ROLE OF PSAMMON MICROINVERTEBRATES IN PHOSPHORUS CYCLING IN HYDROARENAL OF AN EUTROPHIC LAKE

ABSTRACT: Inorganic phosphorus released from littoral bottom sediments plays significant role in phosphorus budget of a whole ecosystem. An aim of the study was to assess a role of small invertebrates in phosphorus remineralization in hydroarenal (See Fig.1 in Preface). Hydropsammon organisms (i.e. bacteria, algae, ciliates, rotifers and crustaceans) living in a layer of submerged sands along the edge of a lake (=hydroarenal) were studied in psammonlittoral of the deep, eutrophic Lake Mikolajskie (North-eastern Poland) in 2005. Sampling cores were taken at a station 1.5 m from water’s edge once or twice a month since April until October 2005. Each time three samples were taken: 5-cm thick water layer (AWL – adjacent water layer), 0.5-cm thick layer of water and sand from the transitory level (EPIH – epihydroarenal) and 2-cm thick slice of sand (ENDOH – endohydroarenal). The rate of phosphorus excretion was calculated using the appropriate regression equations expressing the relation between individual weight of organism and P excretion adjusted to the ambient temperature.

Phosphorus remineralization by the psammon community (calculated for all ciliates, rotifers and crustaceans) was ca. 10 times higher than the maximum rate noted in lake pelagial. The most important role in the process was played by small ciliates, and in periods of high remineralization rate – by small cladocerans. Omnivores, feeding mostly on bacteria and small algae, played the most important role in all three studied layers, especially in periods of the highest rate of P remineralization, thus all kinds of food were used and mineralized. Predators do not seem to play significant role in P remineralization. In hydroarenal significant role seems to be played by processes involved in microbial loop. This suggestion is supported by strong domination of ciliates, main consumers of nanoflagellates, in the process of P remineralization. It seems that phytopsammon and psammic bacteria demands for phosphorus cannot be satisfied merely through the in situ remineralization by microinvertebrates.

KEY WORDS: eutrophic lake, hydropsammon, phosphorus remineralization

1. INTRODUCTION

Littoral zone of lakes is rarely taken into consideration in descriptions of phosphorus cycling in lake ecosystems, although, especially in small water-bodies, phosphorus released from littoral bottom sediments may play significant role in phosphorus budget of a whole ecosystem (Twinch and Peters 1984). It has been also shown that P remineralized in the littoral zone may be transported into pelagial due to nighttime convective circulation (James and Barko 1991a). Benthic algae may modify the exchange of phosphorus between sediment and water and reduce,
in that way, phosphorus pool available for planktonic primary production (Andersen 1997). Epipelic algae have an impact on phosphorus release from sediments through formation of oxic conditions in the upper few millimeters during day and anoxic conditions at night (Carlton and Wetzel 1988). Despite of the importance of benthic algae in nutrient budgets of littoral habitats, their role in lakes is poorly understood relative to the communities in streams or phytoplankton in lakes (Squires and Lesack 2001).

Shallow sandy sediments usually have a thin crust of algae, which are heavily grazed and/or efficiently decomposed (Vadeboncoeur et al. 2006). These dense epipelic mats are characterized by high area-specific primary productivity (Krause-Jensen and Sand-Jensen 1998). It means that phytosammon demands for orthophosphates should be also very high, whereas it has been shown that psammon rotifers do not play a substantial role in delivering remineralized phosphorus into the littoral zone of Mikołajskie Lake (Ejsmont-Karabin 2001). However, psammon involves also other organisms, like ciliates and crustaceans (Kalinowska et al. 2010), which may be more important in the process. Thus, the role of small invertebrates in P release from littoral sediments is still not clear. Taking into account that the upper 0.5 cm microlayer of sand (i.e. epihydroarenal) is occupied by very dense rotifer communities (Ejsmont-Karabin 2008), one may assume that the role of these psammon organisms in phosphorus remineralization should be rather high. Also epibenthic crustaceans seem to occur in higher densities than pelagic ones, as it has been found by Papińska and Prejs (1979), Papińska and Pijanowska (1980), Papińska (1981), Nalepa and Quigley (1985) and Kalinowska et al. (2010).

A lack of a relationship between epipellic chlorophyll content and water-column nutrient concentrations was noticed by Hagerthey and Kerfoot (1998) and Vadeboncoeur and Lodge (2000). The lack may be a result of high availability of nutrients in the interstitial waters (Vadeboncoeur et al. 2006).

The aim of our study was to estimate a role of small invertebrates (ciliates, rotifers and crustaceans) in phosphorus remineralization in hydroarenal.

2. METHODS

Seasonal dynamics of hydropsammon bacteria, nanoflagellates, algae, ciliates, rotifers and crustaceans was studied in three microzones of psammolittoral of the eutrophic Lake Mikołajskie (North-eastern Poland) once or twice a month since April till October 2005.

Sampling cores were taken at a station 1.5 m from water’s edge with a 7.3 cm diameter plastic tube. On each occasion three samples were taken: 5-cm thick water layer (AWL – adjacent water layer), 0.5-cm thick layer of water and sand from the transitory level (EPIH – epihydroarenal) and a deeper 2-cm thick slice of sand (ENDOH – endohydroarenal).

Abundance and biomass of bacteria and heterotrophic nanoflagellates (HNF) were measured in subsamples stained with DAPI (Porter and Feig 1980), filtered through a 1.2 μm pore-size black polycarbonate membrane filters (Millipore), and enumerated by epifluorescence microscopy. HNF biovolume was calculated from measurements of cells and approximations to simple geometrical forms.

For ciliate and algae abundance and biomass samples were examined with light microscope (Nikon Optiphot 2). Biovolume was calculated from measurements of cell dimensions and simple geometric shapes. Methods described by Foissner and Berger (1996) were used to calculate the body weight in ciliates.

Rotifers were determined from sand samples shaken six times with 0.5 l of tap water. The supernatant was filtered through a net with 30 μm mesh-size. Crustaceans were determined from sand samples after swilling them with water infiltrating particular layers. The sampling tube was placed in aquarium filled with tap water, which was infiltrating the sand core from the bottom upwards. The length : wet weight relationship was used to derive the mean body weight of individuals of particular crustaceans (Bottrell et al. 1976) and rotifers (Ejsmont-Karabin 1998).

The rate of phosphorus excretion by ciliates was assessed using the regression equation:
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\[ E = 0.000226 e^{0.096T} W^{0.515}, \]

where: \( E \) = excretion rate in μg P ind.\(^{-1}\) h\(^{-1}\), \( T \) = temperature in °C; \( W \) = dry weight in μg (Bownick-Dylińska 1981).

The remaining formulas used to calculate the excretion rate were:

\[ E = 0.0154 e^{0.096T} W^{-1.27} \] for rotifers
\[ E = 0.519 e^{0.039T} W^{-0.239} \] for cladocerans and
\[ E = 0.299 e^{0.039T} W^{0.647} \] for copepods,

where: \( E \) = excretion rate in μg P mg DW\(^{-1}\) h\(^{-1}\), \( T \) = temperature in °C; \( W \) = dry weight in μg (Ejsmont-Karabin 1984).

3. RESULTS

3.1. Abundance of psammon communities

A comparison of mean biomass of a potential food and its consumers (Table 1) indicates that the main source of food for psammon consumers is phytopsammon. It constitutes 98% of food resources in epihydroarenal and 96% in endohydroarenal. The main trophic group of consumers are omnivores, which constitute 76% of consumer biomass in EPIH and 70% in ENDOH. In total, the ratio of the biomass of a potential food to the biomass of its consumers is 2.4 in AWL, 11.9 in EPIH and 39.7 in ENDOH. Thus, in general, the pressure of consumers is weaker in arenal than adjacent water layers.

3.2. Phosphorus remineralization by hydropsychon communities of microinvertebrates

3.2.1. Role of ciliates, rotifers and crustaceans in the process

Phosphorus excretion rate by psammon community created by ciliates, rotifers and crustaceans was very high, ca. 10 times higher than the rate noted in lake pelagial (Ejsmont-Karabin et al. 1983) and reached up to 6.93 mgP m\(^{-2}\) 24 h\(^{-1}\) in September. The mean excretion rate by AWL communities was lower and accounted for 2.58 ± 0.01 mgP m\(^{-2}\) 24 h\(^{-1}\) whereas the rate by psammon communities was 3.34 ± 2.21 mgP m\(^{-2}\) 24 h\(^{-1}\). However the maximum value of the rate for AWL communities was 2.5 times higher (17.40 mg P m\(^{-2}\) 24 h\(^{-1}\) in June) than the maximum rate of P excretion in hydroarenal (Fig. 1). The taxonomic group deciding on this high rate of P remineralization in AWL were crustaceans which excreted 97% of phosphorus remineralized in the layer. Phosphorus remineralization rate in epihydroarenal was markedly higher than in the endohydroarenal and it increased during the vegetation season (Fig. 1).

The most important role in the process of phosphorus remineralization was played by small ciliates (Fig. 2), which remineralized from 9.3 to 100% (mean 57.0 ± 31.9%) in AWL and from 75.0 to 100.0% (mean 91.5 ± 9.3%) in hydroarenal (EPIH + ENDOH). Such a strong domination of the community in the processes of P remineralization in both

Fig. 1. Phosphorus excretion rate (mg m\(^{-2}\) 24 h\(^{-1}\)) by three taxonomic groups of zooplankton in adjacent water layer (AWL), and zoopsammon in epihydroarenal (EPIH) and endohydroarenal (ENDOH) in a psammolittoral of Lake Mikołajskie.
hydroarenal layers was expected taking into account relatively high biomass (Table 1, Kalinowska et al. 2012) and small body size of these animals. In summer crustaceans played relatively significant role, especially in AWL where they excreted to 97.0% (77.4% in average) of the remineralized phosphorus. Relatively high role played by crustaceans, higher than that of the psammon rotifers was rather unexpected. Rotifer participation in phosphorus remineralization process was slightly higher in endohydroarenal, but even there it was extremely low and reached up to 13.2% (5.3% in average) (Fig. 2).

3.2.2. Sources of remineralized phosphorus, i.e. role of different trophic groups of zooplankton and zoopsammon in the process

Role of different food sources was assessed from data on nutrient remineralization by different trophic groups of Ciliata, Rotifera and Crustacea. It was assumed that about half of the food consumed is assimilated (Olsen and Ostgaard 1985), thus the rate of food consumption, if expressed in phosphorus units, would be nearly twice the rate of P remineralization.

The main group of psammon consumers were omnivores, feeding mostly on bacteria and algae. They played very important role in phosphorus remineralization in all three studied layers (Figs 3 and 4). Their role was the highest in AWL, especially at the beginning of June, when they excreted 17.00 mg P m$^{-2}$ 24h$^{-1}$, i.e. 97.7% of the total phosphorus remineralized at that time. The mean share of omnivores in P remineralization during the season was also highest in AWL (82.4%), and markedly lower in EPIH and ENDOH layers (54.9 and 56.4%, respec-

<table>
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<th>AWL</th>
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<th>ENDOH</th>
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<tbody>
<tr>
<td>Bacteria</td>
<td>77.8</td>
<td>25.2</td>
<td>109.2</td>
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<tr>
<td>NF</td>
<td>18.4</td>
<td>6.8</td>
<td>13.2</td>
</tr>
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<td>Phytopsammon</td>
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<td>1760.2</td>
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</tr>
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<td>Bacterivores</td>
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<td>5.9</td>
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</table>

Fig. 2. The contribution (%) of three taxonomic groups of zooplankton to the rate of phosphorus remineralization in adjacent water layer (AWL), and zoopsammon in ephiphydroarenal (EPIH) and endohydroarenal (ENDOH) in a psammolittoral of Lake Mikolajskie.

Table 1. Mean annual biomass (in mg m$^{-2}$) of organisms inhabiting microzones of psammolittoral in Lake Mikolajskie. AWL – adjacent water layer, EPIH – ephiphydroarenal, ENDOH – endohydroarenal (Kalinowska et al. 2012).
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The role of bacteriophages in P remineralization was most important in spring and autumn in AWL, whereas in both arenal layers bacteria were consumed mostly in April–May (Fig. 3). Alga-feeders remineralized phosphorus mostly in summer months. Their role in P remineralization was rather low in AWL (mean for the season 0.16 ± 0.07 mg m⁻² 24 h⁻¹, i.e. 6.5% of the total P remineralization rate). Phytopsammon seems to be better consumed, as algal-P remineralization constituted 25.0 and 24.1% of the total P remineralization in EPIH and ENDOH layers, respectively. Predators do not seem to play important role in P remineralization. Their contribution to the process is well seen in hydroarenal and nearly negligible in AWL.

Turnover time of phosphorus involved in biomass of bacteria and algae was different in the studied layers and it strongly fluctuated during the season. Bacteria were under the highest pressure by bacteriophagous zooplankton in epihydroarenal as turnover time (TT) of bacterial phosphorus due to consumers' activity was there ca. 5 hours, thus 12 times lower than that for EPIH phytopsammon (Fig. 5). Turnover time for both bacteria- and phytopsammon phosphorus was markedly higher in AWL with mean values 21 and 198 hours, respectively. Mean TT accounted for ca 35 hours for bacteria and 106 hours for phytopsammon in endohydroarenal.

4. DISCUSSION

Most studies on internal P loading from the littoral zone have shown that littoral sediment may play an important role in the P cycling, perhaps more important than sediments from the profundal zone (Andersen and Ring 1999). Liu et al. (2008) showed that
algae, which accumulate in the littoral zones, affect the biogeochemical cycle of phosphorus in eutrophic lakes. They also suggested that the transformations of P compounds in the zones result in a partial release of the accumulated P to the overlying water. Uptake and release of phosphate in littoral sediments is influenced by the season and by light-dark changes and mechanical perturbation (Gerhardt et al. 2010). Among factors influencing the P cycle in the littoral zone there are listed macrophytes, which may increase sedimentation and lower resuspension (Graneli and Solander 1988), and thus may conserve nutrients (Wetzel 1990).

A role of psammon microinvertebrates in phosphorus cycling is less known. Studies by Ejsmont-Karabin (2001) on psammon communities of Lake Kuc showed that remineralization of phosphorus by psammon rotifers may have some importance for P cycling in the littoral zone, but the process plays insignificant role in the whole lake phosphorus budget. However, our results show that rotifers seem to play less significant role than the remaining groups of microinvertebrates. Rotifers constituted 7% of the biomass of epiphydromon microinvertebrates and 27% of the endohydromon ones (Kalinowska et al. 2012). The rotifer role in P remineralization by psammon microinvertebrates was even lower (Figs 1 and 2).

Processes of consumption and remineralization of nutrients are concentrated in a thin layer of epiphydromon, thus in a zone of accumulation of the organic matter settling and, at the same time, high rate of primary production. Primary production rate in the layer is extremely high and markedly higher than that observed in phytoplankton (Krupa et al. 1991, Czernas et al. 1991). As a result phytopsammon assimilate more phosphorus than phytoplankton (Wojciechowski et al. 1991).

The rates of P release from littoral sediments, based on James and Barko (1991b) studies in Eau Galle Reservoir (Wisconsin), averaged 3.6 mg m\(^{-2}\) 24 h\(^{-1}\). These data are in close agreement with our results, as the mean for season rate of P remineralization by psammon organisms was 3.34 mg m\(^{-2}\) 24 h\(^{-1}\). The rate of phosphorus assimilation by hydropsammon in Lake Piaseczno (Czernas 2003) was relatively high and markedly higher in summer (24.5 mg m\(^{-2}\) 24 h\(^{-1}\)) and lower in spring (12.0 mg m\(^{-2}\) 24 h\(^{-1}\)). The rate of phosphorus remineralization by hydropsammon organisms in Lake Mikolajskie was also higher in summer (6.4 mg m\(^{-2}\) 24 h\(^{-1}\)) than in spring (1.9 mg m\(^{-2}\) 24 h\(^{-1}\)). However, the fact is worth emphasizing that in mesotrophic, less productive Lake Piaseczno the assimilation rate of phosphorus was many times higher than the rate of P remineralization in hydroare-
Phosphorus remineralization by psammon organisms. It means that phytopsammon and psammic bacteria demands probably cannot be satisfied merely from internal sources, i.e. through the remineralization by microinvertebrates. According to Czernaś (2003) phytopsammon plays a significant role in drawing and capturing nutrients being washed out from the catchment area into the lake. This conclusion is supported with extremely high turnover time for algal phosphorus in hydroarenal of Lake Mikołajskie (Fig. 5). However, Czernaś (2003) did not study bacterial uptake of phosphorus. Taking into account much lower turnover time for phosphorus involved in the biomass of bacteria we can suppose that bacteria play much more important role than phytopsammon in lake arenal. Thus, it may be concluded that in hydroarenal, and especially in its upper layers, significant role is played by processes involved in so-called microbial loop. This suggestion is also supported by strong domination of ciliates, main consumers of bacteria and nanoflagellates, in the process of P remineralization.

5. REFERENCES


Ejsmont-Karabin J. 1984 – Phosphorus and nitrogen excretion by lake zooplankton (rotifers and crustaceans) in relationship to individual body weights of the animals, ambient temperature and presence or absence of food – Ekol. pol. 32: 3–42.


Foissner W., Berger H. 1996 – A user-friendly guide to the ciliates (Protozoa, Ciliophora), commonly used by hydrobiologists as bioindicators in rivers, lakes, and waste waters, with notes on their ecology – Freshwat. Biol. 35: 375–482.


Papińska K., Prejs K. 1979 – Crustaceans of the near-bottom water and bottom sediments in 24 Masurian lakes with special consideration to cyclopoid copepods – Ekol. pol. 27: 603–624.


Received after revision March 2012