MINIREVIEW

THE ROLE OF CHARACEAN ALGAE IN THE MANAGEMENT OF EUTROPHIC SHALLOW LAKES[1]

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Characeae (charophytes or stoneworts) are anatomically highly developed green algae. The family is divided into two tribes, the Chareae and Nitelleae, which together contain six genera and about 200 species worldwide (Moore 1986). They grow mainly in alkaline freshwater lakes and ponds. The algae are fixed to the sediment by rhizoids, and several species tend to cover the sediment in dense mats, which often are referred to as meadows.

Eutrophication has led to a decline in the charophyte vegetation in many lakes. Over the past decade, numerous restoration projects have been carried out to reduce the negative effects of eutrophication. The main purpose of such projects in shallow lakes has been to change the state of turbid water with dominance by phytoplankton into an alternative stable state with clear water and dominance by macrophytes, including charophytes (Scheffer et al. 1993, Moss et al. 1996). Biomanipulation, mostly comprising a temporary strong reduction of the fish stock, may help to induce the switch to clear water, but a fast return of macrophytes seems crucial for the stabilization of the clear water state (Meijer et al. 1994). Charophytes often play an important role in such projects because they are notoriously rapid colonizers (Crawford 1977, Simons et al. 1994, Beltman and Allegrini 1997). Furthermore, dominance by charophytes can be of special value in recreational waters because the plants normally do not reach the water surface. Such meadows cause less nuisance to swimmers or boats than stands of canopy-forming angiosperms.

This minireview presents some ecological aspects of charophytes and their implications for management of shallow lakes. The first section presents the

history of Lake Veluwemeer (The Netherlands), where the charophyte vegetation disappeared coincident with cultural eutrophication but became dominant again after restoration. The second section considers the main factors that regulate charophyte abundance. The third section describes the effects that charophytes can have on the ecosystem. The last section discusses the stability of charophyte vegetation and the role of charophytes in restoration projects.

LAKE VELUWEMEER: A CASE STUDY

Veluwemeer (surface area ~3300 ha; 1.4 m mean depth) is an artificially isolated part of a large body of water in the center of the Netherlands, called Lake IJsselmeer. In 1952, construction of dams started in the southeastern part of the IJsselmeer around areas that were subsequently turned into polders by pumping out the water. Veluwemeer belongs to a chain of lakes that was left between the newly formed polders and the former shoreline of IJsselmeer.

Over the years, changes in nutrient loading have caused pronounced shifts in the submerged vegetation of Lake Veluwemeer (Coops and Doef 1996, Hosper 1997). In its early years, the lake was known for its clear water and its diverse macrophyte vegetation, including extensive meadows of charophytes. After about 10 years, however, the lake became progressively eutrophied by the discharge of waste water from small cities located along the lake, and the charophyte vegetation declined. By 1969 the average transparency (measured as Secchi depth) had declined to <0.4 m, and the charophyte vegetation had almost completely disappeared (Fig. 1). In the following years the Secchi depth in summer was only 0.25 m due to blooms of cyanobacteria and resuspension of sediments. The only submerged vegetation in the lake consisted of sparse stands of *Potamogeton pectinatus*. In 1979 measures were taken to reduce the external phosphorus load. Inflowing wastewater was treated and the lake itself was flushed with water from the polders, whose water was low in P and rich in carbonate. As a result, the average total P concentration decreased from 0.4 to
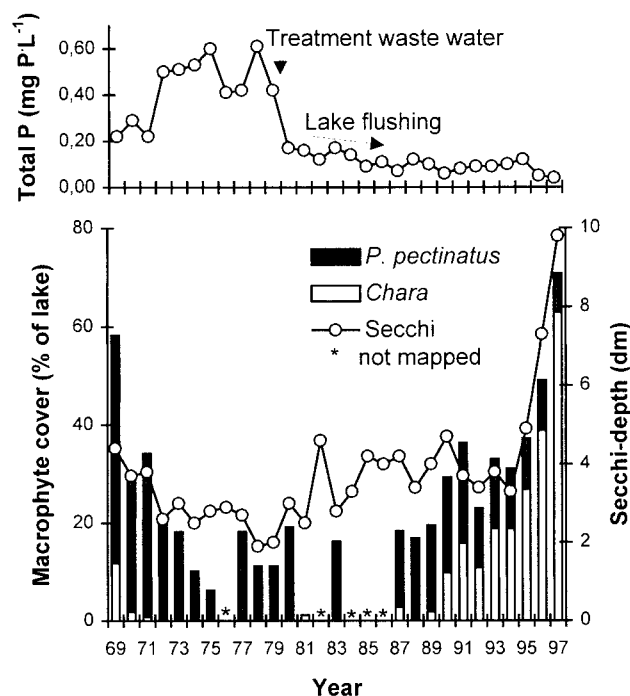
FIG. 1. Cover of *P. pectinatus* and *Chara* over the past 30 years in Lake Veluwemeer in relation to total phosphorus concentration and Secchi depth. Three periods can be distinguished: a tail of the decline of Charophytes in response to increasing eutrophication in the late 1960s, a hypereutrophic period during the 1970s when charophytes were absent, and a period of return in the 1980s after reduction of the phosphorus concentration. Macrophyte cover was estimated from aerial photographs and checked with observations in the field. From 1987 onward, detailed field maps of the charophyte vegetation are available. P data are mean summer values (Noordhuis, unpubl.).
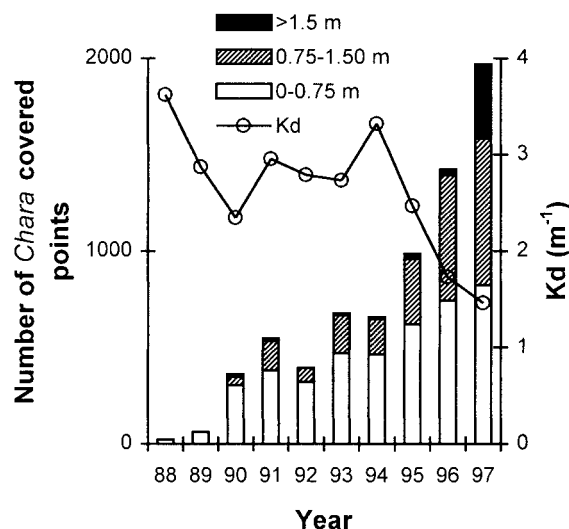

FIG. 2. Depth distribution of *Chara* and the summer average of light attenuation coefficient in Lake Veluwemeer over a period of 10 years. The number of points covered with *Chara* was calculated using a GIS application with grid data of depth (about 4000 sampled points in 1997) and *Chara* cover (about 3000 sample points each year) as input.

0.15 mg·L^{-1}, but the average Secchi depth increased only to 0.45 m. Nonetheless, this moderate increase in transparency probably triggered an increase in the cover of *P. pectinatus* and the return of charophytes. Charophytes reappeared from 1985 onward as Secchi depth increased to >0.4 m. Initially the stands had a variable area and covered only shallow depths (<0.75 m), but after 1990, charophytes expanded steadily with a colonized area of two-thirds of the lake in 1997 and a colonized depth of up to 2.5 m (Fig. 2). During the first years of recolonization, the water over the charophyte meadows became clear in summer (K_d of about 0.8·m^{-1}), which contrasted strongly with the rather high turbidity in the rest of the lake (K_d of about 4·m^{-1}; Van den Berg et al. 1998a). Year by year the water became clearer with average K_d values of about 1.5·m^{-1} in 1997 outside the vegetation. The cover of *P. pectinatus* has decreased, and this formerly abundant species has even disappeared completely at sites with dense charophyte meadows. *Chara aspera* now is dominant with *Chara contraria* and *Nitellopsis obtusa* as accompanying species. The angiosperms *Potamogeton pectinatus, Potamogeton perfoliatus,* and *Myriophyllum spicatum* are widely distributed in the lake,

but their abundance is much lower than that of the charophytes.

FACTORS THAT REGULATE CHAROPHYTE ABUNDANCE

Nutrients. It has long been recognized that charophytes are found particularly in lakes with low inorganic P concentrations (Forsberg 1964, Forsberg et al. 1990, Simons and Nat 1996), and studies have shown that nutrient enrichment of lakes can lead to a decline of charophytes (John et al. 1981, Ozimek and Kowalczewski 1984, Best 1987, Simons et al. 1994). The reason for this apparent negative effect of high nutrient concentrations is uncertain. Early experimental work in the laboratory showed that the addition of 6 μg·L^{-1} PO_4^{-3}–P to the medium was toxic for *Chara hispida* (Forsberg 1964), but recent experiments have not confirmed these findings for other species (Blindow 1988, Simons et al. 1994). Additions of as much as 10 mg·L^{-1} NH_4^+ or NO_3^- have been shown to stimulate a length increase of *Chara* spp., although additions of concentrations higher than 10 mg·L^{-1} of NH_4^+ reduced a length increase (Simons et al. 1994).

The indirect effects of eutrophication on charophytes are probably more important than the direct effects of high nutrient concentrations. As argued in the next section, one of the major problems for charophytes in eutrophic lakes may be light limitation due to an increased growth of phytoplankton and periphyton at high nutrient concentrations.

Turbidity and water depth. The zonation of submerged macrophytes along the water depth gradient is a well-described phenomenon. Because irradiance diminishes with water depth (Kirk 1983), it seems obvious that light is a major determinant of

this zonation (Hutchinson 1975, Spence 1982). However, there are several other factors (e.g. water pressure, substrate, wave action, and temperature) that systematically vary with water depth, which implies that the light level may be only part of the explanation (Spence 1982). At the shallow end of the depth gradient, mechanical damage caused by waves is certainly an important factor in large lakes (Spence 1982, Kautsky 1987, Van Wijk 1988, Scheffer et al. 1994a). Such mechanical disturbance also is thought to affect the occurrence of tall charophytes. Large species (with shoot diameters >1 mm) occur only at sites deeper than 1 m, whereas small charophytes occur also at shallow sites (Blindow 1992a). The absence of cellulose fibers in charophytes (Fox et al. 1994) may reduce the plant's ability to remain intact under mechanical stress (Blindow 1992a).

The role of light limitation in controlling distribution of charophytes is supported by many observations. High turbidity has been implicated as the dominant factor in the decline of charophytes in shallow lakes (Ozimek and Kowalczewski 1984, Hough et al. 1989, Blindow 1992a, Simons et al. 1994, Steinman et al. 1997). In deep lakes too, the biomass and maximum colonized depth of charophytes decline when transparency diminishes (Schwarz et al. 1996, Schwarz and Hawes 1997). In eutrophic systems, a thick epiphyton layer composed of microalgae and other components may further reduce the light reaching macrophytes (Philips et al. 1978, Van Dijk and Van Vierssen 1991). Although charophytes may release growth-inhibiting substances (see next section) they seem to be just as vulnerable to periphytic overgrowth as other plants (Blindow 1987).

Charophytes differ markedly from angiosperms in their response to turbidity. In clear lakes, charophytes often are found at deeper sites than angiosperms. The better ability of charophytes to cope with low light levels is a reasonable explanation for this zonation (Chambers and Kalff 1985, Blindow 1991). The light compensation point for photosynthesis of charophytes ranges from 1 to 7 $\mu mol \cdot m^{-2} \cdot s^{-1}$, which is generally below the lowest values of 8–30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ reported for angiosperms (Van et al. 1976, Andrews et al. 1984, Schwarz et al. 1996, Van den Berg, unpubl.).

In view of this shade tolerance, it is remarkable that the depth limit in turbid water inhabited by charophytes is shallower than that of angiosperms (Fig. 3) (Blindow 1992a, Middleboe and Markager 1997). The difference in growth form is the most likely explanation for this pattern. Charophytes concentrate most of their biomass close to the sediment surface, whereas in sufficiently shallow water, various angiosperms can form canopies just under the water surface, which allows them to ''escape'' from low irradiance caused by turbidity (Scheffer 1998). This pattern is consistent with the shifts in dominant
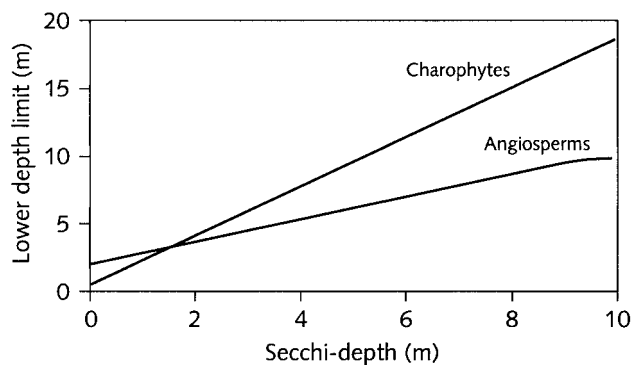

FIG. 3. Schematic relationship between Secchi depth and maximum depth distribution of charophytes and angiosperms (from Blindow 1991).

growth forms that were observed in Lake Veluwemeer. Charophytes disappeared from the lake in the very turbid period, whereas the canopy-forming *P. pectinatus* remained. With increasing transparency, charophytes became dominant again. Similar shifts between *P. pectinatus* and *Chara* spp. have been reported for Swedish lakes (Blindow 1992b).

Although a difference in growth form may explain the fact that canopy-forming angiosperms such as *P. pectinatus* can outcompete charophytes in turbid shallow water, it is not fully understood why charophytes can displace *P. pectinatus* in such shallow systems when turbidity is reduced. Indeed a competition experiment between *Potamogeton pectinatus* and *Chara aspera* under ample light and carbon conditions showed that the biomass of *C. aspera* was reduced by adding *P. pectinatus* plants (Van den Berg et al. 1998b), probably because the canopy of *P. pectinatus* reduced the amount of light reaching the charophytes. Preliminary results of investigations on the use of carbon resources have shown that *C. aspera* may be a better competitor for HCO_3^- than *P. pectinatus*. The former has a much higher growth rate than *P. pectinatus* at a low carbon supply of about 0.5 mM $HCO_3^- \cdot L^{-1}$ (Van den Berg, unpubl.). The efficient use of carbon at low concentrations seems relevant under field conditions because inside *Chara* meadows, strong reductions of the bicarbonate concentration from 2.5 to even less than 0.5 mM HCO_3^- have been observed (Van den Berg et al. 1998a).

Bird grazing and propagule banks. Several enclosure experiments in lakes have shown that the biomass of submerged macrophytes can be reduced due to grazing by water birds (Lauridsen et al. 1994, Van Donk et al. 1994, Schutten et al. 1996, Perrow et al. 1997), but this happens especially in fall and winter when bird concentrations can become very high (Kiorboe 1980). This pattern is also found in Lake Veluwemeer where the charophyte biomass outside bird exclosures is reduced by overwintering waterfowl (Van den Berg, unpubl.). Because most grazing occurs after the end of the growing season, con-

sumption of the above-ground parts may have little effect on the persistence of vegetation. However, the overwintering reproductive propagules (e.g. tubers) also can be exploited heavily by herbivorous birds (Van Wijk 1988). Charophytes such as *Chara aspera* that produce bulbils for overwintering may be subject to such bird exploitation, as illustrated by observations in Lake Veluwemeer (Van den Berg, unpubl.). Although bird grazing may not be of sufficient intensity to eliminate vegetation, it may delay the colonization of lakes by macrophytes after an improvement of water quality (Lauridsen et al. 1994, Meijer et al. 1994, Scheffer 1998).

A lack of seeds and other diaspores is another possible explanation for the observed slow colonization by macrophytes in such restored lakes. In Lake Veluwemeer, for instance, it has taken several years for the charophytes to cover the extensive areas that are colonized today (Fig. 2). Observations of the spatial distribution of oospores and bulbils suggest that the limited dispersion of these diaspores is a major factor limiting the colonization process (Van den Berg, unpubl.). Other studies have shown that charophytes colonize rapidly in new ponds and lakes (Crawford 1977, Crawford 1979, Wade 1990, Simons et al. 1994, Beltman and Allegrini 1997), but most authors suggest that stored diaspores in the sediment may have been a precondition for such a fast colonization. It is not really clear how well charophyte diaspores can be dispersed.

IMPLICATIONS OF CHAROPHYTE DOMINANCE

Transparency. Many studies have shown that macrophytes tend to enhance water transparency (see Scheffer [1998] for an overview). Charophyte meadows in particular have a strong positive effect on water transparency (Crawford 1979), which is even manifested as locally clear spots with sharp borders between clear and turbid (Scheffer et al. 1994b, Van den Berg et al. 1998a). In this section, we argue that it may be the restriction of resuspension and stimulation of sedimentation that explains the strong effect of *Chara* meadows on transparency. Mechanisms such as increased top-down control of phytoplankton and uptake of nutrients may be important as well.

Resuspension of sediment particles by waves contributes strongly to the turbidity of many shallow lakes (Bengtson and Hellstrom 1992, Blom et al. 1994). The presence of macrophytes reduces such resuspension (James and Barko 1990, Petticrew and Kalff 1992). This effect is especially strong in the case of charophytes because these plants often develop a high biomass on the lake bottom, by which the resuspension is reduced and sedimentation is stimulated (Crawford 1979, Scheffer 1998). Transect measurements along a vegetation gradient in Veluwemeer show that the maximum resuspension rate inside charophyte meadows is about two orders of magnitude lower than at adjacent sites without any vegetation (Van den Berg et al. 1998a). In contrast, seasonal measurements inside *Potamogeton* stands showed no strong effect on suspended matter concentration compared to sites without vegetation, suggesting less effect on reduction of resuspension (Van den Berg, unpubl.).

Besides the reduction of the resuspension rate, the sedimentation probably increased due to reduction of the effective mixing depth. The concentration of suspended heavy particles (larger than 30 μm) decreased much more strongly than that of less heavy particles (smaller than 5 μm diameter) along an increasing *Chara* vegetation gradient. Also, the phytoplankton composition changed into dominance by motile algae, such as *Cryptomonas* sp. and *Rhodomomas* sp., that can escape from sedimentation. In addition, large phytoplankton cells (except for cyanobacteria) disappeared inside the *Chara* meadow (Van den Berg et al. 1998b). Other factors, such as nutrient uptake, increased zooplankton grazing, and release of allelopathic substances, may explain the strong effect of charophytes on transparency as well. *Chara* may reduce the phytoplankton biomass by taking up nutrients like NO_3^--N, PO_4^{-3}–P, CO_2, and HCO_3^- from the water (Kufel and Ozimek 1994, Van den Berg et al. 1998a). In addition, the density of zooplankton (Pereyra-Ramos 1981, Blindow 1991) and the grazing pressure by zooplankton on phytoplankton (Van den Berg et al. 1998a) are higher inside dense *Chara* than outside the vegetation. Also the release of allelopathic substances by *Chara* has been shown to reduce the growth of phytoplankton (Anthoni et al. 1980, Wium-Andersen et al. 1982, Blindow 1991). Laboratory experiments, however, show that extracts of charophytes are not more toxic than extracts of other macrophytes (Jasser 1995). In fact, the overall effect of allelopathic substances by macrophytes in keeping the water clear is still speculative since no convincing field studies have yet been carried out (Forsberg et al. 1990).

Fauna community. Macrophytes have pronounced effects on the composition of fish, bird, and invertebrate communities in shallow lakes (Scheffer 1998). In this section, we argue that charophytes are very important for the animal community relative to other macrophytes. The early disappearance of charophytes in response to eutrophication may have negative consequences for the biodiversity of the ecosystem.

With respect to fish, specific information about the role of charophytes is sparse, but results from Lake Veluwemeer indicate that the charophyte meadows are dominated by spined loach (*Cobitis taenia*) and ten-spined stickleback (*Pungitius pungitius*). The fish community outside the vegetation is characterized by roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) (Lammens, unpubl.).

Macrophytes are known to be a major factor de-

termining the abundance and composition of the macroinvertebrate community (e.g. Gilinsky 1984, Cyr and Downing 1988, Diehl 1988, Kornijów 1989). In view of their dense cover and high biomass, charophytes can be expected to be an especially suitable habitat for macroinvertebrates. Indeed, in a Swedish lake the biomass of macroinvertebrates was found to be much higher in dense *Chara* vegetation than in parts covered by stands of *Potamogeton pectinatus* and in unvegetated parts (Hargeby et al. 1994). Similar results have been found for other lakes (Hanson 1990, Van den Berg et al. 1997). The dense *Chara* vegetation may diminish the risk of predation (Hanson 1990) or may provide epiphyton scrapers with more food (Underwood et al. 1992). Gastropods, gammarids and some chironomid species are abundant in dense *Chara* meadows.

Macrophyte-dominated shallow lakes may be very important feeding areas for water birds during fall migration or wintering (e.g. Fox et al. 1994, Hanson and Butler 1994). The charophytes may be of special importance for wintering birds since their above-ground biomass tends to stay available longer in winter than that of angiosperms (Pereyra-Ramos 1981, Nichols and Schloesser 1986). Furthermore, charophytes may be easier to digest than angiosperms because of their lower fiber content (Fox et al. 1994).

Several observations indicate that charophytes may be a major food source for herbivorous birds. Numbers of coots (*Fulica atra*) and mute swans (*Cygnus olor*) are positively correlated with the presence of charophytes in lakes (Hargeby et al. 1994). Also, observations in Lake Veluwemeer on the foraging activity of coots, mute swans, and a number of other species indicate that the herbivorous birds spend most of the time at areas covered by *Chara*. Analysis of the feces of coot and mute swan confirms that charophytes are a main food source. Red crested pochard (*Netta rufina*) also is reported to have charophytes in its diet (Allouche et al. 1988).

THE STABILITY OF CHAROPHYTE VEGETATION AND MANAGEMENT IMPLICATIONS

Charophytes can be viewed as a ruderal group relative to other macrophytes because of their reproductive characteristics such as high investment in small propagules. Some species are particularly found in ephemeral or disturbed habitats where they are present for short periods of time (Brock and Casanova 1991, Grillas et al. 1993, Bonis et al. 1995). Also, in newly created water bodies charophytes are among the first colonizers and are rapidly replaced by other macrophytes (Crawford 1979), sometimes even within 1 year (Portielje 1994). Some charophytes, such as *Tolypella* spp., have a very short life cycle and are able to survive in temporal ponds (Hutchinson 1975). However, the charophyte vegetation is certainly stable in other lakes. Charophytes are present for over 30 years in lakes (Wood 1950),

and as described earlier, charophytes may also replace angiosperms when conditions change.

Various studies consider the idea that lakes may have two alternative stable states: one with clear water and dominance by macrophytes and one with turbid water and dominance of phytoplankton (Hosper 1989, Scheffer et al. 1993). It is hypothesized that each state is stable as the result of several mechanisms. An important mechanism in stabilizing the macrophyte-dominated state may be the effect of vegetation on turbidity (Scheffer et al. 1993, Scheffer 1998). A detailed explanation is beyond the scope of this review, but in short, the idea is that by reducing turbidity, macrophytes improve the conditions for their own growth, thereby stabilizing their dominance. As a result, they may persist for a long time in lakes that are becoming progressively eutrophic. However, when they disappear, their absence allows a sharp increase in turbidity, and under such turbid conditions recolonization is difficult. This implies that recolonization after eutrophication control is expected at much lower nutrient levels than the critical level for disappearance.

As mentioned earlier, charophytes can have an especially strong effect on turbidity. Therefore, one would expect to observe alternative stable states in lakes where charophytes are the dominant vegetation. Indeed, a markedly discontinuous response of charophytes to the P concentration is found in Lake Veluwemeer. During eutrophication the charophytes disappeared at the same Secchi depth as they returned after de-eutrophication, suggesting that Secchi depth was critical for occurrence. However, in the period of decline of charophytes, the P concentration was near 0.3 mg $P \cdot L^{-1}$ compared to 0.1 mg $P \cdot L^{-1}$ during their return in the 1980s after P reduction (Fig. 1). Although the interpretation of such time series has many caveats (Scheffer 1998), these observations suggest that charophyte vegetation can indeed be a self-stabilizing alternative state.

The rich animal community and high water transparency that often are associated with charophyte dominance in shallow lakes may make *Chara*-dominated lakes desirable from a management perspective. The question of how a charophyte-dominated state can be achieved by specific management measures is still far from resolved. Nonetheless, some general patterns emerge from the studies summarized in this review. Long-term dominance by charophytes occurs in large shallow lakes, but only when nutrient loading is low. Nutrient reduction is the first precondition to induce the recovery of lakes that have lost their charophytes, and a temporary reduction of the fish stock may help to trigger the switch to charophyte dominance. In The Netherlands, about 50% of 22 lake restorations switched to the clear-water state (Meijer, unpubl.). In six of the nine cases where the course of the macrophyte cover and species composition is known, charophytes played an important role. Colonization by charo-

phytes occurs particularly in lakes with a former abundant *Chara* cover. Introduction of propagules also may stimulate charophyte colonization, but so far, there is no experience with large-scale application of this approach.

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