Phosphorus release of metazoan zooplankton in two bays with different trophic status in Lake Taihu (China)

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ABSTRACT

The contribution of metazoan zooplankton to internal phosphorus (P) cycling was investigated in Meiliang and Wuli Bays of Lake Taihu, a eutrophic, shallow lake in China by determining biomass and biomass specific P release rates. The zooplankton community of eutrophic Meiliang Bay was dominated by cladocerans, particularly Daphnia spp. and copepods, while dominant groups in hypereutrophic Wuli Bay included rotifers, copepods, and cladocerans. Release rates of PO$_3^{−}$-P ranged from 0.20 to 0.57 mg·g$^{-1}$·h$^{-1}$ in Meiliang Bay and 0.20 to 0.76 mg·g$^{-1}$·h$^{-1}$ in Wuli Bay. In most cases, P release rates were higher in Wuli Bay than Meiliang Bay. Phosphorus fluxes from zooplankton excretion varied from 5.34 to 57.41 mg·m$^{-2}$·d$^{-1}$ in Meiliang Bay and 8.20 to 70.02 mg·m$^{-2}$·d$^{-1}$ in Wuli Bay. Since P released by zooplankton in this study was in a form available to phytoplankton, zooplankton may represent a significant source of P contributing to high phytoplankton biomass in Lake Taihu.

RÉSUMÉ

Rejet de phosphore par le zooplancton métazoaire dans deux baies d’état trophique différent du lac Taihu (Chine)

Mots-clés : lac Taihu, lac subtropical, zooplancton métazoaire, rejet de phosphore

La contribution du zooplancton métazoaire à la circulation du phosphore interne (P) a été étudiée dans les baies Meiliang et Wuli du lac Taihu, un lac eutrophe, peu profond en Chine, par la détermination de la biomasse et les taux de libération de P par biomasse spécifique. La communauté du zooplancton de la baie eutrophe Meiliang a été dominée par les cladocères Daphnia spp, en particulier, et des copepodes, tandis que les groupes dominants dans la baie hypereutrophe Wuli comprenaient des rotifères des copepodes, et des cladocères. Les taux de libération de PO$_3^{−}$-P variaient de 0,20 à 0,57 mg·g (poids sec)$^{-1}$·h$^{-1}$ dans la baie Meiliang et de 0,20 à 0,76 mg·g$^{-1}$·h$^{-1}$ dans la baie Wuli. Dans la plupart des cas, les taux de rejet en P étaient plus élevés dans la baie de Wuli que dans la baie Meiliang. Les flux de phosphore provenant de l’excrétion du zooplancton varient de 5,34 à 57,41 mg·m$^{-2}$·d$^{-1}$ dans la baie Meiliang et de 8,20 à 70,02 mg·m$^{-2}$·d$^{-1}$ dans la baie Wuli. Comme le P libéré par le zooplancton dans cette étude était dans une forme disponible pour le phytoplancton, le zooplancton peut représenter une source importante de P contribuant à la biomasse phytoplanctonique élevée dans le lac Taihu.

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INTRODUCTION

Phosphorus (P) is often a key factor controlling eutrophication in lacustrine systems. Major P sources typically include urban and agricultural runoffs and internal fluxes. In shallow, eutrophic lakes, P flux from the sediment is an important internal process maintaining a high water column P pool (Søndergaard et al., 2012). Excretion by zooplankton also is considered an internal source of P (Lehman, 1980b; Urabe et al., 1995; Kowalczewska-Madura and Goldyn, 2010). Grazing by large zooplankton, particularly cladocerans, can regulate phytoplankton biomass and species composition (Carpenter et al., 1987; Reynolds, 1994; Sommer and Sommer, 2006). However, nutrient excretion by zooplankton may also affect the supply and stoichiometry of nutrients and thereby influence phytoplankton and lake trophic status (Lehman, 1980a; Elser et al., 1988; Sterner and Hessen, 1994; Kowalczewska-Madura et al., 2007).

The role of zooplankton has been well studied in temperate lakes, but and less so in tropical and subtropical systems where zooplankton are smaller and likely to be less efficient in grazing phytoplankton (Jeppesen et al., 2010; Havens and Beaver, 2011). However, small zooplankton exhibit high P release rates and may thus play a significant role in nutrient cycling in tropical and subtropical lakes (Pinto-Coelho and Greco, 1999). Lake Taihu is a subtropical freshwater lake in China’s Yangtze delta, with a surface area of 2338 km² and mean depth of 1.89 m. Situated in one of the most rapidly industrializing and populous regions of the world, Lake Taihu has suffered greatly from anthropogenic eutrophication since the 1980s (Qin et al., 2007). Although the lake is well-mixed and usually turbid due to sediment resuspension and high phytoplankton biomass, a clear water phase may be observed in spring and early summer due to Microcystis blooms, while large zooplankton, particularly Daphnia spp., decrease in density, most likely due to increased fish predation and reduced food quality (Yang et al., 2008; Song et al., 2010; De Kluijver et al., 2012). In this study, the role of zooplankton in nutrient cycling in Lake Taihu was evaluated through estimates of P release and flux by metazoan zooplankton were estimated compared with data on P release from sediments and external P loading gleaned from the literature. The work contributes to a better understanding of the role of zooplankton in subtropical lakes.

STUDY SITE

Two areas with contrasting trophic states (Song et al., 2010) located in the north part of Lake Taihu (Figure 1) were selected for this study. Meiliang Bay (area 124 km², average depth 2.1 m) exhibits total nitrogen levels ranging from 2.3 to 5.2 mg·L⁻¹ and total phosphorus ranging from 0.12 to 0.31 mg·L⁻¹, and experiences severe summer algal blooms dominated by cyanobacteria. Wuli Bay (area 9 km², average depth 1.8 m), considered the most polluted area of main Lake Taihu, is isolated artificially from Meiliang Bay by a dam. Total nitrogen here ranges from 3.13 to 8.85 mg·L⁻¹ and total phosphorus from 0.15 to 0.24 mg·L⁻¹ (Table I).

MATERIALS AND METHODS

Vertical integrated water samples from the surface to a depth of about 1.5 m were taken with a tube sampler biweekly in March–May 2004 in Meiliang Bay and Wuli Bay (Figure 1). For identification and enumeration of zooplankton, samples were filtered with a 63-µm sieve into plastic vials and preserved with 5% formalin solution. Zooplankton were identified according to Wang (1961), Zhuge (1997), Shen (1979) and Chiang & Du (1979). Animals were counted, and the lengths of 20–30 individuals were measured using a microscope. Zooplankton biomass (Bz), expressed as mg (dry weight)·L⁻¹ or g·m⁻³, was estimated according to length-weight relationships given in the literature (Dumont et al., 1975; Huang and Hu, 1986).
Figure 1
Sampling stations in Meiliang Bay and Wuli Bay, Lake Taihu.

Table I
Mean and range of environmental variables in Meiliang Bay and Wuli Bay.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Meiliang Bay</th>
<th></th>
<th>Wuli Lake</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Water Depth (m)</td>
<td>2.1</td>
<td>1.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Secchi Depth (cm)</td>
<td>25</td>
<td>15–32</td>
<td>38</td>
<td>27–49</td>
</tr>
<tr>
<td>Total nitrogen (mg·L⁻¹)</td>
<td>3.34</td>
<td>2.32–5.20</td>
<td>5.25</td>
<td>3.13–8.85</td>
</tr>
<tr>
<td>Total phosphorus (mg·L⁻¹)</td>
<td>0.19</td>
<td>0.12–0.31</td>
<td>0.20</td>
<td>0.15–0.24</td>
</tr>
<tr>
<td>Chlorophyll a (mg·m⁻³)</td>
<td>32.91</td>
<td>9.20–65.88</td>
<td>54.30</td>
<td>38.25–73.85</td>
</tr>
</tbody>
</table>

Table II
Incubation temperatures for zooplankton P release experiments.

<table>
<thead>
<tr>
<th>Date</th>
<th>9 Mar</th>
<th>18 Mar</th>
<th>26 Mar</th>
<th>6 Apr</th>
<th>15 Apr</th>
<th>22 Apr</th>
<th>16 May</th>
<th>25 May</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (°C)</td>
<td>12.0</td>
<td>11.0</td>
<td>11.8</td>
<td>17.0</td>
<td>15.8</td>
<td>25.0</td>
<td>20.5</td>
<td>24.0</td>
</tr>
</tbody>
</table>

On each experiment day, zooplankton were collected from each bay with horizontal hauls using a 63-µm mesh net. Although a plankton net of such mesh size could result in loss of smaller sized rotifers, a smaller sized net was not practical since it is difficult to separate animals from algae. After collection from the lake, zooplankton were transferred immediately into a 20-L tank containing filtered lake water, which was transported to the laboratory where zooplankton were concentrated with a 63-µm sieve. After rinsing three times with distilled water, animals were transferred into three experimental flasks containing 500 ml filtered (0.45-µm) lake water. Temperature was maintained at or near in situ lake temperature (Table II). Three reference flasks without animals were run during each experimental series as controls. After incubation (1 h), a 200-ml water sample was taken by a pipette with the tip opening covered with a fine-mesh net to prevent the introduction of particles, such as feces. Water samples were analyzed for PO₃⁴⁻-P according to Murphy and Riley (1962). All experiments were carried out between 10 h and 15 h.

At the end of the experiments, animals in each flask were filtered onto GF/C filters and dried at 60 °C for 24 h. Dry biomass was determined using a microbalance. Phosphorus (PO₃⁴⁻-P) release rates were calculated as the difference between experimental and control flasks. Biomass specific P release rate (Rp) was expressed per gram dry biomass per hour (mg·g⁻¹·h⁻¹). Daily zooplankton community P flux (Pfz) was estimated by following formula:

\[
Pfz = Rp \times ZB \times 24
\]
Figure 2
Biomass (dry weight) composition of metazoan zooplankton of Meiliang Bay and Wuli Bay, Lake Taihu during the study period.

Where \( P_{fz} \) is daily zooplankton community P flux, \( mg \cdot m^{-2} \cdot d^{-1} \); \( R_p \) is biomass specific P release rate, \( mg \cdot g^{-1} \cdot h^{-1} \); \( Z_B \) is zooplankton biomass expressed as \( g \cdot m^{-2} \). \( Z_B = Z_b \times D \), where \( Z_b \) is zooplankton biomass (\( g \cdot m^{-3} \)), and \( D \) is the mean depth of the study area (m).

**RESULTS**

Metazoan zooplankton community composition during the study period was similar in the two bays, but there were differences in dominant species. In Meiliang Bay, the dominant species included cladocerans *Daphnia hyalina*, *D. longispina*, *D. pulex*, *Moina* spp., *Bosmina* spp. and copepods *Sinocalanus dorrill*, *Cyclops vicinus vicinus*, *C. strenuus*, and *Thermocyclops taihokuensis*. However, in Wuli Bay, the dominant zooplankton species were rotifers *Brachionus calyciflorus*, *B. angularis*, *Asplanchna priodonta*, *Keratella tropica*, *Polyarthra* spp., *Filinia longiseta*, copepods *Cyclops vicinus vicinus*, *Cyclops strenuus*, *Thermocyclops taihokuensis*, *Mesocyclops thermocyclopoides* and cladocerans *Moina* spp. Biomass (dry weight) of metazoan zooplankton in Meiliang Bay was variable (Figure 2). Cladocerans, dominated by *Daphnia* spp. from March to April and *Bosmina* spp. and *Moina* spp. in late May, were the largest component of zooplankton biomass, followed by copepods, while the biomass of rotifers was negligible.

In Wuli Bay, however, rotifers contributed a significant proportion of metazoan zooplankton biomass. Although cladocerans also were an important contributor to zooplankton biomass, the proportion was lower than in Meiliang Bay, and copepod biomass was similar in the two bays.

Mean P release rates ranged from 0.20 to 0.57 \( mg \cdot g^{-1} \cdot h^{-1} \) in Meiliang Bay and 0.20 to 0.76 \( mg \cdot g^{-1} \cdot h^{-1} \) in Wuli Bay (Figure 3). In most cases, P release rates were higher in Wuli Bay than Meiliang Bay although only four experiments yielded statistically significant results. Based on biomass and release rates, zooplankton contribution to internal P cycling was estimated (Figure 4). Phosphorus flux varied from 5.34 to 57.41 \( mg \cdot m^{-2} \cdot d^{-1} \) in Meiliang Bay and 8.20 to 70.02 \( mg \cdot m^{-2} \cdot d^{-1} \) in Wuli Bay. Maximal values for P flux occurred at highest zooplankton biomasses.
DISCUSSION

Zooplankton are an important influence on phytoplankton succession during spring and summer via grazing activity (Sommer et al., 1986). However, nutrient regeneration by zooplankton also is an important factor determining phytoplankton composition (Kowalczewska-Madura et al., 2007). Earlier studies revealed that most soluble P is released by zooplankton as PO$_4^{3-}$P and, therefore, is available for phytoplankton growth (Lehman, 1980a). During our study, large zooplankton were abundant in Lake Taihu. The highest biomass of *Daphnia* spp. was more than 2.0 mg·L$^{-1}$. Zooplankton P release rates were variable but fall within ranges reported in other studies (Table III). In an experimental study, Lehman (1980b) reported a range of 0.58–0.83 mg·g$^{-1}$·h$^{-1}$ for zooplankton P release rates. Urabe et al. (1995) showed that zooplankton P release rates in Lake Biwa ranged from 0.01 to 0.11 mg·g$^{-1}$·h$^{-1}$. In a tropical reservoir, Pinto-Coelho and Greco (1999) reported zooplankton P excretion rates from 0.49 to 1.05 mg·g$^{-1}$·h$^{-1}$.

Our results showed differences in P release rates between the two bays with different eutrophication levels. In most cases, P release rates were higher in Wuli than Meiliang Bay, which may be attributed to differences in zooplankton community structure. Wuli Bay is close to the urban area of Wuxi and receives (treated and untreated) sewage. There were more rotifers in Wuli than in Meiliang Bay, while the number of large zooplankton, mainly *Daphnia*...
Table III
Literature comparison of P release rates by zooplankton.

<table>
<thead>
<tr>
<th>Zooplankton</th>
<th>P release rate (mg·g⁻¹·h⁻¹)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zooplankton community</td>
<td>0.20–0.76</td>
<td>Our study</td>
</tr>
<tr>
<td>Zooplankton community</td>
<td>0.49–1.05</td>
<td>Pinto-Coelho and Greco, 1999</td>
</tr>
<tr>
<td>Daphnia pulex</td>
<td>0.58–0.83</td>
<td>Lehman, 1980b</td>
</tr>
<tr>
<td>Daphnia magna</td>
<td>0.31–2.12</td>
<td>Ruan, 1999</td>
</tr>
<tr>
<td>Zooplankton community</td>
<td>0.07–0.13</td>
<td>Gulati et al., 1995</td>
</tr>
<tr>
<td>Zooplankton community</td>
<td>0.01–0.11</td>
<td>Urabe et al., 1995</td>
</tr>
</tbody>
</table>

Table IV
Comparison of P fluxes from different sources of Lake Taihu.

<table>
<thead>
<tr>
<th>Sources</th>
<th>P fluxes (mg·m⁻²·d⁻¹)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zooplankton P release (PO₄-P)</td>
<td>5.3–70.0</td>
<td>Our study</td>
</tr>
<tr>
<td>Sediment P release (PO₄-P)</td>
<td>3.0</td>
<td>Fan and Wang, 2007</td>
</tr>
<tr>
<td>External P loading (TP)</td>
<td>10.0</td>
<td>Qin et al., 2007</td>
</tr>
</tbody>
</table>

spp., in Meiliang Bay was higher than in Wuli Bay. Nutrient release rates are related inversely to zooplankton size (Pérez-Martínez and Gulati, 1999; Ruan, 1999). Given equal biomass, small zooplankton, such as rotifers, should play a more important role in P cycling than large-sized zooplankton, such as daphnids (Ejsmont-Karabin, 1983; Ejsmont-Karabin et al., 2004). Variation in zooplankton community composition likely is a main factor in the different P release rates between Meiliang and Wuli Bay.

The contribution of zooplankton to internal P cycling was estimated by multiplying biomass specific excretion rates by integrated biomass on each sampling date. The lowest estimate was 5.34 mg·m⁻²·d⁻¹ in Meiliang Bay when zooplankton biomass was lowest, while the highest value of 70.02 mg·m⁻²·d⁻¹ was observed when both zooplankton biomass and P release rate were high in Wuli Bay. A recent study showed that mean PO₄³⁻-P release from Meiliang Bay sediments was below 3.0 mg·m⁻²·d⁻¹ (Fan and Wang, 2007). The external loading of total P to Lake Taihu was ~10.0 mg·m⁻²·d⁻¹ (Qin et al., 2007), which is the same order of magnitude as PO₄³⁻-P flux from zooplankton excretion (Table IV). Considering that P released by zooplankton in this study was in a form available to phytoplankton, zooplankton may supply a significant source of P contributing to high phytoplankton biomass in Lake Taihu.

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