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Changes in submerged macrophyte colonization in shallow areas of an oligo-mesotrophic lake and the potential role of groundwater

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ABSTRACT

Groundwater influx can significantly contribute to nutrient budgets of lakes and its influence is strongest in shallow littoral areas. In oligo- or mesotrophic systems, additional nutrient supply by groundwater influx may affect benthic primary producers and their interactions. Potential changes can be expected in community composition, biomass, stoichiometry and interactions between submerged macrophytes and epiphyton.

This study aimed at investigating whether enhanced epiphyton growth at sites with groundwater discharge may have contributed to a significant change in shallow littoral macrophyte abundance reported from oligo-mesotrophic Lake Stechlin during the last 50 years. In the 1960s, shallow littoral areas were dominated by small charophyte species such as *Chara aspera, C. filiformis* and *C. rudis*. Recent mappings indicated a strong decline of this shallow water charophyte community from 42 ha to 3 ha and a shift to the occurrence of macrophyte species typical of eutrophic lakes such as *Potamogeton perfoliatus, P. pectinatus* and *Myriophyllum spicatum.* We analyzed the nutrient content of macrophytes, and measured epiphyton growth at sites with different groundwater influence. Water column nutrient enrichment may have increased the abundance of eutrophic species, but this did not explain the decrease of charophytes. Our data suggest that enhanced epiphyton growth in shallow littoral areas with groundwater influx could impair the development of small charophytes by shading, increasing drag forces and the charophytes' sensitivity to herbivory.

1. Introduction

Submerged macrophytes have important functions in littoral zones of many lakes by influencing suspended solid retention, sediment oxygenation, and providing shelter or support for other primary producers and grazers (Carpenter and Lodge, 1986). They have been suggested to stabilize clear-water conditions in both shallow (Scheffer et al., 1993) and deeper lakes (Hilt et al., 2010; Sachse et al., 2014). During the last century, higher nutrient loading to temperate lakes resulted in a decrease of charophytes (Baastrup-Spohr et al., 2013; Blindow, 1992) and an increase of faster growing macrophyte species such as *Potamogeton pectinatus* (recently named *Stuckenia pectinata)*, *Myriophyllum spicatum*, or *Ceratophyllum demersum* (Sand-Jensen et al., 2000). Eutrophication has also reduced the maximum colonization depth (Middelboe and Markager, 1997), caused a shift to species with a shorter vegetation period (Hilt et al., 2013; Sayer et al., 2010) and ultimately led to a complete decline of submerged macrophytes (Körner, 2002; Sand-Jensen et al., 2000).

A major nutrient-promoted process impeding macrophytes is the development of phytoplankton and epiphyton competing for light. As macrophytes in deeper water are first affected by shading, maximum colonization depth of macrophytes are widely used as an indicator for lake water quality (Kolada et al., 2014; Lyche-Solheim et al., 2013; Penning et al., 2008; Søndergaard et al., 2013). In the shallow littoral, however, macrophytes are supposed to be less affected by turbid water. Macrophytes therefore often find a refuge in shallow water of highly eutrophic lakes (Hilt et al., 2013). However, additional stress factors can affect macrophyte growth even in shallow waters. Macrophytes in the upper littoral may be influenced by water level fluctuations (Deegan et al., 2012), shading by shore vegetation (Köhler et al., 2010) and by epiphyton (periphyton growing on macrophytes, Phillips et al., 1978; Sand-Jensen and Søndergaard, 1981; Tóth and Palmer, 2016) and wave action (Chambers and Kalff, 1987; Schutten et al., 2004). Shallow macrophytes may also be influenced by groundwater inflow (in the

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following termed lacustrine groundwater discharge, LGD), which predominantly takes place close to the shoreline (McBride and Pfannkuch, 1975; Rosenberry et al., 2015).

LGD may constitute a significant component of the nutrient budget in nutrients-limited lakes (Lewandowski et al., 2015). Groundwater-borne nutrients may influence macrophyte biomass (Frandsen et al., 2012; Lillie and Barko, 1990; Lodge et al., 1989; Loeb and Hackley, 1988), and the stoichiometry (Sebestyen and Schneider, 2004) and total phosphorus (TP) content of their tissue (Ommen et al., 2012). LGD, however, can also promote epiphyton growth (Hagerthey and Kerfoot, 1998, 2005) which may increase shading and drag forces on macrophytes in shallow habitats (Périllon and Hilt, 2016).

Here, we evaluate the changes in the abundance and species composition of shallow littoral macrophytes in a groundwater-fed oligo-mesotrophic hardwater lake and the potential role of LGD in this process. In a previous study, a potential impact of groundwater-mobilized nutrients on periphyton growth has been shown for this lake (Périllon et al., in press). We hypothesize that this process may contribute to a change in macrophyte species composition towards a community with more species typical for eutrophic lakes and a decline of charophytes in shallow littoral areas. To test these hypotheses, we compared the macrophyte species composition and abundance in shallow areas in 1962, 2002, 2007, 2008 and 2014. In addition, macrophyte tissue nitrogen (N) and phosphorus (P) concentrations were measured in five macrophyte species at locations with and without LGD in 2014. Epiphyton development was monitored in summer 2014 on artificial substrates at four locations with or without LGD.

2. Materials and methods

2.1. Lake Stechlin

Lake Stechlin is a temperate, monomictic hard-water lake in north-eastern Germany (Table 1), fed by groundwater and rainfall, with a stable water level since 1962. Short-term water level changes are controlled by climatic conditions such as wind and precipitations (Kirillin et al., 2013a).

In summer 2012, a piezometer campaign aimed at localizing areas with LGD using stable isotopes as indicators (Périllon et al., in press). We generalized these data for the present study area (0–2 m deep) using the Voronoi polygons tool (QGIS 2.12.0) and selected the area situated between the shore and the 2 m depth line, using a bathymetric map (Fig. 1A). The areas located next to a piezometer with low $\delta^{18}O$ signature (between −10‰ and −6‰) were characterized as “LGD” and areas with higher $\delta^{18}O$ values (between −6‰ and −2‰) as “C” (control). The most eastern bay was excluded from the analysis due to its anthropogenic use as beach area (Fig. 1A). The main locations for LGD are in the southern, south-eastern and western littoral, while the outflow is concentrated in the northern littoral of the lake. All our sampling points were located in areas with stable groundwater flow direction, apart from the eastern control which could show inter-annual variation in flow direction, e.g. after wet years (Holzbecher, 2001).

Table 1
Topographical, morphological, hydrological, and chemical parameters of Lake Stechlin (Krey, 1985; IGB, unpublished data).

Parameter	Mean ± sd
Drainage basin	12.6 km^2
Forested area in drainage basin	95%
Maximum depth	69.5 m
Surface area	4.3 km^2
Volume	96.9×10^6 m^3
Mean depth	23.3 m
Effective fetch	2 000 m
Water retention time	> 40 yrs
Water temperature[c]	19.1 ± 3.1 °C
Secchi transparency[a]	6.4 ± 1.7 m
Calcium[b]	49.6 ± 6.9 mg L^{-1}
Dissolved inorganic carbon[b]	20.6 ± 1.9 mg L^{-1}
NO$_3^-$-nitrogen[b]	16 ± 24 µg L^{-1}
NH$_4^+$-nitrogen[b]	32 ± 30 µg L^{-1}
Total phosphorus[b]	11 ± 3 µg L^{-1}
Soluble reactive phosphorus[b]	2 ± 1 µg L^{-1}

[a] seasonal average, May–September, 2001–2010.

[b] seasonal averages, May–September, 2000–2008, pooled samples, surface, 5 m, 10 m.

[c] seasonal averages, May–September, 2014, pooled samples, surface, 5 m, 10 m.

2.2. Macrophyte mapping

Macrophyte surveys have been performed during the summers 1962 (Krausch, 1964), 2002, 2007 (unpublished data of Landesumweltamt Brandenburg), 2008 (Van de Weyer et al., 2009), and 2014 (Van de Weyer et al., 2015; Fig. 1B). From 1962 we could only access the maps (Fig. 1B) and the list of species present in the whole lake (Table 2). In 2002, 2007, 2008 and 2014, macrophytes have been surveyed on 7 identical transects (straight lines that begin perpendicular to the shore). 13 further transects were surveyed in 2008 and 2014.

The mappings performed in 2008 and 2014 (20 transects) were most detailed. First, vegetation zones were mapped in June/July from a boat using an underwater camera and macrophyte were identified after sampling with a rake. Additionally, a diver followed the borders of specific populations of vegetation with a GPS buoy. Finally, divers mapped 20 transects to define more precisely macrophyte habitats and identify maximum colonization depths. Macrophyte species were determined following Van de Weyer and Schmitt (2011) and the macrophyte zones were identified after Berg et al. (2004). For each vegetation zone, the coverage was estimated in the field using the decimal Londo scale (Londo, 1976) and then translated into percentage of coverage, with values ranging between 0.1% (single macrophyte) to 97.5% (single species continuous cover).

Macrophyte species were classified following the indicator values defined in Schaumburg et al. (2015) for the lake type TKg13 (carbonate-rich stratified water body of northern German lowlands with small watershed). “A” species are typical for pristine undisturbed conditions characteristic of this lake type, “B” species are more indifferent and “C” species indicate a deviation from reference conditions for this lake type (Schaumburg et al., 2004). The classification of charophytes (Kabus and Mauersberger, 2011) and angiosperms (Ristow et al., 2006) in red list categories for Brandenburg, are presented in Table 2.

For data evaluation, we selected macrophyte data from the two first meters depth using QGIS. The indicator values were attributed following the species and the depth limits of vegetation zones: when the zone upper limit were shallower than 1m, the indicator values corresponding to 0–1 m (Schaumburg et al., 2015) were attributed to the macrophytes. Indicator values corresponding to 1–2 m were attributed to deeper zones.

First data analysis consisted of the comparison of the number of macrophytes species present at 0–2 m depth, in the 7 common transects studied in 2002, 2007, 2008 and 2014 (Fig. 2A). The number of macrophyte species typically growing in shallow littoral, are also represented for the year 1962 (Fig. 2A).

Further analysis required the calculation of coverage data within transects, using the data from 20 transects, in 2008 and 2014. The coverage of each macrophyte species were added for each indicator value and transects. The percentage of the littoral area covered by the vegetation zones were used as an adjustment value. Often species were observed as single plants, or only in few transects, therefore the obtained values averaged among transects and species, are low.