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# Ecology of rotifers and their unappreciated source of nitrogen and phosphorus in temperate northeastern American bogs

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With 6 figures and 2 tables

**Abstract:** Peatlands are one of the world's most important ecosystems, storing approximately 30 % of all terrestrial soil carbon as peat. Rotifers living in interstitial water within *Sphagnum* mats and in pitchers of *Sarracenia purpurea* are capable of regenerating large amounts of nitrogen ($NO_3$, $NH_4$) and phosphorus ($PO_4$). However, ecological research on rotifers living in bog interstitial waters has been neglected to date. We hypothesized that spatial variability of rotifer abundance and their nutrient contribution is uniform within bogs (i.e., at a local scale), and shows seasonal and geographic variability (i.e., at regional scales), and that rotifers contribute significantly to the nutrient budget of peatlands. To test these hypotheses, we assessed and quantified the role of rotifers in nutrient cycling (as nitrogen and phosphorus regeneration) in bog ecosystems at local, regional, and global scales. We present data on the spatial distribution and abundance of rotifers in bogs, and their effect on nutrient regeneration patterns during the growing season. We estimate that nutrient regeneration by rotifers may account for the regeneration of approximately 3.2–9.7% in Europe and 4.6–6.7% in North America, and be a major source of inorganic phosphorus. We estimate that, through nutrient regeneration, rotifers worldwide may provide 0.12 million tons of N and 0.17 million tons of P to bogs every year.

**Keywords:** Rotifera; peatlands; nutrient regeneration; global cycling

## Introduction

Peatlands cover ≈ 3 % of the global land and area (≈ 4 million km$^2$), represent approximately one-third of the world's wetlands, and store ≈ 30 % of all terrestrial soil carbon as peat (Chapman et al. 2003; Limpens et al. 2008; Parish et al. 2008). Peatlands have been acting as sinks of atmospheric carbon for millennia, but may become sources of carbon if destabilized by global warming and high nitrogen (N) deposition (Vitousek et al. 1997; Heijmans et al. 2002; Driscoll et al. 2003; Parish et al. 2008; Wu et al. 2015). Peatlands also are important for biodiversity conservation, climate regulation, human welfare, and carbon and water storage; their conservation and management are essential for global sustainability (Parish et al. 2008).

In natural bog ecosystems, the source of most N and phosphorus (P) absorbed by plants and algae is the release by mineralization of organic matter (Fellman & D'Amore 2007). However, microbial mineralization is not the only source of nutrients. The other important groups providing a significant amount of nutrients in bog ecosystems are testate amoebae, ciliates, and rotifers (Błędzki & Ellison 2002; Mieczan 2012). Rotifers excrete significant amounts of nitrogen ($NH_4$-N and $NO_3$-N) and phosphorus ($PO_4$-P) via well-studied

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metabolic pathways (Ejsmont-Karabin 1983; Ejsmont-Karabin 1984; Wen & Peters 1994; Gulati et al. 1995; Błędzki & Ellison 2002). As a result, they are one of the essential groups of aquatic invertebrates responsible for nutrient regeneration, through the excretion of inorganic nutrients following consumption of organic matter (Ejsmont-Karabin 1984; Den Oude & Gulati 1988). Nutrient regeneration is a fundamental process that maintains primary production in freshwater environments (Vanni & McIntyre 2016), with nutrient regeneration by rotifers well known, but usually reported from lakes (Hudson et al. 1999; Ejsmont-Karabin et al. 2004). However, nutrient regeneration is underappreciated in, and rarely reported from, peatlands (Błędzki & Ellison 2002). The efficiency of nutrient regeneration declines along a productivity gradient, such that nutrient-poor environments (ombrotrophic bogs) are more efficient at recycling their nutrients than nutrient-rich environments (Hudson et al. 1999). Bacteria are also consumers of mineral phosphorus, as it has been shown that they can compete for P with algae in lakes (Currie & Kalff 1984; Currie 1990) and bogs (Wyatt & Turetsky 2015).

Rotifers in peatlands live in bog ponds (if present), interstitial water of *Sphagnum* mats, and in the water-filled pitchers of *Sarracenia purpurea* (present in many bogs throughout North America (Buckley et al. 2003)), and are capable of regenerating high amounts of N and P (Błędzki & Ellison 1998; Błędzki & Ellison 2002; Błędzki & Ellison 2003). Many species of rotifers have been reported from bog ponds or *Sphagnum* mats (Burger 1948; Wallace 1977; Bateman & Davis 1980; Francez 1981; Francez 1984; Francez 1987; Francez 1988; Francez & Pourriot 1984; Stemberger 1990; Chittapun et al. 1999; Błędzki & Ellison 2003; Kaya et al. 2010; Bielańska-Grajner et al. 2011a; Bielańska-Grajner et al. 2017). However, many of these rotifer species have not been observed since they were described (Harring 1913; Harring 1916; Harring & Myers 1922; Harring & Myers 1924; Harring & Myers 1926; Harring & Myers 1928; Harring & Myers 1930; Nogrady et al. 1995). Although the ecology of rotifers living in lakes and ponds has been very well documented (e.g., Obertegger & Flaim 2015; Sommer et al. 2016; Takamura et al. 2017; Yang et al. 2017), research on rotifers living in bogs has been neglected for many decades (Wallace et al. 2013).

The goal of this study is to fill gaps in our knowledge of the ecology of rotifers in bog habitats, and estimate their contribution to N and P cycling in peatland ecosystems at local, regional, and global scales. We hypothesized that rotifers contribute significantly to the nutrient budget of peatlands. We also hypothesized that the spatial variability of rotifer abundance and their nutrient contribution is uniform within bogs (i.e., at a local scale), and shows seasonal and geographic variability as a function of latitude, longitude, and elevation (i.e., at regional scales).

## Material and methods

### Study sites

To assess local (small-scale) spatial and seasonal variability we sampled two peatlands. Hawley Bog is a mineral poor fen located on the Berkshire Plateau of northwest Massachusetts (USA 42° 34′ 32.34″ N, 72° 53′ 21.96″ W; Fig. 1). This 3-ha stream-side headwater peatland is situated in a 40-ha glacial depression with around 12 meters of peat in the center (Moizuk & Livingston 1966; Johnson 1985; Gotelli & Ellison 2002). Located at an elevation of 542 m a.s.l., Hawley Bog is the remnant of an old glacial lake. Sources of water supply for Hawley Bog are drainage water from the surrounding hills, freshwater springs, and precipitation falling onto the mat. There is one outlet for excess water, but drainage is incomplete and the water table of the floating *Sphagnum* mat area is fairly constant throughout the year (Moizuk & Livingston 1966). Plant communities are dominated by *Sphagnum* mosses with hummock and hollows; pitcher plants (*Sarracenia purpurea*) and ericaceous shrubs *Rhododendron groenlandicum*, *Chamaedaphne calyculata*, *Myrica gale*, *Kalmia* spp. and *Vaccinium* spp. on the floating mat; and *Acer rubrum*, *Picea mariana,* and *Abies balsamea* at the perimeter of the bog (Moizuk & Livingston 1966).

Mer Bleue Bog is located 10 km east of Ottawa, Ontario, Canada (45° 24′ 33.9″ N, 75° 31′ 7.35″ W; Fig. 1). It is a 2,800-ha raised ombrotrophic bog located in the melt-water channel of the postglacial Ottawa River at 67–76 m a.s.l. (Wu et al. 2015). The lagg at the edge of the bog has been dammed by beavers (*Castor canadensis*), creating a zone of fluctuating water levels that influence the groundwater flow in wetter and drier years. Plant communities are dominated by ericaceous shrubs (*C. calyculata, R. groenlandicum, Kalmia angustifolia*) and *Sphagnum* mosses with hummock and hollows (Bubier et al. 2006). A detailed description of Mer Bleue Bog is given in Wu et al. (2015).

To assess regional patterns and geographic relationships, we surveyed 31 New England bogs (Fig. 1) in Vermont, Massachusetts, and northwestern Connecticut that occur in the eastern range of North American *Sphagnum*-dominated peatlands (Halsey et al. 2000; Błędzki & Ellison 2003). We sampled relatively undisturbed bogs identified in consultation with state agencies and conservation organizations (The Nature Conservancy, Audubon Society, and state Natural Heritage programs). Latitude, longitude, and elevation of each bog were determined using a Trimble GPS unit (Trimble Instruments, Sunnyvale, California, U.S.A). Bog area was determined from digitized aerial photographs, using ArcView 3.2 (ESRI, Inc., Redlands, California, U.S.A.).

### Sample collection

Surface pore-water samples for rotifer spatial and seasonal analysis were collected at Hawley Bog in August 1999 along three transects (spaced 15 m apart) with six sampling sites at 5-m intervals along each transect, and weekly from July to Oc-

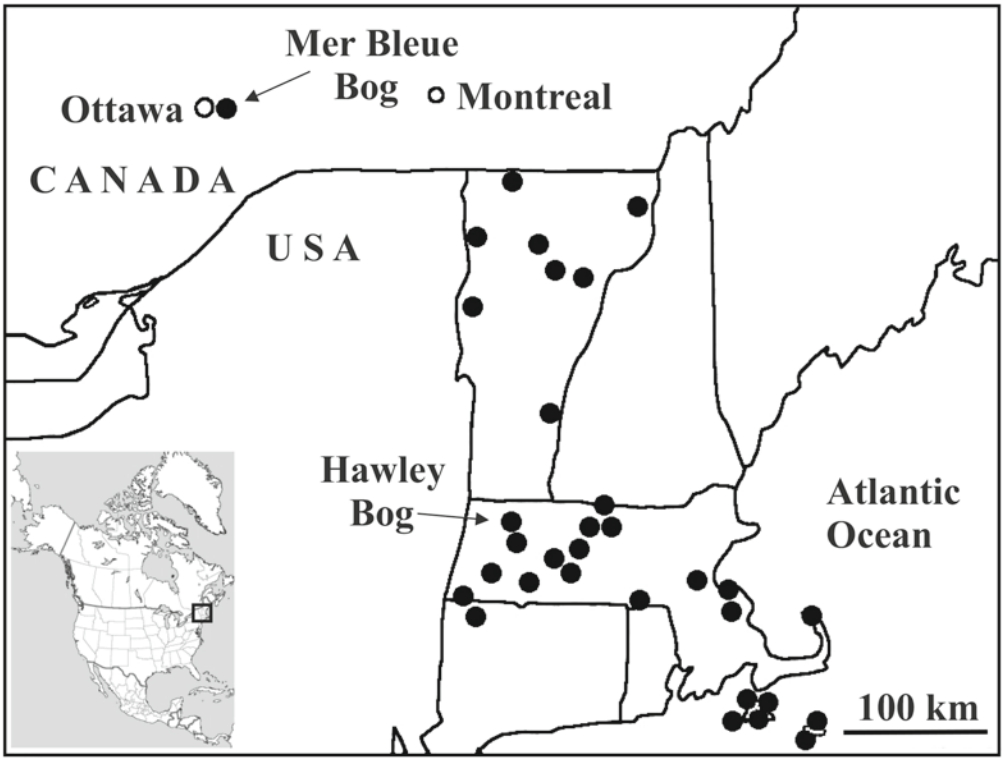

**Fig. 1.** Map showing approximate positions of the sampling locations.

tober 2000, along one transect with six sampling sites spaced at 5-m intervals. The sampled area was between the pond and shrubs on the forest edge, and was covered by *Sphagnum* moss. Samples for spatial analysis at Mer Bleue Bog were collected in July 2009 along a transect from the center toward the edge of the bog with 50 m between sampling sites, and again in June 2013 on a similar transect from the drier to wetter sites, including 5 hummocks and 5 hollows.

At each sampling site, we collected two replicate 50-ml unfiltered pore water samples in a 50-ml plastic Falcon conical centrifuge tube pressed down into the *Sphagnum* mat. These single survey samples were collected from the center of the *Sphagnum* mat; the two replicates were spaced 10 m apart. Tubes readily filled with water in a few seconds and then were transported in a cooler to the laboratory for live rotifer identification and counting (Hawley Bog samples). Samples subsequently were preserved in a 1 % solution of formaldehyde. Samples from Mer Bleue Bog and the other surveyed bogs were preserved on site in a 1 % solution of formaldehyde and processed in the lab within a few weeks. Before counting, samples were concentrated to 5 or 10 ml volume depending on the amount of detritus in the sample. The concentrated sample was placed on a Ward counting wheel and rotifers were counted using a Leica MZ 12.5 stereomicroscope. The identification of rotifers was made under a Leica DMLS compound microscope; detailed rotifer diversity of Hawley Bog and the other New England surveyed bogs was described separately (Błędzki & Ellison 2003).

Rotifer biomass, based on abundance and the body volume-dry weight (DW) relationship, was estimated based on volumetric measurements (assuming $1\,\mu l = 1\,\mu g$) using species-specific formulae and dry biomass conversion of 0.04 % for *Habrotrocha rosea* and other soft-bodied species (Błędzki & Ellison 1998), and 10 % of their wet mass for all other species (Bottrell, et al. 1976; Ejsmont-Karabin 1983; Ejsmont-Karabin 1998).

Nitrogen ($NO_3$-N and $NH_4$-N) and phosphorus ($PO_4$-P) regeneration rates by rotifers (live excretion per hour of nutrients in forms available for uptake by plants and algae) were measured experimentally (Błędzki & Ellison 1998). We sampled rotifers that had been cultured in 20-mL vials to obtain high abundance, and that were then gently pipetted into a new vial to obtain ~5,000 individuals. These were transferred onto small nets (15-µm mesh size), and washed with deionized water to remove the yeast food and organic debris. The rotifers were then transferred into a watch glass filled with deionized water and maintained there for 10 minutes to remove food remnants from their intestines (cf. Ejsmont-Karabin 1984). Prior to each experimental run, replicate 1-mL subsamples of 20-mL liquid were removed from the vials, and the rotifers in each subsample were counted with a Ward counting wheel. For each experiment, ~5,000 rotifers were transferred on 15-µm mesh nets into 300-mL watch glasses containing 100 mL of deionized water. The concentration of nitrate, ammonium, and phosphate was measured in the water before rotifers were placed into the watch glasses and again 5 hours after the rotifers had been placed into the watch glasses. $NO_3$-N concentration was measured using cadmium reduction spectrophotometry, $NH_4$-N with salicylate spectrophotometry, and $PO_4$-P with ascorbic acid spectrophotometry using standard methods (APHA 1992). Five replicates and blank controls (no rotifers) were tested at each of pH 3, 4, 5, and 6 all maintained at 22 °C. Rotifers were

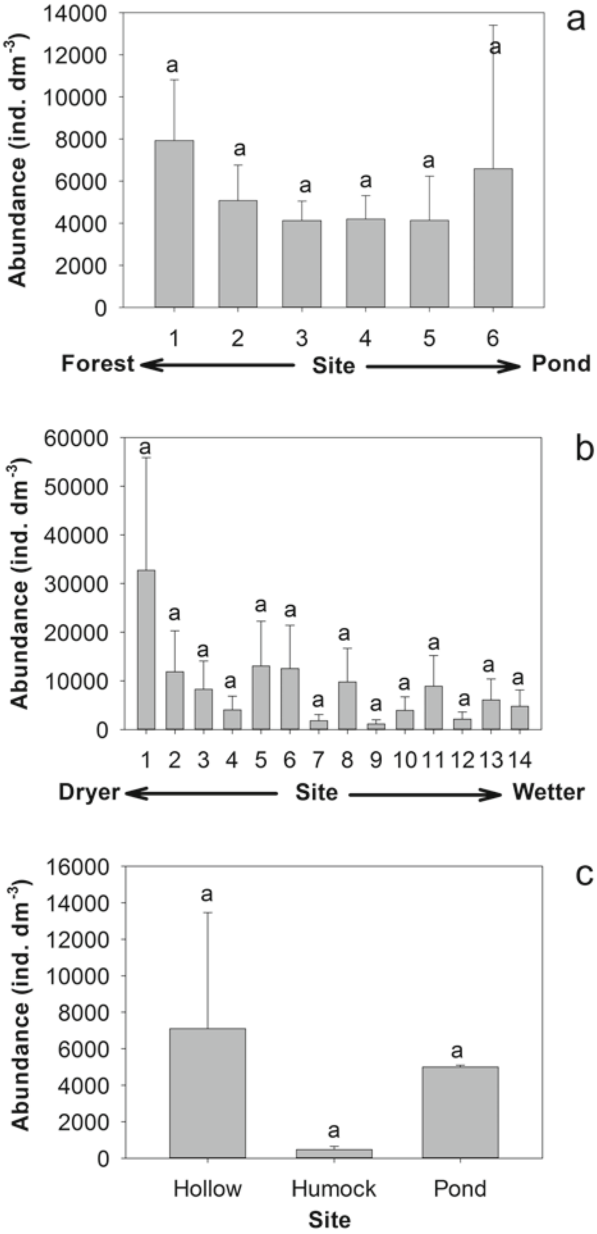

**Fig. 2.** Abundance of rotifers at Hawley Bog on transect between the forest and pond **(a)**, at Mer Bleue Bog between drier and wetter (near the pond) sites **(b)**, and at Mer Bleue hollow and hummock sites and the pond **(c)**. Common letters above the bars denote no statistically significance difference ($p > 0.05$) using One-Way ANOVA and Tukey's post-hoc test for multiple comparisons among means. Error bars illustrate +1 SE (standard error of the mean).

re-counted at the end of each experiment to check for dead or contracted individuals; these were rare. Rotifers were not fed during these experiments. Nutrients excreted by starved rotifers are metabolized from food stored within their bodies as lipids. Nutrient excretion rates of starved rotifers are ~2 times lower those than fed ones (Ejsmont-Karabin 1983; Den Oude & Gulati 1988; Nogrady et al. 1993; Wen & Peters 1994; Gulati et al. 1995). Based on previous work of Ejsmont-Karabin (1984) and Błędzki & Ellison (2002), the average net excretion rate was estimated for a single specimen of *H. rosa*, other bdelloids, and soft bodied species for $N = 0.54$ ng $hr^{-1}$ and $P = 2.04$ ng $h^{-1}$ and for all other species for $N = 0.0879\,DW^{-1.01\ e0.088T}$ and $P = 0.0154\,DW^{-1.27\ e0.096T}$, (where DW is the rotifer dry weight and T is temperature).

Semi-annual contributions by rotifers to nutrient budgets were then estimated for a 6-month growing season as a function of rotifer species biomass (estimated from abundance per $dm^3$ and expressed per $m^2$ assuming experimental estimation to draw the average volume of 2.5 $dm^3$ of water with rotifers from 1 $m^2$) of *Sphagnum* mats at surveyed bogs according to regeneration rates measured experimentally and provided by Ejsmont-Karabin (1983), Błędzki & Ellison (1998), and Błędzki & Ellison (2002). To scale N and P regeneration to North American and global peatlands, we used the peatland area estimation by Joosten (2009).

### Statistical analysis

We used one-way ANOVA and Tukey's HSD post-hoc test for multiple comparisons among the rotifer abundance means at seasonal and small-spatial scales. We used transect-means for within bog comparisons to verify whether two replicate samples taken at the center of each bog were sufficient for a bog representation. We then used regression analysis to test the relationship between geographic variables (latitude, longitude, elevation and area of sampled bogs) and rotifer richness, abundance, and N and P regeneration on large spatial scales. Data were log-transformed where appropriate to ensure normal distribution. Statistical tests were done using Minitab (2003) for ANOVA and Tukey's HSD post-hoc test for multiple comparisons among means, and with JMP (2012) for regression; assumptions of ANOVA and regression (Gotelli & Ellison 2012) were tested and confirmed prior to analysis.

## Results

### Spatial and seasonal variability of rotifers

We recorded 38 rotifer species from New England bogs (Table 1). *Habrotrocha rosa* was the most frequent species, followed by *Lecane pyriformis*, *Cephalodella gibba*, *L. lunaris* and *Polyarthra vulgaris*. Most of the species (29) were found in interstitial waters, followed by ponds (16) and pitcher-plants (5). The most abundant interstitial species were *H. rosa* (31 % of the community) and *Keratella mixta* (31 %), followed by *L. lunaris* and *P. vulgaris* (8 % and 7 %, respectively). Rotifer biomass was dominated by *H. rosa* (60 %, Table 1).

Samples of pore-water rotifers collected weekly at Hawley Bog from July to October 2000 did not show statistically significant spatial variability of rotifer abundance along a transect between the forest and pond (one-way ANOVA $F_{5,66} = 0.62$, $p = 0.68$, Fig. 2a). Similarly, there were no significant differences in ro-

**Table 1.** Frequency, abundance and biomass of Rotifera species collected during the survey of 31 New England bogs, in three habitats (interstitial water between *Sphagnum*, bog ponds and in pitcher of *S. purpurea*).

| Species | Interstitial frequency | Bog pond frequency | In pitcher of *Sarracenia* frequency | Mean interstitial ind. dm$^{-3}$ | Mean interstitial DW µg dm$^{-3}$ |
|---|---|---|---|---|---|
| *Asplanchna priodonta* Gosse 1850 | | 1 | | | |
| *Cephalodella anebodica* Berzins 1976 | | | 1 | | |
| *Cephalodella gibba* (Ehrenberg 1832) | 19 | | | 170.5 | 13.62 |
| *Colurella colurus* (Ehrenberg 1830) | 4 | | | 20.8 | 0.23 |
| *Colurella obtusa* clausa (Hauer 1936) | 12 | | | 142.5 | 0.67 |
| *Euchlanis incisa* Carlin 1939 | | 2 | | | |
| *Euchlanis myersi* Kutikova 1959 | 1 | | | 107.3 | 3.58 |
| *Habrotrocha rosa* Donner 1949 | 31 | | 22 | 1834.2 | 218.27 |
| *Kellicottia bostonensis* (Rousselet 1908) | | 5 | | | |
| *Keratella cochlearis* (Gosse 1851) | 1 | 4 | | | |
| *Keratella mixta* (Oparina-Charitonova 1925) | 12 | | 1 | 1826.7 | 28.31 |
| *Keratella serrulata* (Ehrenberg 1838) | 1 | 3 | | 0.03 | 0.001 |
| *Keratella taurocephala* Myers 1938 | 1 | 2 | | 0.8 | 0.04 |
| *Lecane agilis* (Bryce 1892) | 1 | | | 0.03 | 0.002 |
| *Lecane bulla* (Gosse 1851) | 1 | | | 0.8 | 0.03 |
| *Lecane closterocerca* (Schmarda 1859) | 1 | | | 20.0 | 0.21 |
| *Lecane lauterborni* Hauer 1924 | 6 | | | 0.02 | 0.01 |
| *Lecane ludwigii* (Eckstein 1885) | 1 | | | 1.7 | 0.04 |
| *Lecane luna* (Müller 1776) | 7 | 2 | | 240.8 | 12.40 |
| *Lecane lunaris* Ehrenberg1832 | 17 | 2 | 1 | 459.5 | 11.28 |
| *Lecane pyriformis* (Daday 1905) | 22 | 3 | | 321.8 | 14.35 |
| *Lecane pyrrha* Harring & Myers 1926 | | 4 | | | |
| *Lecane satyrus* Harring & Myers 1926 | 1 | | | 0.03 | 0.001 |
| *Lecane signifera* (Jennings 1896) | 3 | 3 | | 61.7 | 2.28 |
| *Lecane tryphema* Harring et Myers 1926 | 2 | | | 8.3 | 0.13 |
| *Lepadella amphitropis* Harring 1916 | | 2 | | | |
| *Lepadella ehrenbergi* (Perty 1850) | 1 | | | 4.2 | 0.07 |
| *Lepadella ovalis* (Müller 1786) | 3 | | | 41.7 | 0.66 |
| *Lepadella patella* (Müller 1773) | 1 | | | 41.7 | 0.74 |
| *Lepadella triba* Myers 1934 | 2 | | | 59.2 | 0.30 |
| *Macrochaetus collinsi* (Gosse 1867) | 1 | | | 25.0 | 0.52 |
| *Monommata grandis* Tessin 1890 | 7 | | | 63.3 | 4.75 |
| *Mytilina macrocera* (Jennings 1894) | 1 | | | 125.0 | 13.30 |
| *Notholca acuminata* (Ehrenberg 1832) | | 1 | 1 | | |
| *Polyarthra euryptera* Wierzejski 1892 | | 1 | | | |
| *Polyarthra vulgaris* Carlin 1944 | 16 | 5 | | 414.2 | 13.75 |
| *Trichocerca rosea* (Stenroos 1898) | 1 | | | 62.0 | 14.06 |
| *Trichotria tetractis* (Ehrenberg 1830) | | 1 | | | |
| **number of species: 38** | **29** | **16** | **5** | | |

tifer abundance among the three Hawley Bog transects (sampled in August 1999, one-way ANOVA $F_{2,15} = 2.79$, $p = 0.09$, Fig. 3). Transects at Mer Bleue Bog also did not show statistically significant spatial variability of pore water rotifer abundance in July 2009 (one-way ANOVA $F_{13,14} = 1.68$, $p = 0.17$; mean (± se) = 8,641 ± 1,907 ind. dm$^{-3}$, range 330–46,464 ind. dm$^{-3}$ (from 14 sites, Fig. 2b), or in June 2013 at

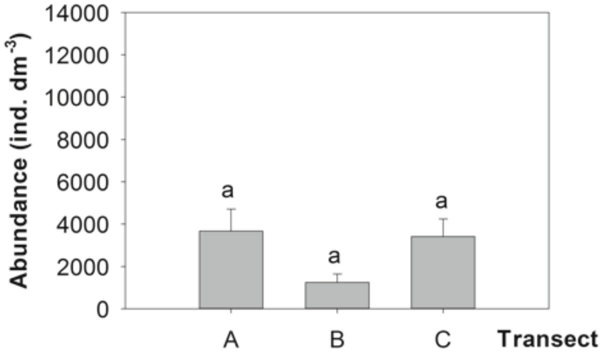

**Fig. 3.** Variation of rotifer abundance between transects (A, B, C) at Hawley Bog. Common letters above the bars denote no statistically significance difference ($p > 0.05$) using One-Way ANOVA and Tukey's post-hoc test for multiple comparisons among means. Error bars illustrate +1 SE (standard error of the mean).

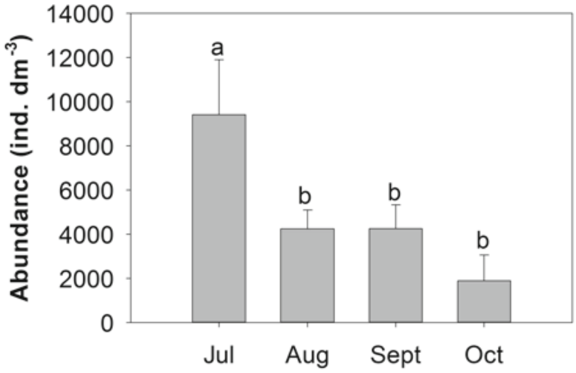

**Fig. 4.** Seasonal variation of rotifer abundance observed on Hawley Bog. Different letters above bars indicate statistically significant differences ($p < 0.05$) using One-Way ANOVA and Tukey's post-hoc test for multiple comparisons among means. Error bars illustrate +1 SE (standard error of the mean).

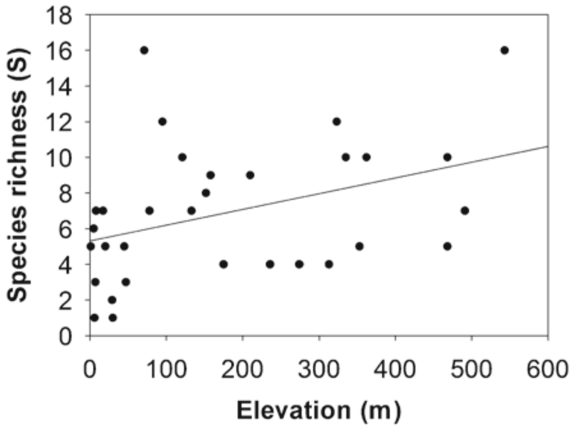

**Fig. 5.** Rotifera species richness ($S$) as a function of bog elevation (m a.s.l.), described by regression model $S = 5.315 + 0.009 \times$ elevation ($r^2 = 0.15$, $p = 0.03$).

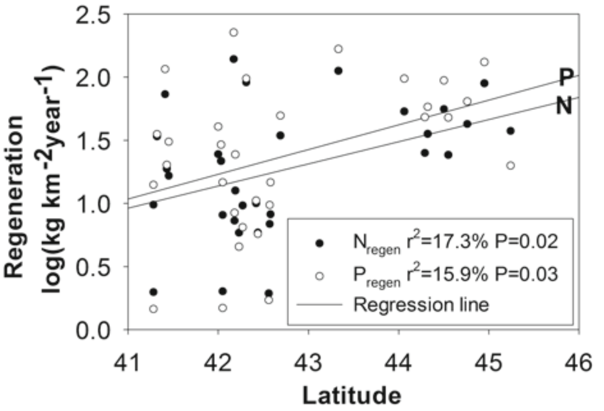

**Fig. 6.** Regeneration of nitrogen (N) and phosphorus (P) by rotifers as a function of latitude, described by regression models: log N = −6.24 + 0.1757× latitude ($r^2 = 0.17$; $p = 0.02$) and log P = −7.004 + 0.1961× latitude ($r^2 = 0.16$ %; $p = 0.03$).

the drier (hummock), wetter (hollow) and pond sites (one-way ANOVA $F_{2,3} = 1.70$, $p = 0.32$; mean (± se) = 4,295 ± 2,323 ind. $dm^{-3}$, range 700–23,200 ind. $dm^{-3}$ (Fig. 2c). However, rotifer abundance was seasonally variable at Hawley Bog, with the maximum observed in July (one-way ANOVA $F_{3,68} = 3.32$, $p = 0.025$, Fig. 4). Rotifer abundance ranged from 0 to 32,820 ind. $dm^{-3}$ over the growing season with a mean = 5,344 ± 808 ind. $dm^{-3}$.

Rotifer species richness ($S$) increased significantly with bog elevation (Fig. 5) for the 31 bogs sampled, but was not associated significantly with latitude, longitude, or bog area. Rotifer abundance in *Sphagnum* pore water across the New England region ranged from 150 to 51,250 ind. $dm^{-3}$ (mean 5,931 ind. $dm^{-3}$) and was not associated significantly with latitude, longitude, bog area, or elevation.

The biomass (DW) of rotifers at Hawley Bog showed similar seasonal and spatial patterns as abundance on the transect between forest and pond. Between July and October 2000, it ranged from 0 to 3,873 µg $dm^{-3}$, with the mean biomass of 399.7 ± 82.4 µg $dm^{-3}$ (one-way ANOVA $F_{5,66} = 0.14$, $p = 0.98$).

## N and P regeneration

The annual growing season rate of N and P regeneration, respectively, by rotifers was estimated (based on Hawley Bog samples) to be 32 mg $m^{-2}$ $yr^{-1}$ (range 11–53 mg $m^{-2}$ $yr^{-1}$) and 47 mg $m^{-2}$ $yr^{-1}$ (range 16–79 mg $m^{-2}$ $year^{-1}$). We estimated the mean contribution of N and P to regeneration by the dominant species *H. rosa* and *P. vulgaris*, respectively, to be 41 % and 53 % of N, and 33 % and 55 % of P. The N and P regeneration es-

**Table 2.** Global peatland area from Joosten (2009) and estimated annual N and P regeneration by rotifers.

| Region | Peatland area ($10^3$ km$^2$) | N regeneration (tons year$^{-1}$) | P regeneration (tons year$^{-1}$) |
|---|---|---|---|
| Russia (including European part) | 1,376 | 44,032 | 64,672 |
| North America | 1,358 | 43,456 | 63,826 |
| Europe (excluding European part of Russia) | 267 | 8,544 | 12,549 |
| Other | 626 | 20,032 | 29,422 |
| Global | 3,627 | 116,064 | 170,469 |

timates for all surveyed bogs were not associated significantly with species richness, longitude, bog area, or elevation, but were a function of latitude (Fig. 6) and abundance described by regression models for the average annual regeneration:

mg N per m$^2$ = –51.62 + 24.82 logAbundance ($r^2 = 0.17, p = 0.02$)

mg P per m$^2$ = –68.27 + 34.34 logAbundance ($r^2 = 0.14, p = 0.04$).

The estimated average global rates of N (116,064 tons year$^{-1}$) and P (170,469 tons year$^{-1}$) regeneration attributable to rotifers are shown in Table 2, assuming the global peatland area to be $3{,}627 \times 10^3$ km$^2$.

## Discussion

The estimate of 38 rotifer species, a mean per liter of bog pore water abundance of 5,931 specimens, and a mean biomass of 350 µg DW dm$^{-3}$ is rather conservative. During a more extensive sampling effort, Pejler & Bērziņš (1993) found 328 rotifer species living between *Sphagnum* on 10 bogs, but they did not provide any information on rotifer abundance. More intensive and extensive sampling effort, including methods described by Peters et al. (1993), and larger sample size would provide probably a larger and more accurate estimation.

We found little spatial variability in rotifer distribution and abundance at Hawley and Mer Bleue Bogs. Similar observations related to rotifers inhabiting *Sphagnum* moss were published by Bielańska-Grajner et al. (2011b). Moisture is one of the most important factors structuring rotifer community seasonally and spatially with wetter hollows having higher species diversity and abundance (Bateman & Davis 1980; Kaya et al. 2010; Bielańska-Grajner et al. 2017). During our research at Mer Bleue, the moisture conditions during a relatively dry season did not create enough of a gradient to influence rotifer spatial variability. Other environmental conditions (pH, conductivity, organic carbon, nitrate, phosphate) and a complex mixture of biogeochemical cycles and activities also are important in structuring rotifer communities (Pejler 1995; Bragazza et al. 1998; Bielańska-Grajner et al. 2011b; Mieczan et al. 2012; Mieczan et al. 2014).

Seasonal variability of rotifer abundance was expected from previous studies of lakes, ponds, reservoirs, and rivers (Błędzki 1989; Błędzki 2004; Błędzki et al. 1992), and of interstitial water of psammic habitats (wet sandy region extending from the water's edge a few meters into the terrestrial habitats) (Wallace & Smith 2010; Lokko et al. 2017). Highest rotifer density in summer also has been generally observed (Bielańska-Grajner et al. 2011a; Bielańska-Grajner et al. 2011b; Bielańska-Grajner et al. 2017), most strongly influenced by pH, conductivity and moisture, and indirectly by total organic carbon.

The significant increase in species richness with bog elevation (but not with latitude, longitude or bog area), was surprising and merits further research. However, this phenomenon may be related to harsher environmental conditions resulting in less competition and predator pressure at higher elevations. Such a trend was observed on the gradient from mineral-rich fen to environmentally harsher environmental conditions on poor *Sphagnum*-fens (Křoupalová et al. 2013).

Regional variation in rotifer abundance (Table 1), is likely to be mostly dependent on local environmental conditions, for example pH, moisture and temperature (Bielańska-Grajner et al. 2011a; Bielańska-Grajner et al. 2011b; Bielańska-Grajner et al. 2017). Concentration of pore-water $NO_3$ and $PO_4$ in the sampled New England bogs increased from northwest to southeast and decreased with elevation; neither pH nor $NH_4$ varied geographically (Gotelli et al. 2008). Very often small, sometimes undetectable, concentrations of $NO_3$ also were observed in bogs (Hemond 1983; Rattle 2006). This can be caused by three main factors. First, *Sphagnum* has been shown to make immediate use of $NO_3$ fixed by *Sphagnum*-associated *Nostoc* colonies (blue-green-algae) (Basilier 1980). Second, nitrifying bacteria require a relatively high pH, so the acidic conditions in bogs may inhibit nitrification and promote denitrification (Bridgham et al. 1996). Third, in the top 5–10 cm of moss $NO_3$ from rain can be rapidly uptaken by bryophyte plants (Urban at al. 1988).

In low-N bog environments, N excreted by rotifers – an alternative way to bypass the microbial mineralization loop (Bridgham et al. 1996; Jonasson & Shaver 1999) – is likely to be an important source of available N to the ecosystem. Further, rotifer P regeneration may be equal to or higher than bacterial mineralization, and N regeneration could be just slightly smaller than bacterial mineralization (Fellman & D'Amore 2007).

Our regional and global estimates of N and P regeneration rates – the first of which we are aware – could be incorporated into future models of N and P cycling. Although rotifer N and P regeneration is missing in all local and global cycling assessments and models, (e.g., Hemond 1983; Holland et al. 2005; Phoenix et al. 2006; Bobbink et al. 2010), we estimate that rotifers account for regeneration of ≈ 3–10 % and 5–7 % of total N inputs, respectively, in Europe and North America (see also Howarth et al. 2002; Holland et al. 2005). Similarly, rotifers may be a major source of P in bog ecosystems. Our estimate of rotifer phosphorus regeneration of 47 kg $km^{-2}$ $yr^{-1}$ is more than an order of magnitude higher than atmospheric deposition rates (Tipping et al. 2014). The observed range of regeneration was a function of latitude (Fig. 6) and may be related to mean annual temperature and precipitation.

Bacteria associated with living *Sphagnum* moss regenerate ≈ 2,500 mg N $m^{-2}$ $yr^{-1}$ and fix ≈ 1,000 mg N $m^{-2}$ $yr^{-1}$, while atmospheric deposition is ≈ 250–700 mg N $m^{-2}$ $yr^{-1}$ (Tjepkema et al. 1981; Hemond 1983; Howard-Williams 1985; Likens & Borman 1995). Atmospheric deposition of N ranges from 0.5 to 1.0 g $m^{-2}$ $yr^{-1}$ in our study sites of New England and southern Canada and at Mer Bleue; Tanja Zivkovic (pers. comm.) estimated $N_2$ fixation rates in the surface *Sphagnum* at the Mer Bleue bog to be 0.2 g $m^{-2}$ $yr^{-1}$, and increased with a decrease in the N:P ratio in *Sphagnum*. There is a strong link between P content and $N_2$ fixation, so the release of P by rotifers would stimulate $N_2$ fixation in the *Sphagnum*. Our estimate that rotifers can regenerate ≈ 50–110 mg N $m^{-2}$ $yr^{-1}$ suggests that rotifers alone can supply ≈ 5 % of the available N in *Sphagnum*-dominated peatlands. In these ecosystems, $NO_3$ is rapidly taken up by bryophytes from precipitation in the top 5–10 cm of moss, outcompeting denitrifying bacteria in the underlying layers. The use of $NH_4$ by many bog plants is strongly inhibited by the low pH (Bridgham et al. 1996).

*Habrotrocha rosa* can live between wet *Sphagnum* litter and is the most frequent rotifer species in peatlands, responsible for 40–50 % N and P regeneration by rotifers. Similarly, *H. rosa* may supply 9–43 mg of N and 18–88 mg of P directly into the leaves of growing pitcher plants during the growing season (Błędzki & Ellison 1998). *Sarracenia purpurea* is widely distributed across North American bogs (Buckley et al. 2003). Although we lack an estimate of pitcher-plant density across North America, Schwaegerle (1983) estimated > 150,000 pitcher plants growing on a 1.2-ha bog. If only 1 % of North American bogs have pitcher plants growing at only 50 % of this density, then given the above supply of N and P by *H. rosa* per pitcher, we would add an additional 2,648 tons of N and 5,398 tons of P annually to the amounts estimated in Table 2.

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