Restoration of submerged vegetation in shallow eutrophic lakes –
A guideline and state of the art in Germany

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Abstract

One of the most serious problems caused by eutrophication of shallow lakes is the disappearance of submerged macrophytes and the switch to a turbid, phytoplankton-dominated state. The reduction of external nutrient loads often does not result in a change back to the macrophyte-dominated state because stabilising mechanisms that cause resilience may delay a response. Additional internal lake restoration measures may therefore be needed to decrease the concentration of total phosphorus and increase water clarity. The re-establishment of submerged macrophytes required for a long-term stability of clear water conditions, however, may still fail, or mass developments of tall-growing species may cause nuisance for recreational use. Both cases are often not taken into account when restoration measures are planned in Germany, and existing schemes to reduce eutrophication consider the topic inadequately. Here we develop a step-by-step guideline to assess the chances of submerged macrophyte re-establishment in shallow lakes. We reviewed and rated the existing literature and case studies with special regard on (1) the impact of different internal lake restoration methods on the development of submerged macrophytes, (2) methods for the assessment of natural re-establishment, (3) requirements and methods for artificial support of submerged macrophyte development and (4) management options of macrophyte species diversity and abundance in Germany. This guideline is intended to help lake managers aiming to restore shallow lakes in Germany to critically assess and predict the potential development of submerged vegetation, taking into account the complex factors and interrelations that determine their occurrence, abundance and diversity.

Keywords: Charophytes; Eutrophication; Invasive species; Lake management; Lake restoration; Macrophyte re-establishment; Nuisance species; Propagules; Shallow lakes; Submerged macrophytes

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Introduction

One of the most serious problems caused by eutrophication of shallow ponds and lakes is the disappearance of submerged macrophytes and switch to the turbid, phytoplankton-dominated state (Scheffer, 1989; Scheffer, Hosper, Meijer, Moss, & Jeppesen, 1993). The decline of submerged macrophytes in shallow lakes in Denmark (Sand-Jensen, Riis, Vestergaard, & Larsen, 2000), Great Britain (Moss, 1980), Sweden (Blindow, 1992) and The Netherlands (Best, De Vries, & Reins, 1984) has been well studied. However, in Germany, comprehensive studies on the extent of the decline in submerged macrophyte abundance due to eutrophication are lacking. Körner (2002a) reported a low abundance of submerged macrophytes in 66% of 100 investigated lakes in Brandenburg in the 1990s. A change back to the clear, macrophyte-dominated state in response to the reduction of external nutrient loads is often delayed by stabilising mechanisms that cause resilience. Macrophyte recolonisation can be hampered due to enhanced turbidity, enhanced sediment resuspension, grazing by herbivorous birds, disturbance by fish or lack of viable propagules in the sediment (Jeppesen et al., 1991, 1999; Körner, 2001; Körner & Dugdale, 2003; Ten Winkel & Meulemans, 1984; Van den Berg, Scheffer, Coops, & Simons, 1998). A delayed response of submerged macrophytes after reoligotrophication has been reported, e.g. in a study comparing 35 temperate lakes (Jeppesen et al., 2005) and in a study on 100 Brandenburg shallow lakes (Körner, 2002a). In contrast, undesired spontaneous re-establishment or colonisation of submerged plants often occurs in shallow lakes after reduction of external nutrient loading, changes in the water regime or fish stock. The possibility of natural and uncontrolled development is mostly ignored in the management of shallow lakes. Dense stands of aquatic vegetation may cause nuisance for boating, swimming and other recreational use (Van Nes, Scheffer, Van den Berg, & Coops, 2002).

In Germany, both the desired and undesired establishment of submerged plants are often not taken into account when restoration measures are planned. Decision support schemes to assess the potential development of submerged vegetation, comparable to those available for manipulation of fish communities (Mehner et al., 2004) or for control of the internal P cycle (Schäuser, Lewandowski, & Hupfer, 2003), are lacking. Although information on macrophyte development is available (Brouwer, Bobbink, & Roelofs, 2002; Moss, Madgwick, & Phillips, 1996a), existing decision schemes to reduce eutrophication (e.g. Rast & Holland, 1988; Schäuser et al., 2003) often consider the topic inadequately.

In order to support lake managers aiming to restore shallow lakes in Germany, we reviewed and rated the existing approaches described in the literature and developed a step-by-step guideline to assess the chances of submerged macrophyte re-establishment. While shallow lakes are traditionally defined either by a certain mean depth (e.g. $<5$ m, Jeppesen et al., 1990) or polymeric conditions (LAWA, 1998), we here consider all lakes in which submerged macrophytes play a significant role for the stabilisation of clear-water conditions. We consider the impact of different internal lake restoration measures on the development of submerged macrophytes, and also summarise case studies on the artificial support of submerged macrophyte colonisation in Germany.

Guideline for assessing the chances of macrophyte re-establishment in shallow lakes

Restoration measures to decrease turbidity in degraded shallow lakes

The initial steps for the development of a restoration strategy are the definition of goals, and the accurate identification of the problems associated with a certain water body. Pilot surveys are necessary to define the current and the best possible state under optimal but realistic conditions reflecting current land and water use. Since the turbid, phytoplankton-dominated state is often caused by excessive total phosphorus (TP) concentrations, an external TP load reduction is in the majority of cases the essential prerequisite for turbidity to fall below a threshold value specific for this lake. But internal feedback loops in eutrophic systems, such as nutrient release from sediments and long water residence times, maintain high phytoplankton production even after loading is curtailed. Therefore, additional internal measures (Cooke, Welch, Peterson, & Nichols, 2005) can help to shorten the relaxation time after external P load reduction and to compensate undesirable effects of insufficient reduction of external load. Common internal restoration measures for shallow lakes aiming at an increase of the water clarity include measures with and without a decrease of the TP concentrations (Table 1).

The choice of an appropriate internal restoration measure in the first instance requires detailed knowledge of the lake and vegetation type to be restored. The majority of lakes (and therefore of available literature on restoration measures) in Germany are eutrophied, alkaline lakes. Dystrophic (peat) lakes are typically mildly acidic, brownish in colour with high levels of dissolved organic substances associated with leaching from adjoining peat vegetation in the catchment. The typical vegetation consists of Sphagnum spp., Nymphaeaceae and Utricularia spp. Characteristic macrophytes in soft water lakes have an extensive root system and short rosette leaves, e.g. Littorella uniflora and...
Isoetes lacustris. In such lakes, sediment dredging and the recovery of the original level of alkalinity seem an essential prerequisite to restore the original vegetation (Roelofs, Brouwer, & Bobbink, 2002).

Although wind stress and sediment conditions may also limit the distribution of submerged macrophytes (Schutten, Dainty, & Davy, 2005), light is the most important factor in eutrophic alkaline lakes (Duarte & Kalff, 1986; Van den Berg, Joosse, & Coops, 2003). In general, all internal measures that result in an improvement of the light conditions should therefore have positive effects on the development of macrophytes. Some measures, however, might also have negative effects, like sediment removal and coverage, inactivation of phosphorus and oxidative measures (Table 1). To our knowledge, a systematic assessment of the potential effects of internal measures on the development of submerged macrophytes is lacking (some information is available in Moss et al., 1996a and Roelofs et al., 2002).

Dredging is often used to increase the P export from the system and to shorten the response time to a decreased external P loading. Furthermore, dredging may decline turbidity by reduced resuspension of unconsolidated sediments and stop the aggradation of very shallow lakes. Sediment removal can affect the macrophyte colonisation in different ways. Beside improved light conditions the removal of water rich sediment layers increases the stability of substrate for rooted macrophytes. Moss, Stansfield, Irvine, Perrow, and Phillips (1996b) state that macrophyte establishment is seriously impaired if the eutrophicated sediment layer is not removed completely. Otherwise, sediment removal may also eliminate seeds, oospores and vegetative reproduction units needed for a fast recoloniisation when clear water conditions recurred. Alternatively, sediment removal may reduce the sludge layer above a viable, long-lived seed bank. Macrophyte recovery from a relict seed bank depends on whether buried seeds are positioned within their physical limits of emergence, can receive germination cues, or are in a physiological state to respond (De Winton, Clayton, & Champion, 2000). De Winton et al. (2000) found viable seeds in 15 cm sediment depth and in lakes with an absence of submerged vegetation for 23 years. Removal of accumulated sapropelium strongly stimulated the germination of soft water macrophytes under experimental conditions in shallow soft water lakes in The Netherlands (Roelofs et al., 2002). Regeneration of soft water macrophytes via seed bank can occur after 20–40 years of absence (Kaplan & Muer, 1990). New establishment of other species, however, is relatively rare (Roelofs et al., 2002). In Lake Beuven, a stable community of soft water macrophytes was established after reduction of external nutrient load and sediment removal (Brouwer & Roelofs, 2001). Sediment dredging, however, was often not successful in decreasing water P concentration because the role of sediments as temporary P storage was overestimated in comparison to external P sources (Annadotter et al., 1999).

Sediment capping, i.e. the physical or chemical isolation of the sediment from the water to decrease sediment P release, can be achieved by several methods (e.g. gravel, plastic films, pulverised fly ash, calcareous mud). These measures most probably have negative effects on the development of submerged macrophytes since a physical barrier buries propagules into deeper sediment strata and prevents germination. The physical capping by synthetic non-porous materials (fibreglass, nylon sheets, polyethylene) is even used to restrict plant development (Perkins, Boston, & Curren, 1980; Cooke et al., 2005). Successful applications of physical barriers for the decrease of P in water have not yet been described.

Phosphorus inactivation in sediments by alum, iron or lime applications is used to decrease TP in shallow lakes (Boers, Van der Does, Quaak, & Van der Vlugt, 1994; Table 1. Common measures for increasing water clarity in shallow lakes (for selection criteria see Schauser et al., 2003) and potential effects on the development of submerged macrophytes (X: increased transparency by a decrease of phytoplankton density, * not applicable in polymictic lakes)

<table>
<thead>
<tr>
<th>Restoration measure</th>
<th>Increase of</th>
<th>Positive effects on macrophytes</th>
<th>Negative effects on macrophytes</th>
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<td>With decrease of TP</td>
<td>P-export</td>
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<td>Elimination of propagules</td>
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<td>Sediment removal</td>
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<td>Improved plant fixation</td>
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<td>Mechanical disturbance</td>
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Cooke et al., 2005; Deppe & Benndorf, 2002; Welch & Cooke, 1999). Besides P input and available P in sediments, the efficiency of the salts used for precipitation depends on their stability under the given redox and pH conditions in the sediment and in the lake water in case of wind resuspension. Under anoxic conditions in the sediment a part of iron bound P can be released again by the microbial reduction of iron (III), whereas aluminium bound P is stable under these conditions. In case of resuspension P bound to aluminium and iron can be mobilised by exchange against OH⁻ ions, if the pH in a productive water body is increased to 9–10. Addition of slagged lime (Ca(OH)₂) to hardwater lakes, however, caused an immediate eradication of submerged aquatic plants triggered by a short-term rise in pH (Chambers et al., 2001; Reedyk, Prepas, & Chambers, 2001). Lime addition may therefore not be the preferred measure in cases where recolonisation is expected to occur from scattered macrophyte stands that survived phytoplankton dominated periods. Experimental studies on the effect of alum or iron additions on the macrophyte development are lacking. Sandrock, Scharf, & Dolgner (2006) report successful re-establishment of submerged macrophytes in three lakes in Mecklenburg-West Pomerania after alum treatment. In Barleber See (103 ha, mean depth: 6.7 m, Saxony-Anhalt) macrophytes re-established after an alum treatment using 5.7 mg L⁻¹ Al³⁺ in 1986 (Rönice, Beyer, Titul, Mätzold, & Ruschak, 1995). Alum mixed directly into the sediment might be more toxic to submerged macrophytes than applied to the overlying water. In the stratified Groß-Glienicker See (67 ha, mean depth: 6.5 m, Berlin), submerged macrophytes only recurred 7 years after a treatment with iron salts, although clearwater conditions were immediately restored (Hilt, 2003).

Sediment oxidation includes the aeration with molecular oxygen and the injection of Ca(NO₃)₂ into the lake sediment to stimulate denitrification. Enhanced denitrification can prevent the reductive dissolution of iron and the subsequent release of iron bound P at the sediment surface. Oxidative measures are often combined with addition of ferric chloride to remove H₂S and to form Fe(OH)₃. Long term effects of single molecular oxygen or nitrate addition on the P cycle are not expected. Effects of these treatments on the development of submerged macrophytes including the mechanical disturbance during application are rare. In the shallow urban lake Old Danube in Vienna (Austria), macrophytes were still absent in large areas of the lake after Riplox treatment, i.e. the addition of FeCl₃ buffered with limestone and Ca(NO₃)₂ (Dokulil, Teubner, & Donabau, 2000). Only a drawdown of the water level by 30 cm resulted in a successful recolonisation (Donabau, Pall, Teubner, & Dokulil, 2004). Water level drawdowns in early spring are very efficient to increase light availability for submerged macrophytes (Coops & Hosper, 2002). Depending on lake morphometry and transparency, drawdowns by 30–60 cm might be sufficient to foster macrophyte development.

Biomanipulation can be very efficient to increase water transparency, i.e. in The Netherlands in 90% of all cases (Meijer, De Boois, Scheffer, Portielje, & Hosper, 1999). Long-term stability of the clear-water state can only be expected below certain critical nutrient levels, which depend especially on lake size and depth. Jeppesen et al. (1990) suggested critical TP levels of 0.08–0.15 mg P l⁻¹. Lauridsen, Jensen, Jeppesen, and Søndergaard (2003) concluded that at least the short term potential of macrophyte recolonisation after nutrient loading reduction is higher in biomanipulated lakes than in lakes subjected to loading reduction only. Hosper & Meijer (1993) developed a simple test to assess the chances for clear water following fish stock reduction. In the Swedish Lake Finjasjön a 5-year inefficient dredging was stopped. Only the combination of further external P reduction and a food web manipulation led to increased light transparency and resulting increase of submerged macrophyte coverage from 1% to 20% within 3 years (Annadotter et al., 1999).

Size of lake area potentially covered by submerged macrophytes

When a method has been chosen to increase the light availability, the second question will be to which extent the turbidity should be decreased (Fig. 1). It is still not solved how much area of a shallow lake has to be covered with submerged macrophytes to maintain clear-water conditions. In general, submerged macrophyte colonisation is described by percentage bottom coverage and/or plant volume inhabited (PVI), including the relative height of macrophyte stands compared to the water level. Following Reynolds (1994), > 50% coverage are needed for a successful biomanipulation, Canfield et al. (1984) found major reductions in chlorophyll a and higher transparencies at a PVI of > 30% and Meijer et al. (1999) as well as Norlin, Bayley, & Ross (2005) stated that low algal biomass coincided with a macrophyte coverage of more than 25% of the lake surface area. Portielje & Van der Molen (1999) even report reductions of chlorophyll a at 5–10% coverage.

The area distribution of submerged macrophytes is regulated by the lake morphology and their maximum colonisation depth (z_c), defined by water column light attenuation and minimum light requirement for growth (Canfield, Langeland, Linda, & Haller, 1985; Chambers & Kalff, 1985). Also other parameters like grazing pressure, substrate type and epiphyte shading can affect z_c (Middelboe & Markager, 1997). Depth limits of...
submerged macrophytes differ between growth forms: In lakes with Secchi disc transparencies \((z_s) \leq 4\, \text{m}\), \(z_c\) can be calculated as \(z_c = K + a \cdot z_s\) with \(a = 1.19, 0.95, 0.38\) and \(K = 0.17, 0.37\) and 0.88 for charophytes, caulescent and rosette-type angiosperms, respectively (Middelboe & Markager, 1997). Provided the depth profile of the lake is known, the required Secchi disc transparency to achieve a certain macrophyte coverage can be calculated, i.e. using a scheme offered on the homepage of the Dutch Shallow Lakes Network (www.shallowlakes.net/handboek/modellen/index_modellen.html). A good prediction, however, remains difficult as models forecasting the dynamics of macrophytes based on transparency, water depth, exposure and sediment type showed that sites without macrophytes can be correctly predicted but not those with vegetation (Scheffer, De Redelijkheid, & Noppert, 1992). Examples of maximum macrophyte colonisation depths for 220 lakes in North eastern Brandenburg are given in Mauersberger & Maurersberger (1996).

In large, wind-exposed lakes, stable sediments and strong resuspension can prevent the re-establishment of submerged vegetation (Hamilton & Mitchell, 1996; Schutten et al., 2005). Phytoplankton dominance promotes the accumulation of highly organic, unconsolidated sediments with low cohesive strength, a factor affecting the distribution and abundance of submerged macrophytes that has been largely neglected (Schutten et al., 2005).

**Natural development of submerged macrophytes**

If the water transparency potentially allows a significant macrophyte coverage (50% can be used as a conservative value), the next question should be whether submerged vegetation can develop naturally from a propagule bank, remaining macrophyte stands or by naturally introduced propagation units (Fig. 1). The presence, density and composition of a seed bank can influence the rate and extent of vegetation establishment (De Winton et al., 2000). The number of macrophyte propagules in the sediment has to be estimated and their viability tested when the lake has been free of macrophytes for a period longer than 20 years (De Winton et al., 2000). Propagules seem to be able to survive rather long periods in the sediment. Van den Berg and Delauney (www.shallowlakes.net) developed a model calculating the chance of submerged macrophyte occurrence based on the relationship between seed bank biomass and light availability using data from five Dutch shallow lakes (chance of appearance of submerged plants \(C = \exp(0.116\%ZB – 0.99)/\left(1 + \exp(0.116\%ZB – 0.99)\right)\), with \(ZB\): biomass of seed bank \((g\, m^{-2})\), \(%l\): light availability as percent of incident light at the water surface, \(%l = 100e^{-zk}\); \(z\): water depth \((\text{m})\) and \(k\): attenuation \((\text{m}^{-1})\)). Based on this relationship, a calculation scheme (also considering fetch and sediment conditions) is offered. Under certain circumstances, large-scale establishment of submerged macrophytes seems possible independently of a viable seed bank. In Steinhuder Meer, a large \((29\, \text{km}^2)\) and shallow lake (mean depth 1.4 m) in Lower Saxony, macrophytes re-established in 1999 after a sudden increase of water transparency approximately 40 years after their disappearance (Poltz & Schuster, 2001). The vegetation was dominated by *Elodea nuttallii*, a species that never occurred in that lake before and spreads mainly by vegetative fragments.

Germination of macrophyte seedlings from seed or overwintering buds/turions may also be hampered by the presence of reducing sediments and consequent high production of sulphides and ammonia (Perrow, Moss, & Stansfield, 1994). No general threshold levels can be given for sediment quality parameters. When a negative impact is expected, experimental tests of the sediment suitability by planting test species are recommended.

Next to the lack of propagules and unsuitable conditions for germination, herbivory might delay recolonisation. Especially during the recolonisation phase after oligotrophication, submerged vegetation is susceptible to damage by naturally occurring fish and waterfowl (Körner, 2001; Körner & Dugdale, 2003; Körner, Schreiber, & Walz, 2002; Marklund, Sandsten, Hansson, & Blindow, 2002; Søndergaard, Bruun, Lauridsen, Jeppesen, & Madsen, 1996). A number of macroinvertebrates ingest macrophyte tissue (Lodge,
but also roach (Rutilus rutilus) and ide (Leuciscus idas) seem to eat significant amounts of plant material (Prejs, 1984). Common carp (Cyprinus carpio) and bream (Abramis brama) do not eat the plants directly but uproot plants by sediments sucking (Crivelli, 1983). Young roach and perch (Perca fluviatilis) were found to pluck parts of leaves while searching for invertebrates in the periphyton (Körner & Dugdale, 2003).

Gross, Feldbaum, & Choi (2002) report substantial damage of apical meristems of Potamogeton perfoliatus and Myriophyllum spicatum in the littoral zone of Lake Constance by herbivorous moth larvae (Acentria ephemera, Pyralidae, Lepidoptera). In order to test whether herbivory prevent the re-establishment of submerged macrophytes, enclosure cages have to be installed at suitable sites in the lake at the beginning of the growing season (usually at the end of April) and the biomass development has to be compared with that of unprotected areas. The use of protective exclosures as a restoration tool has been reported (see ‘Methods for artificial support of macrophyte development’), however, no experience exists for their large-scale use, probably due to high costs for material, installation and maintenance and difficulties such as filamentous algal growth and interference with recreational use.

Methods for artificial support of macrophyte development

If a natural development of sufficient macrophyte cover cannot be expected immediately after the return to clear-water conditions, methods for an artificial support of macrophytes might be considered (Fig. 1). In general, we consider that submerged vegetation will naturally develop sooner or later when the conditions in the lake are suitable. The more cost and maintenance intensive artificial support by planting or seeding of submerged plants seems useful if

1. viable propagation units of submerged vegetation are lacking in the sediment and no remaining stands of any submerged species are present in shallower parts of the lake or water bodies connected to the lake,
2. the restoration method only decreased turbidity for a rather short time period, and long-term clear water conditions would require the immediate stabilisation by submerged macrophytes,
3. the restoration method included the introduction of pike (Esox lucius) that need submerged macrophyte stands for successful development or
4. the promotion of specific (low growing) macrophyte species in particular areas of the lake is required to enable recreational use.

Potential negative effects preventing a successful colonisation like unstable or otherwise unsuitable sediments, waves or currents, herbivory or water level fluctuations should be assessed prior to any planting or seeding (see ‘Natural development of submerged macrophytes’). If the establishment of submerged macrophytes is impossible, neither naturally nor with support, a long-term maintenance of clear-water conditions might not be possible in the lake in question (Fig. 1).

Suitable species

Suitable plant species for recolonisation measures should be selected based on:

1. the lake type (alkaline, dystrophic, softwater),
2. the former vegetation of the lake,
3. species typically occurring in that type of water and in the region,
4. the potential uses of the lake,
5. the suitability of the selected species for transplanting/seeding,
6. habitat preferences of the selected species and
7. the potential origin/source of the plants/seeds.

In Germany, experience with the active planting or seeding of macrophytes is limited (Table 3), although we might have missed some cases. In Table 4, we compiled examples based on literature (Cooke et al., 2005; Kadlec & Wentz, 1974; Smart & Dick, 1999) and expert judgement rather than on experimental trials. Species with a high nuisance potential should not be used to avoid predictable conflicts with lake users. Elodea spp. are therefore generally not recommended. Callitriche spp. are not mentioned due to common difficulties with species determination.

Charophyte development might be especially desirable if an intensive recreational use is intended (see ‘Development of desired species’). The sexual reproduction of charophytes is oogamous. Oospores tolerate temperature fluctuations and desiccation and thus germinate even after decades (Krause, 1997). According to De Winton, Casanova, and Clayton (2004) who measured charophyte establishment from oospores in lake sediments exposed to different light regimes, germination under unfavourable light conditions not supporting seedling growth may cause significant losses to oospore banks. Asexual reproduction takes place by means of (1) multicellular bulbils developed from the lower nodes, (2) uni- or multicellular bulbils developed on rhizoids, (3) protonema-like outgrowths from a node or (4) fragmentation (Martin et al., 2003). Bulbils seem...
to be important for short term survival of an established vegetation whereas oospores are adapted to long time survival in a dormant state (Van den Berg, Coops, & Simons, 2001).

Methods
Following Moss et al. (1996a) and Smart & Dick (1999), planting of submerged macrophytes should be carried out early in the season in sheltered bays in depths not exceeding 1 m and requires the following three phases:

1. trials using test species in small exclosures during the first season,
2. further protected plantation of successful species and test of other species if needed during the second season and
3. natural propagation by sexual and vegetative reproduction.

Plants densities of 0.18–0.25 vegetative plant parts m$^{-2}$ (Cooke et al., 2005), ten 10 cm long fragments m$^{-2}$ (Moss et al., 1996a) or 0.4–0.8 complete plants m$^{-2}$ (Smart & Dick, 1999) are recommended. Planting is rather work intensive and might ideally involve volunteers. At the moment, a number of trials using nets or other rotting and non-rotting substrates that keep planted macrophytes on the lake bottom are carried out in Germany (Table 3 and see below). The initial planting of various submerged macrophytes in Lake Weißenstadt in 2003 using rotting nets and help from volunteers or stake holders resulted in a coverage of 5–10% of the lake area in 2005 (Mapping TU Munich; Morscheid, unpublished data). Rott (2005) planted 200 m$^2$ so-called ‘macrophyte islands’ with Myriophyllum spp. and Chara contraria in a 25 ha lake in southern Germany in 2002. One year later, the plants already colonised 53,000 m$^2$, thus corresponding to more than 20% coverage, and a number of species, which had not been planted, appeared in the lake. Plants repressed benthic cyanobacteria that previously formed thick mats on the sediment. Bolender, Prume, Steinhauser, and Trottmann (2001) report the successful re-establishment of Trapa natans after the introduction of nuts into special protection enclosures. Van de Weyer (2005) started trials for the reintroduction of the extinct Najas flexilis in Poland using plants cultivated from viable seeds from Polish sites or, in case of failure, plant material or seeds from the UK or Scandinavia. Different methods of charophyte establishment have been applied in shallow lakes in The Netherlands (www.shallowlakes.net/platform-ehm/index.html). Whole plants and sediments rich in charophyte vegetative propagules or oospores were used with different success. Van den Berg et al. (2001) found that a closed canopy of C. aspera only developed once an oospore density of about 10,000 m$^{-2}$ was exceeded. Crawford (1979) successfully ‘seeded’ C. vulgaris into farm ponds after drainage and sediment removal by bulldozing. We believe that the use of comparatively undemanding species like C. contraria, C. vulgaris, C. globularis (syn. C. fragilis) or Nitella mucronata might be most promising (Table 4). Establishing large, wintergreen species like Nitellopsis obtusa or Chara tomentosa would in principle be desirable, however, these species are not easily propagating. Successful growth would thus be difficult to accomplish. Evidence for the occurrence of Chara spp. (probably C. contraria and C. globularis) in a number of shallow lakes in Brandenburg was found for the past 2000 years using palaeolimnological methods (Hilt & Dilger, 2004). Plant material or sediments rich in oospores should be gained from, e.g. fish ponds in the surrounding at the end of winter or early spring (www.shallowlakes.net) and inserted as early as possible (Smart & Dick, 1999). Nature protection aspects and the potential risk of transferring fish parasites, pathogens or other undesired species should be considered. Again, small-scale trials in exclosures should be carried out prior to a large scale application. At the moment, several trials using different charophytes attached to supporting textile substrates are carried out in Germany (Table 3).

Development of desired species
If a natural development of submerged macrophytes can be expected, the next question will be whether the developing community will consist of desired or nuisance species (Fig. 1). The development of submerged macrophytes in eutrophic lakes is often restricted to a few species and chance effects on a limited suite of species (particularly monocultures) could easily lead to a total collapse of plant populations (Perrow et al., 1994). A diverse plant community is therefore highly desirable. The species composition of a developing macrophyte community, however, is even harder to predict than the potential coverage. An assessment can be made based on the propagule bank, remaining species in the lake and species present in surrounding waters. Depending on the use of the lake (see ‘Conflicts with lake users’), some species such as low-growing charophytes might be especially desired, whereas invasive species, both native and non-natives, are less desired due to their known potential to form mass developments (see below).

Charophytes
For several reasons, a charophyte dominated vegetation represents the optimum state for most shallow lakes:

1. Similar to aquatic angiosperms, a dense charophyte vegetation enhances water clarity and reduces
phytoplankton growth. This effect is caused by enhanced sedimentation and reduced sediment resuspension within charophyte meadows (Van den Berg et al., 1998), efficient nutrient immobilisation (Blindow, 1992; Kufel & Kufel, 2002) and possibly the production of allelopathic substances (Hootsmans & Blindow, 1994; Wium-Andersen, Anthoni, Christophersen, & Houen, 1982).

2. A dense charophyte vegetation can lead to an efficient long-term immobilisation of nutrients. In calcium-rich lakes, both phosphorus and inorganic carbon are precipitated above charophyte beds. Phosphorus is co-precipitated with CaCO₃ by binding in the crystal structure or sorption on mineral particles, and thus efficiently removed from the water column (Crawford, 1977; Kufel & Kufel, 2002). This apatite-bound phosphorus is among the most inert fractions of phosphorus in the sediments and not released to the water column even under anaerobic conditions (Boström & Pettersson, 1982). Additionally, charophytes like higher submerged plants are able to deliver oxygen to the sediment, thus potentially enhancing nitrification/denitrification processes and preventing iron-bound sediment phosphorus from being released to the overlying water (Kufel & Kufel, 2002).

3. Many charophyte species are wintergreen and therefore possibly cause less oxygen-depletion in the lake during winter than annual submerged plants.

4. In contrast to many submerged angiosperms, charophytes rarely grow to the water surface in lakes deeper than 1 m and therefore hardly interfere with boating and swimming activities in the lake. (In very shallow lakes, however, charophytes can become a far more efficient obstacle to boating and swimming than most angiosperms.)

5. Many charophytes are heavily calcified. Therefore, in contrast to most submerged angiosperms, charophyte fragments sink to the lake bottom and do not bother swimmers.

Data on efficient long-term recolonisation of plankton-dominated shallow lakes with charophytes, however, are sparse. Lake Krangesjön (Sweden) shifted spontaneously from the turbid to the clear-water state during 1985–1987. *P. pectinatus* was the first submerged plant to expand, but was later replaced by dense vegetation of *C. tomentosa* as well as *C. rudis* and *C. hispida* covering about 50% of the lake area outside the reed belts (Blindow, 2002). In The Netherlands, Lake Veluwemeer and Lake Wolderwijd have been affected by eutrophication in the late 1960s and 1970s. In the 1990s, the vegetation changed following lake restoration measures. The dominance of *P. pectinatus* decreased, while charophyte meadows expanded over the same time interval. The pattern of change in macrophyte species composition was assumed to result from changes in the underwater light climate (Coops & Doef, 1996).

**Exotic species**

In Germany, aquatic non-native species did not yet receive a lot of attention (but see www.aquatiscineophyten.de), probably because they do not necessarily replace the native community, but can increase the local species diversity, as shown for *Azolla filiculoides*, *Lemma minuta*, *Myriophyllum aquaticum*, *Egeria densa* and *Vallisneria spiralis* that colonised River Erft (North Rhine-Westphalia) due to the influx of geothermically heated water (Hussner & Lösch, 2005). *E. canadensis* and *E. nuttallii* are among the 30 most important invasive species in Germany (www.floraweb.de/neoflora/handbuch.html), with *E. nuttallii* often replacing *E. canadensis* (Barat-Sergreain, 2004; Kummer & Jentsch, 1997; Vöge, 1995). Both species often become a nuisance (Table 2, see below). *E. nuttallii* rapidly spread to 4 km² within 1 year along the shores of the deep oligotrophic surface mining lake Goitsche (Saxony-Anhalt) (Rönice, Angelstein, Schultz, & Geller 2006). In a number of reservoirs of the river Ruhr, *E. nuttallii* developed extensively since 2000 and caused problems with uses for recreation, drinking water supply and hydropower (Podraza, unpubl. data). In Steinhuder Meer, *E. nuttallii* spread from 500 ha in 2001 to 1500 ha in 2002 (approximately 50% of the lake area) and disappeared completely in spring 2003 after overwintering under ice (Poltz, unpublished data). *Crassula helmsii*, invasive from Australia and New Zealand, developed dense stands in a few lakes in North Rhine-Westphalia and other northern federal states (Büscher, Raabe, & Wentz, 1990; Hussner, personal communication), but seems not to spread as rapidly as in England (Hussner, personal communication). In contrast, *Hydrocotyle ranunculoides* is expected to potentially spread rapidly to the western parts of Germany from initial stands reported in North Rhine-Westphalia in 2004 (Hussner & Van de Weyer, 2004; Hussner, Van de Weyer, & Wiehler, 2005). *Myriophyllum heterophyllum* was reported from a number of lakes in North Rhine-Westphalia and Lower Saxony and became a nuisance in some cases (Table 2; Hussner, Nienhaus, & Krause, 2005).

**Weeds**

Pyšek et al. (2004) suggest the term weeds (harmful species, problem plants, pests) for all species (not necessarily exotic) that interfere with human objectives. Although the problem might not be as severe as in tropical and subtropical regions, several, also native, aquatic macrophyte species have the potential to form dense stands in shallow eutrophic lakes in Germany that
reach the water surface and potentially become mechanical obstacles for boating and swimming (Table 2). Interestingly, a number of species that are problematic at some places are otherwise rated as rare and are classified in the Red Data Books of several federal states, like \textit{N. marina}, \textit{P. lucens} and \textit{Ceratophyllum submersum} (Korneck, Schnittler, & Vollmer, 1996). The macrophyte-based assessment of lakes for the implementation of the European Water Framework Directive in Germany ranks polymictic shallow lakes as moderate (class 3) when the percentage of \textit{C. demersum}, \textit{P. pectinatus} or \textit{E. nuttallii/E. canadensis} of the total lake area covered by submerged macrophytes is higher than 80\% (Schaumburg et al., 2004; Stelzer, Schneider, & Melzer, 2005). Regional differences, however, have to be taken into account. In southern Germany, \textit{C. demersum} mainly occurs at highly eutrophic sites whereas in Brandenburg this species is also abundant in mesotrophic lakes (Hoesch & Buhle, 1996).

### Table 2. List of some submerged macrophyte species involved in mass developments that interfered with the anthropogenic use of the lakes with examples (BB: Brandenburg, BA: Bavaria, BW: Baden-Wuerttemberg, LS: Lower Saxony, NRW: North Rhine-Westphalia, SN: Saxony, SA: Saxony-Anhalt)

<table>
<thead>
<tr>
<th>Species</th>
<th>Native</th>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>\textit{Ceratophyllum demersum}</td>
<td>X</td>
<td>Karsee, Lengenweiler See (both BW)</td>
</tr>
<tr>
<td>\textit{Ceratophyllum submersum}</td>
<td>X</td>
<td>Kersdorfer See (BB), Kleiner Nordfeldweiher (NRW)</td>
</tr>
<tr>
<td>\textit{Chara hispida}</td>
<td>X</td>
<td>Unterförhringer See (BA)</td>
</tr>
<tr>
<td>\textit{Crassula helmsii}</td>
<td></td>
<td>Fühlinger See (NRW)</td>
</tr>
<tr>
<td>\textit{Elodea nuttallii/E. canadensis}</td>
<td></td>
<td>Steinhuder Meer (LS), Ruhrstauseen (NRW), Rottuchspeicher (BA), Schwarzenberger Weiher (BA), Goitsche (SN, SA)</td>
</tr>
<tr>
<td>\textit{Hydrocotyle ranunculoides}</td>
<td></td>
<td>Numerous small lakes in NRW</td>
</tr>
<tr>
<td>\textit{Lagarosiphon major}</td>
<td></td>
<td>Schwanensee (BA)</td>
</tr>
<tr>
<td>\textit{Myriophyllum spicatum}</td>
<td>X</td>
<td>Knappensee (SA), Deisendorfer Weiher (BW)</td>
</tr>
<tr>
<td>\textit{M. heterophyllum}</td>
<td></td>
<td>Heider Bergsee, Schluftsee, Willenhofer Maarsee (all NRW)</td>
</tr>
<tr>
<td>\textit{Najas marina s.l.}</td>
<td>X</td>
<td>Neudendorfer See (BB)</td>
</tr>
<tr>
<td>\textit{Potamogeton pectinatus}</td>
<td>X</td>
<td>Großer Weserbogen (NRW)</td>
</tr>
<tr>
<td>\textit{P. perfoliatus}</td>
<td>X</td>
<td>Grünstensee (BA)</td>
</tr>
<tr>
<td>\textit{P. lucens}</td>
<td>X</td>
<td>Sachsenrieder Weiher (BA)</td>
</tr>
</tbody>
</table>

Management options for the development of desired species

If a desired species composition cannot be expected, e.g. due to the lack of a diverse seed bank, lack of viable charophyte oospores or the presence of invasive species, the question arises whether the growth of desired species can be promoted and controlled (Fig. 1). One of the few published examples is an attempt to shift a vegetation dominated by \textit{P. perfoliatus} to a \textit{C. aspera} dominance in Lake Veluwe in The Netherlands (Coops, Van Nes, Van den Berg, & Butijn, 2002). Using the model CHAR-ISMA (Van Nes, Scheffer, Van den Berg, & Coops, 2003), a mowing design with a mowing depth of 30 cm above the sediment rather late in the vegetation period has been developed. In Steinhoëringer Badeseen and Bachtelweiher (Bavaria), polyethylene covers to prevent growth of tall pondweeds and a subsequent introduction of charophyte species as plant material or with textile mats are applied to shift the present vegetation to charophyte dominance (Table 3). Smart, Dick and Doyle (1998) recommend planting of native species in new water bodies to prevent a dominance of exotic species which potentially have a faster colonisation rate. Although herbivores such as the macroinvertebrate \textit{Acentria} or rudd (\textit{Scardinius erythropthalmus}) and roach (\textit{Rutilus rutilus}) prefer certain macrophyte species over others and therefore may change the community composition within submerged macrophyte beds (Gross, Johnson, & Hairston, 2001; Prejs, 1984), their controlled use to change the species composition has not yet been reported, seems rather difficult and time and cost intensive.

Conflicts with lake users

The desired vegetation needs to be adjusted to the use of the lake. Dense beds of tall-growing submerged macrophytes can be a desired and suitable vegetation in shallow lakes, but become a nuisance when lakes are intensively used for boating, fishing or swimming. Information of the public regarding the positive role of submerged macrophytes in shallow lake ecosystems is a first step towards acceptance of the macrophyte development (Körner, 2002b). Still, the interests of recreational users will often conflict with nature conservation because an intermediate level of vegetation biomass with an optimal benefit both for the ecosystem
Table 3. Case studies of supported macrophyte colonisation in Germany (BA: Bavaria, NRW: North Rhine-Westphalia, S: Saxony, SH: Schleswig-Holstein, + successful establishment of introduced plants)

<table>
<thead>
<tr>
<th>Lake</th>
<th>Area (ha)</th>
<th>Depth for planting (m)</th>
<th>Submerged plants used</th>
<th>Measure</th>
<th>Problems</th>
<th>Success</th>
<th>Reference/contact</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reservoir Saidenbach (S)</td>
<td>142</td>
<td>&lt; 6</td>
<td><em>Elodea canadensis, Juncus bulbosus</em></td>
<td>Planting in baskets with and without substrate in combination with swimming textile islands and vertical Aufwuchs-carrier</td>
<td>+ Weise et al. (1992)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Retention-pool for Tävsmoor (SH)</td>
<td>0.37</td>
<td>1.5</td>
<td><em>Eleocharis acicularis, Myriophyllum spicatum</em>, <em>Potamogeton crispus</em>, <em>P. pectinatus</em>, <em>P. lucens</em>, <em>Ranunculus aquatilis</em>, <em>R. cicinatus</em>, <em>Utricularia minor</em>; <em>Ceratophyllum demersum</em>, <em>Myriophyllum spec.</em>; <em>E. canadensis</em></td>
<td><em>E. canadensis</em> mass development</td>
<td>+ Spieker (1996)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Riesenstein quarry (S)</td>
<td>1.77</td>
<td>&lt; 5</td>
<td><em>Chara intermedia</em></td>
<td>Planting in floating pots with clay, fixation with stones removing of organic substances, aeration of hypolimnion Polyethylene coverage to prevent growth of filamentous green algae, planting of Chara</td>
<td>High sedimentation rates covering plants, shading due to morphometry + enhanced visibility up to 5m, spawning activity of perch, pike, roach</td>
<td>+</td>
<td>Wiche (Tauchshop Meißen)</td>
</tr>
<tr>
<td>Stein-höhringer bathing lake (BA)</td>
<td>0.2</td>
<td>&gt;3</td>
<td><em>Chara intermedia</em></td>
<td>Stocking with carp, temporary high nutrient influx via groundwater</td>
<td></td>
<td></td>
<td>Hoesch (Aquarius, München)</td>
</tr>
<tr>
<td>Location</td>
<td>Surface Area</td>
<td>Depth</td>
<td>Treatment Details</td>
<td>Contact Information</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-------------------------------</td>
<td>--------------</td>
<td>-------</td>
<td>------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
<td>------------------------------------------------------------------------------------------------------------------------------------------------------</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bachtel-Weiher (BA)</td>
<td>5</td>
<td>1</td>
<td>Chara spp. (most. <em>fragilis</em>) plants on artificial textile mats and natural substrate following biomanipulation and coverage to prevent growth of tall pondweeds. Filamentous green algae, cyanophytes. Running project (2005).</td>
<td>Mählmann (STFI e.V., Chemnitz), Bohl, Mattukat, Morscheid (Bayer. LA für Umwelt, Wielenbach; Hoesch (Aquarius, München); Herrmann (Ökon, Mützdorf)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baarer gravel pit (BA)</td>
<td>25</td>
<td>2–4</td>
<td><em>C. contraria</em>, <em>Myriophyllum</em> spp. Initial planting with rottable mats by scuba plants fixed with nets and chalk stones upon substrate, following biomanipulation, <em>P. obtusifolius</em> plants, <em>P. alpinus</em> turions and <em>Polygonum amphibium</em> rhizoms were planted.</td>
<td>+ (2005) Rott (Büro für angewandte Ökologie—terre nouvelle), Gem Baar-Ebenhausen Fischereiverband, Hoesch (Aquarius, München) <a href="http://www.geo.uni-bayreuth.de/wasser-verbindet/projektzeitung5.pdf">www.geo.uni-bayreuth.de/wasser-verbindet/projektzeitung5.pdf</a></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Buchreuther Weiher (BA)</td>
<td>0.2</td>
<td>1.5</td>
<td><em>C. fragilis</em>. Six months polyethylene coverage to clear bottom of <em>Elodea</em> mass development. Running project (2005).</td>
<td>Hoesch (Aquarius, München)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4. Potential of selected, recommended submerged macrophytes species for successful use for artificial colonisation in eutrophic shallow lakes in Germany (S: seeds or comparable structure, F: foliage and stems, T: tubers or roots)

<table>
<thead>
<tr>
<th>Species</th>
<th>Potential propagation method</th>
<th>Susceptible to herbivory</th>
<th>Nuisance potential</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ceratophyllum demersum</td>
<td>F</td>
<td>–</td>
<td>Intermediate</td>
<td>C. contraria and C. vulgaris prefer calcium-rich lakes</td>
</tr>
<tr>
<td>Chara contraria, C. globularis (syn. C. fragilis), C. vulgaris, Nitella muconata</td>
<td>S, F</td>
<td>+/-</td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>Eleocharis acicularis</td>
<td>F</td>
<td>–</td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>Myriophyllum spicatum, M. verticillatum</td>
<td>F</td>
<td>–</td>
<td>High</td>
<td></td>
</tr>
<tr>
<td>Najas marina s.l.</td>
<td>S</td>
<td>–</td>
<td>High</td>
<td>two subspecies, do not occur in all federal states</td>
</tr>
<tr>
<td>Potamogeton alpinus P. berchtoldii, P. crispus, P. friesii, P. obtusifolius, P. pusillus, P. pectinatus, P. perfoliatus</td>
<td>F, T</td>
<td>+</td>
<td>Intermediate</td>
<td></td>
</tr>
<tr>
<td>Ranunculus subg. Batrachium</td>
<td>F</td>
<td>–</td>
<td>Intermediate</td>
<td>Ranunculus trichophyllus only in alkaline lakes</td>
</tr>
<tr>
<td>Zannichellia palustris ssp. palustris</td>
<td>S</td>
<td>+</td>
<td>Intermediate</td>
<td></td>
</tr>
</tbody>
</table>

Data are based on Kadlec & Wentz (1974), Smart & Dick (1999), Cooke, Welch, Peterson, and Nichols (2005) and our own judgement. The choice of species suitable for planting or seeding in a certain lake includes knowledge about the lake type (alkaline, dystrophic, softwater), the former vegetation of the lake, species typically occurring in that type of water and in the region, the potential uses of the lake, the suitability of the chosen species for transplanting/seeding, habitat preferences of the chosen species and the potential origin/source of the plants/seeds.

and users may often not be feasible in shallow lakes (Van Nes et al., 2002; Van Nes et al., 1999). This conflict might be solved with trials to shift the vegetation to low-growing Chara species that do not reach the water surface (see ‘Methods for artificial support of macrophyte development’ and ‘Development of desired surface (see ‘Methods for artificial support of macrophyte development’) or a harvesting management of the tall-growing vegetation.

Management options of biomass/coverage

If the lake ecosystem has alternative stable states, harvesting (or other management options like biological control) becomes risky because the vegetation may collapse entirely below a certain, presently and practically unknown, biomass (Van Nes et al., 2002). The use of carp or grass carp often results in a complete loss of submerged macrophytes, like in Herrenwieser Weiher, Bavaria (Morscheid, Mattukat, & Kucklentz, 2005), and is therefore not recommended. In some federal states, the use of grass carp is generally forbidden (Nature Protection Acts of Berlin, Brandenburg, Lower Saxony, North Rhine-Westphalia, Thuringia), but often this species is still introduced to remove macrophytes. At present, any biological control method using herbivorous vertebrates or invertebrates seems inapplicable in shallow lakes due to the risk of overexploitation and switch back to the turbid, phytoplankton-dominated state (Fig. 1). The use of herbicides is not allowed in Germany. Although labour- and cost-intensive, mechanical mowing or harvesting seems the only measure allowing a controlled elimination of part of the macrophyte biomass. Cutting only, without collection of plant fragments, should not be considered. Harvesting removes biomass which otherwise will release nutrients at senescence, and will contribute to an oxygen depletion that may stimulate further nutrient release from reduced sediments (Cooke et al., 2005). In Harkortsee (140 ha, North Rhine-Westphalia) a harvesting boat cleared 15 ha in 4 weeks. Costs for 4–5 people working 10 hours a day summed up to 130,000 Euro, which is approximately 115 Euro per ton fresh weight. The local authority Wasserwirtschaftsamt Kempten (Bavaria) estimated costs of mowing at 650–1000 Euro per day including a mowing boat and two people. In Rottachspeicher (Bavaria), a 35 m deep reservoir (300 ha), yearly costs for mowing E. canadensis/E. muttillii summed up to 19,000–25,000 Euro. In Grünensee (130 ha, Bavaria) P. perfoliatus was mowed at yearly costs of 3500–5500 Euro. Mowing will only be a short-time relief since most nuisance species spread by vegetative fragmentation and loose fragments easily settle at new places and rapidly regain high biomass (Abernethy, Sabbatini, & Murphy, 1996). Harvesting might also remove herbivorous macroinvertebrates living at the apical shoots of submerged plants (Sheldon & O’Bryan, 1996). Remaining stands should still cover 50% of the lake (see ‘Size of lake area potentially covered by submerged macrophytes’), but further detailed studies are needed to investigate the coverage needed to stabilise clear-water conditions. Populations of E. canadensis and E. muttallii were often reported to collapse naturally, the possibility of such an event,
however, is unwarranted as a “do-nothing” approach sensu Simberloff & Gibbons (2004).

Conclusions

The choice of an appropriate internal lake restoration measure should include an assessment of its potential effects on the development of submerged macrophytes to prevent failure of the restoration due to a lack of macrophyte recolonisation or mass development. Further research is needed to elucidate the effects of a number of common restoration measures on the development of submerged macrophytes.

Using the step-by-step guideline, an assessment of potential chances and the degree of the development of submerged macrophytes in degraded, turbid shallow lakes after an increase of the light availability is possible. However, due to the complex nature of factors determining the occurrence, distribution and biomass development of submerged macrophytes, predictions are still limited.

As the re-establishment of submerged macrophytes is essential for the long-term success of a restoration in shallow lakes, measures for their support in case of a hampered natural re-establishment and management measures in case of mass developments should be planned in advance of any restoration effort. Low growing species, such as many Chara species, are the desired vegetation for lakes with extensive recreational use. Experience with measures to arrive at such a sustainable vegetation, however, are limited and further research is needed to find management solutions for shallow lakes where mass developments of submerged macrophytes result in conflicts with lake users. In future, the number of lakes with problematic macrophyte mass developments may increase in Germany as the reduction of external nutrient loads may finally result in improved conditions for macrophyte growth even in lakes without additional internal measures.

Acknowledgements

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References


