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Submerged vegetation development in two shallow, eutrophic lakes

Hugo Coops & Roel W. Doef
Institute for Inland Water Management and Waste Water Treatment (RIZA), P.O. Box 17, 8200 AA Lelystad, The Netherlands

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Abstract

Submerged macrophyte vegetation in two shallow lakes in the Netherlands, Lake Veluwemeer and Lake Wolderwijd, has been affected by eutrophication in the late 1960's and 1970's. Recent changes in the vegetation occurred in the period following lake restoration measures. Between 1987 and 1993, the dominance of *Potamogeton pectinatus* decreased, while Charophyte 'meadows' expanded over the same time interval. The pattern of change of the dominant macrophyte species might result from changes in the underwater light climate. Seasonally persistent clear water patches associated with the *Chara* meadows have been observed in the last few years. The interaction between submerged macrophyte vegetation succession and water transparency in the lakes is discussed.

Introduction

Submerged macrophyte vegetation plays a central role in the functioning of shallow lake ecosystems. Lake restoration measures (e.g., biomanipulation) often aim at recovery of macrophytes as a provision for phytoplankton grazers and piscivorous fish (Hosper, 1989; Moss, 1990). Furthermore, the role of submerged vegetation in lake nutrient dynamics is often stressed (Carpenter & Lodge, 1986). An increase of submerged vegetation may occur after improvement of the underwater light climate (Scheffer et al., 1993), but extensive studies documenting decline and recovery of macrophytes are scarce, because long-term monitoring results are hardly ever available. To evaluate vegetation recovery patterns, more should be known about fluctuations of the plant populations present among and within years.

In Lake Veluwemeer and Lake Wolderwijd, two shallow lakes bordering the Flevo Polders in the Netherlands, eutrophication has affected the submerged vegetation seriously since the late 1960's. Scattered patches of aquatic plants (mainly *Potamogeton pectinatus* L. and *P. perfoliatus* L.) occurred in the resulting turbid water. 'Meadows' of Charophytes, once an important component of the vegetation, disappeared in the late 1960's.

In order to assess the impact of lake restoration measures this paper describes changes in the submerged vegetation of both lakes, prior to and following nutrient reduction (Lake Veluwemeer) and fish removal (Lake Wolderwijd).

Description of the lakes

After disconnection from the sea in 1932, the formerly brackish Zuiderzee estuary in the Netherlands formed Lake IJsselmeer. Freshwater macrophytes (mostly *P. pectinatus*, *P. perfoliatus*, and Characeae) established in the late 1930's and 1940's, following salinity reduction. Lake Veluwemeer (3400 ha) and Lake Wolderwijd (2700 ha) were formed as marginal lakes after embankment of part of Lake IJsselmeer (the so-called Flevo Polders), in 1957 and 1969, respectively. Both lakes are shallow (mean depth ~ 1.5 m) and have been eutrophic since their origin. The water is in the range pH 8–9 and the sediments are predominantly sand and loam. Chloride content in Lake Veluwemeer is 150–200 mg Cl l^{-1} (due to flushing with relatively saline seepage water from the Flevo Polders), and in Lake Wolderwijd 80–150 mg Cl l^{-1}.

Originally, Lake Veluwemeer water was very clear and supported a dense mat of Characeae, while from 1965 onwards other macrophytes (*Potamogeton* spp. and *Myriophyllum spicatum* L.) gradually developed; an increase of turbidity and decrease of macrophytes occurred in the early 1970's. Lake Wolderwijd has been dominated by the blue-green alga *Oscillatoria agardhii* Gomont. since its origin, resulting in a sparse macrophyte vegetation (Berger, 1987). In Lake Veluwemeer, flushing with relatively phosphate-poor, chloride-rich seepage water from the Flevo Polders started in 1979 (Hosper & Meijer, 1986). There was a more or less immediate and marked reduction in total phosphorus from a mean of c. 0.4 mg l^{-1} to c. 0.1 mg l^{-1} which has been sustained ever since. Lake Wolderwijd was subject to a drastic reduction of the fish stock in the winter of 1991, aimed to promote zooplankton grazing and decrease the resuspension of sediments by benthivorous fish (Meijer et al., 1994).

Methods

Macrophytes have been monitored in Lake Wolderwijd and Lake Veluwemeer between 1987 and 1993. Each summer (July), the distributions of aquatic plant species were mapped. Species composition and cover were determined in quadrats located in a grid pattern over the lakes. Area estimates were made in GIS after preparing maps by interpolating gridpoints, following the procedure of Scheffer et al. (1992). The data were added to a previously constructed time series of the vegetation, which was reported in Scheffer et al. (1994).

The biomass of *P. pectinatus* was determined at a site in Lake Wolderwijd (52°20′N 5°35′E) during the vegetation periods of 1991, 1992 and 1993. At the site, eight to sixteen 40 ×40 cm quadrats were harvested at 2- to 3-weekly intervals. Aboveground parts, roots and tubers were separated before determination of ash free dry weight (AFDW) (48 hr at 550 °C).

Results and discussion

Vegetation development

Species composition of submerged vegetation in both lakes stayed relatively constant between 1987 and 1993, except Charophytes (principally *C. contraria* A. Braun ex Kützing and *C. aspera* Deth. ex Willd.) appeared for the first time in Lake Wolderwijd. Both lakes supported relatively abundant *P. pectinatus* and *P. perfoliatus*, with smaller quantities of *P. pusillus* L., *P. crispus* L., *Zannichellia palustris* L. and *Elodea nuttallii* (Planchon) St. John. Remarkable differences between the two lakes were the total absence from Lake Wolderwijd of *Myriophyllum spicatum* and *Alisma gramineum* Lej., which occurred abundantly in Lake Veluwemeer.

The areas occupied by the three dominant taxa, viz. *P. pectinatus*, *P. perfoliatus*, and *Chara* sp., between 1970 and 1993 are shown in Figure 1. The dynamics of the vegetation may be related to a variety of environmental factors, of which water depth and turbidity seem to be of major importance (Scheffer et al., 1992). In contrast to *P. pectinatus*, *P. perfoliatus* and Charophytes showed a strong reduction in Lake Veluwemeer in the early 1970's. Differences in response between the species may be explained by different growth forms, enabling plants to cope with reduced underwater light conditions to a variable degree. Plants with an erect architecture show less irradiance-controlled growth than bottom-dwelling species (Chambers & Kalff, 1987). *P. pectinatus* may tolerate increased turbidity by rapid shoot growth towards the water surface in spring, facilitated by carbohydrate reserves in buried tubers. The leaves form a canopy just below the water surface, thereby exploiting limited light resources efficiently (Van Wijk, 1988). *P. perfoliatus* has a much more pillar-like growth form, which potentially is less efficient in turbid water and is more prone to self shading. Furthermore, such a growth form is more susceptible to mechanical damage through water movement. Development of Characeae, which form dense mats of vegetation just above the soil surface, might strongly depend on high light availability as well as sufficiently high temperatures in spring and summer. Consequently, *Chara* spp. generally inhabited a shallower zone (30–75 cm deep) than *P. perfoliatus* (60–150 cm deep).

The seasonal cycle of *P. pectinatus* has a short duration in the lakes (Figure 2). The overwintering tuber biomass is a determinant of shoot emergence in the next year; its decrease during the winter period could be due to grazing. Several, probably interacting factors might cause the short duration of shoot growth: luxuriant epiphytic growth, high turbulence, as well as grazing by herbivorous birds (Van Wijk, 1988). A general decrease in above-ground biomass was evident between 1991–93, consistent with the increasing *Chara* cover. The area occupied by *Chara* meadows increased markedly after 1988 in Lake Veluwemeer

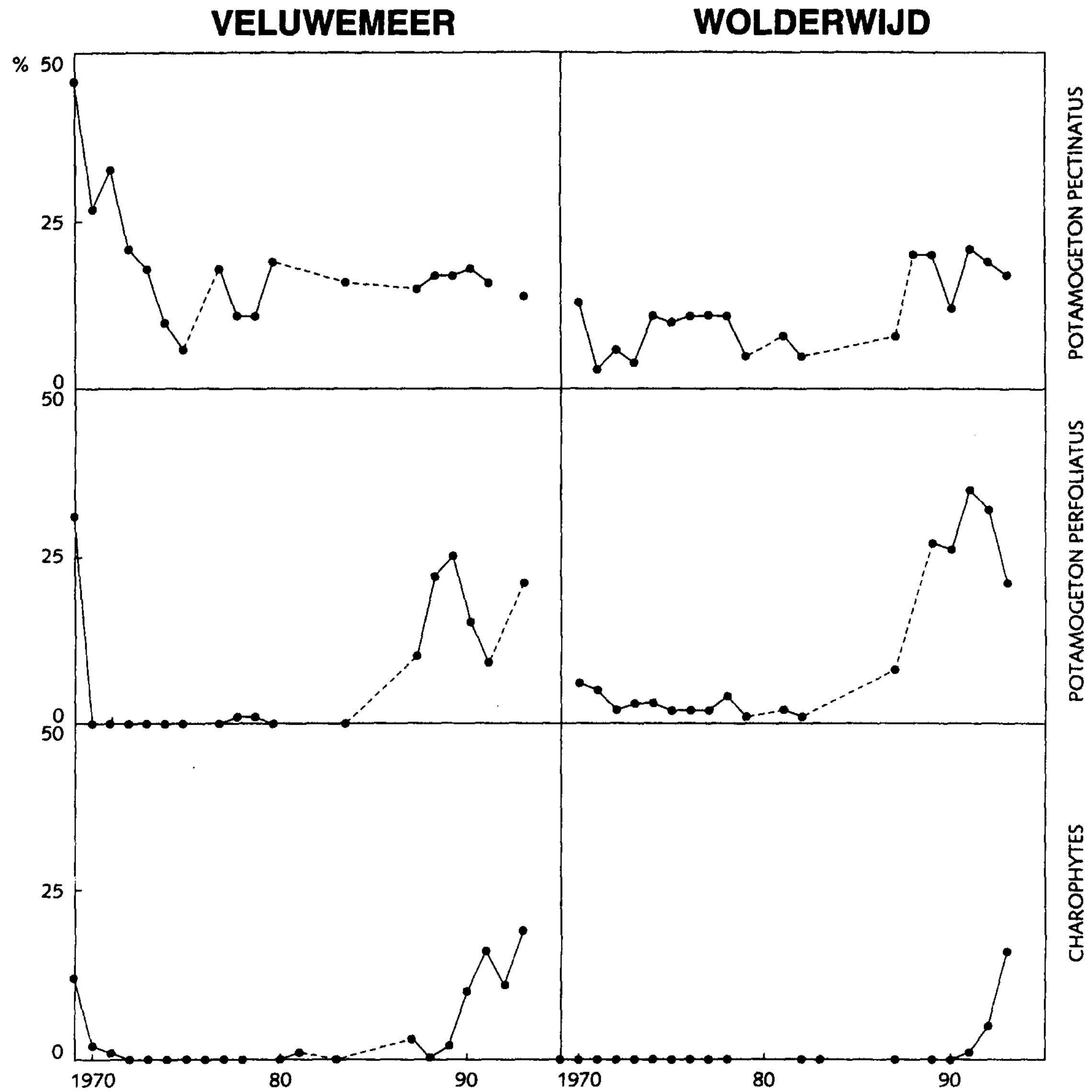

Figure 1. Presence (% of area) of *Potamogeton pectinatus*, *P. perfoliatus*, and *Chara* spp. in Lake Veluwemeer and Lake Wolderwijd between 1969 and 1993.

and after 1990 in Lake Wolderwijd. The recent colonization from 1990 onwards is demonstrated in Figure 3.

Management of the lakes

The recent increase of *P. perfoliatus*, and subsequently of *Chara* sp. indicates a gradual improvement of the water quality in both lakes from about 1985 onwards. Changed light conditions might cause competitive displacement of *P. pectinatus* by Charophytes, starting in the shallowest areas where light conditions are best (McCreary, 1991). Rapid spring growth of Charophytes may pre-empt the seasonal development of *P. pectinatus*.

Turbidity was reduced in the spring following biomanipulation in Lake Wolderwijd (Meijer et al., 1994). It is not clear, however, whether this triggered the simultaneous increase of Charophytes, since the first observations of Charophytes were made in 1990,

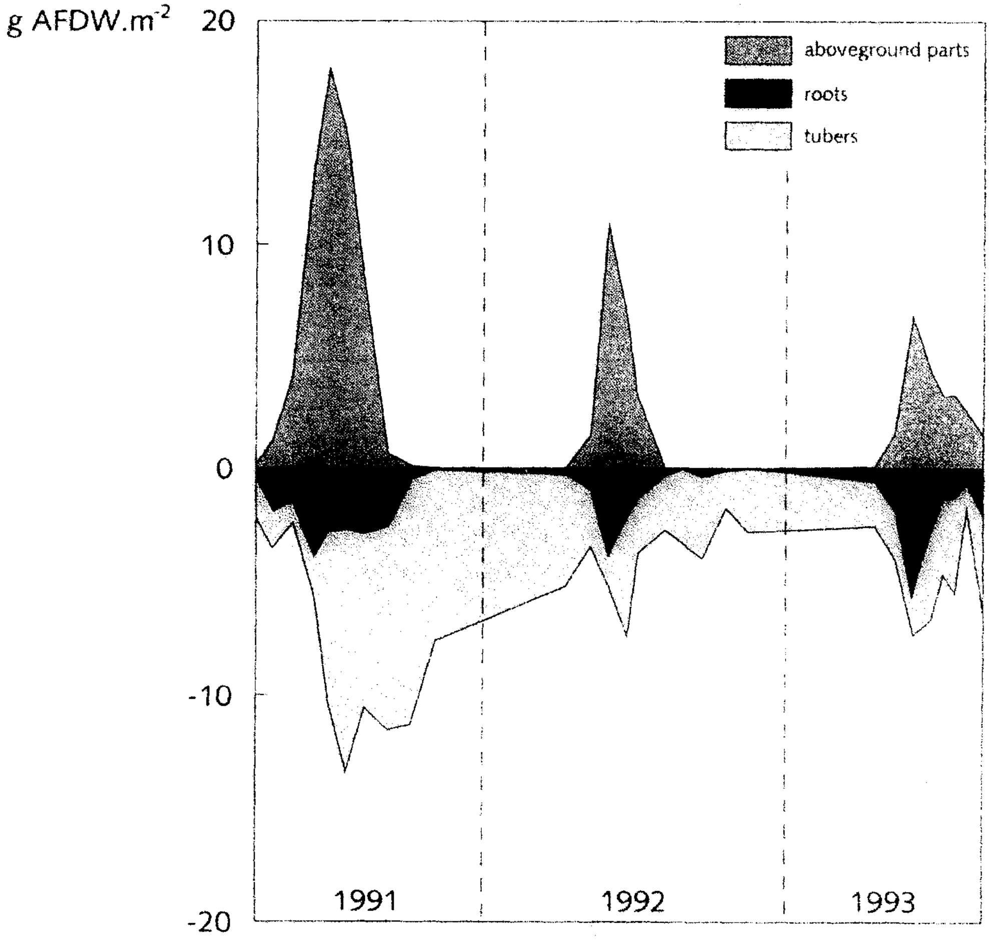

Figure 2. Biomass development and allocation between aboveground parts, roots and tubers of *Potamogeton pectinatus*, harvested from a site in Lake Wolderwijd in 1991, 1992 and 1993.

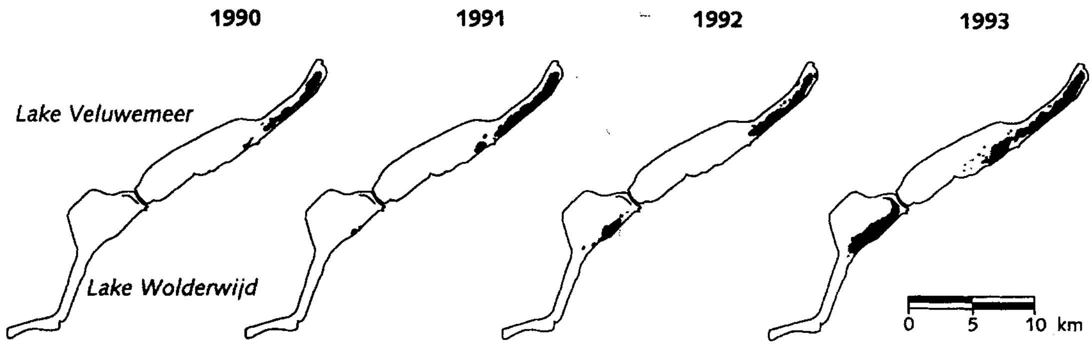

Figure 3. Pattern of distribution of *Chara*-dominated vegetation in Lake Veluwemeer and Lake Wolderwijd between 1990 and 1993.

before the biomanipulation started. Shallow, eutrophic lake ecosystems may potentially exist in one of two alternative states (Scheffer et al., 1992, Blindow et al., 1993): a clear, macrophyte-rich state characterized by cladocerans and predatory fish; and a turbid, phytoplankton-dominated state with benthivorous fish. Shifts from one state to the other due to management interference have been reported (Moss, 1990).

Vegetation has a large influence on ecosystem processes because of the effects of macrophytes on the physico-chemical environment and biota (Carpenter & Lodge, 1986). The coverage of the sediment surface may minimalize resuspension (James & Barko, 1990) Observations in both lakes during 1992 and 1993 of clear water patches above areas with dense Charophyte cover offer a demonstration of this. Imported suspended material may be trapped at the margins of the dense vegetation. Resuspension of sedimentated phytoplankton also might be prevented.

Phytoplankton growth around dense vegetation might also be limited by other mechanisms. Competition for nutrients may occur due to uptake from the water column. Charophytes may fixate relatively large amounts of P during the growing season (Blindow, 1992). However, as they take up nutrients from both water column and soil, no quantitative conclusion regarding their role in nutrient dynamics can be drawn at present. The excretion by Characeae of allelopathic substances that inhibit algal growth is often referred to (Hootsmans & Vermaat, 1991). However, any impact of allelopathy on water transparency in quite large wind-mixed lakes is unproven. Last but not least, dense Charophyte mats may act as a refugium for grazers (cladocerans, molluscs), which might be able to suppress both planktonic and epiphytic algal growth.

It seems likely that the mass emergence of *Chara* in the spring could dictate the appearance of clear water patches in summer. Once vegetation is established, clear water might be maintained, owing to the above mentioned mechanisms. However, their impact and relative importance require further study. The pathway of restoration of aquatic vegetation may involve more than one stage of succession (Figure 4). The colonization of deeper water by Charophytes might occur in interaction with the expansion of clear water patches over some years. Hence a clear lake might appear patchwise, interacting with the development of dense *Chara*-meadows. The influence of herbivorous birds, hydraulic and climatic fluctuations, edaphic factors, and nutrients in the water layer on the stability and future development of the 'partially clear state' of the lakes remains uncertain.

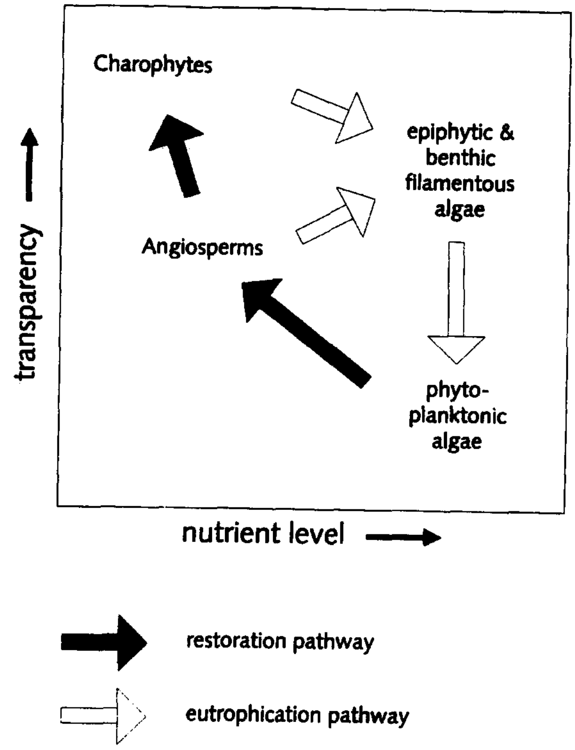

Figure 4. Schematic model of the pathways of submersed vegetation succession and regression in relation to water transparency and nutrient loading of the lakes. Starting from a phytoplankton-dominated system, lowering of the nutrient level and/or increasing water transparency results in the successive dominance of angiosperms and Charophytes. Eutrophication leads to a situation with poor macrophyte growth via enhancement of algal growth.

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