

# Regime shifts between macrophytes and phytoplankton – concepts beyond shallow lakes, unravelling stabilizing mechanisms and practical consequences

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## ABSTRACT

### Regime shifts between macrophytes and phytoplankton – concepts beyond shallow lakes, unravelling stabilizing mechanisms and practical consequences

Feedback mechanisms between macrophytes and water clarity resulting in the occurrence of alternative stable states have been described in a theoretical concept for shallow lakes. Here, I review recent studies applying the concept to other freshwater systems, unravelling stabilizing mechanisms and discussing consequences of regime shifts. Recent modelling studies predict that abrupt changes between clear and turbid water states can also occur in lowland rivers, both in time and in space. These findings were supported by long-term data from rivers in Spain and Germany. A deep lake model revealed that submerged macrophytes may also significantly reduce phytoplankton biomass by 50-15 % in 100-11 m deep and oligotrophic lakes. Some of the mechanisms stabilizing clear-water conditions are still far from fully understood. Available data suggest that the macrophyte community composition affects number and type of mechanisms stabilizing clear-water conditions. Allelopathic effects of macrophytes on phytoplankton are no longer doubted, however, bacterial colonization of macrophytes and phytoplankton, phytoplankton interactions, local adaptations and strain-specific sensitivities have been found to modulate these interactions. New aspects on stability properties of shallow lake ecosystems arose from experimental and modelling studies on terrestrial organic matter input, both in dissolved (tDOM) and particulate (tPOM) form. These suggest that the likelihood that shallow lakes will shift to or stay in the turbid state is enhanced with a predicted future increase in tDOM and tPOM input. Shallow lake restoration still suffers from knowledge gaps such as the role of propagule availability and dispersal for the re-establishment of a diverse submerged macrophyte vegetation. The importance of lake regime shifts, however, is increasingly supported by studies on quantitative consequences for processes such as primary production, carbon emissions and carbon burial.

**Key words:** Allelopathy, bistability, carbon balance, lake restoration, river.

## RESUMEN

### *Cambios entre el régimen de macrófitos y el de fitoplancton: conceptos más allá de los lagos poco profundos, descifrando los mecanismos de estabilización y consecuencias prácticas*

*Existe el concepto teórico para lagos poco profundos de los mecanismos de retroalimentación que ocurren entre los macrófitos y la fase clara del agua y que resultan en estados alternativos de estabilidad. En este trabajo, reviso estudios recientes aplicando este concepto a otros sistemas de aguas continentales, descifrando los mecanismos de estabilización y discutiendo las consecuencias de los cambios de régimen. Modelos recientes predicen que pueden ocurrir cambios abruptos entre estados de aguas claras y turbias también en las partes bajas de los ríos, tanto en el tiempo como en el espacio. Estos resultados se apoyan en largas series temporales de datos en ríos de España y Alemania. Un modelo en un lago profundo reveló que los macrófitos sumergidos también pueden reducir significativamente la biomasa de fitoplancton entre un 50 y 15 % en lagos oligotróficos de entre 11 y 100 m de profundidad. Pero los mecanismos que determinan las condiciones para la estabilidad de la fase de aguas claras están aún lejos de ser bien comprendidos. Los datos disponibles sugieren que la composición de la comunidad de macrófitos afecta el número y tipo de mecanismos que estabilizan las condiciones de aguas claras. No hay duda de los efectos alelopáticos generados por los macrófitos en el fitoplancton, sin embargo, se ha encontrado que la colonización bacteriana en macrófitos y fitoplancton, las interacciones del fitoplancton, las adaptaciones locales y la sensibilidad específica*

*de cada cepa modulan estas interacciones. Están apareciendo nuevos aspectos acerca de las propiedades de la estabilidad en ecosistemas lacustres someros basados en estudios, experimentales o de modelización, de los aportes de materia orgánica de origen terrestre, tanto disuelta (tDOM) como particulada (tPOM). Estos estudios sugieren que la probabilidad de que los lagos someros cambien hacia o permanezcan en un estado de aguas turbias, aumenta con la predictibilidad futura de un incremento en los aportes de tDOM y tPOM. Todavía existen muchas incógnitas en la restauración de lagos someros, como la disponibilidad y dispersión de propágulos para el restablecimiento de una vegetación diversa de macrófitos sumergidos. Sin embargo, la importancia de los cambios en el estado del lago está cada vez más demostrada en trabajos que cuantifican las consecuencias para la producción primaria, las emisiones y el secuestro de carbono.*

**Palabras clave:** Alelopatía, biestabilidad, balance de carbono, restauración de lagos, río.

## INTRODUCTION

Many ecosystems seem to exert multiple stable states and thus respond to changes in external factors with sudden state shifts (Holling, 1973; May, 1977; Scheffer *et al.*, 2001). Barnosky *et al.* (2012) suggested that even the entire biosphere may be approaching a critical transition and finding suitable approaches for detecting or predicting critical transitions has become an emerging topic across many systems and disciplines (Dakos & Hastings, 2013 and references therein). One of the best described examples of multiple stable states in ecosystems are shallow lakes that occur in either a clear, macrophyte-dominated or in a turbid, phytoplankton-dominated regime (Scheffer *et al.*, 1993, 2001; Scheffer & Van Nes, 2007). A theoretical concept has been developed showing how feedback mechanisms between macrophytes and water clarity result in the occurrence of alternative stable states in shallow lakes (Scheffer *et al.*, 1993). The main stabilizing mechanisms of clear-water conditions by macrophytes were suggested to be reduced resuspension of bottom material (James *et al.*, 2004) and increased sedimentation (Vermaat *et al.*, 2000) inside of macrophyte stands, refuge against planktivorous fish for phytoplankton-grazing zooplankton (Timms & Moss, 1984) as well as suppression of phytoplankton growth by competition for nutrients (Kufel & Ozimek, 1994) and excretion of allelochemicals by macrophytes that inhibit phytoplankton growth (Hilt & Gross, 2008). Scheffer (1998) concluded that the intensive work on shallow lakes has led

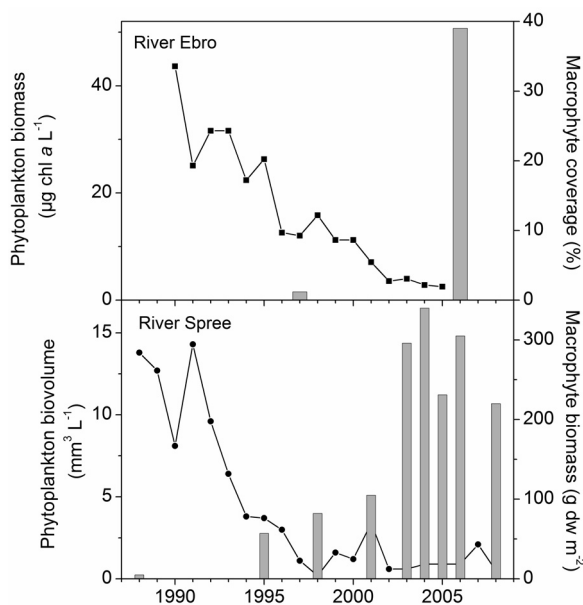
to a vast expansion of our knowledge on these ecosystems, however, the array of poorly understood problems remains equally impressive. He suggested that a combination of approaches ranging from controlled experiments, whole-lake manipulations, minimal models and elaborate simulation models may be the most powerful strategy to resolve the open questions.

Here, I review recent studies that applied the concept of a clear-water stabilizing role of submerged macrophytes to other freshwater systems, namely to rivers and deeper lakes. In addition, I summarize recent findings unravelling stabilizing mechanisms in shallow lakes focussing on effects of macrophyte community composition, studies on inhibition of phytoplankton by allelochemically active macrophytes and on the impact of terrestrial organic matter on shallow lake resilience. Finally, I discuss practical and quantitative consequences of regime shifts in shallow lakes for their restoration and carbon cycling.

## CONCEPTS BEYOND SHALLOW LAKES

### Regime shifts in rivers

An important assumption for alternative stable states in water quality is that the endogenous feedback processes are stronger than exogenous processes (Dent *et al.*, 2002). This assumption may often be violated for rivers that are generally considered to be open ecosystems mainly controlled by exogenous processes, particularly hydrologic regimes (Ryder & Pesendorfer, 1989;



**Figure 1.** Development of phytoplankton and submerged macrophytes in River Ebro (data from Ibáñez *et al.*, 2012) and River Spree (data from Hilt *et al.*, 2011) in the period 1988–2008. River Ebro: annual averaged chlorophyll concentrations (line) and average macrophyte coverage (bars) measured at six locations, River Spree: seasonal means (biweekly sampling from June–September) of phytoplankton biovolume (line) and summer biomass of submerged macrophytes (bars). For years without bars, no macrophyte data were available. Error bars were omitted for clarity. *Desarrollo de fitoplancton y macrófitos sumergidos en el río Ebro* (Ibáñez *et al.*, 2012) y *el río Spree* (Hilt *et al.*, 2011) en el período 1988–2008. *Río Ebro: concentración anual promedio de clorofila (línea) y promedio de cobertura de macrófitos (barras) medidas en seis localidades. Río Spree: medias estacionales (muestreo quincenal de Junio–Septiembre) del biovolumen de fitoplancton (línea) y biomasa de macrófitos sumergidas en verano (barras). Los años sin barras no hubo datos disponibles de macrófitos. Las barras de error se omitieron para una mejor claridad.*

Dent *et al.*, 2002). Consequently, alternative stable states in rivers have been described for geomorphological features, although biotic components sometimes affect geomorphology (Naiman *et al.*, 2000). Planktonic algae are unlikely to dominate in the upper reaches of all rivers and over the whole length of short rivers with a short water retention time. These are dominated by macrophytes or benthic algae and lack multiple stable states (Hilton *et al.*, 2006). The flow of most rivers of the world, however, is regulated by dams (Nilsson *et al.*, 2005) and postglacial lowland regions are often dominated by river-

lake systems. In such systems, river stretches downstream of eutrophic lakes or reservoirs may be strongly loaded with phytoplankton (Köhler, 1994; Neal *et al.*, 2006).

A recently developed spatially explicit simple model predicts that shifts between phytoplankton and macrophyte dominance can also occur in such rivers with high phytoplankton loading (Hilt *et al.*, 2011). Alternative stable states only occur at low flowing velocities and thus high retention times. Hysteresis disappeared with decreasing retention times, but abrupt changes between clear and turbid states were still possible both in time and in space. A local regime shift that occurs upstream may propagate through the whole river due to a domino effect. Restoration measures such as biomanipulation in lakes, planting macrophyte stands (Larned *et al.*, 2006) or reduction of local nutrient loading should thus start upstream and may eventually trigger regime shifts downstream (Hilt *et al.*, 2011). The possibility of steep regime shifts between phytoplankton and macrophyte dominance in slow flowing (lowland) rivers is supported by data from River Spree (Germany) and River Ebro (Spain). Parts of both rivers went through an abrupt regime shift from phytoplankton to macrophyte dominance (Fig. 1) during a period of gradually declining nutrient concentrations (River Spree: Köhler *et al.*, 2010; Hilt *et al.*, 2011; River Ebro: Ibáñez *et al.*, 2012).

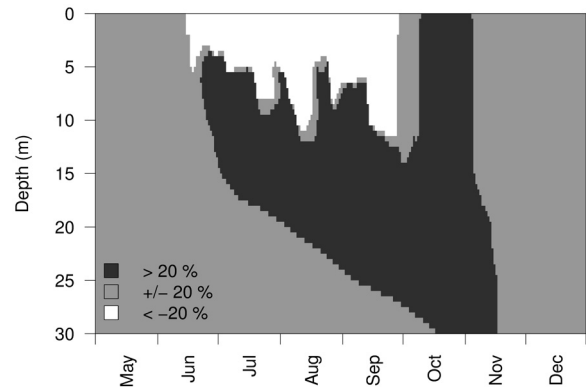
The model developed by Hilt *et al.* (2011) consists of 100 equal, well-mixed sections receiving water from a previous section (the first section gets water from an external source). In each time unit, a fraction of the volume flows to the next section. The model is thus also valid for a chain of connected lakes and may explain the striking co-occurrence of clear-water and turbid conditions in connected shallow lakes detected by Timms & Moss (1984) and Cottenie *et al.* (2001). It may also help comparing management options in chains of shallow lakes (Carpenter & Lathrop, 2014).

### Regime shifts in deeper lakes

In deep lakes and reservoirs only a smaller part of the water body can be colonised by submerged

macrophytes and the vegetation response to changes in turbidity is not discontinuous as in shallow lakes (Scheffer *et al.*, 1993). Submerged macrophytes have thus been widely neglected in deep lake modelling. Genkai-Kato & Carpenter (2005) modelled the effect of submerged macrophytes on water clarity and found no remarkable effect for lakes deeper than 10 m. However, the macrophyte effects were restricted to prevention of phosphorus recycling from the sediment not including other potential interactions of submerged macrophytes within the ecosystem. In contrast, several empirical studies suggest that submerged macrophytes may significantly contribute to the stabilization of the clear-water regime in deep lakes. Hilt *et al.* (2010) observed a sudden and stable shift to clear-water conditions in Lake Scharmützelsee (maximum depth 29.5 m) after a significant increase in submerged macrophyte coverage from < 10 % to 24 %. Rooney & Kalff (2003) detected an inverse relationship between phytoplankton biomass and macrophyte coverage in nine lakes with maximum depths ranging from 2 to 20 m. This indicates a potential impact of macrophytes on phytoplankton in lakes deeper than those allowing full macrophyte coverage. In addition, Lauridsen *et al.* (1996) and Portielje & Van der Molen (1999) showed that low macrophyte coverages in shallow lakes can also significantly contribute to a higher water clarity as compared to lakes without macrophytes. The impact of submerged macrophytes on the water quality in deeper lakes, even if smaller areas are colonized, might thus be underestimated.

Sachse *et al.* (2014) developed a one-dimensional, vertically resolved macrophyte model to test macrophyte effects on water quality in scenarios for lakes with different basin shapes and maximum depths from 11 m to 100 m. Their model simulations revealed that submerged macrophytes can significantly affect the water quality of deep lakes. The presence of submerged macrophytes resulted in up to 50 % less phytoplankton biomass in the shallowest simulated conic-shaped lake (11 m) and still 15 % less phytoplankton was predicted in 100 m deep oli-



**Figure 2.** Relative differences of phytoplankton concentrations in a mesotrophic 30 m deep simulated conic lake with macrophytes as compared to a scenario without macrophytes. Shadings indicate strong negative (white) or positive (dark grey) effects which exceeded  $\pm 20\%$  (modified after Sachse *et al.*, 2014). *Diferencias relativas en la concentración de fitoplancton de un lago simulado mesotrófico y cónico de 30 m de profundidad, entre un escenario con y sin macrófitos. Los colores indican efectos fuertemente negativos (blanco) o positivos (gris oscuro) que exceden  $\pm 20\%$  (modificado de Sachse *et al.*, 2014).*

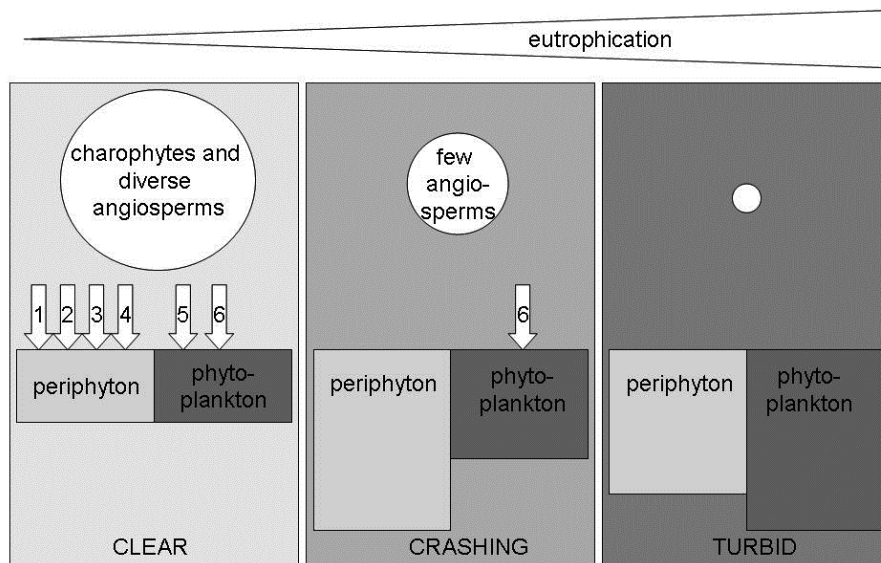
gotrophic lakes as compared to lakes without macrophytes. At intermediate depths (30 m), total phytoplankton biomass was reduced by at least 20 % in the epilimnion throughout the whole summer, but an increase of phytoplankton was predicted for the metalimnion (Fig. 2). Overall, competition for nutrients in the open water was mainly (89 %) responsible for the simulated macrophyte effect in deep lakes. Shading contributed by 8 %, the provision of zooplankton shelter by 3 % and reduced turbulence in macrophyte patches contributed only by 0.1 % to the overall macrophyte effect (Sachse *et al.*, 2014). Hysteresis effects were small in deep lakes, however, their response to changes in nutrient loading may still be discontinuous when the lake is close to the critical threshold level, similar to findings made for rivers (Hilt *et al.*, 2011). Deep lakes that lost their submerged vegetation were thus supposed to also show some resilience to decreasing nutrient loading. Based on these results re-establishment of submerged macrophytes in deep lakes was suggested to be potentially as important during their restoration as in shallow lakes (Sachse *et al.*, 2014).

## MECHANISMS STABILIZING MACROPHYTE DOMINANCE

### Effects of macrophyte community composition

Currently, the importance of the effect of macrophyte community composition on ecosystem functions performed by macrophytes remains largely unknown and seems an emerging topic of research (Bakker *et al.*, 2013). Studies on feedback mechanisms between water clarity and submerged vegetation have often been conducted in shallow lakes with dominance of angiosperms. These differ from those dominated by charophytes and often have higher nutrient concentrations. Blindow *et al.* (2014) hypothesized that different mechanisms prevail depending on whether charophytes or angiosperms are the dominant macrophyte group. Charophytes domi-

nate at lower nutrient concentrations and can develop higher areal biomass than most angiosperms. Their influence on sedimentation, re-suspension and water column nutrients is thus assumed to be higher than that of most angiosperms. In contrast, grazing pressure from zooplankton on phytoplankton is suggested to be low in characeans, but to be the main stabilizing feedback mechanism in most angiosperm-dominated ecosystems. Zooplankton is hampered by low food quality and quantity and at least temporarily by high predation pressure from juvenile fish inside of dense characean stands (Blindow *et al.*, 2014). Allelopathic inhibition of phytoplankton may occur at high densities of allelopathically active species, which are present among both charophytes and angiosperms (Blindow *et al.*, 2014). Experiments and field measurements comparing the effect of charophytes and angiosperms on water clarity



**Figure 3.** Development of shallow lakes during eutrophication: A diverse submerged vegetation of charophytes and angiosperms in clear lakes negatively affects both, periphyton and phytoplankton abundance via reduced sediment resuspension (1), competition for nutrients (2), provision of habitat for macrozoobenthos (3) and piscivorous fish (4), allelopathy (5) and shelter for zooplankton from predation by planktivorous fish (6). In crashing lakes, only a few angiosperms dominate and consequently, most negative effects are lost, especially those affecting periphyton. In turbid lakes, submerged vegetation is almost absent and cannot affect periphyton or phytoplankton. *Evolución en lagos someros durante la eutrofización: una diversa vegetación de carófitos y angiospermas en lagos de aguas claras afectan negativamente la abundancia de perifiton y de fitoplancton vía: la reducción en la resuspensión de sedimento (1), competencia por nutrientes (2), provisión de hábitat para macrozoobentos (3), y peces piscívoros (4), alelopatía (5) y protección de la depredación del zooplancton por peces planctívoros (6). En lagos en fase "crashing" solo predominan unas pocas angiospermas y como consecuencia la mayoría de efectos negativos se pierden, especialmente los que afectan al perifiton. En lagos turbios, casi no hay vegetación sumergida y en consecuencia no afecta al perifiton o al fitoplancton.*

under similar conditions are needed to verify the hypothesized difference between charophytes and angiosperms on water clarity.

These differences in feedback mechanisms may also explain the declining negative effects of submerged vegetation on periphyton and phytoplankton during eutrophication of shallow lakes (Fig. 3). A decline in macrophyte species diversity has often been observed in temperate European shallow lakes during eutrophication already before total macrophyte disappearance (Sayer *et al.*, 2010a, b). A typical sequence starts with a high diversity of charophytes and angiosperms characterised by high water clarity in spring and summer (Fig. 3). This diverse submerged vegetation can negatively affect both competitors for light, periphyton and phytoplankton abundance, via reduced nutrient availability from sediment resuspension, competition for nutrients, provision of habitat for macrozoobenthos and piscivorous fish, allelopathy and shelter for zooplankton from predation by planktivorous fish (Fig. 3). So-called “crashing” conditions are characterized by a dominance of few angiosperm species (*Potamogeton pectinatus*, *P. pusillus*, *Zannichellia palustris*; Hilt, 2006; Sayer *et al.*, 2010b). These can provide shelter for zooplankton from predation by planktivorous fish, whereas other negative effects are lost or much less effective, especially those affecting periphyton (Fig. 3). Consequently, the water is only clear in spring but dominated by phytoplankton in late summer (Sayer *et al.*, 2010b; Hilt *et al.*, 2013). In turbid lakes, submerged vegetation is sparse or absent and thus cannot affect periphyton or phytoplankton (Fig. 3).

### Modulations of macrophyte allelopathic effects on phytoplankton

Proving an allelopathic inhibition of phytoplankton by macrophytes at ecosystem level remains a challenge (Gross *et al.*, 2007; Hilt & Gross, 2008). Some of the recent field and mesocosm experiments (Hilt *et al.*, 2006a; Vanderstukken *et al.*, 2011; Švanys *et al.*, 2014) indicate allelopathic effects of macrophytes on phytoplankton, whereas Lombardo *et al.* (2013) con-

cluded that allelopathy was not explaining *in situ* macrophyte-phytoplankton patterns in their studied lakes. Factors that were suggested to decrease the *in situ* relevance of allelopathic interactions include lake size (Gasith & Hoyer, 1997) but also photolytic and microbial degradation of allelochemicals (Bauer *et al.*, 2012) and environmental adaptation and co-evolution of phytoplankton (Reigosa *et al.*, 1999).

The role of heterotrophic bacteria associated with producing and target cells has long been neglected, although they may both enhance or decrease the allelopathic activity (Gross *et al.*, 2012). Recently, bacteria degrading polyphenols, a common group of aquatic macrophyte allelochemicals (Gross, 2003), have been detected both in the vicinity of the allelochemical-excreting macrophytes (Müller *et al.*, 2007; Hempel *et al.*, 2008, 2009) and attached to target phytoplankton (Bauer *et al.*, 2010; Eigemann *et al.*, 2013a). Different algae species were found to harbour bacterial communities that were species specifically associated. However, a significant contribution of these bacteria to differences in the sensitivities of algae toward allelochemicals could not be shown (Eigemann *et al.*, 2013a).

Al-Sheri (2010) provided first indications for adaptation of phytoplankton to allelochemicals. A green algal strain isolated from a pond with an abundant allelopathically active macrophyte species had a lower sensitivity to macrophyte extracts as compared to an algal strain from a macrophyte-free pond. Local genetic adaptation and a potential co-evolution between allelochemical donor macrophytes and acceptors, however, could not be shown in a study testing 23 different strains of the green alga *Pediastrum duplex* originating from ponds with and without allelopathically active macrophytes (Eigemann *et al.*, 2013b). Differences in sensitivities of strains, however, varied by two orders of magnitude and need to be taken into account if evaluating ecological consequences of allelopathic interactions (Eigemann *et al.*, 2013b).

In addition to the different sensitivities of strains towards allelochemicals, interactions between strains and species have to be considered. Most studies of the effects of macrophyte allelo-

chemicals on phytoplankton were performed with single-species cultures and thus neglected this aspect. Natural phytoplankton assemblages, however, usually contain a high number of species from different phytoplankton groups that compete for nutrients and light (Kayser, 1979) or otherwise interact, e.g. via the excretion of extracellular metabolites (Keating, 1977; Graneli *et al.*, 2008). Chang *et al.* (2012) showed that interactions with a green alga turned the inhibiting effect of allelochemicals on the cyanobacterium *Microcystis aeruginosa* into an enhancement resulting in increased growth rates of *M. aeruginosa*.

### Role of terrestrial organic matter input

The stability properties of shallow lake ecosystems have been discussed along a gradient of nutrient loadings (Scheffer *et al.*, 1993). Regime shifts were attributed to either passing of threshold levels in nutrient loading or strong disturbances such as reductions in fish biomass or macrophyte disappearance after storm events (Scheffer, 1998). The role of inputs of dissolved and particulate organic matter from terrestrial surroundings (tDOM, tPOM) for the stability of shallow lake ecosystems, however, has received less attention. The tDOM loading potentially affects shallow lakes ecosystems by increasing light extinction and thus affecting physical mixing and primary production (Carpenter *et al.*, 1998; Houser *et al.*, 2003; Houser, 2006). An oligotrophic, subarctic lake shifted towards a more heterotrophic food web under experimentally elevated tDOM fluxes (Försström *et al.*, 2013) and both model simulations and empirical studies showed reduced primary production in meso- to eutrophic lakes due to shading by tDOM inputs (Jones *et al.*, 2012; Brothers *et al.*, 2014). A model study by Lischke *et al.* (2014) suggested that also an enhanced tPOM input will reduce the resilience of the macrophyte-dominated clear-water state of shallow temperate lakes. Their results show that tPOM induced an increase in zoobenthos biomass resulting in more benthivorous fish, which reduced light availability due to bioturbation. An increased

zoobenthos biomass by tPOC additions has been experimentally verified in a whole-lake experiment (Scharnweber, 2013; Scharnweber *et al.*, 2014a, b). In addition, Lischke *et al.* (2014) predicted that suspended tPOM reduces the consumption of phytoplankton by zooplankton which increases the turbidity, and that suspended tPOM reduces the light availability for submerged macrophytes. These results resemble the effects of tDOM on light climate in lakes (Ask *et al.*, 2009; Karlsson *et al.*, 2009), but the presumed underlying mechanisms were different. The likelihood that shallow lakes will shift to or stay in the turbid state will thus most probably be enhanced by the predicted future increase in tDOM and tPOM input (Zaehle *et al.*, 2007).

## PRACTICAL CONSEQUENCES OF REGIME SHIFTS

### Lake restoration

Regime shifts between alternative stable states have vast effects on community structure and biodiversity with consequences for ecosystem function (Scheffer *et al.*, 2001). Sand-Jensen *et al.* (2000) and Jeppesen *et al.* (2000) reported a reduction in species richness in lakes with high phytoplankton turbidity. Delays in the recovery of macrophyte abundance (Körner & Dugdale, 2003; Hilt, 2006) and species diversity have often been observed during lake restoration and the diversity present prior to eutrophication may often not return at all (Bakker *et al.*, 2013; Hilt *et al.*, 2013). A significant increase in macrophyte species diversity may take 20 years after start of reductions in external nutrient loading, indicating that patience is needed in allowing the few species of the re-establishment phase to pave the way for a more diverse macrophyte community (Hilt *et al.*, 2013). However, as the re-establishment of submerged macrophytes is essential for the long-term success of a restoration in shallow lakes, measures for their potential support in case of a hampered natural re-establishment and management measures in case of mass developments should be planned in ad-

vance of any restoration effort (Hilt *et al.*, 2006b). A cost and maintenance intensive artificial support by planting or seeding of submerged plants was supposed to be useful only under specific circumstances. These include 1) the lack of viable propagation units of submerged vegetation in the sediment and lack of submerged macrophytes in the lake or connected water bodies, 2) the application of a restoration measure that decreases turbidity only for a short time period, 3) a restoration measure including the introduction of pike (*Esox lucius*) that need submerged macrophyte stands for successful development or 4) the need of promoting specific (low growing) macrophyte species to enable recreational use (Hilt *et al.*, 2006b). In general, the role of propagule availability and dispersal for the re-establishment of a diverse submerged macrophyte vegetation during lake restoration is still fairly unknown. More studies testing the importance of macrophyte diversity for maintaining clear-water conditions are needed for a better guidance of restoration efforts (Bakker *et al.*, 2013).

### Regime shifts and carbon cycling

Apart from qualitative changes, recent studies have indicated that shifts between the separate plant forms also have significant quantitative consequences for shallow lake ecosystems, e.g. for primary production, carbon (C) emissions and C burial. In general, eutrophic lakes with abundant primary producers (either phytoplankton or submerged macrophytes) are often undersaturated in CO<sub>2</sub> and thus could act as net atmospheric CO<sub>2</sub> uptake sites (Kosten *et al.*, 2010; Balmer & Downing, 2011). Brothers *et al.* (2013a) provided empirical and theoretical evidence for higher gross primary production (GPP) in small, eutrophic, shallow lakes dominated by a submerged macrophyte-epiphyton complex as compared to turbid, phytoplankton-dominated lakes of similar nutrient concentrations. Blindow *et al.* (2006) also found a higher net primary production (NPP) in a macrophyte-dominated lake and assumed this to be the reason for increased biomass of higher trophic levels after a shift to a clear-water state. Shifts from a turbid to a clear-

water state are also accompanied by a dominance shift from a pelagic to a benthic food chain and will increase the energy transfer to higher trophic levels (Hecky & Hesslein, 1995; Vander Zanden *et al.*, 2006). Brothers *et al.* (2013b) linked regime shifts from macrophyte to phytoplankton dominance in shallow lakes to a major increase in C burial efficiency due to lower C mineralization and higher calcite precipitation. Their data indicate that nearly all C deposited over an annual period in a phytoplankton-dominated lake was buried in the sediments, compared to only 20% in a macrophyte-dominated lake of comparable size and nutrient concentration (Fig. 4). The lower C mineralization rates in the turbid lake were associated with a decrease in benthic oxygen availability coinciding with the loss of submerged macrophytes. Future research in shallow aquatic systems is thus suggested to address the potential effects of regime shifts between macrophyte and phytoplankton dominance in addition to other factors that influence C burial rates, such as watershed erosion and nutrient loading (Heathcote & Downing, 2012; Theissen *et al.*, 2012; Heathcote *et al.*, 2013).

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