

Zooplankton phosphorus excretion in Swarzędzkie Lake (Western Poland) and its influence on phytoplankton

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Abstract

Zooplankton phosphorus excretion was studied in Swarzędzkie Lake in 2000-2002. Phosphorus excretion rates were high from spring through autumn, but low in winter. The highest value, 203.7 $\mu\text{gP l}^{-1} \text{d}^{-1}$ (vertical profile mean), was recorded in June 2000. The mean rate was 26.6 $\mu\text{gP l}^{-1} \text{d}^{-1}$ and was 10 times greater for rotifers than for both cladocerans and copepods. In most months, the calculated phosphorus excretion rate was greater than the sum of tributary external phosphorus loading and internal bottom sediment loading. Nevertheless, the influence of the zooplankton phosphorus excretion rate on yearly phytoplankton abundance, biomass and chlorophyll *a* was not statistically significant. Yearly variance in phytoplankton variables was best explained by a canonical variable composed of internal loading and zooplankton phosphorus excretion (total redundancy 32.8%).

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INTRODUCTION

Zooplankton excretion is an important mechanism for supplying bio-available phosphorus to the phosphorus pool in lakes (Lampert, Sommer 2001; Arhonditsis et al. 2004). Generally, the smaller an organism is, the higher its rate of phosphorus excretion per unit of biomass (Peters 1983). If small organisms are numerous, then the total phosphorus load from zooplankton excretion can be high (Gulati et al. 1989). Zooplankton phosphate excretion may exceed the total phosphorus demand of phytoplankton and bacteria during some periods (Ejsmont-Karabin et al. 2004). The total amount excreted depends on the abundance and composition of the zooplankton community as well as on water temperature (Kajak 1998, Ejsmont-Karabin et al. 2004). The rate of phosphorus recycling within the lake depends on zooplankton phosphorus excretion. Moreover, as the turnover rate of a unit of phosphorus increases, less of the fraction of input phosphorus is deposited in sediments and more is passed up the trophic food web (Ejsmont-Karabin 1984). The process of nutrient recycling is especially important in oligotrophic lakes, primarily due to organisms in the microbial loop (Teubner et al. 2003). Greater internal loading in eutrophic lakes stimulates the development of larger phytoplanktonic organisms, with relatively high nutrient-storage capacities (Reynolds 1993, Reynolds et al. 2002). Consequently, the importance of the microbial loop in phosphorus recycling in eutrophic lakes decreases and the role of micro- and mesozooplankton increases (Teubner et al. 2003).

By combining the calculations of external (Kowalczevska-Madura 2003) and internal loading from the sediments (Kowalczevska-Madura 2005) in Swarzędzkie Lake with calculations of zooplankton excretion, we compared the importance of each of these phosphorus sources on phytoplankton community parameters (density, biomass and chlorophyll *a*) in a shallow, eutrophic lake.

The aim of this study was to determine the seasonal variation in the zooplankton phosphorus excretion rate and evaluate its role in explaining patterns of phytoplankton abundance and biomass.

MATERIALS AND METHODS

Swarzędzkie Lake (52°25'N, 17°04'E) is located within the town of Swarzędz (Western Poland). It is a throughflow lake of glacial origin, with a total area of 93.7 ha, maximum depth of 7.2 m, and mean depth 2.6 m (Szyper et al. 1994; Gołdyn, Grabia 1998). The lake is polymictic with a very short metalimnion. The mixed depth was 4 m in most cases, but in August 2000, May 2001 and 2002 it was only 3 m, while in August 2002, it was found to be 5 m. The lake is supplied by the Cybina River and the Mielcuch stream. The Cybina,

which is 41 km long, introduces most of the pollution from its largely agricultural catchment and from areas lacking wastewater treatment systems. The Mielcuch is polluted by urban rainwater, some illegal sources of domestic sewage, and the rainstorm overflow from the urban wastewater treatment system of Swarzędz (Gołdyn, Grabia 1998).

Swarzędzkie Lake's catchment covers 17,230 ha and is dominated by farmland (75.5% of the area; Szyper et al. 1994; Gołdyn, Grabia 1998). The lake was heavily polluted in the past due to the discharge of untreated or partially treated sewage from Swarzędz. However, an urban wastewater treatment system was started in November 1991, with treated sewage diverted to the Warta River (Gołdyn, Grabia 1998). Unfortunately, this diversion did not improve water quality. At present, the lake is hypertrophic, with poor water quality, according to an assessment based on the method of Kudelska et al. (1992), which is obligatory for lake monitoring in Poland. Degradation was caused by continued nutrient input from the Cybina and from nutrients released from bottom sediments (Kowalczevska-Madura 2005).

The zooplankton phosphorus excretion rate in Swarzędzkie Lake was calculated monthly from June 2000 through September 2002, by applying published excretion rate equations (Ejsmont-Karabin 1984) to measures of zooplankton abundance and size. Water samples for zooplankton community structure determinations were taken monthly at the deepest site from the surface to 6 m at 1 m intervals. Samples were taken using a 5 l Limnos water sampler and passing 10 l of water through a plankton net (mesh size 40 μm) to remove most zooplankton. Samples were preserved with modified Lugol's solution (Wetzel, Likens 2000). Simultaneously with zooplankton sampling, temperature was measured with a YSI Multiprobe System. Zooplankton was analysed (determined, counted and measured) in a 1 ml Sedgwick-Rafter chamber at a magnification of 100-200x. Zooplankton biomass was calculated by application of length-weight regressions according to Bottrell et al. (1976). Zooplankton community phosphorus excretion rate was calculated by applying the regression equations of Ejsmont-Karabin (1984) to enumerated and measured samples and measured water temperatures. The formulae for the three main zooplankton taxa were:

- for rotifers: $E_p = 0.154 W^{-1.27} e^{0.096T}$
- for cladocerans: $E_p = 0.519 W^{-0.23} e^{0.039T}$
- for copepods: $E_p = 0.299 W^{-0.645} e^{0.039T}$,

where E_p = phosphorus excretion rate ($\mu\text{gP mg DW}^{-1} \text{ h}^{-1}$), W = individual dry weight ($\mu\text{g DW}$), and T = water temperature ($^{\circ}\text{C}$).

Samples for phytoplankton and chlorophyll *a* analyses were taken from the water surface layer. Phytoplankton quantitative analyses (both counts and

measurements) were made from samples fixed with Lugol's solution in 5 ml settling chambers, under an inverted microscope (magnification 400×), after 24 h sedimentation. Phytoplankton biomass was calculated by multiplying taxon abundance by the average volume of one specimen of each taxon. Volume was estimated by applying the most similar geometric formula (Hindak 1978; Wetzel, Likens 2000). Chlorophyll *a* was assessed following the Lorenzen method after extraction in acetone and corrected for phaeopigment *a* (Wetzel, Likens 2000). Data describing phytoplankton (abundance, biomass and chlorophyll *a*) will be published in a separate paper (Kowalczevska-Madura 2005). Phytoplankton showed seasonal changes, with maxima typically found in spring and summer. Timing of these maxima, however, differed amongst phytoplankton measures. For example, phytoplankton abundance reached its maximum (61,300 specimens ml⁻¹) in May 2001, when biomass and chlorophyll *a* were at their mean values (35.8 mg l⁻¹ and 34.7 µg l⁻¹, respectively). Maximal biomass (99.5 mg l⁻¹) and chlorophyll *a* (97 µg l⁻¹) were found in August 2002, during a period of low phytoplankton density (10,900 specimens ml⁻¹). The differences in seasonal changes between phytoplankton variables resulted in our using all of them to characterise phytoplankton community dynamics in the canonical analysis and redundancy analysis.

External loading was calculated every two weeks by multiplying total phosphorus concentration by water discharge in the two tributaries (Kowalczevska-Madura 2003). Internal loading was evaluated using *ex situ* experiments with intact cores of bottom sediments, sampled at 6 stations within the lake basin. Stations were selected to represent diverse lake conditions according to depth, oxygenation of sediments and distance from the shoreline. Experiments were conducted every season under laboratory conditions, taking into account the temperature and oxygen concentration of water present in the lake (Kowalczevska-Madura 2005).

To estimate the significance of changes in the zooplankton phosphorus excretion rate along a vertical profile, an ANOVA test with Tukey's post-hoc test was used (STATISTICA software, version 7.1). The same test was applied to estimate the difference in phosphorus excretion between the zooplankton groups. Canonical correlation analysis (STATISTICA version 7.1) was used to assess the importance of phosphorus supply from three sources (external loading, internal loading from sediments, and zooplankton excretion) in relation to measures of phytoplankton abundance. All analysed data were transformed to a normal distribution. The total redundancy index is very important in this analysis, as it allows us to estimate how much of the variability in one set of parameters (here the phytoplankton related data) is explained by the other (sources of phosphorus). Additionally, RDA analysis was applied (using

CANOCO 4.5 software) to assess more thoroughly the changes in phytoplankton data along the environmental gradients. Because the gradient length of our environmental data was short (0.701), the redundancy analysis (RDA) was selected over canonical correspondence analysis (CCA), as suggested by ter Braak and Šmilauer (2002). The aim of the analysis was to assess the strength and sign of the relationship between the two sets of variables. We assumed that particular sources of phosphorus should have different influences on phytoplankton abundance, as their impact varied seasonally.

RESULTS

Monthly zooplankton phosphorus excretion rates showed marked seasonal variation (Fig. 1). Rates were much higher from spring through autumn than during winter, when they sometimes decreased to zero (Fig. 1). Zooplankton

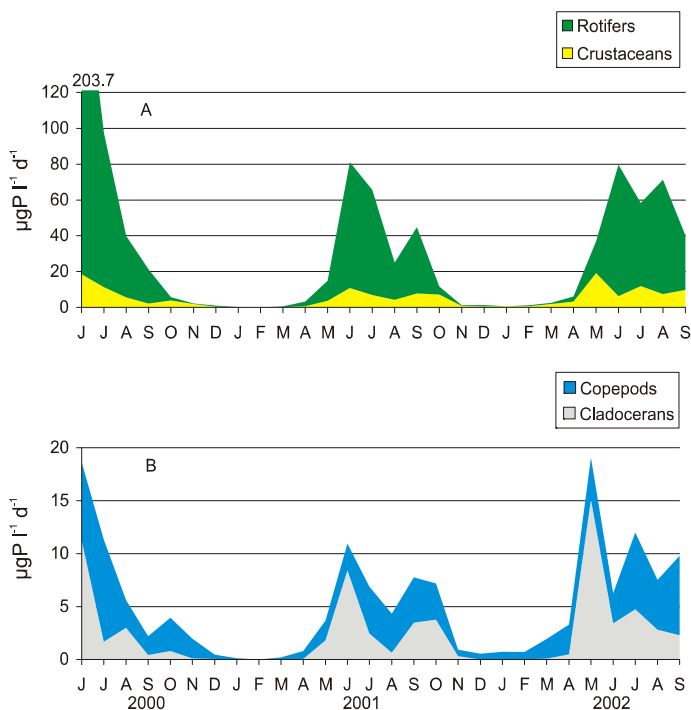


Fig. 1. Seasonal patterns of phosphorus excretion rates (mean values over the vertical profile) of (A) rotifer and crustacean zooplankton, and (B) cladocerans and copepods, in Swarzędzkie Lake in 2000-2002.

excretion rates were greatest overall in June with the highest calculated excretion rate in June 2000 ($203.7 \mu\text{gP l}^{-1} \text{d}^{-1}$). Zooplankton community excretion rates were dominated by rotifers. For example, in June 2000 rotifers were responsible for $185 \mu\text{gP l}^{-1} \text{d}^{-1}$ (Fig. 1). In 2001-2002, zooplankton phosphorus excretion was lower and generally did not exceed $80 \mu\text{gP l}^{-1} \text{d}^{-1}$ for the zooplankton community, or $70 \mu\text{gP l}^{-1} \text{d}^{-1}$ for the rotifers (Fig. 1).

Along a depth profile of the Swarzędzkie Lake, the highest rate of phosphorus excretion was usually observed at a depth of 1 m, which was due mainly to the vertical distribution of rotifers. However, statistically significant differences were observed only between 1 m and 5 or 6 m.

For cladocerans, calculated phosphorus excretion rates ranged from 0 to $15.1 \mu\text{gP l}^{-1} \text{d}^{-1}$, reaching the highest values in spring (maximum in May 2002). In other seasons, cladoceran excretion rates did not exceed $10.0 \mu\text{gP l}^{-1} \text{d}^{-1}$ (Fig. 1). In the vertical profile, the greatest values for cladocerans were observed at 2 m, although the differences between samples from particular depths were statistically non-significant.

For copepods, the maximum phosphorus excretion rate ($9.6 \mu\text{gP l}^{-1} \text{d}^{-1}$) was calculated in July 2000. In all years, copepod excretion rates were the greatest from spring through autumn, and in winter they did not exceed $1.0 \mu\text{gP l}^{-1} \text{d}^{-1}$ (Fig. 1). Along a depth profile, copepod excretion rate peaked at 3 m, however, statistically significant differences between the depths were observed only between 1 m and 6 m as well as 3 m and 6 m.

Comparison of the mean phosphorus excretion rate between analysed zooplankton groups showed that rotifers excreted 10 times more than both cladocerans and copepods ($F = 37.88$, $p < 0.0001$, $n = 170$). No statistical difference was found between cladocerans and copepods (Fig. 2).

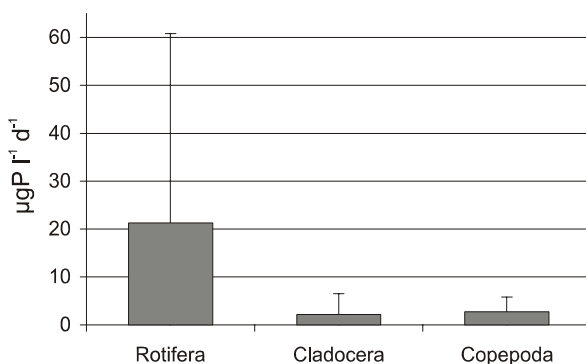


Fig. 2. Comparison of rotifer, cladoceran, and copepod phosphorus excretion rates (means and standard deviations; $n = 170$).

The mean zooplankton community phosphorus excretion rate for the study period was $26.6 \mu\text{gP l}^{-1} \text{d}^{-1}$ (Table 1). The community excretion rate exceeded both the external loading from tributaries (mean $3.9 \mu\text{gP l}^{-1} \text{d}^{-1}$; Kowalczevska-Madura 2003) and the internal loading from bottom sediments ($4.0 \mu\text{gP l}^{-1} \text{d}^{-1}$; Kowalczevska-Madura 2005). Zooplankton community excretion dominated the supply of phosphorus from spring through autumn while external loading was greatest in winter (Fig. 3).

Table 1

Zooplankton phosphorus excretion rates by taxon and season in Swarzędzkie Lake from June 2000 through September 2002 ($\mu\text{gP l}^{-1} \text{d}^{-1}$)

Group	Spring (Mar–May)	Summer (Jun–Aug)	Autumn (Sep–Nov)	Winter (Dec–Feb)	Annual Mean
Rotifers	5.93 ± 6.98	70.95 ± 47.34	10.46 ± 14.82	0.36 ± 0.34	21.93 ± 35.65
Cladocerans	2.92 ± 6.01	4.27 ± 3.43	1.48 ± 1.67	0.02 ± 0.02	2.17 ± 2.19
Copepods	1.9 ± 1.37	5.0 ± 2.52	2.52 ± 1.34	0.41 ± 0.3	2.46 ± 2.07
Total	10.75 ± 2.09	80.22 ± 38.28	14.46 ± 4.91	0.79 ± 0.21	26.56 ± 13.5

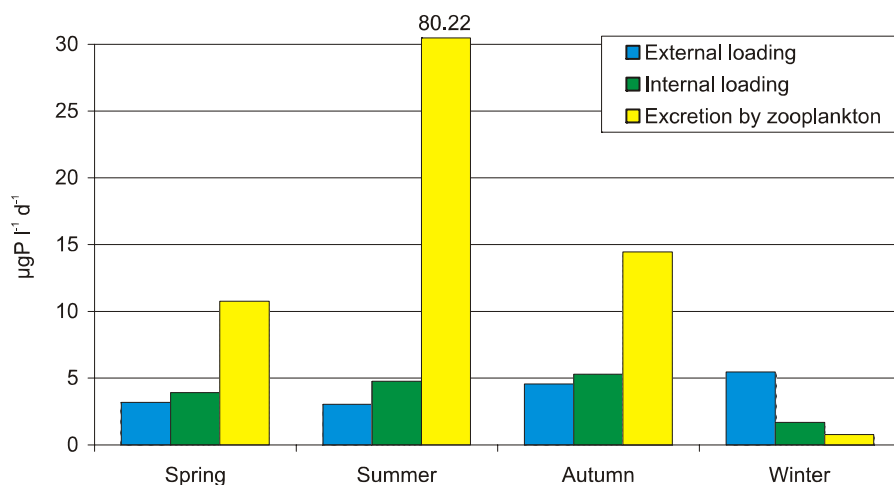


Fig. 3. Seasonal mean phosphorus input into Swarzędzkie Lake due to external loading, internal phosphorus loading from the sediments (Kowalczevska-Madura 2005), and mean calculated zooplankton community phosphorus excretion during the study period.

Canonical analysis of Swarzędzkie Lake plankton data showed that phosphorus excreted by zooplankton alone had a weak influence on the phytoplankton community. Zooplankton phosphorus excretion explained only 20% of the total variance in describing phytoplankton community parameters, i.e. abundance, biomass, and chlorophyll *a* (Table 2). Moreover, zooplankton phosphorus excretion was not statistically significant ($p = 0.17$). Phytoplankton community parameter variance was better explained by a canonical variable that accounted for external loading and internal loading from the sediments (total redundancy index 25.5%; Table 2). Phytoplankton community parameter dynamics also were explained much better by the canonical variable comprised of internal loading from the sediments and zooplankton phosphorus excretion (32.8%; Table 2). Both internal loading from the sediments and zooplankton excretion were temperature dependent and had the highest values in warm seasons, and therefore, they were complementary variables. As a result, their joint influence on phytoplankton community parameters was greater than external and internal loading from the sediments combined (Table 2).

Table 2

Canonical correlation analysis of variables relating to phosphorus loading (left set) and phytoplankton community parameters (density, biomass and chlorophyll *a*; right set) (No. of valid cases = 26)

Canonical Variables – left set	Canonical <i>R</i>	<i>p</i>	Total redundancy (%)
External loading	0.233	0.741	5.41
Excretion by zooplankton	0.447	0.171	19.98
External and internal loading	0.683	0.028	25.52
Internal loading and excretion by zooplankton	0.677	0.026	32.80

RDA analysis demonstrated that external and bottom sediment loading were negatively correlated (opposed to the EXT and INT vectors, Fig. 4). The analysis also confirmed the correlation of internal loading from the sediments with zooplankton phosphorus excretion (acute angle between INT and ZOO vectors). The most interesting result from the RDA analysis was, however, that the influence of particulate sources of phosphorus on different phytoplankton communities was clearly indicated. External loading primarily influenced phytoplankton variables during spring and winter months, internal loading from sediments – during late summer (August and September), while zooplankton excretion influenced phytoplankton variables in early summer (June and July). It is also important that the influence of zooplankton-excreted phosphorus on phytoplankton growth in early summer is greater than the influence of

phosphorus released from bottom sediments on late summer phytoplankton (longer ZOO than INT vectors on Fig. 4). In contrast, external loading had the lowest direct influence on phytoplankton variables (the shortest EXT vector on Fig. 4).

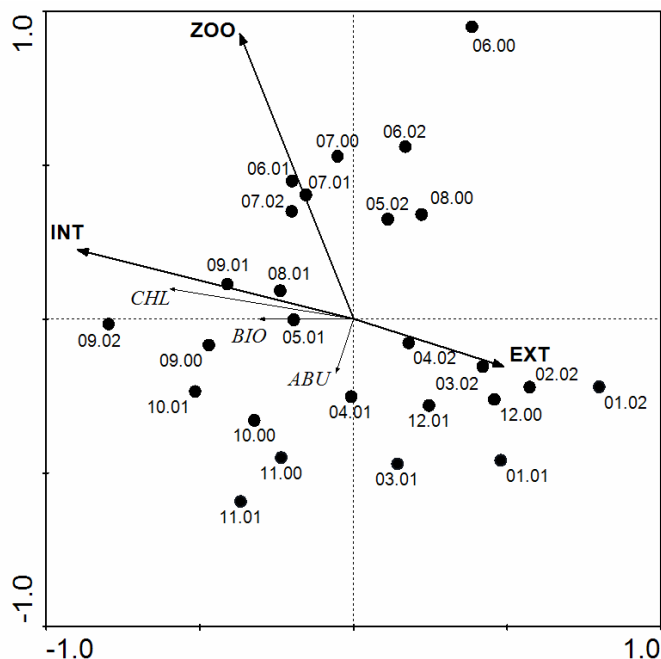


Fig. 4. Redundancy analysis biplot of phytoplankton data from 26 dates (black circles labelled with month and year, and thin vectors) and environmental data (black vectors). Acronyms: ZOO – phosphorus excreted by zooplankton, INT – phosphorus released from bottom sediments, EXT – external load of phosphorus, ABU – density of phytoplankton, BIO – biomass of phytoplankton and CHL – values of chlorophyll a.

DISCUSSION

The greatest zooplankton phosphorus excretion rate in Swarzędzkie Lake, which was noted in early summer 2000, coincided with the highest density of zooplankton (Kowalczevska-Madura 2005). At this time rotifers were particularly important due to their considerable phosphorus excretion rates, small sizes, and high densities (up to 18,000 specimens l^{-1}). In comparison with

other published data, the study lake had high zooplankton phosphorus excretion rates (Gulati et al. 1989; Ejsmont-Karabin et al. 1995; Ejsmont-Karabin et al. 1996a, 1996b; Arhonditsis et al. 2004; Ejsmont-Karabin et al. 2004). However, an even higher rate was observed in Lake Łuknajno (Northeastern Poland), where values up to $400 \mu\text{gP l}^{-1} \text{d}^{-1}$ were calculated for rotifers (Ejsmont-Karabin et al. 1995). The cladoceran excretion rate in the same lake did not exceed $80 \mu\text{gP l}^{-1} \text{d}^{-1}$, but this value was still over five times higher than the highest found in Swarzędzkie Lake. Copepod excretion rates were similar in Lake Łuknajno and in Lake Swarzędzkie: in both lakes it was lower than $10 \mu\text{gP l}^{-1} \text{d}^{-1}$ (Ejsmont-Karabin et al. 1995). In Lake Kujno (Northeastern Poland), calculated phosphorus excretion rates were rather low, ranging from 1.8 to $36.0 \mu\text{gP l}^{-1} \text{d}^{-1}$ (Ejsmont-Karabin et al. 1996b). Due to the marked dominance of rotifers in the zooplankton community of the Pierzchalski Reservoir (Northern Poland), the contribution of this group to the total phosphorus excretion by zooplankton was very high, sometimes exceeding 90% (Bowszys 2003). This value was similar to the mean value found in Swarzędzkie Lake (81.6%). A large portion of the phosphorus supply in Lake Washington (USA) was contributed by zooplankton excretion during the summer months (Arhonditsis et al. 2004), as was found in Swarzędzkie Lake.

The zooplankton community excretes a large amount of nutrients, possibly eliminating nutrient deficiency for phytoplankton and bacteria within the lake ecosystem. Zooplankton excretion does not provide a new phosphorus source but only transforms particulate phosphorus into a soluble form (Kajak 1998). Soluble nutrient forms are more available for phytoplankton use and, therefore, zooplankton excretion-derived phosphorus can be an important contributor to phytoplankton growth in a lake (Gulati et al. 1989). During summer stratification, zooplankton nitrogen and phosphorus is often the main source of nutrients for phytoplankton (Lampert, Sommer 2001). Ejsmont-Karabin et al. (1996a) reported, however, that phytoplankton biomass is sometimes negatively correlated with the rate of phosphorus excretion by zooplankton in the pelagic zone. This finding is correlated with food accessibility for zooplankton. In mesotrophic and slightly eutrophic lakes dominated by nanoplankton, top-down pressure of zooplankton is often observed, as explained by biomanipulation theory (Shapiro et al. 1975, Meijer 2000, Tonno et al. 2003). This reduction of phytoplankton biomass may be achieved not only by large specimens but also by numerous small species (e.g. rotifers), simultaneously increasing excreted phosphorus in the water column (Ejsmont-Karabin et al. 2004). On the contrary, in eutrophic lakes, in which rotifers usually dominate over large cladocerans, selective grazing of small phytoplankton species is observed and simultaneous phosphorus excretion promotes the growth of colonial or filamentous cyanobacteria (Haney 1987; Kozak, Gołdyn 2004).

Phosphorus excreted by zooplankton can be sequestered not only by algae but also by bacteria, which reduces its availability to phytoplankton (Jansson et al. 1999). The studies of Currie and Kalff (1984) have shown that bacteria are superior competitors for phosphorus in comparison to phytoplankton. Klug (2005) showed, however, that this competitive dominance depends on colored dissolved organic matter concentrations (DOM) and therefore may be more important in humic lakes. In eutrophic lakes, which are not phosphorus but carbon-limited, bacteria can stimulate phytoplankton growth by respiration of extracellular DOM released by phytoplankton, in turn providing phytoplankton with an inorganic carbon source (Klug 2005). Under eutrophic conditions protozoans may play an important role (both ciliates and heterotrophic nanoflagellates), because of their bacterivory and nutrient recycling (Fenchel 1987, Dolan 1997, Ejsmont-Karabin et al. 2004).

Statistical analysis demonstrated that phosphorus excreted by zooplankton stimulated phytoplankton growth primarily in the early summer season. In other seasons a greater influence is exerted by external loading and phosphorus released from bottom sediments. Following expectations, the maximum value of phosphorus loading from each source was found to occur in different seasons. The influence of zooplankton-excreted phosphorus on phytoplankton in early summer is greater than that of phosphorus released from bottom sediments on late summer phytoplankton. This result can be explained by small phosphorus supply from the catchment and sediments during June and July (Kowalczevska-Madura 2005), making zooplankton excretion the main phosphorus source at that time. During late summer months both internal sources were synergistic; however, RDA analysis indicated that phosphorus released from bottom sediments was the most important. That external loading had the lowest direct influence on phytoplankton variables was unexpected, even at the time of its maximum values. Although the nutrient load transported to the lake with tributaries in early spring was large (Kowalczevska-Madura 2003), it was not exploited by phytoplankton as intensively as in the summer season. Such factors as light, the temperature gradient and increased flushing rate limited phytoplankton growth in early spring (Lampert, Sommer 2001). The bulk of the phosphorus load that supplied the lake at that time was not exploited by phytoplankton but rather was trapped in bottom sediments (Kowalczevska-Madura 2003). This phosphorus was used by phytoplankton primarily during summer, after being made available in the water column through internal loading from the sediments.

In conclusion, we found that the phosphorus excretion rate in shallow and eutrophic Swarzędzkie Lake was high from spring through autumn and was about 10 times greater for rotifers than for both cladocerans and copepods. The mean zooplankton phosphorus excretion rate was greater than other phosphorus

sources: its mean value was $26.6 \mu\text{gP l}^{-1} \text{ d}^{-1}$, while that from external sources was $3.9 \mu\text{gP l}^{-1} \text{ d}^{-1}$ and from bottom sediments $4.0 \mu\text{gP l}^{-1} \text{ d}^{-1}$. However, our results also showed that zooplankton community phosphorus excretion alone did not exert substantial direct control on phytoplankton density and biomass throughout the year. Zooplankton-excreted phosphorus exerts an important influence on phytoplankton growth mainly during the early summer season (June and July). One third of the variance in phytoplankton community parameters could be explained, however, by the combined effects of internal loading from the sediments and zooplankton community excretion.

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