. In 1998, high Dinophyceae biomass (mainly *Ceratium hirundinella*) dominated the phytoplankton with a maximum of  $23 \text{ mg l}^{-1}$  (92% of the



**Fig. 4.** Seasonal variation of the particulate phosphorus fraction in the surface water of Lake Bützow (A) and Lake Dudinghausen (B) from March to November 1998.



**Fig. 5.** Concentrations of polyphosphate (PolyP) and phospholipid (P-lipid) in Lake Bützow (A) and Lake Dudinghausen (B) from March to November 1998.

phytoplankton communities). In 1997, Dinophyceae also dominated in August, but with a much lower biomass. In 1997 the dominance in the phytoplankton community had the following seasonal sequence: Bacillariophyceae, Chlorophyta, Dinophyceae, Cyanobacteria and Bacillariophyceae.

#### 3.4. Sequential extraction of PP and P-forms

Figure 4 illustrates the seasonal distribution of the phosphorus fractions in both lakes. The dominant fraction and the variability differed considerably in both lakes. In Lake Bützow the dominance changed between the BD-SRP and NaOH-SRP fraction until June, whereas from August to October, NaOH-NRP dominated with 39-42 % of the PP. H<sub>2</sub>O-extractable P con-

tributed 4-20%. The highest concentration of this fraction was measured towards the end of the spring phytoplankton peak in May.

NaOH-NRP dominated (except in June) in Lake Dudinghausen. The percentage values ranged from 10 to 65% PP. NaOH-SRP was higher in spring and dominated with 44% PP in June. BD-SRP and HCl-SRP played a minor role with respect to the PP in Lake Dudinghausen.

PolyP – as the internal reserve compound of organisms – could only be detected in the first half year (until July) in Lake Bützow; its percentage decreased during the year and amounted to 1.6-4.2% of PP (Fig. 5A). In Lake Dudinghausen, polyP was only determined in May and June, making up only 8 and 9% of the organic P fraction (Fig. 5B).

The Plipid content, however, increased in June/July in both lakes and remained constant to the end of the study period. The values ranged from 1-9% of PP in both lakes. During the second half of 1998, the Plipids formed 78 and 68% of the organic P (NaOH-NRP fraction) in June and November in Lake Bützow, respectively. In Lake Dudinghausen the Plipids varied between 4 and 88% of the organic P, with a maximum in November. In Lake Bützow the Plipid content was highly correlated with the phytoplankton biomass (Tab. 3).

#### 4. DISCUSSION

##### 4.1. Trophic level

TP, Chl-*a* and phytoplankton biomass are the classical parameters to classify the trophic level of lakes. Accordingly, both lakes have a clearly different trophic status: Lake Bützow is eutrophic and Lake Dudinghausen is mesotrophic. In shallow lakes the German standard method for lake classification cannot be used because the parameters secchi disk depth and TP are influenced by sediment resuspension. Phytoplankton biomass clearly described the high trophic level for Lake Bützow. Besides the biomass, the dominant taxonomical classes were also different in both lakes. Thus, the phytoplankton biomass, the algae species and the seasonal variation described the different trophic level of the two lakes. The seasonal variation of algae groups was confirmed in both investigations years, but the phytoplankton biomass was very different.

The SRP concentration also characterised the different nutrient status of both lakes. In Lake Dudinghausen the SRP concentrations were below 12  $\mu\text{g l}^{-1}$  in 1998, whereas in Lake Bützow the values never fell under 10  $\mu\text{g l}^{-1}$ . Sas (1989) concluded that the seasonal mean concentration must drop below 10  $\mu\text{g l}^{-1}$  to reduce phytoplankton biomass. Resuspension may explain the high SRP concentration and the bioavailable phosphorus in Lake Bützow. Sediment resuspension has been described as a potential source of nutrients for phytoplankton in shallow lakes (Carper & Bachmann 1984; Canfield & Hoyer 1988; Hamilton & Mitchell 1997). In Lake Dudinghausen, P can be released from the sediment under anoxic conditions only in the hypolimnion during summer stratification (Selig & Schlungbaum 2003).

##### 4.2. Elemental ratios in particulate matter

In contrast to the SRP concentration, the elemental composition (C/N/P ratio) of particulate matter showed a phosphorus deficiency corresponding to the Redfield ratio for phytoplankton growth throughout both years in both lakes. Hecky and Kilham (1988) described particle composition as the simplest and most comparable way

of defining the nutrient status of phytoplankton. Banse (1974b) has dealt with the interpretation of the elemental ratio in marine systems. These results would also apply to limnic systems. The C/P ratio failed to describe the different nutrient status of the two lakes. Particulate matter in lakes was higher and more variable in elemental ratios than particulate matter in oceans (Hecky *et al.* 1993). Especially in shallow lakes, particulate matter consists of plankton, detritus, allochthonous particles and resuspended sediments. The correlation analysis showed a strong relation between POC and Chl-*a*. For Lake Bützow, no relation between the phytoplankton biomass and Chl-*a* concentration was found. The relation of particulate nutrients does not reflect the nutrient status of planktonic organisms in the shallow Lake Bützow. Therefore, this classic parameter of defining the nutrient status of phytoplankton is insufficient to compare shallow lakes with dimictic lakes.

Moreover, the total pool of PP is not available for algal growth in either lake type. Reynolds and Davies (2001) described the ideal instantaneous measure of P bioavailability as the sum of SRP and biomass phosphorus. Chemical extraction was used to define the bioavailable P (Young & DePinto 1982; Dorich *et al.* 1985; House *et al.* 1995; Fabre *et al.* 1996). The interpretation of these results varied strongly depending on the extraction protocols.

##### 4.3. P-Fractionation

The P-fractionation, based on Psenner *et al.* (1984), is used to define the released and available P depending on the variation of environmental conditions in lake water and sediment, especially depending on variation of oxygen conditions. This fractionation procedure has been used to describe the transformation of particulate phosphorus in both: the sediment and the water body (Hupfer *et al.* 1995; Pacini & Gächter 1999). Thus, it can better describe P availability under different conditions in lake water than the fractionation procedure that subdivides the intracellular phosphorus components such as sugar P or nucleic P (Miyata & Hattori 1986). Independent of this fractionation procedure, the two internal P compounds polyP and Plipid were separately determined.

Based on the definition of Boström *et al.* (1988), the sum of H<sub>2</sub>O-TP and NaOH-NRP is the available PP in the pelagic subsystem. Accordingly, 31-76% of the PP in Lake Bützow and 22-85% PP in Lake Dudinghausen was available for autotrophic organisms during the vegetation season. This analysis indicates no P limitation at any time in either pelagic system. BD-SRP as well as NaOH-SRP, which are defined as being available for overlying sediments (Boström 1984), must be characterised as stably bound and unavailable for autotrophic organisms in the oxic water column (Selig 2003).

The inorganic P fraction is only important in Lake Bützow. This reflects the suspended particulate matter in this shallow lake. The relation between PP and PFe was very different in both lakes. Whereas for Lake Dudinghausen no correlations ( $r^2 = 0.25$ ) were found, the correlation was high in Lake Bützow ( $r^2 = 0.75$ ). In the shallow lake we also found a correlation of PFe with the BD-SRP fraction. Pacini and Gächter (1999) described the high importance of BD-SRP in riverine particulate phosphorus during rain events. This fraction characterised the phosphorus binding on particles and showed that colloidal Fe is associated with colloidal P. Whereas the BD-SRP fraction in rivers was increased by higher discharges, in shallow lakes it was primarily increased by resuspension processes. Therefore, the resuspension of muddy sediment particles and the benthic-pelagic coupling influences the P binding and P availability in the pelagic zone of shallow Lake Bützow.

#### 4.4. Polyphosphate and phospholipid as internal P compounds

It has been postulated that the content of polyphosphates in microalgae can be used as a biological indicator for higher P loading and eutrophication. The analysis of TP, Chl-*a* and phytoplankton biomass clearly describe the different trophic status of both lakes. In spite of the also high SRP concentration and higher proportion of available P in the PP, polyphosphate granules were only determined in the first half of each year in the eutrophic Lake Bützow. In Lake Dudinghausen, polyP was only detectable in May and June. Therefore, the analysis of polyP is not confirmed with the different P status and trophic level in both lakes. In freshwater, such reserve compounds have mostly been reported from nutrient-rich waters. For example, Schelske and Sicko-Goad (1990) observed these compounds in bays of Lake Michigan with heavy nutrient load and described their influence on phytoplankton dynamics. Schelske (1994) excluded a P-limitation in the shallow Lake Apopka based on polyphosphate granules, which were found year-round in algae. The same effect could not be found in the also high eutrophic shallow Lake Bützow in our results. Lean (1984) showed that for about a month after SRP concentrations fell, the P stored within the cells could have met the demands of the phytoplankton. Kenney *et al.* (2001) interpreted polyphosphate accumulation in the sediment as an effect of high P load and as accumulation of storage in algae cells. All these authors used polyphosphate granules as an indicator for systems that are sufficiently supplied with phosphorus that is available for algae. Bolier *et al.* (1992) found polyP in phytoplankton cells – independent of the SRP concentration and without prior P starvation – in different parts of the Andelse Maas basin. The present investigation of Lake Dudinghausen and Lake Bützow also shows that polyP granules cannot be used to characterise the differ-

ent trophic status and P availability in both systems. Eixler *et al.* (2006) investigated the accumulation of phosphorus storage in *Chlorella vulgaris* and its dependence on phosphate supply in laboratory experiments. The variation in phosphate concentration in the medium of a well supplied culture had much less effect on the degree of polyP storage than a preceding P starvation phase. These results from laboratory studies confirm the field study of Lake Bützow and Lake Dudinghausen.

The accumulation of polyP in freshwater ecosystems was observed more at the sediment-water interface (Davelaar 1993) or on the thermocline and chemocline in dimictic lakes (Selig *et al.* 2004). In P-rich wastewater systems the absence of polyP accumulation by organisms has been discussed as reflecting stress situations (Kjeldstad *et al.* 1991; Lawrence *et al.* 1998). The higher accumulation rate of polyP in the post-stress condition is among the discussed effects. Feuillade *et al.* (1995) observed a higher polyP concentration in *Chlorella* sp. in the recovery period after P starvation. We cannot explain the presence of the polyP only in the spring in both lakes, and can only speculate at this point in time. We postulated, that permanent or temporary light limitation is a potential stress factor for the phytoplankton in shallow lakes – also for Lake Bützow (Secchi disk depth lower 0.4 m during the whole vegetation period).

In contrast to polyP granules, Plipids are indicators of microbial biomass (Findlay *et al.* 1989). According to Napolitano (1994), Plipid content varied substantially and unpredictably among algae and periphyton under different light regimes. Irradiance also had a significant effect on storage lipids. In the shallow lake we found a strong similarity between phytoplankton biomass and Plipid concentration. This, however, is not valid for the dimictic Lake Dudinghausen. Moreover, no relationship of Plipid to Chl-*a* or to POC was found. Therefore, the Plipids cannot generally be used to detect plankton biomass in freshwater. The relation of Plipids to other P compounds – such as PP, the P fraction or polyP – provides no information about the P status of phytoplankton and P availability.

#### ACKNOWLEDGMENTS

All this would not have been possible without Fred Brezsinski's technical assistance in the field. We thank Sabine Stolle and Regine Paschen for technical assistance in the laboratory.

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Received: January 2006

Accepted: March 2006