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SHALLOW LAKES

Potential for the development of submerged macrophytes in eutrophicated shallow peaty lakes after restoration measures

R. J. W. van de Hateerd · G. N. J. Ter Heerdt

Abstract Biomanipulation of eutropicated peaty lakes has rarely been successful; clear water with dense macrophyte stands fails to develop in most cases. It was unclear whether (1) high turbidity due to resuspension by benthivorous fish or wind is the major cause of low macrophyte density or whether (2) the establishment of submerged macrophyte stands is prevented by a lack of propagules, low cohesive strength of the lake sediment, high concentrations of phytotoxics, grazing by waterfowl and/or shading by periphyton growth. These hypotheses were tested in an experiment in a shallow peat lake in the Netherlands (Terra Nova). Removal of fish from a 0.5 ha experimental site resulted in clear water and the development of a dense (90% coverage) and species-rich (10 species) submerged vegetation. At a fish-stocked site and a control site the water remained turbid and dense macrophyte stands did not develop. The establishment of submerged macrophytes appeared not to be limited by a lack of propagules. Introduced plants grew poorly in turbid water, but very well in clear water. Exclosures showed that bird grazing reduced the plant biomass. In clear water grazing seemed to enhance the vegetation diversity. Periphyton development did not prevent plant growth in clear water. After the experiment, the fish stock was greatly reduced in the whole lake (85 ha), to test if (3) in a large lake, submerged macrophyte stands will not develop after biomanipulation. In the first season after fish reduction, transparency increased and species-rich submerged macrophyte stands developed, covering 60% of the shallow parts of the lake. Most of the species known to have occurred in the past re-established. The results indicate that high turbidity caused by benthivorous fish in combination with bird grazing were the major causes of the absence of submerged macrophyte stands in this lake. Abiotic conditions after the clearing of the lake were suitable for the growth of macrophytes. We infer that the restoration potential of submerged macrophyte stands in eutrophicated peaty lakes can be high, and results can be obtained quickly.

Keywords Shallow peaty lake · Restoration · Biomanipulation · Macrophytes · Herbivory · Periphyton

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Shallow lakes in a changing world

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Introduction

Many of the freshwater lakes in the Netherlands originate from peat digging and are very shallow (<2 m). Once the water was oligotrophic and clear, but during the 20th century external nitrogen (N) and phosphorus (P) loading caused eutrophication. At first, this resulted in increased macrophyte growth and increased biodiversity. Since the 1950s, cyanobacterial blooms have resulted in high turbidity, poor underwater light climate and loss of submerged vegetation in most lakes. Restoration measures have been employed to reduce the external loading, but the clear water and macrophyte-dominated state generally did not return. For the history of the eutrophication and restoration of shallow lakes, see Van Liere & Gulati (1992), Scheffer (1998) and Gulati & van Donk (2002).

One of the reasons why nutrient reduction does not result in the return of a clear water state is the presence of large numbers of planktivorous and benthivorous fish. Planktivorous fish prevent zooplankton from becoming abundant and grazing down phytoplankton blooms. Benthivorous fish stir up the sediment, resuspending large amounts of detritus. A drastic reduction of fish stocks, a form of biomanipulation or biological control, often results in a shift from a turbid state towards one with clear water (Jeppesen et al., 1997; Scheffer, 1998; Gulati & van Donk, 2002). However, unlike results obtained in lakes with mineral sediment, biomanipulation in peaty lakes in the Netherlands has rarely been successful (Van Liere & Gulati, 1992; Meijer et al., 1999; Gulati & Van Donk, 2002).

The failure of restoration measures might be caused by poor colonisation of the lake sediment by submerged macrophytes (Hansson et al., 1998; Körner, 2002). Macrophytes are able to absorb large quantities of nutrients, thereby suppressing algal blooms, and they stabilise the sediment surface, reducing resuspension of detritus. Macrophytes also function as a refuge for zooplankton and are the habitat of predatory fish (Scheffer, 1998; Hansson et al., 1998; Gulati & Van Donk, 2002). A sustainable clear water situation requires the development of a dense submerged macrophyte cover (Jeppesen et al., 1997; Scheffer, 1998; Gulati & Van Donk, 2002). The process of colonisation by submerged macrophytes can be hampered by factors like a lack of propagules, shading by abundant periphyton growth, insufficient light conditions in deeper water and grazing by waterfowl (Jeppesen et al., 1997; Hansson et al., 1998; Scheffer, 1998; Van Donk & Otte, 1996). In peaty lakes, the development of submerged macrophytes may also be limited by high turbidity, due to resuspension of sediment by wind and wave action (Meijer et al., 1999), low cohesive strength of the lake sediment in combination with wave action (Schutten & Davy, 2000; Schutten et al., 2005) or high concentrations of phytotoxics such as sulphide (Smolders & Roelofs, 1993; Lamers et al., 1998). Hence, biomanipulation in peaty lakes may be less successful than in lakes with a mineral sediment. Meijer et al. (1999) showed that biomanipulation results for peaty lakes were indeed less favourable than those for other lakes, but did not clarify whether this was caused by insufficient fish removal or by the factors and conditions mentioned above.

Waternet is the water quality manager of many shallow peaty lakes in the region south of Amsterdam and restoration projects are going on or planned for several of these turbid lakes to restore the clear-water and macrophyte-dominated state. Before starting drastic and expensive measures, we wanted to make sure that macrophytes would be able to colonise peaty lakes rapidly. As part of a large-scale biomanipulation experiment, we started a pilot study of the colonisation by submerged macrophytes in two small (0.5 ha) and shallow (0.7 m) experimental sites. In this part of the experiment we tested the following hypotheses:

(1) High turbidity is the major cause of low macrophyte density.
(2) The establishment of submerged macrophyte stands is prevented by a lack of propagules, low cohesive strength of the lake sediment, high concentrations of phytotoxics, grazing by waterfowl and/or shading by periphyton growth.

Even if the colonisation by macrophytes is not inhibited in the enclosed sites, it would still not be certain that biomanipulation would work in larger peaty lakes, where waves and poorer light conditions due to greater depth (1.75 m) might prevent macrophyte establishment. Therefore we also performed a whole-lake biomanipulation experiment in an 85 ha lake, testing the following hypothesis:

(3) In a larger lake, submerged macrophyte stands will not develop after biomanipulation.

Materials and methods

Study area

This study was performed at Lake Terra Nova, also called Lake West Loenderveen (LWL). Lake Terra Nova is an 85 ha shallow peaty lake in the centre of the Netherlands, originating from peat excavation and subsequent erosion, and forming part of the Loosdrecht lake system (Hofstra & Van Liere, 1992). In 1941, more than 50% of the lake bottom was covered by submerged macrophytes, dominated by Characeae. Water transparency was 2–2.5 m Secchi depth (Leentvaar & Mörzer Bruijns, 1962; Best et al., 1984). Between 1941 and 1980, several observations indicated that species-rich macrophyte stands were present in Lake Terra Nova. In 1980–1982, dense stands of Characeae, *Elodea* sp., *Najas marina* and *Potamogeton* spp. were found, totalling 26 submerged macrophyte species (Table 1, Best et al., 1984). Secchi depth in summer was 1.2–1.9 m. Between 1977 and 1983, the average total phosphorus content in summer gradually increased from 0.04 to 0.08 mg/l, and remained around that level since.

Blooms of cyanobacteria appeared in 1987 (Dekker et al., 1992), while transparency decreased to 0.4 m Secchi depth from that date onwards. In 1994, a quick scan revealed very sparse growth of *Ceratophyllum demersum*, *Potamogeton lucens*, *Potamogeton obtusifolius*, *Potamogeton pectinatus*, *Myriophyllum spicatum* and some specimens of *Stratiotes aloides*. In 2003, we found only a very few specimens of *C. demersum*, *Elodea nuttallii*, *P. obtusifolius* and *Chara globularis*. *Nymphaea alba* and *Nuphar lutea* fields were present in shallow parts of Lake Terra Nova.

Experimental setup

Two experimental sites of 0.5 ha each were constructed by building dams between parallel banks in the western part of Lake Terra Nova (Fig. 1). Behind these dams, waves were greatly reduced, and water exchange and fish migration were no longer possible. Water depth at these sites ranged between 30 and 90 cm. The bottom was covered with a 0.9 m organic mud layer. At both sites, we greatly reduced the fish stock, using fykes, seine nets, gill nets and electro fishery. Petersen's mark and recapture method was used to estimate the fish population before and after fishing (Klinge et al., 2003). Fishing was repeated until the stock was below 25 kg fresh weight (FW) of benthivorous fish ha^{-1} and below 15 kg FW of planktivorous fish ha^{-1}. One site—referred to below as ''fish-stocked''—was restocked with 180 kg FW cyprinids ha^{-1} (the average density in the lake) in April 2003. In December 2003, the fish population at the fish-stocked site had increased to 320–400 kg FW of cyprinids ha^{-1}. At the other site, which was not restocked—referred to as ''fish-less'', the fish stock had increased to 82.4 kg FW of cyprinids ha^{-1} in December 2003. Next to the experimental sites, a third, morphologically identical but unenclosed site served as control. The fish stock in the control site was estimated at 180 kg FW of cyprinids ha^{-1}. In the winter of 2003–2004, the fish stock had increased to 244 kg FW of cyprinids ha^{-1}.

We expected that the water of the ''fish-less'' site would become clear, and that the restocked and control sites would remain turbid. If our first hypothesis should be true, submerged macrophytes should develop much better at the clear ''fish-less'' site. If significant submerged macrophytes should develop, this would mean that lack of propagules, low cohesive strength of the lake sediment and high concentrations of phytotoxics do not prevent macrophyte development.

To test the effect of bird grazing, eight 4 m^2 exclosures were constructed at each of the three sites, with nets to keep birds out (Fig. 1). Next to each exclosure an unprotected 4 m^2 plot was

Table 1 Submerged macrophyte species found in Lake Terra Nova between 1949 and 1983 (Best et al., 1984; unpublished data), at the experimental sites in 2003 and in the lake in 2004, with indications of abundance

Species	Lake 1943–1983	2003 control	2003 fish-stocked	2003 fish-less	Lake 2004
Ceratophyllum demersum	xx	xx	xx	xx	Very common
Elodea nuttallii	xx	xx	xx	xx	Common
Potamogeton obtusifolius	xx	x	xx	xx	Common
Nitella mucronata				xx	Common
Najas marina	xx			x	Common
Utricularia vulgaris	xx				Common
Potamogeton crispus	x			xx	Fairly common
Potamogeton lucens	xx				Fairly common
Chara globularis	xx		x	xx	Fairly common
Stratiotus aloides	xx			x	Less common
Elodea canadensis	xx				Less common
Potamogeton pectinatus	xx	x			Fairly rare
Potamogeton pusillus	xx				Fairly rare
Potamogeton mucronatus	+			xx	Fairly rare
Myriophyllum spicatum	xx				Fairly rare
Potamogeton compressus	+				Rare
Nitella flexilis				xx	Rare
Nitellopsis obtusa	xx				1 individual
Potamogeton perfoliatus	x				1 individual
Chara vulgaris	xx				
Fontinalis antipyretica	xx				
Myriophyllum verticillatum	xx				
Potamogeton trichoides	xx				
Ranunculus circinatus	xx				
Utricularia minor	x				
Ranunculus aquatilis	+				

'+' means present with unknown abundance; 'x' means found once or twice; 'xx' means found more often

marked, where birds had free access. Vegetation developments in the exclosures and unprotected plots were assessed and compared; any significant difference was attributed to bird grazing. In view of the possibility that plants would not establish due to lack of propagules, we introduced plants at each site, viz. in four of the exclosures and in four of the adjacent unprotected plots (Fig. 1). The species introduced had all been found growing in Lake Terra Nova during the past 10 years and had different growth forms: *P. lucens*, *C. demersum* and *E. nuttallii*. Ten young plants of each species were individually planted in half-open pots, mounted in a 50 × 50 cm metal frame that was sunk into the sediment, one frame per species per plot.

Light conditions

Water transparency and vertical light attenuation were both measured each week from April to September and once every 2 weeks in winter. Transparency was measured with a Secchi disk. The vertical light attenuation coefficient (K_d) was calculated as: $K_d = (\ln(I_0/I_Z))/Z$, where I_0 and I_Z are the intensities of the Photosynthetically Active Radiation (PAR) just under the water surface and at a depth $Z = 0.5$ m (Scheffer, 1998). I_0 and I_Z were measured with two LI-192SA underwater quantum sensors, mounted in a frame, 0.5 m apart. Measurements were taken every second for 30 s, using a LI-1400 data logger. K_d was calculated as the average of 3–10 of such 30-s series, 1 min apart.

Light attenuation by periphyton

Thin 1.5 cm^2 glass discs were used to measure shading by periphyton (Van Dijk, 1993). Ten glass discs were placed at a depth of 10 cm below the water level, and ten other plates at a depth of 50 cm. The incubation time was 14 days, as this is

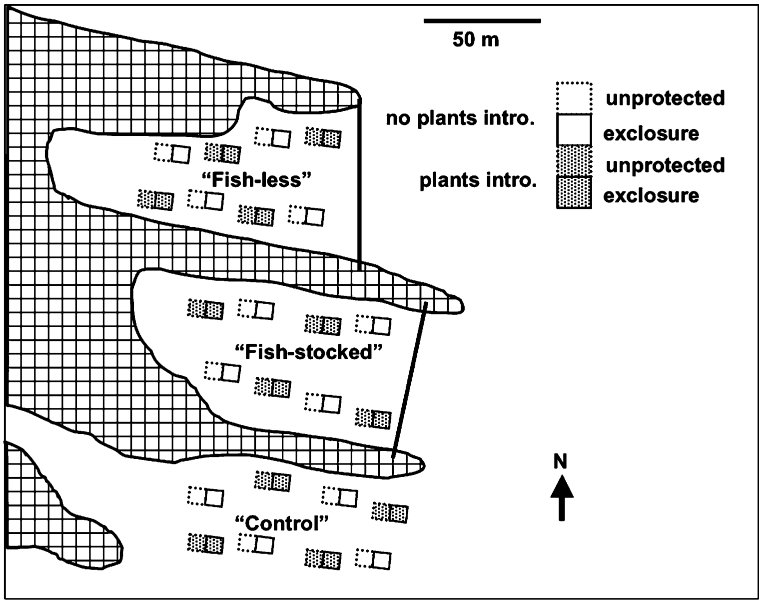

Fig. 1 Overview of the experimental setup

approximately the lifespan of leaves of submerged plants (Hootsmans, 1994). After 14 days, when the discs had become covered with a periphyton layer, light attenuation (% PAR) was compared with that of a clean glass disc, using two LI-COR underwater sensors.

Vegetation sampling

The percentage cover of the submerged macrophytes and of the floating-leaved species at each site was estimated on a decimal scale (adapted from Londo, 1975). Measurements were made weekly from April to September 2003 and fortnightly in the winter of 2003–2004. Estimations were made visually, using a hydroscope when needed, and with a rake when transparency was poor. On 23 June and 11 August 2003, the vegetation was surveyed in detail, by estimating the plant cover at the three experimental sites in 35 evenly distributed plots of approximately 0.25 m^2.

To determine plant biomass, all 4 m^2 plots were harvested in August 2003. If the volume of the plants collected from a plot was more than approximately 10 l, a representative subsample (1/2, 1/4 or 1/8) was taken. Species were separated, washed to remove detritus and stored in paper bags, and the dry weight of the plants (70°C, 48 h) was determined.

Statistical analysis

Differences in species biomass were tested with multiple regression analysis using Genstat 7.1. The data were log-transformed and model checking was applied. Post-hoc contra *t*-tests were carried out according to *t*-values. Least significant differences at a 5% level were used to test differences between factor classes of the exclosure/unprotected plot treatments. Blocks were used for the fish-less, fish-stocked and control sites. Differences in total biomass were log-transformed and tested with a *t*-test. Differences in light attenuation by periphyton layers at different depths were also tested with a *t*-test. The average number of species per treatment was tested with a Mann–Whitney *U*-test, because they were not normally distributed.

Whole-lake biomanipulation experiment

In the winter of 2003/2004, the fish stock in the whole Lake Terra Nova was reduced from 244 kg fresh weight ha^{-1} to 48 kg fresh weight ha^{-1} (estimated with Petersen's mark and recapture technique; Klinge et al., 2003). Turbidity and vegetation cover were measured once a month at six locations, with four plots (4 m^2) each. The percentage cover of each species was estimated visually if the water was clear enough, using a decimal scale (adapted from Londo, 1975). Afterwards, all plants in the plots were collected with a rake. In August, total dry biomass in the plots was determined as described above.

The vegetation of the lake was mapped in August by identifying homogeneous areas, surveying the species (visually and with a rake) in each area and estimating their percentage cover on a decimal scale (adapted from Londo, 1975).

Results

Light conditions at the experimental sites

After biomanipulation in the winter of 2002–2003, the water in the fish-less site became clear in April 2003, while the water in the fish-stocked site and in the control site remained turbid (Fig. 2). In summer, light conditions decreased at all three sites, but light conditions at the fish-less site remained better than at the other sites. Secchi-disc measurements showed that the bottom of the fish-less site was visible all year round, while it was rarely visible at the other sites.

Effects of turbidity on plant growth and number of species

The percentage cover of the submerged macrophytes (Fig. 3) at the clear-water fish-less site slowly increased in May and June. In July and August, the cover increased rapidly until it reached 90% by the end of August. At the other two, turbid sites, the cover by submerged macrophytes remained below 25%.

At the clear-water fish-less site, ten macrophyte species were found, eight of which were found more than twice. At the persistently turbid sites, only four submerged macrophyte species were found (Table 1).

There was no significant difference in total plant biomass between the turbid control and the fish-stocked sites, nor between the plots with or without introduced plants (*t*-tests, see Table 2). The total biomass at the clear-water fish-less site was significantly higher than at the two turbid sites, both with and without introduced plants (*t*-tests, see Table 2). At species level, the same effect was seen for the plots without introduced species (Fig. 4): the dominant *E. nuttallii* and the

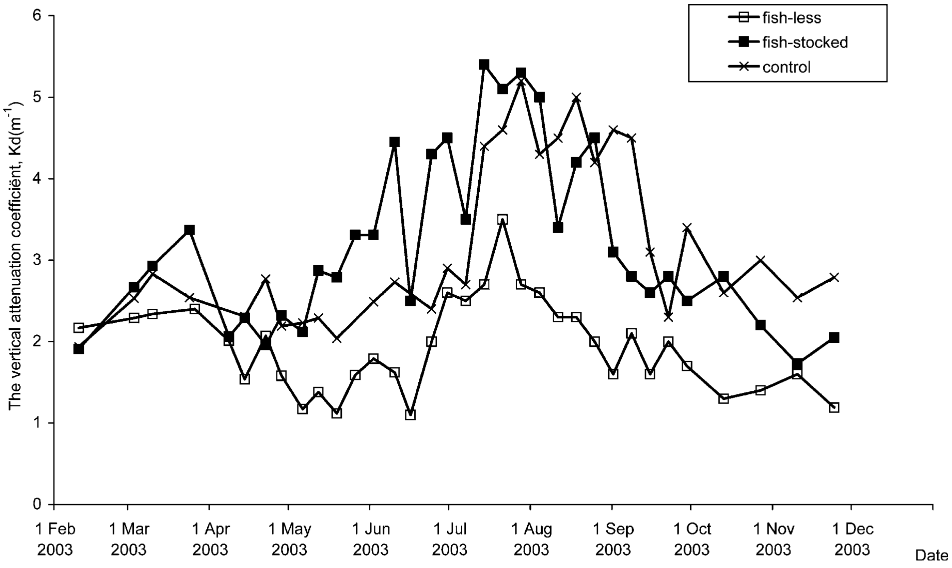

Fig. 2 Light conditions under water at the experimental sites in 2003

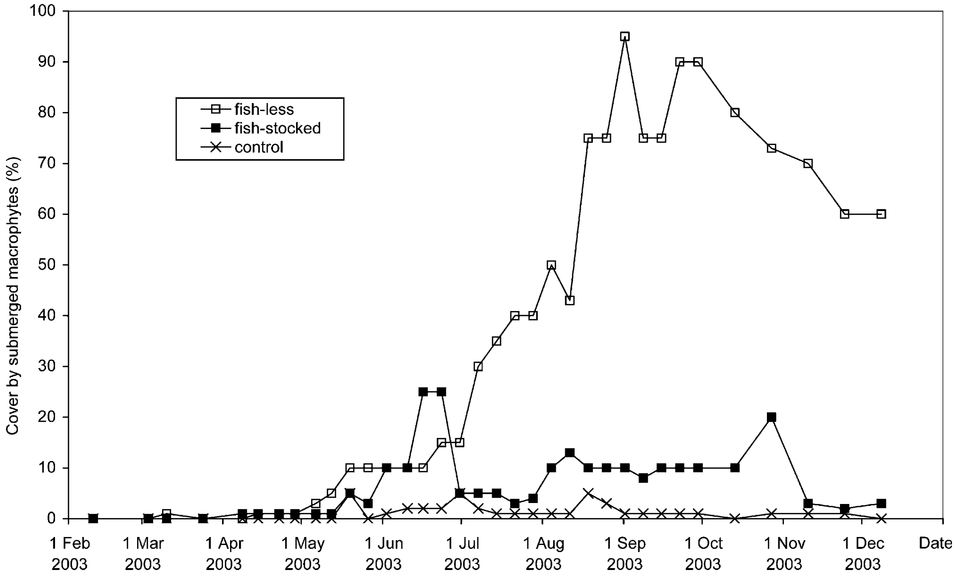

Fig. 3 Development of cover by submerged macrophytes during 2003 at the three experimental sites

less abundant Characeae both had significantly higher biomass at the fish-less site, whereas the control site and the fish-stocked site did not differ significantly (regression post-hoc *t*-tests, see Table 3). For the plots with introduced species, the pattern seemed similar (Fig. 5), but a significant effect was only found for *E. nuttallii*, and not for the dominant *P. lucens* (regression post-hoc *t*-tests, Table 3).

Light attenuation by periphyton

The light attenuation by periphyton, measured as the periphyton layer on glass discs after 14 days in the water, was not significantly different between the two depths of 10 and 50 cm (*t*-test, $t = 0.629$, $n = 830$, $P = 0.53$). Light attenuation by this periphyton layer generally remained below 20% (Fig. 6).

Table 2 Differences in total biomass at the sites, as tested with a *t*-test

With introduced species	
Control–fish-stocked	$t = -.918$, $n = 16$, $P = .374$
Control–fish-less	$t = -3.546$, $n = 15$, $P = .006$
Fish-stocked–fish-less	$t = -2.826$, $n = 15$, $P = .019$
Without introduced species	
Control–fish-stocked	$t = -.676$, $n = 15$, $P = .511$
Control–fish-less	$t = -8.478$, $n = 16$, $P < .001$
Fish-stocked–fish-less	$t = -6.527$, $n = 15$, $P < .001$

Effects of bird herbivory

At the fish-less site, *E. nuttallii* grew up to the water surface inside the exclosures. Outside the exclosures, it rarely did, as it was “clipped” a few decimetres below the water surface, a pattern which is consistent with grazing by herbivorous waterbirds (Common coot *Fulica atra* was actually observed eating *E. nuttallii*). At the unprotected plots without introduced plants in clear water, all common species (*E. nuttallii*, *C. demersum*, *P. obtusifolius* and *C. globularis*) established, and *E. nuttallii* became dominant. At the sites with turbid water, however, hardly any biomass developed in the unprotected plots (Fig. 4).

The biomass of the dominant species (*P. lucens* with and *E. nuttallii* without introduction) was significantly higher inside than outside the exclosures (regression post-hoc *t*-tests, Table 3). This was true for all three sites, both with and without introduction, with only one exception, viz. the fish-less site without introduction.

In the plots without introduced plants at the fish-less site, the average number of species outside the exclosures was 4.3, whilst the number

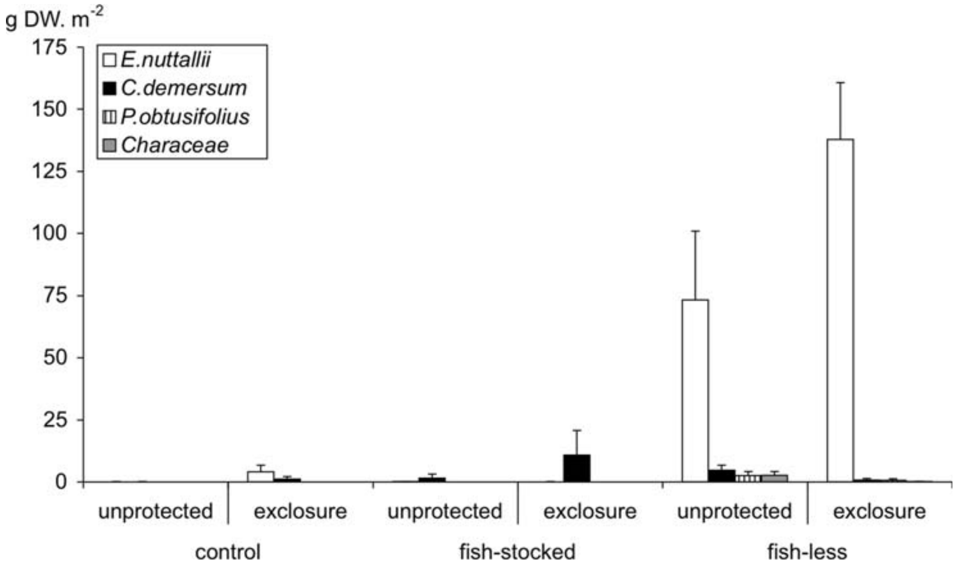

Fig. 4 Average biomass of the plots without introduced plants. For each treatment condition, the biomass in the plots open to bird grazing and in the exclosures is presented separately. *Potamogeton crispus* and *Najas marina* (not shown) occurred only in the unprotected plots of the fish-less site, with a very low biomass (too low to be visible). Error bars represent standard error of the average biomass

of species inside the exclosures was 2.3. However, this difference was significant only at the 10% level (Mann–Whitney $U = 2$, $n = 8$, $P = 0.074$).

Whole lake biomanipulation experiment

Biomanipulation of the whole Lake Terra Nova in the winter of 2003–2004 resulted in clear water (Fig. 7; for details see Ter Heerdt & Hootsmans, 2007). Submerged macrophytes quickly developed in the shallow parts (<1.4 m) of the lake. Plants were occasionally present in the deeper parts, but average cover remained below 1%. In August, submerged macrophytes covered about 30% of the whole lake, and 60% of the shallow parts (<1.4 m), although they remained absent from a few shallows. A total of 19 submerged macrophyte species, including four species of Characeae, were found in 2004 (Table 1). Whereas the vegetation at the fish-less experimental site was dominated by *E. nuttallii* (with almost 100% coverage), the vegetation in the lake as a whole was more diverse (Fig. 8). The shallowest parts (<1.1 m) were co-dominated by *C. demersum, Najas marina* and *P. obtusifolius*, in a patchy pattern. The cover of individual species hardly ever exceeded 70%. Characeae were frequently observed in the shallowest parts; high cover by Characeae only occurred at a few locations. At relatively sheltered, 1.1–1.4 m deep locations, only *C. demersum* covered more than 10%. At the more exposed places, *Potamogeton lucens* formed scattered stands at depths between 1.3 and 1.7 m.

Discussion

Effect of turbidity on colonisation by macrophytes

After the water had cleared, many submerged macrophyte species established, both at the experimental site and in the lake as a whole. Macrophytes reached a high cover, which did not happen at the turbid fish-stocked experimental site. We therefore conclude that the high turbidity was the major factor limiting the development of submerged macrophytes in Lake Terra Nova. The negative effect of high turbidity on the biomass of the dominant species was significant at the plots without introduced species, but not at the plots with introduced species. This difference suggests that high turbidity has a negative effect on the establishment of plants, rather than on their growth rate.

Table 3 Results of the regression analysis

Fitted terms: constant + blocks + grazing		With introduced plants			Without introduced plants	
		ln(*E. nuttallii*)	ln(*C. demersum*)	ln(*P. lucens*)	ln(*E. nuttallii*)	ln(characaea)
Regression summary						
N		22	22	22	23	23
F		5.3	4.7	9.0	38.5	4.1
P		0.007	0.012	<.001	<.001	0.021
R^2		0.36	0.33	0.51	0.84	0.30
Parameter estimates						
Constant		0.745	0.768	3.707	–0.611	–2.619
t, P		$t = 1.04$, $P = 0.312$	$t = 1.72$, $P = 0.101$	$t = 6.58$, $P = <.001$	$t = –1.16$, $P = 0.259$	$t = –6.38$, $P = <0.001$
Blocks fish-stocked		0.833	1.192	0.284	-0.973	0.045
t, P		$t = 0.95$, $P = 0.355$	$t = 2.18$, $P = 0.041$	$t = 0.41$, $P = 0.685$	$t = –1.47$, $P = 0.158$	$t = 0.09$, $P = 0.931$
Blocks fish-less		2.769	1.864	1.124	5.456	1.39
t, P		$t = 3.15$, $P = 0.005$	$t = 3.41$, $P = 0.003$	$t = 1.63$, $P = 0.119$	$t = 8.54$, $P = <0.001$	$t = 2.78$, $P = 0.012$
Grazing		–1.689	–0.666	–2.774	–0.966	0.633
t, P		$t = –2.35$, $P = 0.029$	$t = –1.49$, $P = 0.151$	$t = –4.92$, $P = <.001$	$t = –1.81$, $P = 0.087$	$t = 1.51$, $P = 0.147$
Post-hoc t-tests						
Effect of fish in unprotected plots						
Control unprot.	Fish-stocked unprot	ns	$P < 0.05$	ns	ns	ns
Control unprot.	Fish-less unprot	$P < 0.05$	$P < 0.05$	ns	$P < 0.05$	$P < 0.05$
Fish-stocked unprot	Fish-less unprot	$P < 0.05$	ns	ns	$P < 0.05$	$P < 0.05$
Effect of fish in exclosures						
Control excl.	Fish-stocked excl	ns	$P < 0.05$	ns	ns	ns
Control excl.	Fish-less excl	$P < 0.05$	$P < 0.05$	ns	$P < 0.05$	$P < 0.05$
Fish-stocked excl	Fish-less excl	$P < 0.05$	ns	ns	$P < 0.05$	$P < 0.05$
Effect of exclosures (grazing)						
Control unprot.	Control excl	$P < 0.05$	ns	$P < 0.05$	$P < 0.05$	ns
Fish-stocked unprot	Fish-stocked excl	$P < 0.05$	ns	$P < 0.05$	$P < 0.05$	ns
Fish-less unprot	Fish-less excl	$P < 0.05$	ns	$P < 0.05$	ns	ns

Only significant regressions are shown (regression of *P. obtusifolius* and *C. demersum* at the plots without introduction were not significant)

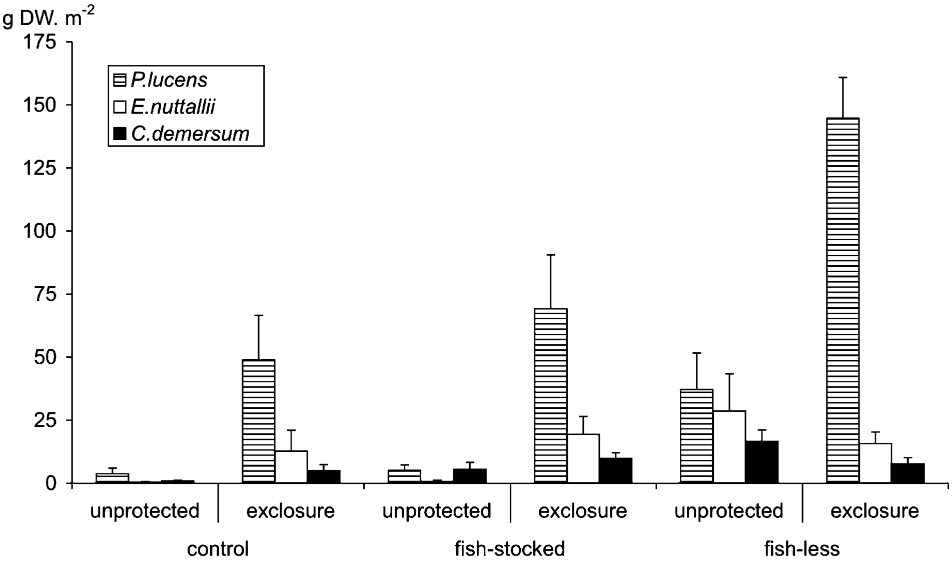

Fig. 5 Average biomass of the plots with introduced plants. For each treatment condition, the biomass in the plots open to bird grazing and the exclosures is presented separately. Error bars represent standard error of the average biomass

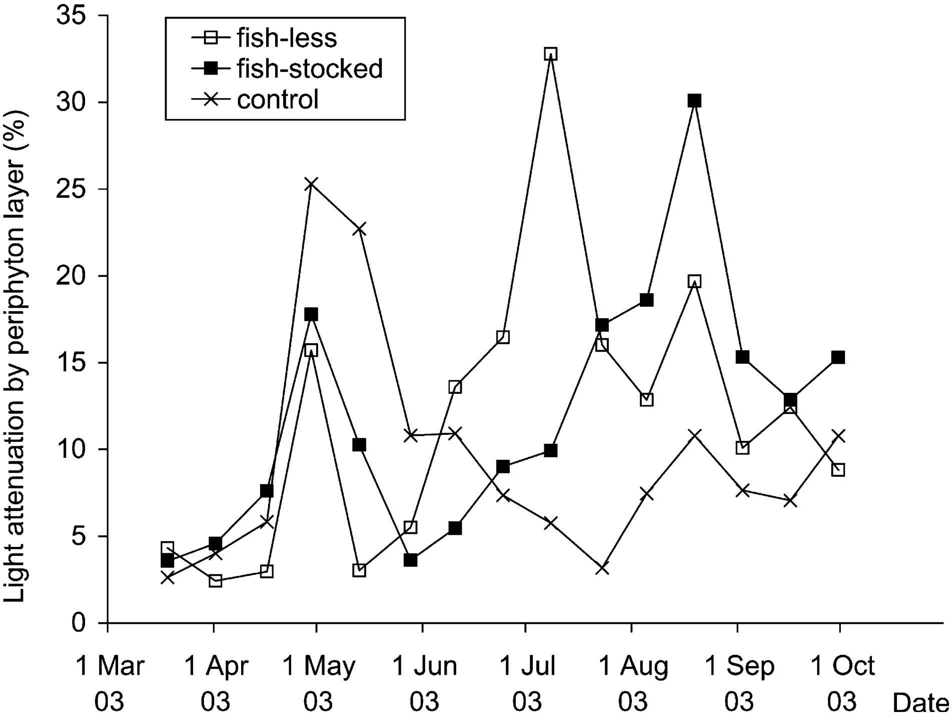

Fig. 6 Light attenuation by a periphyton layer growing on a glass disc submerged for 14 days at the experimental sites

Colonisation

The large number of species found and the rapid colonisation of the lake indicate there was no lack of propagules in Lake Terra Nova. Most species known to have occurred in the past recovered in 2004, including some rare species. Although some of the species found in 2004 had been encoun-

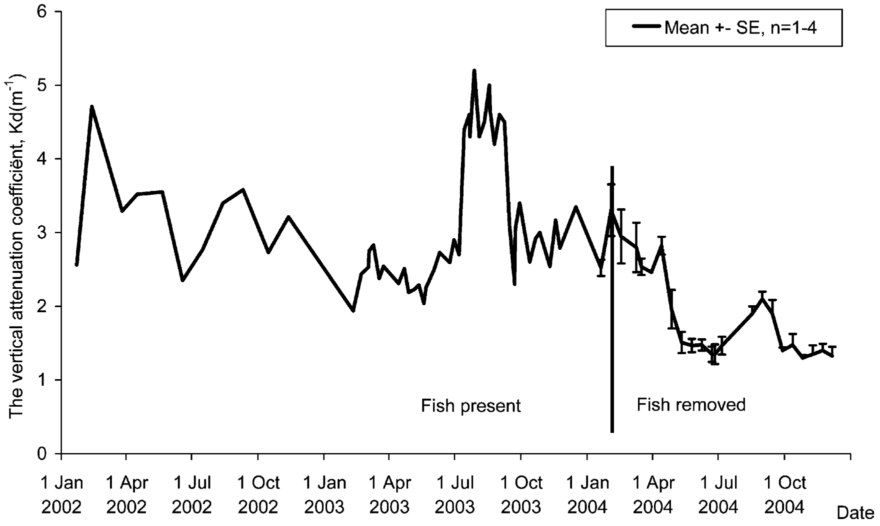

Fig. 7 Development of the vertical light attenuation coefficient in Lake Terra Nova (excluding the dammed off experimental sites)

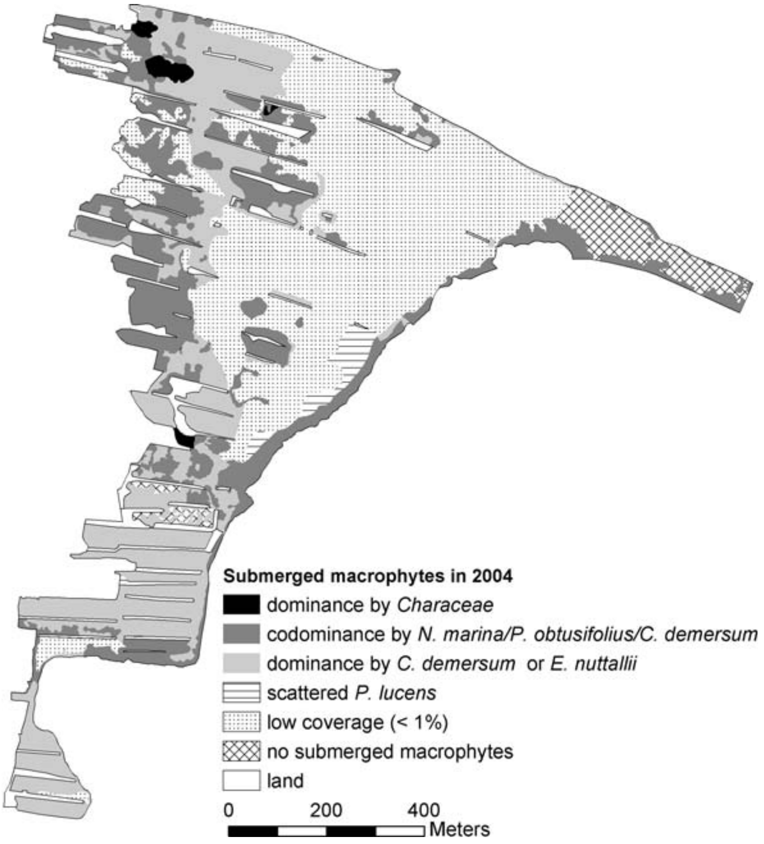

Fig. 8 Map of the submerged macrophytes in Lake Terra Nova in 2004

tered regularly in the lake since 1984, most had not been observed. Some of these species probably re-established from soil seed banks, such as Characeae, which are known to have persistent seed banks (Thompson et al., 1997). Transport of diaspores by water is also known to play an important role in the establishment of submerged macrophytes, especially *E. nuttallii* and *C. demersum* (Boedeltje et al., 2003, 2004). Birds are known to transport propagules of aquatic plants frequently, at least at a local scale, both by endozoochory (internal transport of seeds, e.g. those of *Potamogeton* species) and ectozoochory (external transport of vegetative parts, e.g. those of *Elodea* species) (Figuerola & Green, 2002). Large numbers of geese, ducks and swans visit Terra Nova and thus may import propagules from a wide area. Vegetation development in the lake started with only a few individuals, but expanded exponentially (Fig. 3). As the processes summarised above are quite common, it seems reasonable to assume that propagules will be present in many other lakes too. This implies that the restoration potential may also be high in similar lakes.

The low cohesive strength of the lake sediment and the presence of phytotoxics were apparently no major constraints in Lake Terra Nova, as most shallow parts became covered by submerged macrophytes.

Grazing by waterbirds

Exclosures yielded higher biomasses than unprotected plots, where grazing and uprooting by birds could occur. Because the effect was observed not only at the fish-stocked and control sites, but also at the fish-less site, we conclude that grazing by birds reduces the total biomass. In turbid water, grazing reduced biomass to almost zero, whereas in clear water, the reduction of the biomass of the dominant species seemed to result in a higher number of species. It is well-known from terrestrial grasslands (e.g. Olff & Ritchie, 1998), that grazing (at least extensive grazing) often results in higher plant diversity. We suggest that also in macrophyte stand, a reduction of the competition between species by a reduction of the dominant species results in higher vegetation diversity.

Light attenuation by periphyton

Although plant growth is reduced even by moderate shading, we do not consider 20% light attenuation by a periphyton layer (grown in 14 days) to be a major obstacle to plant growth in clear and shallow water. Van Dijk & Van Vierssen (1991) found that 26% shading did not have a significant effect on the growth of *P. pectinatus* in Lake Veluwe, whereas 45% and 73% shading did have significant effects on the growth of this species.

Restoration experiment in the whole lake

The vegetation that developed at the (shallow) experimental fish-less site differed from the vegetation in shallow parts of the lake as a whole. Whilst the experimental fish-less site was dominated by one species (*E. nuttallii*; covering nearly 100%), the vegetation in the other shallow parts was less dense and mostly co-dominated by two or three species. We suspect that the difference in wind dynamics played a role. Why some parts of the lake were not colonised by submerged macrophytes, despite being sheltered, shallow and clear, remains to be studied.

A clear water state in the first year after biomanipulation sometimes returns to turbid state after a few years (Meijer et al., 1999). Our results do not allow us to conclude whether the restoration of Lake Terra Nova is sustainable or whether supplementary measures will be required. We are optimistic because of the development of a dense submerged macrophyte cover in the lake, but will continue to study the lake over the next few years.

Conclusions

At Lake Terra Nova, a reduction of the fish stock to 48 kg ha^{-1} of cyprinids resulted in clear water in 2004. Turbidity was the major factor limiting the growth of submerged macrophytes in Terra Nova. In this lake, which has been turbid since 1988, the density of propagules enabled colonisation of shallow parts of the lake within 1 year. Grazing by birds reduced the total biomass, and hardly any biomass remained in turbid water. In clear water, the reduction of the biomass of the dominant species seemed to enhance vegetation diversity. Periphyton growth generally did not limit light conditions to such an extent that plant growth was prevented in the shallow parts.

This study has shown that the potential for restoration of species-rich submerged macrophyte stands in peaty lakes is high, even after two decades in a turbid state. Whether the restoration of Lake Terra Nova is sustainable or whether supplementary measures will be required, cannot be concluded from the results.

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