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Recovery of *Potamogeton pectinatus* L. stands in a shallow eutrophic lake under extreme grazing pressure

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Abstract

In shallow lakes, submerged macrophytes contribute to the stabilization of the clear water state. If lost, a number of mechanisms prevent re-colonization. Lake Müggelsee (730 ha) lost its submerged vegetation due to increasing eutrophication and switched to phytoplankton dominance in 1970. After the reduction of nutrient loading in 1990, *Potamogeton pectinatus* L. started re-colonizing the lake. During the following years, it spread at a mean rate of 2.5 ha per year to all available areas <80 cm depth. Between 1993 and 1999, decreasing maximum biomass indicated hampered growth. Exclosure experiments revealed that herbivory reduced the aboveground biomass by more than 90%. Both waterfowl and fish were found to contribute to the grazing pressure despite a low abundance of the known herbivorous fish species and waterfowl in spring and summer. Protection of stands against grazing resulted in higher biomass of shoots, whereas shoot and tuber density did not change. Both shading by phytoplankton and periphyton, as well as grazing pressure, prevented the submerged vegetation of Lake Müggelsee from developing back to a dense zone that contributed to the reduction of turbidity.

Introduction

Eutrophication due to anthropogenic impacts caused a decline of submerged vegetation in many shallow, north temperate lakes (e.g. Körner, 2002). This reduction is mainly explained by the shading effects by phytoplankton and epiphyton (Phillips et al., 1978). Besides turbidity and sediment re-suspension, it has been proposed that grazing by herbivorous birds hampers the re-colonization after reductions of external nutrient loads and/or biomanipulation (e.g. Lauridsen et al., 1993; Søndergaard et al., 1996). Perrow et al. (1997), however, state that there is little evidence in the literature to support this hypothesis and Van Donk et al. (1994) and Mitchell & Wass (1996) could not find a significant effect of waterfowl grazing on the (re-) establishment of submerged plants. Other investigations do suggest an impact of fish, usually rudd (*Scardinius erythrophthalmus*) on macrophyte growth (Prejs, 1984; Van Donk et al., 1994). Several authors proposed that grazing might be critical for macrophyte development in lakes at the nutrient threshold where both a clearwater and a turbid state may occur (Søndergaard et al., 1996) and when light or other conditions for macrophyte growth are marginal (Mitchell & Wass, 1996).

In the following study the re-establishment of *Potamogeton pectinatus* L. stands in a eutrophic shallow lake was investigated a decade after starting the reduction of external nutrient loads. Conditions were appropriate for macrophyte growth, but nutrient concentrations around

0.1 mg P l^{-1} still caused summer cyanobacteria blooms (Körner, 2001) and high periphyton biomass (Roberts et al., 2003). It was hypothesised that the impact of grazing on the development of submerged plant stands might be crucial during this stage of recovery.

Description of sites studied

Lake Müggelsee is a eutrophic, shallow lake in Berlin (Germany) with an area of 7.3 km^2 and a mean depth of 4.9 m (description in Driescher et al., 1993). At the beginning of the 20th century, a diverse submerged vegetation covered one third of the lake. At least 20 species occurred in the lake, with *Potamogetonaceae* dominating the shallower areas and *Fontinalis antipyretica* forming a belt in the deeper regions. Increasing eutrophication lead to the total disappearance of submerged plants around 1970 and a switch to phytoplankton dominance (Körner, 2001). *P. pectinatus* probably did survive in small stands during the 1970s and 80s. Since 1990, external nutrient loads have been reduced, resulting in a spring clearwater phase and re-appearance of submerged macrophytes, mainly *P. pectinatus* (Körner, 2001). Between 1999 and 2001 nutrient (total phosphorus: 112 ± 16 (standard error) $\mu g\ l^{-1}$, NH_4^+–N: 0.12 ± 0.02 mg l^{-1}, NO_3^-–N: 0.29 ± 0.08 mg l^{-1}) and chlorophyll concentrations (27 ± 4 $\mu g\ l^{-1}$) and Secchi depths (April–June: 2.3 ± 0.3 m, July/August: 1.2 ± 0.1 m) did not change significantly.

Material and methods

The submerged vegetation of Lake Müggelsee was mapped and biomass determined in 1993 (Awe & Körner, unpublished), 1999 and 2000 (for methods see Körner, 2001). The development of selected *P. pectinatus* stands has been followed during the vegetation period of 1999 and 2000 at the wind-exposed northern (N) and sheltered western (W) shore in 0.5 m water depth. Effective fetch for the prevailing wind directions W/SW of the exposed and sheltered site was 0.43/1.44 km and 0/0 km, respectively. Biomass of *P. pectinatus* was harvested at monthly intervals using a tube corer (0.181 m^2, four replicates). Aboveground shoots, tubers, roots and rhizomes were dried separately at 60 °C until weight constancy.

In order to determine the influence of herbivorous birds and fish on *P. pectinatus* growth, two sets of exclosure cages with 2 cm mesh size were placed at 0.5 m water depths at the N and W shore in the lake in April 2001. One set of cages (four at each location) was fully closed to protect macrophytes against all birds and fish above 2 cm body width ($1 \times 1 \times 0.5$ m), whereas the other was open for 25 cm above the sediment to allow fish to enter ($1 \times 1 \times 0.25$ m). Biomass in the cages and the unprotected surrounding was harvested in June (one sample per cage, four samples at randomly selected unprotected locations) and dry weight, length and number of aboveground shoots, rhizomes and tubers were recorded. Means were compared separately for the exposed and sheltered site using a one-way analysis of variance (ANOVA) ($p < 0.05$) and a subsequent multiple comparison using Tukey's test (SPSS). Exponential rates of net plant aboveground biomass increase (d^{-1}) were calculated for the interval 23rd of March (biomass approximately 1 g dw m^{-2}) until the harvesting as $(\ln dw_2 - \ln dw_1)/t$, where dw_2 and dw_1 are the final and initial mean biomass and t is time (days). Grazing rates of fish and birds were calculated from the differences between growth rates of differently protected stands. Herbivorous water birds were counted between May 2000 and May 2001 every 2–4 weeks.

Results

The area colonized with submerged macrophytes in Lake Müggelsee increased between 1993 and 1999 from 6 ha to 22 ha (Fig. 1), resulting in an average colonization rate of 2.5 ha per year. Total area covered, maximum and average colonization depth (1.5 m and 0.8 m, respectively) and colonization density did not change from 1999 to 2000. *P. pectinatus* was the dominating species, covering 99% of the colonized area. It germinated from tubers at the end of March and became senescent in August. Plants did not reach the water surface and did not flower. Maximum biomass at the sheltered W shore was significantly higher than at the exposed N shore (Fig. 1). Values declined between 1993 and 1999 at the N shore and between

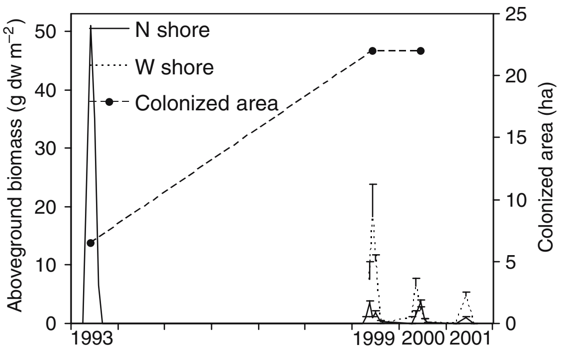

Figure 1. Development of aboveground biomass (+ standard error) of *P. pectinatus* in 0.5 m water depth at the wind-exposed northern (N) from 1993 to 2001 and at the sheltered western (W) shore from 1999 to 2001 and colonized area in Lake Müggelsee.

1999 and 2001 at the W shore (Fig. 1). Tubers germinated in April and above-ground shoots disappeared in August. Average maximum shoot length (June, 1999–2001) was significantly lower at the exposed shore (5.0 ± 0.1 cm) compared to the sheltered shore (8.0 ± 0.3 cm). Shoot densities (730 ± 220 at N and 1350 ± 320 at W) did not differ significantly between shores. Sheltered stands had significantly more tubers compared to the exposed stands at the beginning (333 ± 76/28 ± 13) as well as at the end of the growing season (157 ± 23/21 ± 10, data from 2000). Significantly less tubers at the end of the growing season compared to the beginning were found at the exposed shore in 1999 (401 ± 99/3 ± 2). The maximum aboveground biomass of the stands was independent of the tuber bank size (Fig. 2). Mean individual tuber weight was significantly higher at the sheltered shore at the end of the growing season in 2000 (7.2 ± 0.5/0.8 ± 0.6).

Protection of *P. pectinatus* stands against herbivory from fish and waterfowl resulted in significantly higher biomass and longer shoots compared to the unprotected stands at both shores (Fig. 3). Shoot biomass of stands in cages protected against bird herbivory only (half closed) resulted in an intermediate biomass at the sheltered stand, but was not significantly different from the unprotected stand at the exposed shore. Shoot length differed significantly between differently protected stands with longest plants in the fully closed cages, intermediate in the half closed and lowest in the unprotected stands. A significant reduction of the rhizome biomass in unprotected stands was only found at the exposed site, whereas a reduction of the total tuber biomass could only be found at the sheltered site. Grazing by birds and fish did not reduce shoot and tuber densities and individual tuber weight (Fig. 3).

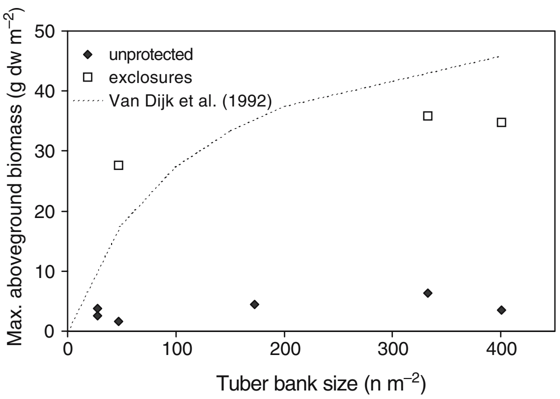

Figure 2. Data pairs of mean maximum aboveground biomass of unprotected stands and stands in exclosures and mean size of tuber bank of *P. pectinatus* in Lake Müggelsee in 1999 and 2000. The dotted line shows the relationship derived for *P. pectinatus* in Lake Veluwe in 1987 by Van Dijk et al. (1992).

Potentially herbivorous birds present were swans (*Cygnus olor*), coots (*Fulica atra*), mallards (*Anas platyrhynchos*), tufted ducks (*Aythia fuligula*), pochards (*Aythia farina*) and goldeneyes (*Bucephala clangula*). Coot numbers increased from about 1 coot ha^{-1} from May to July to 6 coots ha^{-1} in December. Numbers of diving ducks increased from 0.06 ha^{-1} in summer to 0.85 ha^{-1} in winter. Total numbers of swans varied between 0.01 and 0.04 ha^{-1}, with more swans at the W compared to the N shore.

Discussion

In Lake Müggelsee, *P. pectinatus* spread rapidly between 1993 and 1999 to all available areas shallower than 80 cm depth. Re-colonization occurred probably from remaining stands by vegetative propagation as plants do not flower and extensive seed-baring stands are lacking upstream (unpublished). Although nutrient concentrations and therefore shading by phytoplankton and periphyton did not increase, maximum biomass declined between 1993 and 2001. Only a few studies report such low values for *P. pectinatus*, whereas shoot

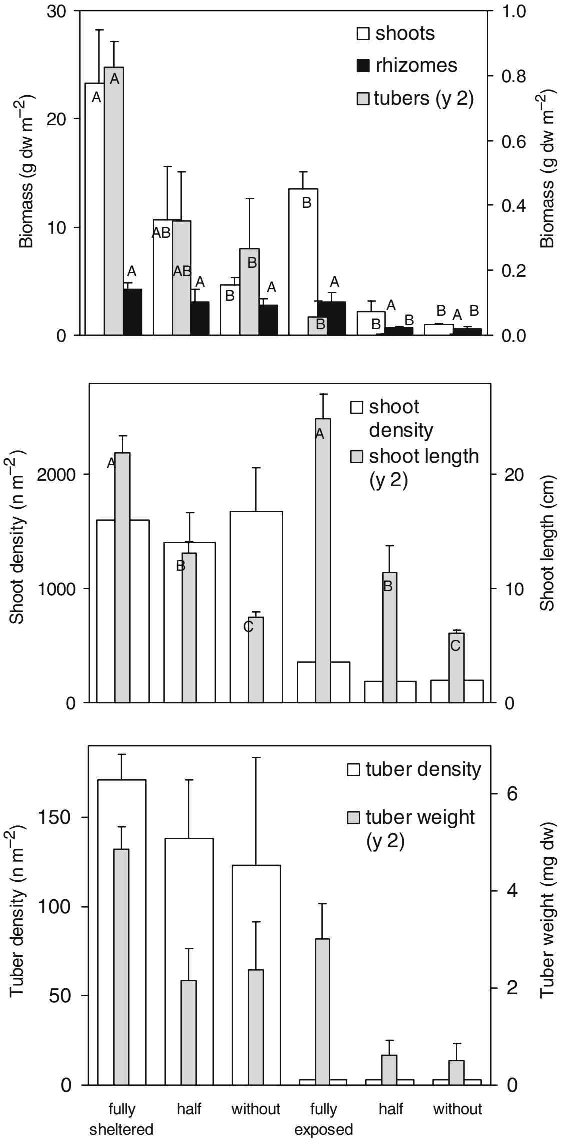

Figure 3. Biomass (+ standard error) of shoots, rhizomes and tubers, shoot density and length, and tuber density and weight of *P. pectinatus* stands in 0.5 m water depth at the sheltered western (W) shore and the wind-exposed northern shore in Lake Müggelsee in June 2001. Stands were protected against herbivory from birds and fish (fully), birds only (half) or not protected (without). Different letters indicate significant differences at $p < 0.05$ (one-way ANOVA with subsequent multiple comparison test (Tukey)). Shoot and tuber density and tuber weight were not significantly different.

densities were high (e.g. Ozimek et al., 1986). Due to the low shoot length *P. pectinatus* did not reach the water surface and could therefore not escape turbid conditions during cyanobacteria blooms in July and August. Growth of stands at the exposed and sheltered site probably differed due to differences in wave stress (Ozimek et al., 1986) and/or grazing pressure, as the contents of organic matter in the sediment were comparable (unpublished) and periphyton densities were not significantly different (Roberts et al., 2003).

Contrary to the findings of Van Donk et al. (1994), macrophyte consumption by vertebrate grazers did negatively affect the recovery of submerged macrophytes in Lake Müggelsee, as protection resulted in significantly higher biomass. Exclosure experiments revealed that fish have a higher impact than waterfowl although the known herbivorous fish species like rudd (*S. erythrophthalmus*) or carp (*Cyprinus carpio*) were not abundant in the lake. Plants were obviously not totally pulled out of the sediment as e.g. by grass carp (Prejs, 1984), as shoot densities were not reduced. An impact of young roach (*Rutilus rutilus*) was suggested from studies using underwater videos (Körner & Dugdale, 2003). Surprisingly, tuber density and individual tuber weight were also not significantly reduced, although tuber production is positively correlated to the aboveground biomass (Van Dijk et al., 1992; Figure 2). Tuber densities at the end of the vegetation period in August were, however, lower than at the beginning in some cases in the unprotected stands.

The net growth rate of fully protected *P. pectinatus* in 2001 was significantly higher at the sheltered (0.070 d^{-1}) compared to the exposed shore (0.051 d^{-1}). Both were lower than the optimum growth rate reported by Nielsen & Sand-Jensen (1991) (25% or 46%, respectively). Still, protected stands reached the water surface and contrary to Mitchell & Wass (1996) it is therefore concluded that grazing pressure has a high impact on the re-establishment of submerged vegetation even if growth conditions are appropriate. Fish grazing rates were higher at the exposed shore (0.046 d^{-1}) and comprised 92% of total grazing compared to the sheltered shore (0.027 d^{-1}), where bird grazing rates of 0.012 d^{-1} contributed 30% to total grazing. The bird grazing rates were higher than those reported by Mitchell & Wass (1996) for black swan at densities of up to 25 ha^{-1}. The calculated grazing rates probably overestimate the ingested material as plant growth is supposed to be slower with grazing.

It was concluded that the impact of grazing on the development of *P. pectinatus* in shallow lakes can be crucial when conditions for macrophyte growth are only appropriate in shallow areas due to summer cyanobacteria blooms and periphyton growth. Grazing probably hampers the growth of *P. pectinatus* resulting in high calculated grazing rates of fish and birds despite low abundances of waterfowl and the apparent absence of herbivorous fish.

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