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Facilitation of Lake Eutrophication by Altered Feedback Loops Between Submerged Macrophyte Vegetation and Phosphorus Retention

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ABSTRACT

1. Charophytes (stoneworts) often dominate the submerged vegetation in nutrient-poor hardwater lakes, where they support high benthic phosphorus (P) retention. As a consequence, epilimnion P concentrations remain low and water clarity high, resulting in a positive feedback. When perennial charophytes, retaining P all year round, are replaced by vascular macrophytes, P is retained only during summer but rapidly released during decomposition in the autumn and winter. Epilimnion P thus becomes available to phytoplankton in the following growing season, reducing lake water clarity and further shifting plant dominance from bottom-dwelling charophytes to taller vascular species.
2. We tested the hypothesis that changes in lake P concentrations may be partly related to changes in the structure of submerged macrophytes in a deep hardwater lake that experienced a dramatic increase in total P (TP) concentrations over a decade with no evidence of changes in external P loading. We repeatedly measured water transparency, macrophyte maximum colonisation depth (MCD) and abundance between 2008 and 2022 and determined macrophyte tissue P content in 2020 to test whether changes in submerged vegetation could explain gaps in the lake's P budget and shifts in P sink/source functions of littoral areas.
3. In 2008, charophyte communities were dominated by wintergreen *Nitellopsis obtusa*. The subsequent decline of the species was negatively correlated with the spring TP concentration in the upper water layer (0–20 m) of the lake and positively correlated with Secchi depth and macrophyte MCD, which decreased from 13.5 to 9.5 m. In contrast, the cover of annual vascular macrophytes (mainly rootless hornwort, *Ceratophyllum demersum*) increased and was positively correlated with P losses from the upper water layer in summer and negatively correlated with Secchi depth and MCD.
4. Budget calculations showed that the littoral zone was a P source during the period when *N. obtusa* declined. Despite the relatively low contribution of P directly released from lost charophyte biomass, declines of *N. obtusa* partly explained the temporary P source function of the littoral zone and the increasing P concentrations in the upper water layer at the beginning

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of May. This was most probably due to the positive effects of charophytes on particle retention and the negative effects on sediment resuspension. Conversely, the growth of *C. demersum* can explain P losses from the upper water layer, turning the littoral zone into a temporal P sink during summer. However, most of this P is likely to return to the upper water layer during the decomposition of plant biomass after the growing season.

5. In conclusion, our data indicate that replacement of charophytes by submerged vascular plants can facilitate rapid lake eutrophication due to changes in the feedback loop between submerged vegetation, benthic P retention, epilimnion P availability, water transparency, and MCD.

1 | Introduction

Submerged macrophytes are an integral part of many lakes, where they fulfil numerous ecological functions and provide a variety of ecosystem services (Hilt et al. 2017, 2022) such as the stabilisation of clear-water conditions in both shallow (Scheffer et al. 1993; Genkai-Kato and Carpenter 2005) and deeper lakes (Hilt et al. 2010; Sachse et al. 2014). Mechanisms include (i) the uptake and temporary storage of nutrients such as phosphorus (P) in macrophyte tissue, attached periphyton and calcite encrustations (Kufel and Kufel 2002); (ii) increased sedimentation and reduced sediment resuspension (Hamilton and Mitchell 1996); (iii) protection of zooplankton from fish predation (Burks et al. 2002); and (iv) allelopathic growth inhibition of phytoplankton (Hilt and Gross 2008). In nutrient-poor hardwater lakes of temperate climates, macrophyte communities are typically dominated by charophytes, which form dense meadows and can occur at depths of up to 60 m (Frantz and Cordone 1967). However, this type of vegetation has strikingly declined over the last century (Blindow 1992a; Sand-Jensen et al. 2000, 2017; Auderset Joye et al. 2002). As a result, most charophyte species are now threatened (Baastrup-Spohr et al. 2015), to the extent that the remaining oligo-mesotrophic hardwater lakes with charophyte vegetation have been protected under the European Union's Habitats Directive (EC-DGENV 2007) since 1992.

Charophytes can take up nutrients from both the water column (Kufel and Kufel 2002) and sediments (Wüstenberg et al. 2011). They appear to do so more efficiently than many vascular submerged macrophytes, but as nutrient loading of lakes increases, charophytes lose this competitive advantage (Hidding et al. 2010; Richter and Gross 2013). Subsequent increases in vascular macrophytes, often canopy-forming species, have typically been associated with reduced light availability in lakes (Blindow 1992a; Brodersen et al. 2001; Bazarova and Itigilova 2006). Therefore, declines in charophyte abundances have been mainly attributed to lake eutrophication. However, charophytes have also disappeared from shallow areas in the littoral zones of clear-water lakes (Périllon et al. 2018) and from deeper waters, partly as a result of invasions by non-native aquatic vascular plants (Wells et al. 1997). Although in recent decades external nutrient loading of many lakes has been greatly reduced in many regions (Jeppesen et al. 2005; Stich and Brinker 2010), and charophytes have regained dominance over vascular plants during the re-oligotrophication of such lakes (Richter and Gross 2013; Brzozowski et al. 2021), widespread declines of charophyte vegetation have continued (Alirangues-Núñez et al. 2023; Krambeck et al. 2024). Shading by periphyton, damage or removal by benthivorous fish, and exposure to herbicides have been discussed as potential reasons (Alirangues-Núñez et al. 2023; Krambeck et al. 2024). In general, however, the

underlying mechanisms and consequences of charophyte declines remain poorly understood.

Here, we present data on submerged macrophytes from a temperate hardwater lake that recently underwent a dramatic increase in P concentrations despite no evidence of external P loading, but indications of internal P release from littoral areas (Gonsiorczyk et al. 2024). We hypothesised that the observed rapid increase of total P (TP) concentrations in the lake was partly related to concomitant rapid changes in the community structure of submerged macrophytes, facilitated by feedback loops supporting a dominance of either charophytes or vascular aquatic plants (Figure 1). Specifically, we posited (i) that replacement of wintergreen charophytes by annual vascular plants contributed to decreased benthic P retention during the autumn and wintertime, increased P availability in the epilimnion, reduced water transparency and maximum macrophyte colonisation depth (MCD), together favouring conditions for vascular plant dominance (Figure 1); (ii) that the reduced benthic P retention is facilitated by the high P tissue content and rapid release during senescence and decomposition of annual submerged macrophytes during autumn and winter; and (iii) that these changes in submerged vegetation partially explain gaps in the lake's P budget and shifts in P sink/source functions of littoral areas of lakes.

2 | Materials and Methods

2.1 | Study Site

Lake Stechlin is a dimictic clear-water lake located in north-eastern Germany (53°09'5.6" N 13°01'34.2" E, Figure S1, <https://geo.igb-berlin.de/maps/972/view/#/>). The lake surface area is 4.23 km² and the volume is 99.7 × 10⁶ m³ at a mean and maximum depth of 23.6 and 69.5 m, respectively. The lake is mainly fed by precipitation and groundwater and has a water retention time of at least 40 years (e.g., Kasprzak et al. 2017). The regulated water level has fluctuated little (i.e., by about 30 cm) in recent decades (Pöschke et al. 2018). The catchment is dominated by managed forest. Macrophyte surveys between 1962 and 2008 indicated that shallow-water charophyte communities had been replaced by either bare sediment or vascular submerged macrophyte species, suggesting a deviation from reference oligotrophic conditions (Périllon et al. 2018). Between 2010 and 2020, the formerly oligotrophic lake experienced a rapid eutrophication related to a quadrupling of TP concentrations (Gonsiorczyk et al. 2024). This led to increased phytoplankton and zooplankton biomass and size of vendace, the dominant pelagic fish, while water transparency declined (Selmečzy et al. 2019; Kröger et al. 2023; Mehner et al. 2023).

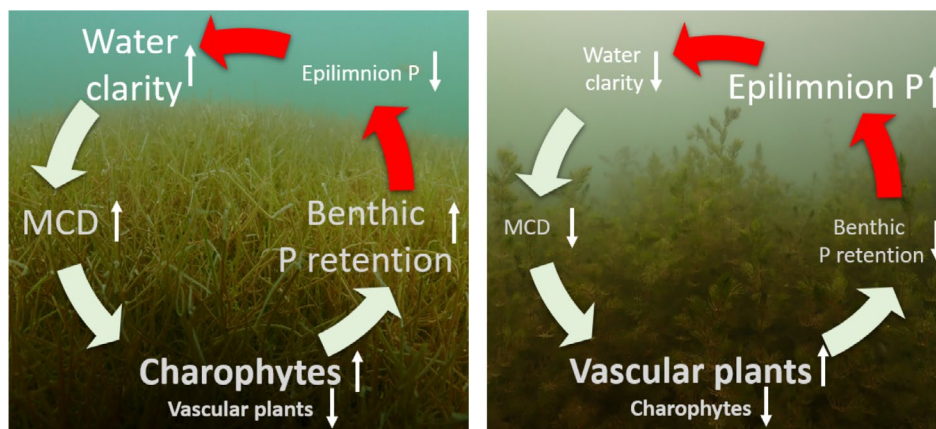


FIGURE 1 | Proposed feedback loop between submerged macrophytes, benthic phosphorus (P) retention, epilimnion P concentrations, water clarity and maximum colonisation depth (MCD) of macrophytes in oligotrophic hardwater lakes under charophyte (left) or vascular plant (right) dominance. Red and light green arrows indicate negative and positive effects, respectively, and font sizes and small arrows represent lower versus higher values under charophyte or vascular plant dominance.

2.2 | Water Clarity, Phosphorus Concentrations and Sedimentation Rates

Secchi disk transparency was determined fortnightly at the deepest point of the lake from May to October and monthly during the rest of the year between 2008 and 2022. Water samples from 5 different depths (0, 5, 10, 15 and 20 m) were also collected fortnightly (May to October) or monthly (mixed sample from 0, 5 and 10 m) during the rest of the year. The upper 20 m of the water column roughly corresponded to the euphotic zone and to the former MCD of submerged macrophytes. Total phosphorus (TP) concentrations in the water samples were determined as described in Gonsiorczyk et al. (2024).

Sedimentation rates of P from the upper water layer (20 m) into the hypolimnion were determined with four cylindrical traps (100 cm height, 9 cm diameter) deployed at 20 m depth from 2009 to 2012 and from 2016 to 2022. Formaldehyde was added to the traps before they were filled with lake water (0.13% final concentration) to preserve the settled material. The traps were retrieved every 6 weeks, the contents passed through a 500- μ m mesh to remove mesozooplankton, pooled across the four traps, and an aliquot of the suspension was filtered through glass-microfiber filters (MGF, Sartorius, Germany). The remaining material was left to settle and, to minimise contamination by solutes in the overlying water, the supernatant was successively decanted before drying the material at 105°C. The TP content of the dried material was determined spectrophotometrically as soluble reactive P (SRP) after digestion of 5–10 mg dry sediment in a solution of 2 mL 5 M H_2SO_4 , 2 mL 30% H_2O_2 , and 20 mL demineralised water at 150°C for 8 h.

2.3 | Macrophyte Mapping and Tissue Phosphorus Content

In 2008, 2014 to 2016, 2020 and 2022, the abundance of submerged macrophyte species was determined along 13 transects of Lake Stechlin by scuba diving surveys according to Pätzolt (2007). See Figure S1, Table S1 and <https://geo.igb-berlin.de/maps/972/view/#/> for the exact locations and coordinates. The 13 transects were selected to be representative of the submerged vegetation of the lake as part of the monitoring required

by the EU Water Framework Directive for all European lakes larger than 50 ha (van de Weyer et al. 2015). In addition, the spatial extent of the following vegetation zones was recorded: (a) shallow-water stonewort community, (b) starry stonewort community (*Nitellopsidetum obtusae*), (c) deep-water community with filamentous green algae and mosses (*Cladophora spec.*, *Vaucheria spec.*, *Fontinalis antipyretica*, *Platyhypnidium riparioides*), (d) community with vascular submerged macrophytes (*Potamogeton lucensis*, *Najas intermediae*), (e) reed community (Phragmites), including sedge reed (*Magnocaricion*), and (f) vegetation-free areas. The depth distribution and length of each vegetation zone were determined, and a semi-quantitative survey using the Londo (1976) scale was carried out for all encountered macrophyte species down to the MCD. The *Vaucheria* and *Cladophora* clades from the deep zone were not identified.

In addition, the extent of the vegetation zones (see above) was mapped in the entire lake in September 2008, 2014, and 2022 using a method developed by van de Weyer et al. (2009). First, the vegetation was mapped from a boat in transects perpendicular to the shore at 100 m intervals along the shoreline. This survey was carried out with a rake, a double rake, and an underwater video camera. The depth limits and exact locations of the vegetation zones were recorded using GPS. In addition, lists of all encountered macrophyte species were compiled for each sampling site. The boundaries between vegetation zones were delineated by scuba divers recording tracks by holding a line attached to a surface buoy mounted with a GPS. Biomass samples of the most common submerged macrophyte species in September 2020, *Ceratophyllum demersum* and *Nitellopsis obtusa*, were harvested at four transects using a rake. The collected plant material was sorted, dried at 60°C to constant weight, ground, digested, and analysed using the ammonium molybdate spectrophotometric method for tissue P content.

2.4 | Contribution of the Littoral Zone to the Phosphorus Budget of the Upper Water Layer

We calculated the potential contribution of the littoral area of Lake Stechlin to P gains or losses in the upper water layer (P_{0-20m}) during summer (May–October) as:

$$P_{0-20m} = P_{traps} - (P_{May} - P_{Oct}) - (P_{import} - P_{export})$$

The P content of the upper water layer (0–20m) in May and October (P_{May} , P_{Oct}) was calculated as the volume-weighted mean TP concentration of the individual depth layers that were sampled, multiplied by the corresponding water volume of those layers. Vertical P fluxes from the upper water layer (top 20 m) into the hypolimnion (P_{trap}) during summer stratification (May–October) were determined from the rates of P accumulation in the sediment traps. To assure comparability of the sedimentation fluxes and changes in the upper water layer, the values were interpolated in all considered years to the reference period from the 1st of May to the 31st of October. The external P load into the upper water layer (P_{import}) was estimated at 90 kg for May to October, and the losses of P to groundwater ($P_{export} = 24.3 \pm 11.6$ kg) were calculated based on a retention time of 40 years (Gonsiorczyk et al. 2024).

2.5 | Data Analyses

Linear regressions were performed between the sum of vegetation cover by starry stonewort communities over all 13 transects (sum of cover over all 13 transects) and (i) the P content of the upper water layer (0–20m) at the beginning of the vegetation period (1st of May), (ii) mean annual Secchi depth, and (iii) MCD. Additional linear regressions were calculated between the sum of vegetation cover by vascular plant communities over all 13 transects and (i) the summer P loss (1st of May until 31st of October) of the upper water layer (0–20m), (ii) Secchi depth, and (iii) MCD.

3 | Results

3.1 | Shallow Water Phosphorus Concentrations and Water Transparency

The mean annual TP concentration in the upper water layer (0–20m) of Lake Stechlin increased from $14 \mu\text{g L}^{-1}$ in 2008 to $40 \mu\text{g L}^{-1}$ in 2020 and had declined to $33 \mu\text{g L}^{-1}$ by 2022. A distinct seasonal pattern with the highest TP concentrations during winter and early spring (January to early March) and a subsequent decline during summer stratification from May to October was observed each year (Figure 2a). Until 2017, minimum TP concentrations remained between 9 and $12 \mu\text{g L}^{-1}$ in most years, while maximum TP concentrations increased from $21 \mu\text{g L}^{-1}$ in March 2008 to $64 \mu\text{g L}^{-1}$ in March 2020 (Figure 2a). At the beginning of May, the P content in the upper water layer (0–20m) ranged from 780 kg in 2008 to 3624 kg in 2021 (Figure 2b). In October, these values were always lower, except for 2008, ranging between 549 and 1335 kg (Figure 2b). Mean annual Secchi disk readings decreased significantly between 2008 and 2022 (Figure 2c) and were negatively correlated with yearly mean TP concentrations in the upper water layer ($r = 0.91$; $p < 0.001$).

3.2 | Submerged Macrophyte Maximum Colonisation Depth, Cover and Tissue Phosphorus Content

The maximum colonisation depth (MCD) of submerged macrophytes in Lake Stechlin decreased by about 5 m from 14.1 to

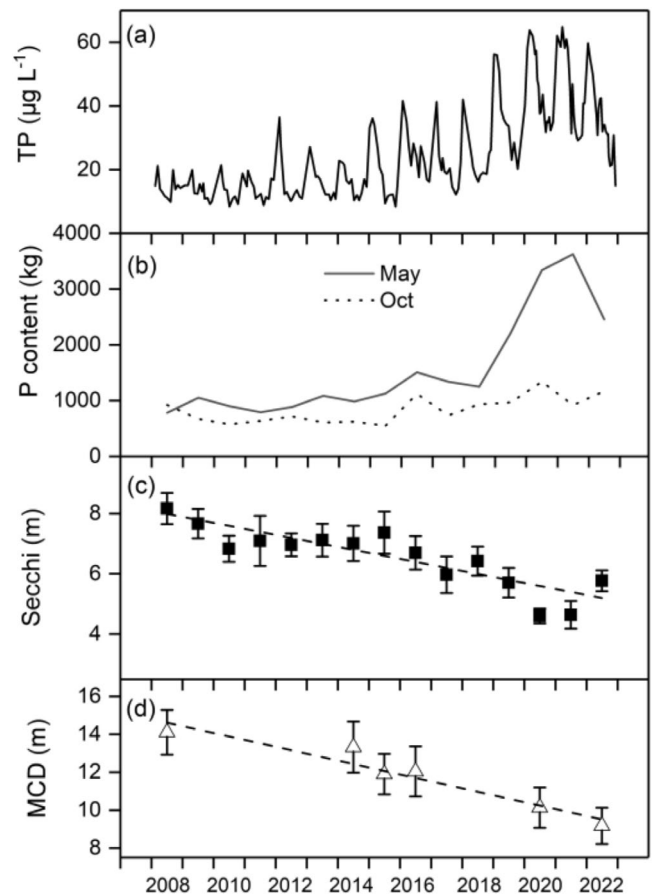


FIGURE 2 | Concentrations of total phosphorus (TP) in the upper water layer (0–20m) (a), P content in the upper water layer (0–20m) in May and October (b), mean annual Secchi depth ($\pm$ standard error, $N = 12$) (c) and mean maximum colonisation depth (MCD, $\pm$ standard error, $N = 13$) of submerged macrophytes determined at 13 transects (d) in Lake Stechlin between 2008 and 2022.

9.2 m between 2008 and 2022 (Figure 2d). Submerged macrophyte cover was dominated by charophytes, green algae, and mosses, and the starry stonewort *Nitellopsis obtusa* was the most abundant species in all years except 2020 (Figure 3a). Cover by vascular plant species, particularly hornwort, *Ceratophyllum demersum*, increased strongly over the years, with a peak observed in 2020 (Figure 3b). Major changes were detected between 2008 and 2022 for the contribution of different macrophyte communities to the total plant cover along the 13 transects (Figure 4). The starry stonewort community and the deep-water community consisting of filamentous green algae and mosses, declined by 12% and 29%, respectively, while areas with vascular plants or sparse submerged vegetation increased by 17% and 26%, respectively (Figure 4).

The starry stonewort community cover in transects was negatively correlated with the TP content in the upper water layer at the beginning of May (Figure 5a), and positively correlated with mean Secchi depth (Figure 5b) and the MCD of submerged macrophytes (Figure 5c). The vascular plant community cover in transects was positively correlated with losses of TP from the upper water layer (0–20m) during summer (May to October) (Figure 5d), and negatively correlated with Secchi depth (Figure 5e) and the MCD of submerged macrophytes

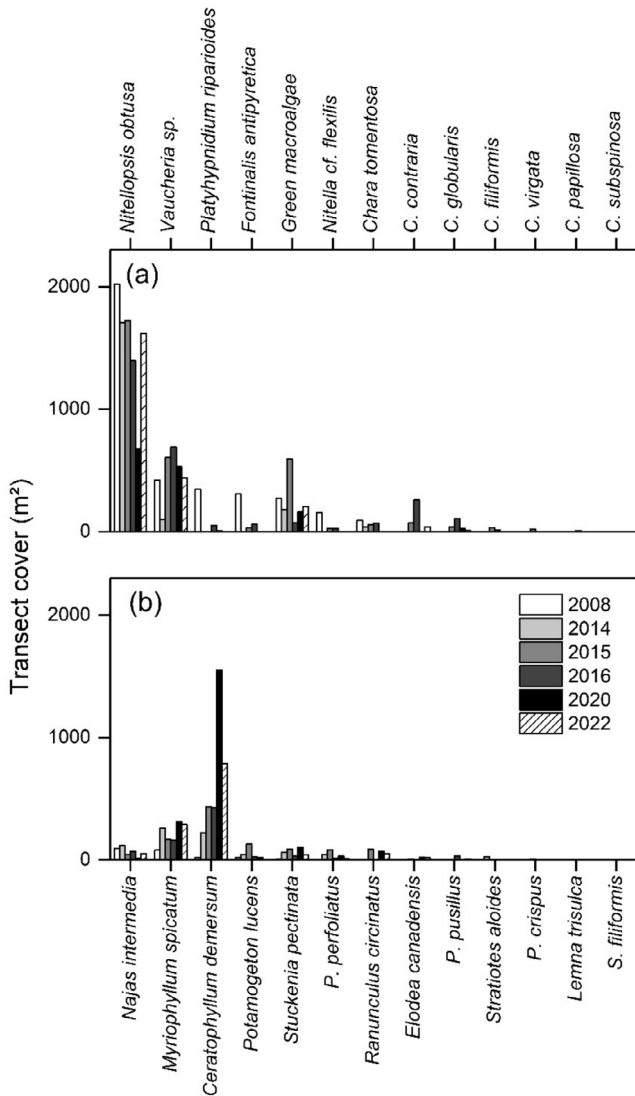


FIGURE 3 | Sum of the transect cover of charophytes, mosses and filamentous green algae (a), as well as vascular plants (b), along 13 transects monitored in Lake Stechlin on 6 occasions between 2008 and 2022. Taxa are ordered from left to right according to their importance in 2008.

(Figure 5f). Mean tissue P content in *C. demersum* harvested in September 2020 varied between 2.4 and 3.5 mg g⁻¹ dry mass, while values in *N. obtusa* were about 2–4 times lower (Figure 6). Total vegetation cover mapping of the whole lake in 2008, 2014 and 2022 showed a loss of 0.14 km² of charophytes (41%), most of it (0.12 km²) between 2008 and 2014, and an increase of vascular plant communities by 0.45 km² (346%) to 0.58 km² between 2008 and 2022 (Figure 7c).

3.3 | Contribution of the Littoral Zone to the Phosphorus Budget of the Upper Water Layer

The calculated differences in the P content between May and October (Figure 2b) amounted to losses of between 155 (2011) and 2707 kg P (2021) from the upper water layer (0–20 m) during summer (Figure 7a). The material collected in sediment traps between May and October (measured over 11 years, the exceptions

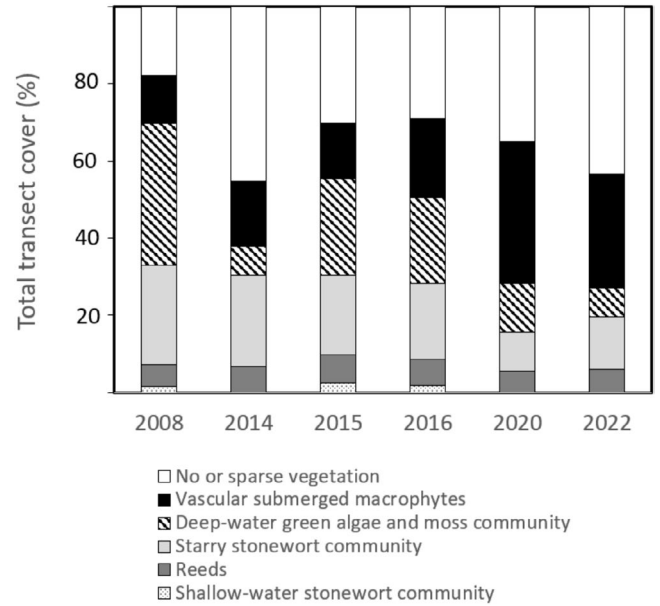


FIGURE 4 | Proportion of different macrophyte communities and bare sediment along 13 transects in Lake Stechlin monitored by scuba-diving surveys on 6 occasions between 2008 and 2022.

being 2008 and 2013 to 2015) indicated vertical P fluxes from the upper (0–20 m) to deeper water layers between 301 kg (2022) and 1045 kg (2012) (Figure 7b). Based on the estimated external P inputs to and exports from the upper water layer (see Materials and Methods), we assessed the sink versus source function of the littoral area in the P budget of the upper water layer during the summer. Accordingly, the littoral zone functioned as a P source between 2009 and 2018, releasing an average of 296 kg P per year during summer but turned into a P sink from 2019 to 2022, accumulating between 645 and 2345 kg P (mean 1381 kg) during the summer (Figure 7b).

4 | Discussion

The results of our analysis support the hypothesis that shifts in submerged macrophyte communities from charophytes to submerged vascular plants facilitate internal P loading, leading to increased TP concentrations in the epilimnion of stratified lakes. This, in turn, could exacerbate the shift in macrophyte communities and result in feedback loops that stabilise the dominance of submerged vascular plants or charophytes in hardwater lakes (Figure 1).

4.1 | Contribution of Charophyte Decline to Phosphorus Enrichment of the Upper Water Layer

To assess whether the strong decline of charophyte cover in Lake Stechlin between 2008 and 2022 (Figures 4 and 7c) could explain the additional P availability in the upper water layer (0–20 m), we first converted the loss in charophyte area (0.14 km²) determined by our whole-lake mappings in 2008 and 2022 into charophyte biomass loss based on literature values (0.3–1.5 kg dry mass m⁻² reported by Blindow (1992a) and Kufel et al. (2020), respectively). Combined with the mean tissue P content we measured

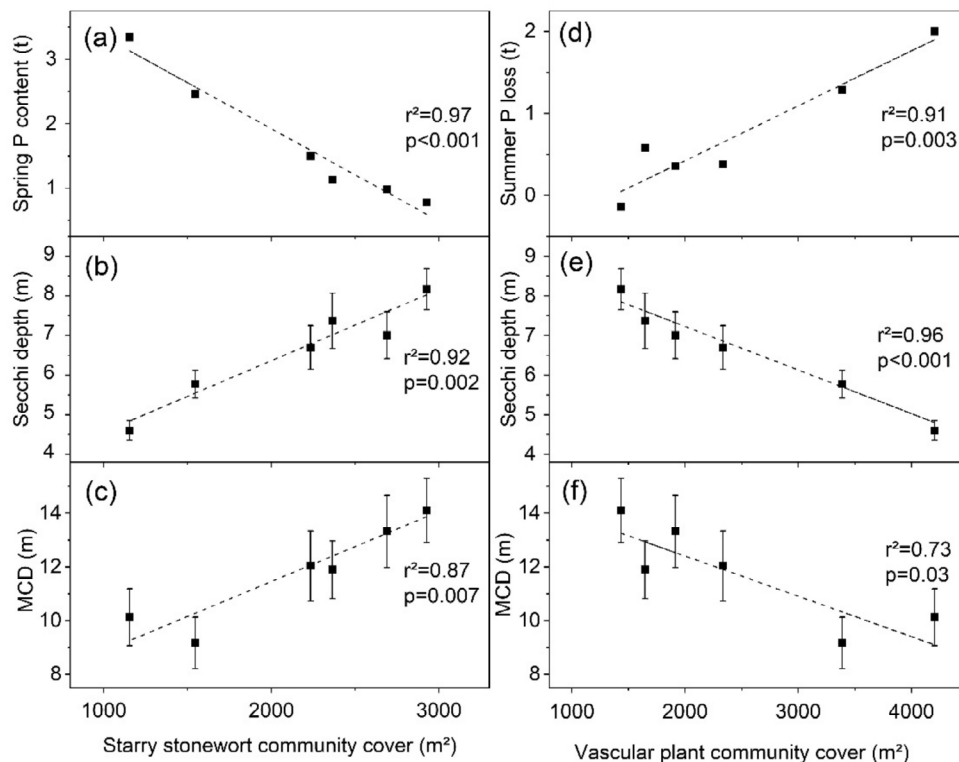


FIGURE 5 | Correlations between vegetation cover of starry stonewort communities (a–c) and vascular plant communities (d–f), respectively, in Lake Stechlin monitored along 13 transects by scuba-diver surveys in 2008, 2014, 2015, 2016, 2020 and 2022 (sum of the cover across 13 transects), and total phosphorus (TP) content of the upper water layer (0–20 m) in May (a) or summer P loss in the upper water layer (0–20 m) (d), annual mean ($\pm$ standard error) Secchi disk transparency (b, e), and maximum colonisation depth (MCD, mean $\pm$ standard error, $N = 13$) of submerged macrophytes (c, f).

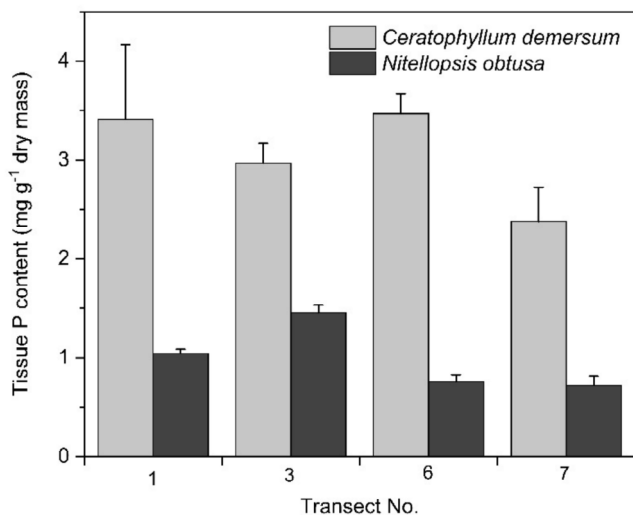


FIGURE 6 | Tissue phosphorus (P) concentrations of *Ceratophyllum demersum* and *Nitellopsis obtusa* harvested in September 2020 in 2 m water depth at four different transects in Lake Stechlin.

in 2020 (1 mg g^{-1} dry mass), this biomass loss resulted in a direct P release from charophyte biomass of 42–209 kg in 14 years (2008–2022), which accounts for 1%–5% of the average littoral P release in Lake Stechlin ($296 \text{ kg P/summer (May–Oct)}^{-1}$). This range ($0.3\text{--}1.5 \text{ g P m}^{-2}$) corresponds well with published data on P storage by charophyte communities (Królikowska (1997):

0.19 g P m^{-2} ; Blindow (1992b): 0.4 g P m^{-2} ; Pereya-Ramos (1981): $0.5\text{--}1.7 \text{ g P m}^{-2}$). The tissue P contents in *N. obtusa* we determined once in September 2020 are in good agreement with other published data (Table S2). In 2022, a partial recovery of *N. obtusa* stands was observed along with a decrease in the P availability in the upper water layer (0–20 m), indicating an increase in P retention and supporting the link between charophyte cover and P availability in the upper water layer.

Charophytes also offer surfaces for the growth of periphyton, which in Lake Stechlin accumulated up to 35 mg P m^{-2} of plant surface area in four weeks (Périllon et al. 2017). Assuming a surface area of *N. obtusa* of $560 \text{ cm}^2 \text{ g}^{-1}$ dry mass (Sher-Kaul et al. 1995), and a biomass of $0.3\text{--}1.5 \text{ g dry mass m}^{-2}$, the loss of charophytes between 2008 and 2022 translates to $2.4\text{--}11.8 \text{ km}^2$ of lost surface area for periphyton and a release of up to $84\text{--}412 \text{ kg P}$ or up to 10% of the observed average littoral P release. The contribution of P released from calcite encrustations, which often cover charophytes in hardwater lakes, can account for 12%–21% of the P associated with these plants (Siong et al. 2006; Kufel et al. 2013; Klamt et al. 2019).

Additionally, charophyte stands trap suspended particles containing P and also prevent P loss from sediments as a result of resuspension by either hydrodynamics or burrowing activities of animals (Zambrano et al. 2001; Blindow et al. 2014 and references therein). This effect could be large, given that maximum resuspension in a shallow lake was two orders of magnitude lower within charophyte stands than at adjacent sites lacking

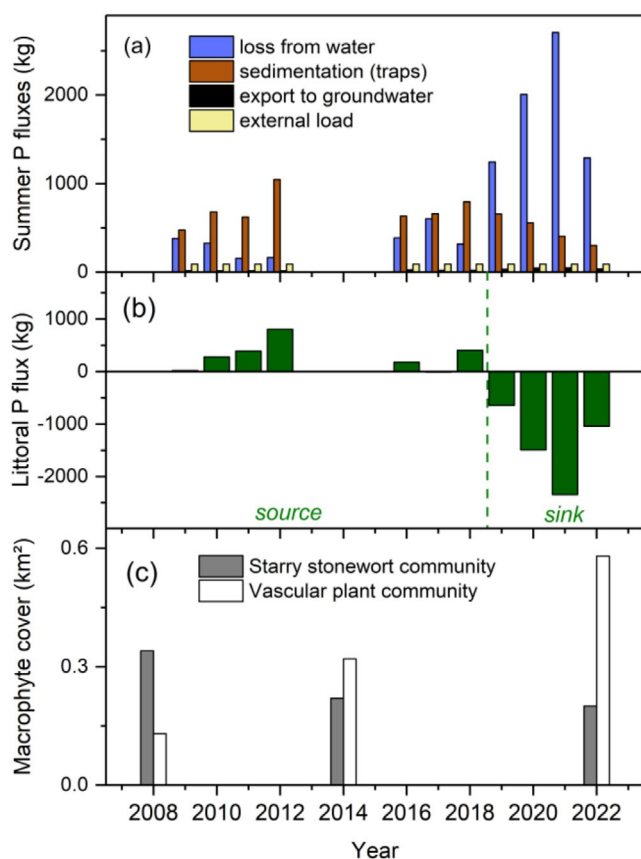


FIGURE 7 | Summer phosphorus (P) fluxes in Lake Stechlin with losses determined as the difference in P content in the upper water layer (0–20 m) between May and October, sedimentation losses determined with traps deployed at 20 m depth (no data for 2008 and 2013–2015), export to groundwater, and external P load (a); contribution of the littoral zone to the P budget of the upper water layer, which changed from a source (2009–2018) to a sink function (2019–2022) (b); and cover of major vegetation types (starry stonewort community and vascular plant community) in 2008, 2014 and 2022 (c).

vegetation cover (van den Berg et al. 1998). Sediment resuspension is expected also to occur in deeper littoral areas of Lake Stechlin, due to internal waves (Kirillin et al. 2009) and activities of benthivorous fish (see Section 4.3). Cyr et al. (2009) reported increased TP concentrations just above the surface of littoral sediments (5.0–5.5 m) of an oligo-mesotrophic stratified lake after movement of the thermocline and suggested that sediment resuspension was a likely mechanism contributing to this internal P loading. Conceivably, therefore, the effects of charophyte beds on sediment resuspension could have outweighed the P immobilisation function of plant biomass and associated periphyton. Importantly, these mechanisms would be effective all year because *N. obtusa* in Lake Stechlin is wintergreen, thus retaining P permanently as long as charophyte stands remain intact. Accordingly, the decline of *N. obtusa* might have significantly contributed to the temporary P source function of the littoral zone despite the relatively low contribution of P directly released from lost charophyte biomass in Lake Stechlin.

Wintergreen deep-water communities of filamentous green algae and mosses, covering the zone below the charophytes due to their lower light requirements (Middelboe and Markager 1997),

also decreased during the study period, especially between 2008 and 2014 (Figure 4). In contrast to charophyte cover, that of filamentous algae and mosses was not significantly correlated with spring TP content, Secchi depth or MCD ($p > 0.05$; Figure 5a–c). However, when data from both communities are combined, these correlations were significant for Secchi depth ($p = 0.02$), and nearly significant for spring TP content ($p = 0.07$) and MCD ($p = 0.054$). Assuming similar effects on P enrichment compared to charophytes, the area of filamentous algae and mosses lost between 2008 and 2022 (0.06 km²) would add about 40% to the charophyte effects on P fluxes. This percentage is probably an overestimate, however, since wind-induced sediment resuspension decreases with water depth (Hamilton and Mitchell 1997).

4.2 | Contribution of *C. demersum* to Lake Phosphorus Dynamics

In contrast to *N. obtusa*, the submerged vascular plant species replacing it (*C. demersum*) senesces, dies off, and decomposes in autumn and winter. As a consequence, much of the P immobilised in *C. demersum* biomass and associated periphyton and calcifications during the growing season in spring and summer can be released back to the water column during autumn and winter. Kufel et al. (2004) found a 50% release of P from decomposing *C. demersum* within 12–50 days in Polish lakes. In line with other reports (Table S2, Kufel and Kufel 2002), we found tissue P concentrations of *C. demersum*, which assimilates nutrients mostly from the water column (Denny 1972), to be higher than those of *N. obtusa*. Therefore, interannual and seasonal variation in *C. demersum* biomass would potentially result in a correspondingly large variation in TP concentration in the epilimnion. This variation could be accentuated by the fact that *C. demersum* can increase its tissue P content when P concentrations in the water increase (Li et al. 2018). Indeed, strong interannual and seasonal variation was observed in Lake Stechlin, the latter particularly in years when *C. demersum* biomass and TP concentrations were highest (Gonsiorczyk et al. 2024; Figure 2a).

The positive correlation we found between *C. demersum* areal cover and P loss from the upper water layer during summer is in accordance with these reflections and our second hypothesis. Given a total area of vascular plant communities dominated by *C. demersum* of 0.58 km² in 2022, with biomass ranging from 0.41 to 1.5 kg dry mass m⁻² according to Goulder (1970) and Wells et al. (1997), respectively, and an average tissue content of 3.1 mg P g⁻¹ dry mass, the plants may have assimilated 737–2700 kg P between May and October. These figures are similar to, or even exceed, the littoral P uptake from the upper water layer (0–20 m) of 1041 kg P estimated for Lake Stechlin in the summer of 2022 (Figure 7b). Calculated daily areal P uptake rates for *C. demersum* in Lake Stechlin between May and October 2022 (7–25.8 mg P m⁻² d⁻¹) are within the range of published removal rates (0.6–32.8 mg P m⁻² d⁻¹; Pietro et al. 2006).

Tissue P contents of *C. demersum* can reach much higher values than determined in our study (Table S2), especially in poly- and hypertrophic waters. Furthermore, the tissue P contents we measured in September 2020 are expected to be lower than in spring and summer when the TP concentrations in the lake water were higher. In addition, increased periphyton growth

at increased lake water P concentrations (Alirangues-Núñez et al. 2023) would be expected to further promote P accumulation. Thus, our estimates of P accumulated by the plants and associated periphyton are likely to be conservative. It is remarkable, therefore, that P immobilisation by vegetation and periphyton can still explain the P loss from the upper water layer between May and October. This suggests that *C. demersum* and associated periphyton contributed to the P sink function of the littoral zone in Lake Stechlin during the summer months (May to October) in the period from 2019 to 2022.

4.3 | Potential Reasons for Macrophyte Community Shifts

Several processes in addition to nutrient availability may have triggered the decline of *N. obtusa* and concomitant expansion of *C. demersum* by shifting the competitive balance between the two species before feedback mechanisms (Figure 1) exacerbated the shift. First, feeding preferences for charophytes of common herbivorous fish such as rudd (*Scardinius erythrophthalmus*) would directly impact charophytes more than *C. demersum* (Lake et al. 2002). In addition, physical sediment disturbance by benthivorous cyprinids in the lake, such as bream (*Abramis brama*) (Anwand et al. 2003), can directly and indirectly impact charophytes (Laguna et al. 2016; Ten Winkel and Meulemans 1984; Alirangues-Núñez et al. 2023), whereas the burrowing activities of these fish would have little effect on floating *C. demersum*. That both mechanisms could play a role is underlined by observations regularly made by the scuba divers conducting the macrophyte surveys (van de Weyer et al. 2015); *N. obtusa* invariably showed signs of herbivory, and burrowing traces were manifest as characteristic sediment craters indicating physical disturbance, most likely by benthivorous fish. Similar arguments may hold for invasive crayfish, particularly *Faxonius limosus*, a widespread invasive species in the area (Haertel-Borer et al. 2005), whose diet is often dominated by macrophytes (Chybowski 2007), and related species clearly prefer charophytes over *C. demersum* (Chambers et al. 1991) or other vascular macrophyte species (Wood et al. 2018). Secondly, an extreme summer storm in July 2011, followed by a sharp decline in Secchi depth by up to 5 m over 4 weeks (Kasprzak et al. 2017) could have triggered a decline of deep-water charophyte communities (and mosses and filamentous green algae) as a result of light limitation. Indeed, the first strong increase in epilimnion P concentrations to almost $40 \mu\text{g L}^{-1}$ was measured in spring 2012 (Figure 2a).

Other potential causes are more speculative. They include, thirdly, climate warming, for example, through prolonged summer stratification that could increase light limitation by promoting phytoplankton development (Selmečzy et al. 2019; Kröger et al. 2023). Overall, however, the existing data on climate change effects are inconclusive. This is also true for a positive effect of moderate warming ($+2^\circ\text{C}$) on charophytes (Choudhury et al. 2019), but not on *C. demersum* (Hyldgaard and Brix 2012) found in mesocosm experiments, a result that would be at variance with the community shifts observed in Lake Stechlin. Another possible reason is, fourthly, that charophytes were infected by a pathogen, but here, too, the available data (Gibbs

et al. 2011) are too sparse to allow a meaningful assessment of the likelihood of this potential stressor. Finally, interactions of multiple drivers need to be considered. A case in point is increased shading of periphyton induced by nutrient availability as a result of groundwater influx (Pérrillon et al. 2017), which may increase the susceptibility of macrophytes to herbivory (Hidding et al. 2016).

In conclusion, our results provide evidence that the shift from charophytes to submerged vascular plants, a common sequence of macrophyte degradation in lakes, can lead to changes in the feedback loop between submerged vegetation, benthic P retention, epilimnion P availability, water transparency, and MCD. A corollary of such a feedback loop is that the replacement of charophytes is likely to be not only a consequence but also a cause of lake eutrophication, notwithstanding that the initial triggers of the community shifts remain largely speculative. Understanding the mechanisms behind the replacement of charophytes and the potential feedback mechanisms will be essential to mitigate the nutrient enrichment of clearwater lakes affected by internal P loading and to develop strategies for the protection and restoration of charophytes in the littoral zone of lakes.

Author Contributions

Conceptualization: Sabine Hilt, Thomas Gonsiorczyk, Michael Hupfer, Mark O. Gessner. Developing methods: Sabine Hilt, Klaus van de Weyer. Conducting research and data analysis: Sabine Hilt, Thomas Gonsiorczyk, Michael Hupfer, Marta Maria Alirangues-Núñez. Writing and editing: all authors.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data of Lake Stechlin are available in the IGB Freshwater Research and Environmental Database (FRED) at <https://doi.org/10.18728/water-chemistry> and <https://fred.igb-berlin.de/data/package/941> (sedimentation rates, macrophyte coverage).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.