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Restoring macrophyte diversity in shallow temperate lakes: biotic versus abiotic constraints

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Abstract Although many lake restoration projects have led to decreased nutrient loads and increased water transparency, the establishment or expansion of macrophytes does not immediately follow the improved abiotic conditions and it is often unclear whether vegetation with high macrophyte diversity will return. We provide an overview of the potential bottlenecks for restoration of submerged macrophyte vegetation with a high biodiversity and focus on the biotic factors, including the availability of propagules, herbivory, plant competition and the role of remnant

populations. We found that the potential for restoration in many lakes is large when clear water conditions are met, even though the macrophyte community composition of the early 1900s, the start of human-induced large-scale eutrophication in Northwestern Europe, could not be restored. However, emerging charophytes and species rich vegetation are often lost due to competition with eutrophic species. Disturbances such as herbivory can limit dominance by eutrophic species and improve macrophyte diversity. We conclude that it is imperative to study the role of propagule availability more closely as well as the biotic interactions including herbivory and plant competition. After abiotic conditions are met, these will further determine macrophyte diversity and define what exactly can be restored and what not.

Guest editors: Zhengwen Liu, Bo-Ping Han & Ramesh D. Gulati / Conservation, management and restoration of shallow lake ecosystems facing multiple stressors

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Introduction

Macrophytes play an important structuring role in shallow freshwater bodies (Scheffer et al., 2001; Burks et al., 2006). Macrophytes have traits that affect the ecosystem services that shallow water bodies provide as they can maintain clear water and nutrient retention, while they also strongly improve aquatic biodiversity by providing a habitat and food for many aquatic organisms (Carpenter & Lodge, 1986). The ongoing

eutrophication of freshwater bodies (Carpenter et al., 1998; Tilman et al., 2001) has induced a decline or disappearance of macrophytes from many shallow water ecosystems (Sand-Jensen et al., 2000; Brouwer & Roelofs, 2001; Gulati & van Donk, 2002; Lamers et al., 2002). This has been observed in many shallow lakes in densely populated areas, for instance in the Loosdrecht lakes (Best et al., 1984; Gulati & van Donk, 2002; Van de Haterd & Ter Heerdt, 2007) and Lake Veluwemeer (Van den Berg et al., 1999; Ibelings et al., 2007) in The Netherlands, Lake Fure (Sand-Jensen et al., 2008) and Lake Arresø (Jeppesen et al., 2007) in Denmark and the Müggelsee in Germany (Korner, 2001). Increased nutrient availability can initially stimulate macrophyte growth as long as the water remains clear (Lombardo & Cooke, 2003; Nagasaka, 2004; Feuchtmayr et al., 2009). However, with increasing nutrient loading, phytoplankton biomass may increase, creating water turbidity which may result in light limitation and disappearance of submerged macrophytes (Scheffer et al., 1993). However, before the water becomes turbid, there can be direct shading of macrophyte leaves by the accumulation of epiphyton or filamentous algae, which causes macrophyte decline or inhibits their return (Phillips et al., 1978; Weisner et al., 1997; Jones & Sayer, 2003; Roberts et al., 2003; Irfanullah & Moss, 2004; Hilt et al., 2010). Besides the indirect effect of nutrients on macrophyte growth (via light limitation), certain nutrients can be toxic for macrophytes, including ammonium which can be toxic at high concentrations for many macrophyte species (Smolders & Roelofs, 1996), whereas nitrate has been shown to reduce the growth of *Chara* species (Lambert & Davy, 2011). Furthermore, sulphide, which is formed at high sulphate concentrations in the water or sediment, can be toxic for macrophytes (Van der Welle et al., 2006). Nutrient addition may also induce changes in the fish community which may lead to increased turbidity due to the predation on zooplankton by planktivorous fish or sediment resuspension by benthic feeders (Jeppesen et al., 1997; Gulati & van Donk, 2002). Due to a shift from clear to turbid water with increasing eutrophication, shallow water bodies may eventually become dominated by algae, many species of which can occur in heavy blooms, especially cyanobacteria of certain toxic strains. This has jeopardised several of the important services of shallow waters, including use for drinking water and recreational activities such as

swimming (Guo, 2007). To restore ecosystem services and aquatic biodiversity, many restoration programmes have been set up to induce backward shifts from the turbid, algal-dominated state to a clear state dominated by macrophytes (Moss, 1989; Scheffer et al., 1993; Jeppesen et al., 2005a, b). As macrophytes play a crucial role in the maintenance of this clear water state, the targets and success of these restoration efforts are often measured in terms of the extent of return of submerged macrophytes. Therefore, most restoration measures try to realise clear water conditions, reasoning that, by restoring clear water conditions, macrophytes will return, which, on their turn, will maintain the clear water state. Restoration measures that can be taken to induce a shift from a turbid to a clear water state have been thoroughly reviewed recently (Gulati & van Donk, 2002; Sondergaard et al., 2007; Gulati et al., 2008; Sondergaard et al., 2008). However, restoring clear water does not always lead to the return of macrophytes or the return of desired species (Lauridsen et al., 2003a; Jeppesen et al., 2005a, b; Sondergaard et al., 2008), nor can macrophytes always maintain the clear water state (Bakker et al., 2010). In this review, we want to pay specific attention to the restoration of macrophyte communities and the factors that determine the biodiversity of this restored vegetation. We limit this review to freshwater submerged macrophytes, including vascular species and charophytes.

We focus on the importance of biotic factors, including the availability of propagules, the amount of herbivory and role of remnant populations, whereas macrophyte requirements for abiotic conditions, such as light and nutrient availability or shelter from the wind are recently reviewed in Bornette & Puijalon (2011). Furthermore, we address the importance of the composition and abundance of the macrophyte vegetation as these may affect the performance of ecosystem functions and conservation value of the vegetation. The study is focused on highlighting potential constraints for the return of a diverse macrophyte vegetation to lakes where abiotic conditions have been restored.

Where do the returning macrophytes come from?

If the right abiotic conditions exist (i.e. mainly enough light, nutrients and shelter), macrophytes can return to

a restored shallow water body in the short-term, varying from a few weeks to a few years (Casanova & Brock, 1990; Portielje & Roijackers, 1995; Brouwer et al., 2002; Ter Heerdt & Hootsmans, 2007), although numerous exceptions have been reported (Lamers et al., 2002; Jeppesen et al., 2005a, b; Geurts et al., 2008; Sarneel et al., 2011). Table 1 lists examples of restoration projects where nutrient loading has been reduced or sediment disturbing and zooplanktivorous fish has been removed and the effect on the restoration of the macrophyte community composition. The recovery of the vegetation raises questions about the origin of the returning plants: are propagules already present as a propagule bank or as a remnant population or is there a massive dispersal of macrophyte propagules from other source populations?

Dispersal of propagules

Seeds, oospores and vegetative propagules of submerged macrophytes are most likely dispersed by water, but also by wind and animals (Boedeltje et al., 2002, 2003, Charalambidou & Santamaria, 2005; Soons et al., 2008). In terrestrial ecology, the probability of dispersal via water is quantified by the buoyancy of the seed (Kleyer et al., 2008), assuming that long floating time enhances dispersal. Surprisingly, data on the buoyancy of seeds and other propagules from submerged macrophytes are lacking, but recent studies (Xie et al., 2010) reveal that at least vegetative propagules can float for several months. In shallow lakes, wind plays an important role in the dispersal route as the wind-induced currents transport the seeds (Sarneel, 2010; Soomers et al., 2010). Also, for charophytes, wind dispersal may play a role as spores are very light and generally easily dispersed by the wind. Propagules of aquatic macrophytes are also dispersed by waterfowl, fish and invertebrates (Green et al., 2002; Charalambidou & Santamaria, 2005; Brochet et al., 2010; Figuerola et al., 2010; Pollux, 2011). Especially the smaller-sized propagules are more likely to survive the gut passage in birds feeding on them and germinate afterwards (Soons et al., 2008). After passing through the gut, the frequency of propagule germination for many plants increases, e.g. in *Chara* spp., *Potamogeton pectinatus*, *P. nodosus*, and *P. pusillis* (Brochet et al., 2010; Figuerola et al., 2010). However, the overall probability of the digested propagules to establish successfully in a new habitat may well be low. Nevertheless, dispersal

via animals provides macrophyte species with an opportunity to disperse over long distances, stretching up to 3000 km (Soons et al., 2008). Genetic analyses support the exchange of propagules among distant and upstream populations (Green et al., 2002; Pollux et al., 2009). Therefore, dispersal is a powerful mode for the submerged macrophytes to return to the restored water bodies. However, the undesired species (e.g. eutrophic, very common or invasive species) may often have the highest probability to colonise new sites after restoration, leaving a low probability for colonisation by rare, endangered and desired species. But perhaps, propagules of such target species might already be present in the propagule bank.

The role of the propagule bank

Propagule bank studies of submerged lake sediment are rather scarce, although propagule banks of riparian zones did receive attention. Table 2 shows an overview of the literature available on the presence of macrophytes in both submerged and riparian propagule bank samples. Because the most commonly used seedling emergence test has been developed for terrestrial vegetation, there is no standardisation for sampling the submerged soils: sampling designs vary, with core depth ranging from 2.5 to 26 cm and germination conditions from moist soil to 60 cm flooding. Such large differences will strongly affect the results of the propagule bank assays. Based on trials, Boedeltje et al. (2002) recommend to further standardise aquatic propagule bank research by using moist, but not submerged sediment.

Reported propagule densities range from 0 to 40,000 propagules m^{-2} for submerged macrophytes (Table 2) indicating that in some cases, macrophytes may not return simply because of a lack of propagules, but in other cases generally high densities ensure their return. The occurrence of propagules of submerged macrophytes is not restricted to the lake bottom sediment but they may also occur in sediment from riparian zones and floodplains. In general, riparian propagule banks have somewhat higher propagule densities compared with propagule banks in lake sediments. From the literature on lake sediments, it is clear that particularly propagules from *Chara* species can be very abundant (Table 2; De Winton et al., 2000). This may well explain their relatively rapid return in case of many restoration projects (Casanova

Table 1 Examples of lake restoration projects with effects on macrophyte community composition

Lake	Reference	Restoration measures	Duration of study	Effect on transparency	Effect on macrophyte abundance	Effect on species richness	Speed of recovery	Full recovery of macrophyte community	Reason of limited recovery
Lake Fure (Denmark)	Sand-Jensen et al. (2008)	Reduction external P loading	35 years since P reduction	Increased gradually	Increase	Increase	Gradually	No, community composition different and less species compared to ± 100 years ago	Oligotrophic species regionally rare, sediment less suitable, competition with taller fast-growing species
Loch Leven (UK)	Dudley et al. (2012), Carvalho et al. (2012)	Reduction external P loading	40 years since first P reduction	Increased after 5 years	Increase esp. since 15 years	Increase	Gradually, most change after 20 years	No, approx. 80% returned compared to ± 100 years ago	Still increased nutrient levels
Schlachtensee (Germany)	Hilt et al. (2010)	Reduction external P loading	25 years since P reduction	Increased after 4 yrs	Increase	Increase	Delay > 10 yrs	No, community composition different and less species compared to ± 100 years ago	Many species regionally rare
Lake Tegel (Germany)	Hilt et al. (2010)	Reduction external P loading	20 years since P reduction	Increased gradually	Increase	Increase	Delay > 10 years	No, community composition different and less species compared to ± 100 years ago	Many species regionally rare
Lake Finjasjön (Sweden)	Strand & Weisner (2001)	Removal of fish	6 years since fish removal	Increased	Increase	Increase	Immediately	Unknown; charophytes found in seed bank were not in vegetation	Unknown
Lake Terra Nova (Netherlands)	Van de Haerd & Ter Heerdt (2007)	Removal of fish	2 years since fish removal	Increased immediately	Increase	Increase	Immediately	No, approx. 70% returned compared to 20–60 years before	Unknown
Lake Zwemlust (Netherlands)	Van de Bund & Van Donk (2002)	Removal of fish	10 years and 2 years since fish removal	Increased immediately	Increase	Increase	Immediately, second fish removal after 2 years	Unknown	Competition with filamentous algae; high nutrient loading

Table 2 Overview of macrophyte occurrence in propagule bank analyses with a short description of the sampling site

Habitat type	Lake sediment					Lake + riparian zone					River					Temporary marsh					Freshwater tidal		Estuary		Salt marsh																		
	A	B	C	D	E	F	F	G	H	I	I	I	I	J	J	J	K	L	M	M	M	M	M	M	M	N	N	O	O	P	P	W1	W1										
References																																											
Method	C	FI	FI	W1	FI	W1	W1	M	M	M	M	M	M	FI	FI	W1	Nd	FI	FI	FI	FI	FI	FI	FI	FI	FI	FI	All	All	All	All	All	All	All	All	All	All	All	All				
Seedlings × 1,000 (m ⁻²)	Nd	Nd	Nd	6.2	0.01	0.3	0.1	1.2	10.2	3.3	2.8	0.5	Nd	Nd	Nd	32.2	1.5	238.6	168.7	617.4	363.9	0.3	43.3	43.3	0.3	0.3	72	72	72	72	72	72	72	72	72	72	72	72	72				
Species	96	92	16	75	3.8	8.1	11	0.1	8.1	39																																	
Characeae																																											
<i>Ceratophyllum</i> sp.																																											
<i>Callitriche</i> sp.	1.3													0.1	0.4	1	22.3	0.2	0.2	0.4	0.2	15																					
<i>Elodea nuttallii</i>																																											
<i>Hottonia palustris</i>																																											
<i>Hydrilla verticillata</i>	7.6				8.1	14	0.2	2	39																																		
<i>Lamprothamnium macropogon</i>			0.6																																								
<i>Lepilaena</i> sp.			4.2																																								
<i>Myriophyllum</i> sp.	0.3	69			2.3	1.8	0.3																																				
<i>Najas</i> sp.			0.1		7.7	20	15	3.6																																			
<i>Ottelia alismoides</i>																																											
<i>Potamogeton</i> sp.			31	25	33	19	1	11																																			
<i>Ruppia</i> sp.	0.7		1.7																																								
<i>Suaeda pectinata</i>																																											
<i>Trappa natans</i>																																											
Other species	1.7	0.4	0	77.4	0	44.6	80	39.2	95.8	88.9	100	50	99.9	99.6	99	77.7	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	99.1	

Methods used are: All seeds were counted with the microscope (C); seedling emergence with flooded soil (FI) or moist soil (M). Data are percentage contribution of each submerged macrophyte species to the total propagule bank. Other species include all species that are not submerged macrophytes. References are indicated in the footnotes (A, Grillas et al. (1993); B, Harwell & Havens (2003); C, Ozimek (2006); D, Porter et al. (2007); E, Strand & Weisner (2001); F, Xiao et al. (2010); G, Li et al. (2008); H, Liu et al. (2006); I, Liu et al. (2009); J, Boedeltje et al. (2002); K, Boedeltje et al. (2003); L, Spencer & Ksander (2002); M, Bonis et al. (1995); N, Capers (2003); O, Riddin & Adams (2009); P, Espinar & Clemente (2007) *Nd* not determined

Table 3 Available longevity values of seeds of submerged macrophytes in the LEDA trait base based on seed bank analyses (Kleyer et al., 2008)

Species	Longevity
<i>Callitriche palustris</i> L.	1
<i>Callitriche stagnalis</i> Scop.	0.67
<i>Callitriche truncata</i> Guss.	1
<i>Elodea nuttallii</i> (Planchon) St John	0
<i>Myriophyllum spicatum</i> L.	0
<i>Najas flexilis</i> (Willd.) Rostk. & W.L.E. Schmidt	0.4
<i>Potamogeton pectinatus</i> L.	0.07
<i>Potamogeton perfoliatus</i> L.	0
<i>Potamogeton pusillus</i> L.	0.5
<i>Ruppia maritima</i> L.	0.67
<i>Utricularia minor</i> L.	0
<i>Utricularia vulgaris</i> L.	0.6
<i>Zannichellia palustris</i> L.	0.89

Longevity values in this database are binary: 0 = transient (<1 year), 1 = persistent (>1 year). The longevity value presented here gives the mean of documented case studies per species

& Brock, 1990). Other species are less frequently encountered in soil samples, and investigated macrophyte species mainly exhibit transient to short-term persistent propagules (Table 3; Kleyer et al., 2008). Therefore, a lack of propagules may actually inhibit macrophyte return after restoration in some lakes (Strand & Weisner, 2001).

Germination

Aquatic macrophytes may germinate poorly in the field. From the yearly production about 15% of *Chara aspera* spores germinate (Van den Berg et al., 2001). Recruitment from the dispersed propagules and from the propagule bank may depend on the environmental conditions, including light, soil moisture and nutrient availability (Sederias & Colman, 2007, 2009). Although data on germination of submerged macrophytes are scarce, seedling emergence tests show that propagules of submerged macrophytes can germinate as well on moist and wet sediment (Boedeltje et al., 2002; De Winton, 2000; Espinar & Clemente, 2007) as under water (Harwell & Havens, 2003; Porter et al., 2007). Moreover, *P. pectinatus* is known to recruit more from seeds with decreasing latitude, due to a higher probability of summer drought at these latitudes, which

reduces survival of tubers and thus also their clonal reproduction (Santamaria & Garcia, 2004).

However, many macrophytes do not depend only on recruitment from seeds as they can easily regenerate from fragments. Some even produce specialised vegetative dispersal organs, turions and other vegetative propagules which can regrow easily, even under very low light conditions (Xie et al., 2010). Generally, the clonal recruitment through vegetative propagules is considered to prevail over that from seeds and oospores as they often outnumber seeds in trapping experiments (Boedeltje et al., 2002, 2003). Capers (2003) found that about 60% of the individuals that colonised bare soil in freshwater tidal areas originated from vegetative propagules. Genetic studies, however, show that recruitment from vegetative propagules versus seeds and oospores is very species specific (Nilsson et al., 2010; Bornette & Puijalon, 2011).

The importance of remnant populations

In addition, species can also colonise restored shallow water bodies by expansion of local remnant populations. As most macrophyte species are clonal, theoretically only a single individual needs to survive until favourable conditions return. Generally, the occurrence of macrophyte species shows only a weak relationship with the nutrient concentration in the water (Vestergaard & Sand-Jensen, 2000; Penning et al., 2008; Sondergaard et al., 2010). Possibly, the species temporarily can tolerate the less favourable conditions (Blindow, 1992a; Van den Berg et al., 1999). Based on their long-term dataset (100 years), Sand-Jensen et al. (2008) elegantly show that the return of macrophytes after improved abiotic conditions in Lake Fure in Denmark, was strongly determined by the presence of clones of several species that had originated from the time before eutrophication. The historical presence of clones of species in the lake was a much more powerful predictor of vegetation composition after restoration than the altered nutrient conditions. Thus, in the restoration of shallow water bodies remnant populations, especially for species of high conservation value, deserve special attention and should, if possible, remain unscathed by the restoration measures taken.

On the other hand, the historical presence could also form a threat to successful restoration if undesirable species, e.g. eutrophic or invasive species, are

present in the area. These are then also very likely to re-colonise after restoration, especially if restoration measures have not led to an anticipated decrease in the nutrient loading, for example in some cases where biomanipulation is used as a restoration measure (Gulati & Van Donk, 2002; Gulati et al., 2008).

Herbivory on returning macrophytes

When macrophytes return after restoration of shallow water bodies, waterbirds are attracted to this new and abundant food source (Noordhuis et al., 2002). The question is whether grazing by waterfowl and large fish can also prevent or inhibit the re-colonisation of shallow water bodies after restoration? Vertebrate herbivores can strongly reduce macrophyte vegetation, but their impact varies among study sites (Marklund et al., 2002). The question whether herbivores can prevent the colonisation of macrophytes in restored shallow water bodies is debated. Experiments where macrophytes were transplanted in restored lakes showed that herbivores (large fish and waterfowl) strongly reduced macrophyte biomass (Lauridsen et al., 1993; Sondergaard et al., 1996; Lauridsen et al., 2003b; Irfanullah & Moss, 2004; Van de Haterd & Ter Heerdt, 2007; Moore et al., 2010). However, Perrow et al. (1997) and Strand & Weisner (2001) found no significant reduction due to herbivory by fish and birds in restored lakes of the biomass of macrophytes that had developed spontaneously, whereas Hilt (2006) found a more than 90% reduction of *P. pectinatus* vegetation through grazing. Even if the herbivores do not completely prevent the colonisation of macrophytes, they may retard the vegetation development. As the macrophytes that appear when clear water is restored, are required to maintain this clear water state, a rapid colonisation, i.e. increased coverage by macrophytes of the water body is crucial. If herbivores inhibit the increase in coverage of macrophytes or the biomass that they attain, the colonisation process may become too slow and the clear water phase may disappear, thereby decreasing the probability of macrophyte establishment and dominance (Van de Bund & Van Donk, 2002; Sondergaard et al., 2008). However, in addition to reducing macrophyte biomass, herbivores may also affect macrophyte community composition by selective consumption of certain species in favour of other

species. For example, in Lake Zwemlust in the Netherlands, the macrophyte vegetation that had developed after the lake's restoration by biomanipulation, was markedly grazed down by coots and rudd, shifting the dominance of *Elodea nutallii* to co-dominance by *Ceratophyllum demersum* and *Potamogeton berchtholdii* (Van Donk & Otte, 1996). Waterfowl has been documented to graze selectively on *P. pectinatus*: in Matsalu bay in Estonia, herbivores selectively removed *P. pectinatus* plants in favour of the charophytes (Hidding et al., 2010a), whereas in the Lauwersmeer in The Netherlands, waterfowl suppressed dominance of *P. pectinatus* in favour of subordinate *Zannichellia palustris* and *Potamogeton pusillus* (Hidding et al., 2010b).

The role of macrophyte species in ecosystem stability

Macrophytes differ in their efficiency to retain nutrients (Engelhardt & Ritchie, 2001), in their suitability as substrate for macrofauna (McAbendroth et al., 2005; Declerck et al., 2011) and in their importance as food for herbivores (Dorenbosch & Bakker, 2011). Several studies have reported enhanced water clarity above charophyte vegetation (Scheffer et al., 1994; Van Donk & Van de Bund, 2002; Hargeby et al., 2007), although this clearing effect is not limited to charophytes (Kosten et al., 2009b). Charophytes can attain high biomass and form dense stands (Blindow, 1992b; Van Nes et al., 2002; Bakker et al., 2010), which may improve the trapping of sediment. Furthermore, the occurrence of charophyte stands may be more stable than for example those of *Potamogeton* spp. (Van den Berg et al., 1999) that occur more stochastically. Combined with a strong allelopathic activity of charophytes (Vermaat et al., 2000; Kufel & Kufel, 2002; Mulderij et al., 2003; Hilt & Gross, 2008), clear water conditions may be achieved relatively easily. Waters dominated by eutrophic species such as *Potamogeton* spp. on the other hand seem to switch more readily to a turbid state (Van Nes et al., 2002). This may be because eutrophic species grow at nutrient-rich conditions which favour algal growth or because of the morphology of these species leading to more biomass allocation towards the water surface and lesser biomass density. Also a switch from a macrophyte community dominated by charophytes to a

Potamogeton-dominated vegetation is accompanied by a substantial reduction in the seasonal duration of macrophyte dominance and a greater tendency of incursions by phytoplankton (Sayer et al., 2010). Therefore, the macrophyte community composition seems to affect the ecosystem functions performed by macrophytes. Currently, the importance of the effect of macrophyte community composition remains largely unknown as this is just an emerging topic of research.

Macrophyte biodiversity

The number of species in submerged macrophyte vegetation is generally rather low compared to terrestrial vegetation (Edwardsen & Okland, 2006). Field studies show that macrophyte richness is related to several lake variables, including lake area, altitude, shoreline complexity, connectivity, trophic state, conductivity and water and sediment quality (Rorslett, 1991; Murphy, 2002; Makela et al., 2004; Declerck et al., 2005; Scheffer et al., 2006; Geurts et al., 2008). This makes macrophyte species richness generally hard to predict (Edwardsen & Okland, 2006). However, some general mechanisms and patterns can be acquired from field surveys. As for terrestrial plant species, coexistence in macrophytes is highest at optimal light conditions. Under-water light conditions, which reflect turbidity, are an important limiting factor for macrophyte diversity: for example in fens, macrophytes are restricted to water depths <4 m and to water bodies with a turbidity <20 ppm Pt and for red list species <12 ppm Pt (Geurts, 2010). Shading, including that caused by other macrophytes, may also reduce diversity. Macrophyte species richness follows an optimum curve over a productivity gradient, as earlier described for terrestrial vegetation (Al-Mufti et al., 1977): macrophyte richness peaks at intermediate standing crop, indicating light limitation at high plant production and suboptimal conditions for growth of many species at low productivity due to nutrient limitation (Willby et al., 2001; Murphy, 2002). Therefore, the return of large amounts of macrophytes does not need to coincide with the highest species richness. This is for instance observed in restoration projects in shallow eutrophic lakes, where upon the increase of water transparency, fast-growing eutrophic species such as *Elodea nuttallii* or *C. demersum* may

initially become dominant, leading to a large coverage of macrophytes, but low species diversity (Hilt et al., 2006). Similarly, the spread of invasive macrophytes can lead to high coverage and large macrophyte biomass, but a low species diversity, as native species may become outcompeted due to shading (Stiers et al., 2011).

Nutrient levels in shallow water bodies do affect macrophyte diversity indirectly through changing light conditions, but also directly through the accumulation of toxic substances. The sediment Fe:PO₄ ratios may be used as a diagnostic tool to determine optimal macrophyte diversity. Generally species richness is highest and red list species occur more often at high Fe:PO₄ ratios (>10 mol mol⁻¹) because of a higher probability of strong P release, associated with algal blooms and toxic sulphide formation, at ratios below this threshold (Smolders & Roelofs, 1996; Van der Welle et al., 2007; Geurts et al., 2008). The concentration of nitrate in the surface water in winter has also been reported as an important predictor of macrophyte or charophyte species richness in the field (James et al., 2005; Lambert & Davy, 2011); and nitrate loading can also reduce macrophyte species richness under experimental conditions (Barker et al., 2008). This relationship is explained by increased competition at higher nitrate availability resulting in a shift towards floating-leaved macrophyte species and thus light limitation (James et al., 2005) and a toxic effect of nitrate on charophytes (Lambert & Davy, 2011). Macrophyte species richness declined above a threshold concentration of 1–2 mg N-NO₃ l⁻¹ in winter (James et al., 2005) or 0.6 mg N-NO₃ l⁻¹ (corresponding to 1.5 mg TN l⁻¹) under experimental conditions (Barker et al., 2008). Charophyte species richness declined above a threshold of a mean annual concentration of ca. 2 mg N-NO₃ l⁻¹ (Lambert & Davy, 2011).

Even though the role of abiotic factors in determining macrophyte diversity is gradually becoming established, little is yet known about how biotic factors affect macrophyte diversity. It is for example virtually unknown whether the composition of macrophyte vegetation is limited by propagule availability or local conditions, which may affect colonisation, establishment and growth. Analyses of patterns of macrophyte diversity among lakes for examining the role of the regional species pool, by including a distance parameter, revealed that local in-lake

conditions are more strongly related to local macrophyte diversity than the distance to a propagule source (Rorslett, 1991; Vermond et al., 2010). However, experimental or mechanistic tests of the role of the species pool and propagule pressure in determining macrophyte diversity are still lacking.

Furthermore, the role of food web interactions as determinants of macrophyte diversity remains largely unknown. Whereas connectivity improves propagule availability, which could improve macrophyte diversity, isolation is known to increase macrophyte diversity in ponds. An explanation for the counter-intuitive relationship between isolation and species richness is that isolated ponds frequently lack benthivorous fish, which create turbid conditions through their foraging in sediment. Isolated ponds that lack those fish have higher richness of macrophyte species because they become turbid less easily if habitat conditions deteriorate (Scheffer et al., 2006). However, at high macrophyte productivity, moderate levels of disturbance may actually increase macrophyte diversity. Herbivores that graze on the dominant plant species and create moderate sediment disturbance create recruitment opportunities for subordinate plants, thereby improving macrophyte diversity (Sandsten & Klaassen, 2008; Hidding et al., 2010b). Similarly, water level fluctuations can enhance macrophyte diversity (Rorslett, 1991): drawdowns particularly have been shown to improve richness of submerged macrophytes (Van Geest et al., 2005).

Restoration measures

How do restoration measures affect the return of species rich vegetation? There are several well-documented examples of restoration projects where external nutrient loading has been reduced and the effects on the vegetation have been placed in a long-term context (Table 1). These examples show that reducing external nutrient loading does result in a return of macrophytes and an increase in species richness 20–40 years after peak nutrient loading, when macrophytes had almost disappeared (Table 1). Macrophyte return is slow and there can be a delay in recovery, where macrophytes do not yet colonise even though transparency has increased in response to reduced nutrient loading, a phenomenon also observed in other studies of nutrient reduction (Jeppesen et al.,

2005a, b; Phillips et al., 2005). Furthermore, whereas macrophytes returned and species richness improved after reduction of nutrient loading, a longer term comparison shows that the species richness and macrophyte community is different from the records about a century ago, from the early 1900s, which was the start of human-induced large-scale eutrophication (Table 1). The authors suggest that this may be due to an impoverished regional species pool, where species are nowadays rare, altered sediment characteristics and competition from tall growing eutrophic species, which inhibits the return of smaller, rare, oligotrophic species (Sand-Jensen et al., 2008; Hilt et al., 2010; Dudley et al., 2012). This observation raises the question whether the changes to the aquatic habitat, particularly the sediment, and plant communities induced by eutrophication are reversible.

In contrast to the reduction of nutrient loading, biomanipulation can create an almost immediate response of both enhanced light availability and macrophyte growth (Lauridsen et al., 2003a, b; Table 1).

Clear water is the foremost requirement to allow optimal under-water light conditions for macrophytes to germinate and grow. In lakes where sediment contributes most to water turbidity and sediment dynamics prevent macrophyte recruitment, the creation of shelter and removal of sediment disturbing fish will be necessary; as shown by lake biomanipulation studies (Gulati & Van Donk, 2002; Sondergaard et al., 2007; Gulati et al., 2008). When optimal light conditions are re-established, plants can respond fast by germination and colonisation of the shallow water body (Van de Haterd & Ter Heerdt, 2007). However, whereas biomanipulation can initially result in a strong expansion of macrophyte vegetation, which can be species rich, the community often rapidly changes and becomes dominated by eutrophic species. On one hand the abundance of eutrophic species may enhance water transparency, but on the other hand the species that dominate and grow to the water surface will limit light deeper in the water column, which will reduce the number of species that can grow under these conditions (Sand-Jensen et al., 2008). Additionally, dominance by eutrophic species does often not result in a stable vegetation and a relapse to the turbid state can occur within 10 years (Sondergaard et al., 2008). To prevent the deterioration of the vegetation and clear water state, low nutrient levels are required,

as indicated by the thresholds mentioned in the previous paragraph. To achieve such low nutrient levels, both external and internal nutrient loading should be reduced, depending on the nutrient loading of the sediment, for which many methods are available (Cooke et al., 1993; Hickey & Gibbs, 2009). Most of these measures are not harmful for the macrophyte habitat, apart from removal of nutrient-rich sediment. Even though decreased nutrient availability after dredging can result in clear water, it will also remove a large part of the macrophyte propagule bank. But, we still do not know if this hampers macrophyte recovery as the role of the propagule bank in restoring macrophyte vegetation remains largely unknown.

Water fluctuations will generally benefit the submerged vegetation by providing recruitment sites (Coops & Hosper, 2002). However, this also depends on the effects on water quality, as in some cases shallow water may be prone to algal blooms facilitated by the increased temperatures in a shallow water layer.

If there is uncertainty whether macrophyte species will colonise the restored areas and sustain the restored clear water state, planting them might be an option (Hilt et al., 2006). However, first the abiotic conditions for the growth of submerged macrophytes should be met as well as a reduction in the population of sediment disturbing fish or crustaceans including (invasive or stocked) crabs and crayfish. Subsequently one should wonder why macrophytes are not spontaneously returning to the restored water body. This may indicate that growing conditions are still not good enough and in that case transplanting will be unsuccessful. For macrophytes to maintain a clear water state a minimum coverage of the lake seems to be required; as a rule of thumb 30% coverage has been used as a minimum threshold (Jeppesen et al., 1994; Van Nes et al., 2002; Janse et al., 2008; Kosten et al., 2009a), which is in the range of 10%–40% reported by Sondergaard et al. (2010), but others report the need for higher coverage (50% Tatrai et al., 2009, 60% Blindow et al., 2002). In warm lakes in tropical and subtropical regions, a higher coverage of macrophytes may be needed as the grazing of zooplankton on phytoplankton is low due to high fish predation (Jeppesen et al., 2007; Kosten et al., 2009a). As this requires a tremendous effort, large-scale planting of macrophytes has not often been used. In China, subtropical Lake Huizhou (West Lake) has been planted completely with submerged macrophytes after

removal of fish and has been clear for 6 years since planting it, with continued fish removal (Chen et al., 2010), even though it is assumed that (sub)tropical lakes are much harder to maintain in the clear water state (Jeppesen et al., 2005a, b).

Perspectives and conclusions

In view of the money spent and efforts put in restoration of submerged macrophytes, it is somewhat surprising that we still do not know exactly why the restoration of vegetation with high biodiversity fails in many lake restoration studies. In lake restoration, most attention has been paid to switch eutrophic lakes with highly turbid waters to a clear water state, with the assumption that the macrophyte vegetation will appear as soon as the water is clear and maintain this clear water state. However, the first bottleneck for lake restoration may be the absence of species either in the propagule bank, or in the form of relic populations that survived the period of unfavourable conditions. Currently, the intriguing question is: where do macrophytes come from after restoration? As long as we do not know how important propagule availability and dispersal are for the re-establishment of diverse macrophyte vegetation, it is not possible to take directed measures to improve the recruitment of a diverse vegetation other than creating the right abiotic conditions as is currently been attempted by many. We conclude that it is imperative to study the recruitment phase of macrophytes more closely for restoring diverse macrophyte communities as well as the biotic interactions including herbivory and plant competition. These essential study objectives will further determine the probability of macrophyte restoration and define what exactly can be restored and what not. The composition of the vegetation, in turn, affects the ecosystem functions that macrophytes have. A better understanding of the species specificity and of the importance of diversity of macrophyte vegetation in the fulfilling of ecosystem functions will both advance our knowledge of the role of macrophytes in shallow water bodies and lead to a better guidance of restoration efforts.

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