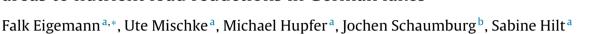
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Biological indicators track differential responses of pelagic and littoral areas to nutrient load reductions in German lakes



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ABSTRACT

External nutrient loading was reduced over the past decades as a measure for improving the water quality of eutrophic lakes in western Europe, and has since been accelerated by the adoption of the European Water Framework Directive (WFD) in 2000 (EC, 2000). A variety of eutrophication-related metrics have indicated that the response of biological communities to this decreased nutrient loading has been diverse. Phytoplankton, a major component of the pelagic community, often responded rapidly, whereas a significant delay was observed for submerged macrophytes colonizing littoral areas. In this study we tested whether assessment methods developed for phytoplankton and macrophytes in lakes during Germany's implementation of the WFD reflect this differential response. An assessment of 263 German lakes confirmed that a lower ecological state was recorded when based on the biological quality element (BQE) for macrophytes than the BQE for phytoplankton during the investigated period (2003-2012). On average, lakes had a moderate ecological status for both phytoplankton and macrophyte BQEs, but differences of up to three classes were observed in single cases. Long-term data were available for five lowland lakes subject to strong reductions in phosphorus loading. Their phytoplankton-based assessments indicated a constant improvement of the ecological status in parallel to decreasing water phosphorus concentrations. In contrast, macrophyte-based assessments indicated a 10–20 year delay in their ecological recovery following nutrient load reduction. This delay was confirmed by detailed data on the temporal development of macrophyte species diversity and maximum colonization depths of two lakes after nutrient load reduction. We conclude that the available WFD assessment methods for phytoplankton and macrophyte BQEs are suitable to track the differential response of pelagic and littoral areas to nutrient load reductions in German lakes.

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1. Introduction

Most European lakes experienced severe deteriorations of water quality due to eutrophication during the 20th century. As a consequence, many lakes completely lost their submerged macrophyte communities (Sand-Jensen et al., 2000; Hilt et al., 2013) and shifted to a phytoplankton-dominated state (Scheffer et al., 1993). In recent decades, substantial efforts were made to improve the ecological state of lakes (Sas, 1989; Jeppesen et al., 2005; Van Puijenbroek et al., 2014). This process has been further intensified by European legislation adopted in 2000, the Water Framework Directive

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http://dx.doi.org/10.1016/j.ecolind.2015.10.045 1470-160X/© 2015 Elsevier Ltd. All rights reserved. (WFD, European Commission, 2000), which commits all members to achieve a good ecological status for their water bodies. Traditionally, lake water quality assessments mainly focused on nutrient concentrations. Along with the WFD, biological quality elements (BQEs) were introduced to determine the ecological integrity of lakes (Lyche-Solheim et al., 2013). Phytoplankton and macrophytes are two of these BQEs, which are key response variables for reduced nutrient loading (Carvalho et al., 2013; Poikane et al., 2014).

Despite reductions in nutrient loading to lakes in several European countries, macrophyte recovery has often been delayed whereas phytoplankton showed an almost immediate response (Jeppesen et al., 2005; Coops et al., 2007) when internal loading was low (Søndergaard et al., 2003). Potential reasons for this delay include high nutrient availability in the sediments, the major nutrient source for rooted macrophytes (Barko and Smart, 1981), longer generation times of macrophytes compared to phytoplankton (Jeppesen et al., 2005), dispersal limitations (Hilt et al., 2013), a lack of viable seed banks, and herbivory (Bakker et al., 2013).





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WFD assessment methods for macrophytes condense the taxonomic and distributional information gained from surveys into water quality metrics (Penning et al., 2008; Kolada et al., 2014). However, the highly complex and variable distribution of macrophytes and the delayed response to nutrient load reductions may cause uncertainty in their use as biological indicators (Capers et al., 2010; Dudley et al., 2013). Cellamare et al. (2012) and Stelzer et al. (2005) suggested that phytoplankton was the best indicator for seasonal and short-term changes in lake water quality. Nevertheless, macrophytes may better reflect the long-term consequences of eutrophication in littoral areas, which can affect the ecological status of lakes for decades (Schneider et al., 2014).

In this study, we tested whether the WFD BQEs for phytoplankton and macrophytes reflect a differential response of the pelagic and littoral areas of lakes to nutrient load reductions. We hypothesized that lakes with decreasing nutrient loading would be rated a poorer ecological status when macrophytes were considered, rather than phytoplankton. To test this hypothesis, we compared the assessment data for macrophyte and phytoplankton BQEs from 263 German lakes investigated between 2003 and 2012. Data on lake-specific changes in nutrient loading were not available, but we assumed a decrease for the majority of lakes due to the overall changes in most catchments (Behrendt et al., 2002; Jeppesen et al., 2005).

We also compared temporal changes in the ecological statuses provided by phytoplankton and macrophyte BQEs during the past 5–20 years in five lakes for which a strong decrease in nutrient loading had been established, based on measurements of TP concentrations. In addition, we compared the ecological status provided by the BQE for macrophytes with data on temporal changes in macrophyte species diversity and maximum colonization depth development for two lakes following nutrient load reductions.

2. Material and methods

2.1. Ecological status of lakes based on phytoplankton and macrophytes in Germany

We used the assessment results of the German Phyto-See-Index based on phytoplankton, and the module "macrophytes" within the German PHYLIB system for lakes. Both assessment methods have a five status classification (1 = high, 2 = good, 3 = moderate, 4 = poor, 5 = bad) with their status result being adjusted against the status of reference lakes unaffected by human impact or in relatively undisturbed locations.

The assessment of the ecological status of phytoplankton consists of the metrics biomass, algae classes and the Phytoplankton-Taxa-Lake-Index (PTLI) (Mischke et al., 2008). The biomass metric is based on the arithmetic average of the separate valuations of three parameters: The total biovolume of phytoplankton in the epilimnion or euphotic zone, the average and the maximum chlorophyll *a* concentration (Mischke et al., 2008). The algae class metric categorizes the added biovolumes of all cyanobacteria, chlorophyceae, dinophyceae and cryptophyceae, and the PTLI grades the trophic state of the lake based on phytoplankton species composition. The overall calculation of the PTLI is carried out by calculating the mean of the single metrics, with different weighting factors depending on lake type (Mathes et al., 2002; Riedmüller et al., 2013).

To evaluate the ecological status of macrophytes in German lakes, Schaumburg et al. (2004, 2011) and Stelzer et al. (2005) mapped species distributions and abundances across depth gradients in lake transects. An index to classify three different macrophyte groups (A: dominant in the reference system, B: neutral species, C: degradation indicator) is calculated, which varies by lake type (Mathes et al., 2002). Besides species composition and abundances, vegetation depth limits also influence the evaluation of the ecological status of macrophytes, as well as some additional metrics such as the mass stands of eutraphent species. Macrophyte status and benthic diatoms are the only biological modules in the German PHYLIB assessment system (Schaumburg et al., 2011).

2.2. Fundamental data

In this study, we compared the assessment results from the phytoplankton and macrophyte BQEs for 263 German lakes from 2003 to 2012. Altogether, 375 direct matches for macrophyte and phytoplankton assessments in the same lake and year were accessible, originating from 13 different lake types (Table 1). While a national data collection for macrophyte indices was performed for our study, the phytoplankton indices were already available. Phytoplankton data were exported from the database PHYTOSEE (Mischke and Böhmer, 2013) and macrophyte data were exported (after merging all available data) from the database PHYLIB (Schaumburg et al., 2004). For calculations and comparisons of the different ecological statuses, the variable "macrophyte evaluation decimal" was used for the macrophytes and the variable "PHYTOSEE index" was used for the phytoplankton.

Longer-term assessments of the ecological status of macrophytes and phytoplankton were available for five German lakes which had been subject to various restoration measures, producing declining total phosphorus (TP) concentrations (Table 2). TP concentrations were exported from the phytoplankton database PHYTOSEE where possible. In cases where TP values were not available from the PHYTOSEE database, TP data were obtained from the Ministry of Farming, Environment and Consumer Protection Mecklenburg-Western Pomerania, and TP concentration means were calculated from April to October within the (estimated) euphotic depths of each lake (see instructions for PHYTOSEE evaluation). For Lake Tollensesee, TP concentrations before 1999 were taken from Nixdorf et al. (2004).

2.3. Response of macrophyte species numbers and colonization depths to P load reductions

Data on changes in species number and maximum colonization depths of macrophytes in response to TP load reductions were available for two lakes (Table 2). Data were recorded during surveys conducted in Lake Müggelsee in 1999 and 2006 along the entire lake's littoral zone using an aquascope and a rake, and in 2011 and 2014 by Scuba diving along 25 and 8 transects, respectively. In Lake Tegel, data for 1988 were based on literature values (Hilt et al., 2010) and in 2007 and 2012, surveys were conducted along 29 and 12 transects, respectively, by Scuba diving (Van de Weyer and Krautkrämer, 2012).

2.4. Statistical analyses

Comparisons between assessment results of macrophytes and phytoplankton were executed using Student's *t*-tests. Pearson correlations were calculated to test for the relationships between different parameters. To test for different discrepancy levels between lake types, a one-way ANOVA with a subsequent Tukey's LSD post hoc test was executed. The significance level for all tests was set to p = 0.05. All statistical analyses were performed with the software package R (R Development Core Team, 2008).

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