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Changes in macrophyte community structure in Lake Christina (Minnesota), a large shallow lake, following biomanipulation

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Abstract

Macrophyte community structure in Lake Christina, a large shallow lake in west-central Minnesota, changed in response to a biomanipulation treatment in 1987. Three years of pre-treatment and 11 years of post-treatment data were analyzed. Using a combination of cluster analysis and indicator species analysis, three distinct macrophyte communities were identified: a pre-treatment community of low plant abundance, an early post-treatment community dominated by *Najas flexilis*, *N. marina*, *Myriophyllum sibiricum* and *Ruppia maritima*, and a late post-treatment community characterized by *Chara vulgaris*, *C. canescens*, *Potamogeton pectinatus*, and *P. pusillus*. Canonical correspondence analysis (CCA) showed that these changes in plant community structure are associated with improvements in water clarity and annual variation in abundance of filamentous algae.

Keywords: Aquatic macrophytes; Aquatic plants; Macrophyte community; Multivariate analysis; Shallow lakes

1. Introduction

The abundance and composition of the rooted aquatic macrophyte community has a great effect on a lake ecosystem, particularly for shallow lakes (Carpenter and Lodge, 1986; Blindow et al., 1998). Many shallow lakes are thought to alternate between a clear and

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a turbid state (Scheffer et al., 1993; Scheffer, 1998). Shallow lakes that support abundant submerged vegetation when the water is clear may be degraded by excessive nutrient inputs from sewage effluent, agriculture, or internal loading caused by the excretion and foraging activities of fish. Such degraded lakes often are turbid and devoid of submersed macrophytes.

Biomanipulation treatments have become a common method for restoring water clarity in degraded shallow lakes (Hosper, 1997). Initial water clarity improvements following these treatments are often attributed to top–down effects (Hosper, 1997; Jeppesen et al., 1997; Hansson et al., 1998), and specifically to increased grazing pressure by cladocerans. However, these top–down effects may not maintain a long-term clear-water state (Hanson and Butler, 1994a,b; Beklioglu and Moss, 1996). In fact, zooplankton grazing has been shown to have little impact on water clarity in lakes with abundant submerged macrophytes (Blindow et al., 2000).

Shapiro (1990) emphasized the need to make the clear-water period resulting from a biomanipulation persist for longer time periods. Many authors recognize that the presence of macrophytes can play a key role in the long-term success of biomanipulation efforts (Hanson and Butler, 1994a; Perrow et al., 1997; Hansson et al., 1998). Submersed macrophytes contribute to the stability of the clear-water state by stabilizing the bottom sediments (Balls et al., 1989; McQueen et al., 1990; Moss, 1990; Blindow et al., 1993), providing refuge for invertebrates (Timms and Moss, 1984; Schriver et al., 1995), sequestering nutrients (Van Donk et al., 1989), and reducing sediment resuspension (James and Barko, 1990; Petticrew and Kalff, 1992; Van den Berg et al., 1998a; Vermaat et al., 2000).

Although plants are important in the maintenance of the clear-water condition of shallow lakes (Ozimek et al., 1990; Weisner et al., 1997), little is known about long-term plant community composition and succession in lakes that have undergone biomanipulation treatments (Kowalczewski and Ozimek, 1993; Coops and Doef, 1996). Although there are many studies documenting the increase in abundance of plants after biomanipulation treatments (Ozimek et al., 1990; Strand, 1999), few look at long-term plant community composition.

In this paper, we examine the long-term changes in the plant community after the biomanipulation treatment of Lake Christina (46°05′N, 95°44′W, Minnesota, USA) a large (1600 ha) shallow (mean depth = 1.5 m) lake. This lake has been restored from the degraded, algal-dominated condition to a clear-water condition twice in the past half-century, both times facilitated by biomanipulation treatments. In 1965, the lake was treated with toxaphene. Prior to that treatment, macrophytes were sparse, but they increased in abundance after the treatment. However, by the late 1970s water clarity had decreased (average Secchi depth 1977, 45 cm), and by the early 1980s the lake was again nearly devoid of plants and waterfowl (Hanson and Butler, 1994b, Fig. 5, p. 462). During this time there was little change in land use in the small watershed of Lake Christina (average total phosphorus ranging from 140 $\mu g\,l^{-1}$ in 1960 to 130 $\mu g\,l^{-1}$ in 1985).

In an attempt to restore the waterfowl habitat, the Minnesota Department of Natural Resources, applied 63,000 l of rotenone to the lake in the fall of 1987. Prior to this treatment a limnological study of the lake was initiated in 1985 and lasted through 1998. During this study, chlorophyll-*a* (chl-*a*) ranged from an annual average of 70 $\mu g\,l^{-1}$ in 1985 to a post-treatment low of 10 $\mu g\,l^{-1}$ in 1990, annual average Secchi depth ranged from a low of 28 cm in 1985 to a high of 176 cm in 1990, the coefficient of light attenuation ranged from a high of 4.0 in 1985 to a low of 0.9 in 1993. The lake was re-vegetated within 3 years of the treatment and waterfowl use of the lake increased dramatically (Hanson and Butler, 1994a). Here we examine the plant community changes that took place in the lake over a 14-year period from 1985 to 1998 with multivariate techniques including cluster analysis (CA), indicator species analysis (ISA) and canonical correspondence analysis (CCA). Multivariate methods provide an ideal way to evaluate the responses of multiple plant species in relation to changes in environmental conditions.

2. Materials and methods

Basic sampling techniques and processing procedures have remained consistent since limnological evaluation of Lake Christina began in 1985 (Hanson and Butler, 1990, 1994a,b). Since 1985, light attenuation, Secchi depth, and turbidity have been measured every two to four weeks during the open water period (late April to mid October) at a minimum of five locations on the lake, and in recent years at up to 12 locations. Water samples from the same locations were analyzed on a monthly basis by the Minnesota Department of Agriculture lab for chlorophyll-*a* (chl-*a*), total suspended solids (TSS), total phosphorus (TP), and total Kjeldahl nitrogen (TKN). Waterfowl surveys were conducted by airplane during the migration season every fall.

Submersed plants were surveyed annually in mid August each year from 1985 to 1998. Thirty-five stations were sampled with a weighted plant rake, with four rake throws made in opposing directions at each station. Each plant species was ranked from 0 to 5, according to the number of rake throws in which it was found. A ranking of 5 was given if the plant was extremely abundant on each of the four rake throws (Jessen and Lound, 1962).

2.1. Multivariate analyses

Several multivariate techniques were used to determine if there was structure in the plant community data, if this structure changed through time, and whether variation in the plant community could be explained by environmental changes that occurred in Lake Christina. Cluster analysis, indicator species analysis, principal components analysis, and canonical correspondence analysis were performed with the PC-ORD program (McCune and Medford, 1997). Cluster analysis was used to group years with similar plant communities from 1985 to 1998. Indicator species analysis (Dufrene and Legendre, 1997) was then performed to see which plant species were characteristic of the groups generated by the CA. CCA was then performed to determine whether variance in the plant community data could be explained by environmental variables. PCA, an indirect ordination technique, was performed to verify results of CCA, a direct ordination technique. CCA results can be misleading if irrelevant environmental variables are chosen for analyses. Similar results of PCA and CCA will indicate that relevant environmental variables were used (Ter Braak, 1995; Okland, 1996). Stepwise selection in CCA provided an efficient way to eliminate environmental variables that did not explain significant variation in the plant community. With CCA, one can analyze multiple species and environmental relationships at once, avoiding the time consuming task of comparing each species and environmental variable separately.

CA was performed using Euclidian distance and the group linkage method of flexible beta with a value of −0.25. Clusters were tested for significance with the multi-response permutation procedure (MRPP) (Biondini et al., 1988). Because we were making multiple comparisons, P-values were adjusted using a sequential Bonferroni technique (Rice, 1990). Indicator species were tested using a Monte Carlo simulation test (1000 runs). Indicator values were determined by combining relative frequency and relative abundance of plant species in a given group of years, as in Dufrene and Legendre (1997).

The variance–covariance option in PCA was chosen to emphasize the dominant species in the analysis. The correlation option puts more emphasis on rare species, but our objective was to look at gross changes in the plant community structure by seeking differences in the dominant species from year to year. Axes generated by PCA were tested for significance with the Fisher proportion test (Fisher, 1958).

CCA ordination was tested for significance with a Monte Carlo test (1000 runs). Graphing of CCA was based on scores derived as linear combinations of environmental variables because the plant community variation explained by the environmental variables was of greatest interest. These scores best show the relationship between the environmental and the species data, and are recommended by Palmer (1993) and Ter Braak (1994).

Aquatic plant growth in shallow eutrophic lakes is largely determined by the amount of light reaching the plants (Scheffer et al., 1992). This light is dependent upon incident light at the water surface, how much that light is attenuated by the water column, and the depth of water the light must pass through before it reaches the plants. Therefore, Secchi depth and water depth were recorded at each plant sampling station. Other environmental data available included light attenuation, TP, TKN, chl-*a* concentrations. It has been suggested that waterfowl can impact plant development and community composition by their grazing activity (Lauridsen et al., 1993; Van Donk and Gulati, 1995; Moss et al., 1996; Van Donk and Otte, 1996; Scheffer, 1998). We used peak fall waterfowl counts from the previous year in our analysis since waterfowl grazing in the fall may affect the number of plant propagules for the following spring. Abundance of filamentous algae was also a potential environmental variable since these algae may have a detrimental impact on rooted aquatic vegetation (Ozimek et al., 1991; Perrow et al., 1997b). The abundance of filamentous algae in Lake Christina differs greatly from year to year, and may impact some species of plants. The presence of filamentous algae was noted during the plant surveys and its abundance scored in the same manner as for submerged plants.

The number of environmental variables used in the CCA should be limited by the number of sites to avoid the problem of multicollinearity (Ter Braak, 1986), thus only three of the eight environmental variables could be included in the final CCA model. Each environmental variable was tested separately for marginal effects, or how well each individual environmental variable alone explained the variance in the species matrix. The environmental variables that produced a significant CCA axis were ranked by eigenvalue and tested for conditional effects by forward selection (Ter Braak and Verdonschot, 1995). The latter is done because environmental variables may only explain a significant amount of variance if they are combined with other environmental variables, or the same variance may be explained by two or more different environmental variables. P-values were adjusted with a sequential Bonferroni correction (Rice, 1990) in both the marginal and conditional effects tests. A 1000-run Monte Carlo simulation was done for all tests. These steps ensured that only pertinent environmental variables were used in the final CCA analysis.

For the purpose of these analyses, plant ranks for each species were averaged over all sampling stations, resulting in a mean rank for each plant species for each year. Environmental data were averaged in the same way and standardized by maximum to remove the inconsistencies of units of measurements for different variables (Ter Braak, 1986).

3. Results

Three distinct groups of years were revealed by cluster analysis of the plant community (Fig. 1), all of which differed significantly from each other (Table 1). The first division separated pre-rotenone years (1985–1987) from post-rotenone years (1988–1998). These post-treatment years were further divided into two groups consisting of the years 1988–1991 and 1992–1998. The same clusters were also apparent in PCA (Fig. 2).

Of the 11 plant species, 8 were indicators according the indicator species analysis (Table 2). The second (1989–1991) and the third group (1992–1998) each had several

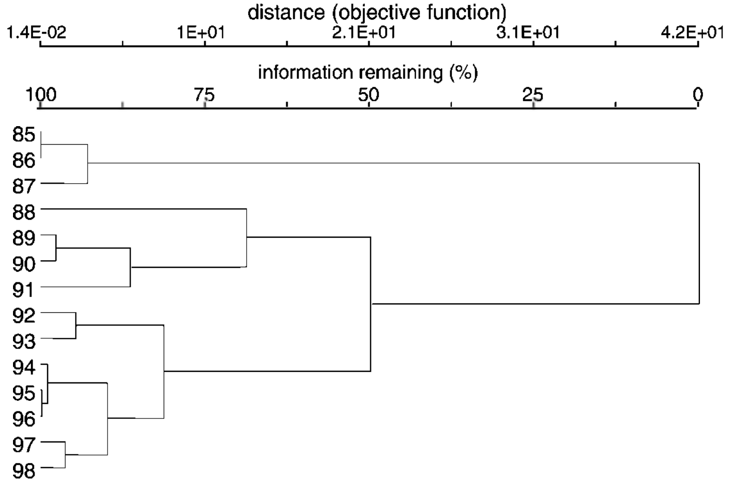

Fig. 1. Cluster analysis of Lake Christina plant community composition over the period 1985–1998.

Table 1
Multi-response permutation procedure testing of three groups of years identified with cluster analysis (Fig. 1)

Overall P	1985–1987 vs. 1988–1991	1988–1991 vs. 1992–1998	1985–1987 vs. 1992–1998
0.00003034*	0.0318**	0.0007**	0.0015**

The overall P-values determines if there are any significant differences among the groups. Since the overall P did indicate a significant difference somewhere among the groups, these groups of years are then tested in pairs to determine which specific groups are significantly different from each other.

* $P < 0.05$.

** Significant with sequential Bonferroni correction at $P < 0.05$.

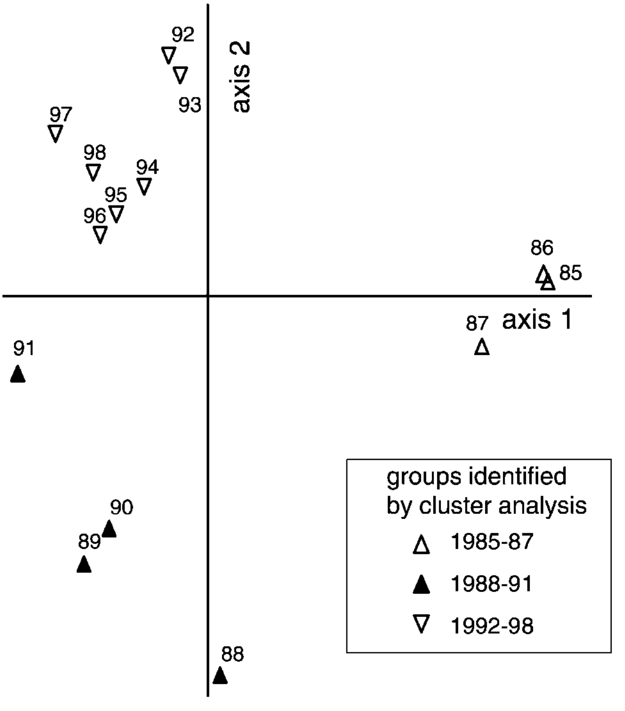

Fig. 2. Principal components analysis plot of Lake Christina plant community 1985–1998. The first two axes were significant with the first PCA axis explaining 66% ($P = 0.0002$) of the variance in the plant data and the second explaining an additional 19% ($P = 0.004$).

Table 2
Indicator values and Monte Carlo P-values for each species based on relative frequency and relative abundance in groups generated by cluster analysis, and species abbreviations for Figs. 3 and 4

Species	Abbreviation	Group indicator[a]	Indicator value	P
Myriophyllum sibiricum	Ms	2	60.5	0.003*
Najas flexilis	Nf	2	63.5	0.041*
Najas marina	Nm	2	78.1	0.029*
Ruppia maritima	Rm	2	66.6	0.001*
Chara canescens	Cc	3	85.7	0.011*
Chara vulgaris	Cv	3	52.7	0.002*
Potamogeton pectinatus	Pp	3	56.9	0.002*
Potamogeton pusillus	Ppu	3	77.5	0.009*
Potamogeton friesii	Pf	2	20.5	0.885
Zannichellia palustris	Zan	2	20.6	0.937
Potamogeton richardsonii	Pri	3	61.1	0.085

[a] Group 2: 88–91; group 3: 92–97.
* $P < 0.05$.

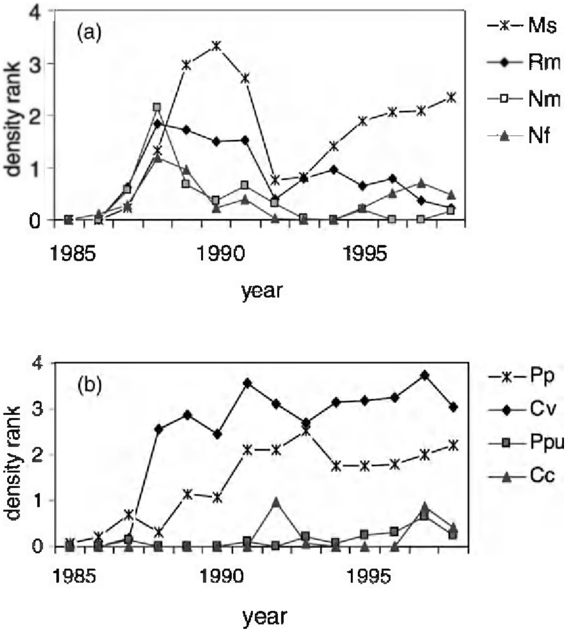

Fig. 3. Average plant density rankings for significant indicator species from 1985 to 1998 (see Table 2). (a) Indicator species for group 2: (b) indicator species for group 3 (species abbreviation key in Table 1).

indicator species, but there were no indicator species for the 1985–1987 group. Fig. 3 shows how the average density ranks of these indicator species have changed over the years of the study.

Testing for marginal effects in the CCA identified three significant variables: light attenuation, filamentous algae, and total phosphorus, but total phosphorus was eliminated when all of the variables were combined to test for conditional effects (Table 3). In the final

Table 3
Results of canonical correspondence analysis with Monte Carlo simulation (1000 permutations) testing for marginal and conditional effects of environmental variables (see Section 2)

Environmental variable	Marginal effects		Conditional effects	
	Eigenvalue	P	Eigenvalue	P
Light attenuation	0.123	0.0010*	0.131	0.006*
Filamentous algae	0.114	0.0080*	0.055	0.001*
Total phosphorus	0.113	0.0015*	0.014	0.102
TKN	0.085	0.696	–	–
Chl-*a*	0.080	0.092	–	–
Secchi depth	0.073	0.245	–	–
Waterfowl	0.065	1.400	–	–
Depth	0.043	2.456	–	–

* Significant at $P < 0.05$ with sequential Bonferroni correction.

Table 4
Summary of CCA on plant communities and environmental data over 14 years of data on Lake Christina (1985–1998)

	Axis 1	Axis 2
Eigenvalue	0.144	0.055
Variance explained (%)	38	16
Pearson correlation between species and environment (P-value)[a]	0.87 (0.011)	0.91 (0.001)
Canonical coefficients		
Light attenuation	−0.394	−0.428
Filamentous algae	0.320	−0.466
Intraset correlations		
Light attenuation	−0.875	−0.484
Filamentous algae	0.804	−0.595

[a] Determined by Monte Carlo simulation (1000 permutations).

CCA model (Table 4), the first two axes were significant and together explained 54% of the variance. CCA axes are interpreted using intraset correlations and canonical coefficients. Canonical coefficients are the best weights for the environmental variables that make up each biplot axis. Intraset correlations indicate how well these weights correlate with each environmental variable (Ter Braak, 1995). Intraset correlations are illustrated in the biplot by vectors representing each significant environmental variable. Canonical coefficients indicate that axis one is a gradient of decreasing light attenuation and increasing filamentous algae, whereas axis two is a gradient of decreasing light attenuation and filamentous algae (Table 4). The Pearson correlations between species and environment are relatively high and are significant (Table 4).

CCA produced a biplot (Fig. 4) consisting of patterns slightly different from the cluster analysis, but still interpretable. Looking first at temporal patterns, the years 1985–1988 were clearly associated with high light attenuation or low water clarity. The first year, 1985, did not group tightly with the other pre-treatment years, indicative of extremely low water clarity in 1985. The first post-treatment year, 1988, grouped closer to 1986, 1987, and 1989 occupied an intermediate position between the highly turbid years and years 1990–1997 with clearer water (or low light attenuation). The year 1998 also fell in a somewhat intermediate position between years of highly turbid water and years of clearer water. Several years were characterized by high abundance of filamentous algae, especially 1992, 1993, and 1997.

Plant species in the CCA biplot (Fig. 4) show a pattern that corresponds to results from the cluster and indicator species analysis. *Myriophyllum sibiricum* L. (milfoil), *Ruppia maritima* L., and *Najas flexilis* (Willd.) Rostk. and Schmidt and *N. marina* L. were associated with the years immediately after treatment, while *Chara canescens* Desv. and Lois, *C. vulgaris* L., *Potamogeton pectinatus* L., and *P. pusillus* L. were associated with the most recent years. *Chara* and *Potamogeton* spp. were associated with low light attenuation. Several species also appear to have been inversely associated with filamentous algae. *Najas* spp., *Ruppia maritima*, and *Myriophyllum sibiricum* all appear to have been less abundant in the years when filamentous algae were abundant. Three of the *Potamogeton* spp. were positively associated with filamentous algae. Both species of *Chara* were positively associated with

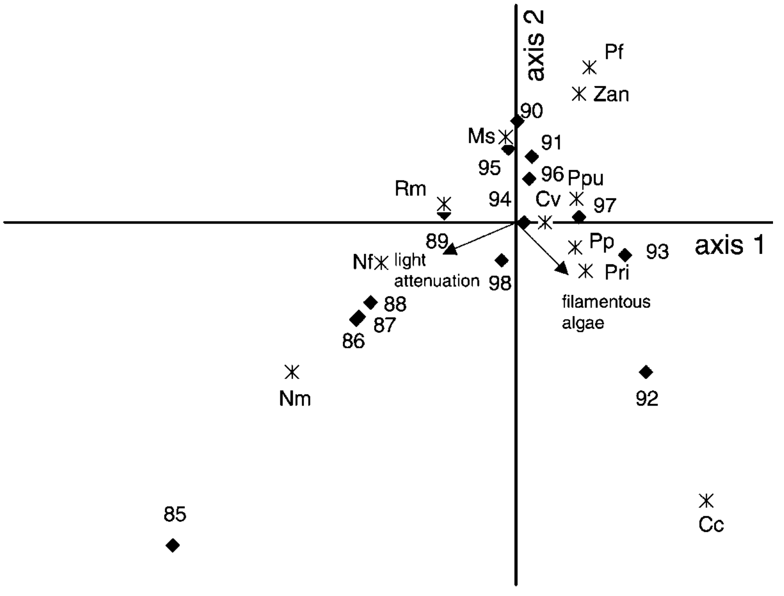

Fig. 4. Canonical correspondence analysis biplot of Lake Christina plant community data from 1985 to 1998 and environmental vectors (species abbreviation key in Table 1).

filamentous algal abundance, but *Chara canescens*, a relatively uncommon species in Lake Christina, showed a very strong positive association with filamentous algae.

4. Discussion

Multivariate techniques were extremely useful for characterizing changes in Lake Christina's plant community following the biomanipulation treatment, as well as in illustrating how this community varies along gradients of water clarity and filamentous algal abundance. Pre-treatment, the lake was largely devoid of plants with only sparse occurrences of sago pondweed and *Najas*. Two distinct communities characterized post-treatment years. The summer after treatment, a pioneer plant community started to develop and was characterized by *Najas* spp., *Myriophyllum sibiricum*, and *Ruppia maritima*. Later (1992–1998), the lake was dominated by a *Chara vulgaris* and *C. canescens* under-story and a *Potamogeton pectinatus* and *P. pusillus* canopy (data not shown). Cluster analysis, indicator species analysis, and PCA were most useful in characterizing differences in the plant communities among years in Lake Christina, whereas CCA showed how changes in plant community composition related to environmental conditions.

Three of the plant species found in the lake were not indicators of any of these three communities (Table 2). These plants were rare species in that they were found only in one particular year and only in a few locations in the lake. Plants in the pioneer community (*Najas* spp., *Myriophyllum*, and *Ruppia*) may be more turbidity-tolerant than *Chara* and the

Potamogeton species (Sand-Jensen and Vindbæk Madsen, 1991). The *Najas* spp. are annuals and would be expected to colonize new habitats. *Chara* especially is known to be intolerant of turbid conditions (Blindow, 1992a,b; Van den Berg et al., 1998a,b). The presence of pioneer plants altered abiotic conditions by improving and stabilizing water clarity (Van den Berg et al., 1998a) and consolidating sediments, thus allowing light sensitive *Chara* and the perennial sago pondweed to become the dominant plants.

Potamogeton pectinatus is a perennial species that grows mainly from over-wintering tubers in the spring (Van Wijk, 1989; Kantrud, 1990). Tuber production may be limited in turbid conditions (Van Dijk and Van Vierssen, 1991). The tuber bank for this species was likely depleted during turbid years and was not fully restored until after several years of clear-water conditions.

A shift to or from *Chara* dominance has been documented in other shallow lakes similar to Lake Christina. Sago pondweed and other aquatic angiosperms have been replaced by *Chara* in Lakes Veluwemeer, Wolderwijd, Takern, and Krankesjön, all shallow lakes in Europe which have undergone improvements in water clarity (Blindow, 1992b; Coops and Doef, 1996). *Chara* has also declined in some European lakes due to eutrophication (Blindow, 1992a; Simons and Nat, 1996). *Chara* abundance declined as water quality deteriorated in Lake Botshol but increased after restoration measures were implemented (Simons et al., 1994).

These changes in the plant community composition can be related to changes in certain environmental variables tested. Of these variables, waterfowl use and water depth were the least significant when tested for marginal effects. Water depth is an important factor in determining plant abundance (Scheffer et al., 1992). Because water depth did not vary much from year to year, this variable alone does not account for a significant amount of the variation in the plant data.

Although waterfowl grazing has been important in structuring plant communities in other lakes (Jupp and Spence, 1977; Lauridsen et al., 1994; Van Donk and Gulati, 1995; Søndergaard et al., 1996; Van Donk and Otte, 1996; Strand, 1999); it did not explain a significant amount of variance in the plant community of Lake Christina. Perrow et al. (1997b) report that timing of grazing determines whether grazing changes plant communities. Grazing early in the season before reproductive structures form has a much greater impact compared to grazing that occurs later in the season. The most intense waterfowl grazing at Lake Christina occurs during the fall waterfowl migration and usually lasts about one month. By this time, the plants have already formed their reproductive structures and are senescent. Lodge et al. (1998) suggested that the pressures of seasonal, but long-term, grazing have not been tested. Lake Christina plant data indicate that high grazing pressure in consecutive autumns (Fig. 5) has had little effect on the plant communities of future years. Submerged plants have remained abundant in Lake Christina despite 10 years of heavy but temporary waterfowl grazing especially by American coots (*Fulica americana*) and diving ducks such as greater and lesser scaup (*Aythya marila* and *A. affinis*, respectively), canvasbacks (*Aythya valisineria*) and ring-necked ducks (*Aythya collaris*). Peak canvasback migration counts on Lake Christina reached 105,000 birds in 1994. Coot numbers were especially high in 1994 and 1997 with peak counts reaching 390,000 and 450,000, respectively.

Plants are light-limited in most lakes, especially those lakes that are eutrophic (Chambers and Kalff, 1987; Sand-Jensen and Vindbæk Madsen, 1991; Scheffer et al., 1992; Scheffer

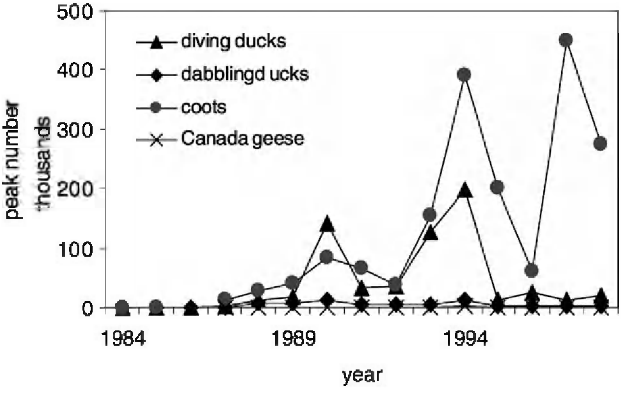

Fig. 5. Peak fall counts of migratory waterfowl on Lake Christina from 1984 to 1998. Coots (*Fulica americana*) were usually the dominant species on Lake Christina during fall migration. Diving ducks were particularly abundant in some years. In 1990, lesser and greater scaup (*Aythya affinis* and *A. marila*, respectively) peak migration counts reach 127,000 birds, and in 1993 and 1994 canvasbacks (*Aythya valisineria*) were abundant.

et al., 1993; Middleboe and Markager, 1997). Light attenuation was the best single environmental variable for explaining the variance in the plant community in Lake Christina. Past studies show that turbidity in Lake Christina was caused by a combination of factors including calcite precipitation in the form of microscopic crystals suspended in the water, resuspended sediments and phytoplankton (Hanson et al., 1990). Chl-*a*, an indicator of algal abundance, did not significantly explain any of the plant community variance, as other sources of turbidity likely played an equal or greater role in overall light attenuation. Filamentous algae also played a significant role in structuring the plant community in Lake Christina. Perrow et al. (1997b) reported that filamentous algae have negative impacts on the plant community in shallow lakes in England, and Ozimek et al. (1991) reported that filamentous algae hindered plant development in lab studies. Large mats of *Cladophora* are especially abundant some years in Lake Christina but almost absent in other years. Macrophytes often became entangled in these mats of algae. The entangled plants are uprooted when the mats of filamentous algae float to the surface or are shifted by the wind. Filamentous algae also use the plants as a substrate on which to grow, thereby preventing plants from getting adequate light. Milfoil had a strong negative association with filamentous algae; this plant routinely matted at the water surface (while *Potamogetons* in Lake Christina typically did not form dense surface mats) and may have been more susceptible to physical damage caused by the floating mats of filamentous algae. However, abundant filamentous algae may also enhance water clarity, by competing with planktonic algae for nutrients and protecting the sediments from resuspension. Some macrophytes species are positively associated with filamentous algae, for example *Chara canescens*. This species' position on the CCA biplot would indicate that it has a strong positive relationship with filamentous algal abundance, and the highest light requirements of all the plant species found in Lake Christina (Fig. 4).

Scheffer's models (Scheffer et al., 1993; Scheffer, 1998) indicate that shallow lake ecosystems may switch, in either direction, between a state with clear water and abundant plants, and an alternative, phytoplankton-dominated state; Lake Christina illustrates this concept of "alternative stable states" well. Plants quickly re-vegetated Lake Christina after the biomanipulation treatment, but the plant community continued to change over the subsequent decade. Successional changes in the plant community of a biomanipulated lake are to be expected, but detailed analyses such as we present here are scarce. Additional analyses of long-term data sets may shed more light on how changes within aquatic plant communities of shallow lake systems relate to Scheffer's models of alternative stable states.

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References

Balls, H., Moss, B., Irvine, K., 1989. The loss of submerged plants with eutrophication. I. Experimental design, water chemistry, aquatic plant and phytoplankton biomass in experiments carried out in ponds in the Norfolk Broadland. Freshwater Biol. 22, 71–87.

Beklioglu, M., Moss, B., 1996. Existence of a macrophyte-dominated clear water state over a wide range of nutrient concentrations in a small shallow lake. Hydrobiologia 337, 93–106.

Biondini, M.E., Mielke Jr., P.W., Berry, K.J., 1988. Data-dependent permutation techniques for the analysis of ecological data. Vegetation 75, 161–168.

Blindow, I., 1992a. Decline of charophytes during eutrophication: comparison with angiosperms. Freshwater Biol. 28, 9–14.

Blindow, I., 1992b. Long- and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. Freshwater Biol. 28, 15–27.

Blindow, I., Andersson, G., Hargeby, A., Johansson, S., 1993. Long-term pattern of alternative stable states in two eutrophic shallow lakes. Freshwater Biol. 30, 159–167.

Blindow, I., Hargeby, A., Andersson, G., 1998. Alternative stable states in shallow lakes: What causes a shift? In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), The Structuring Role of Submerged Macrophytes in Lakes. Springer, New York, pp. 353–360.

Blindow, I., Hargeby, A., Wagnet, B., Andersson, G., 2000. How important is the crustacean plankton for the maintenance of water clarity in shallow lakes with abundant submerged vegetation? Freshwater Biol. 44, 185–197.

Carpenter, S.R., Lodge, D.M., 1986. Effects of submersed macrophytes on ecosystem processes. Aquat. Bot. 26, 341–370.

Chambers, P.A., Kalff, J., 1987. Light and nutrients in the control of aquatic plant community structure. I. In situ experiments. J. Ecol. 75, 611–619.

Coops, H., Doef, R.W., 1996. Submerged vegetation development in two shallow, eutrophic lakes. Hydrobiologia 340, 115–120.

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Fisher, R.A.,1958. Statistical methods for research workers. 13th ed. Hafner, New York.

Hanson, M.A., Butler, M.G., Richardson, J.L., Arndt, J.L., 1990. Indirect effects of fish predation on calcite, supersaturation, precipitation, and turbidity in a shallow prairie lake. Freshwater Biol. 24, 547–556.
Hanson, M.A., Butler, M.G., 1990. Early responses of plankton and turbidity to biomanipulation in a shallow prairie lake. Hydrobiologia 200–201, 317–327.
Hanson, M.A., Butler, M.G., 1994a. Responses of plankton, turbidity, and macrophytes to biomanipulation in a shallow prairie lake. Can. J. Fish. Aquat. Sci. 51, 1180–1187.
Hanson, M.A., Butler, M.G., 1994b. Responses to food web manipulation in a shallow waterfowl lake. Hydrobiologia 279–280, 457–466.
Hansson, L.A., Annadotter, H., Bergman, E., Hamrin, S.F., Jeppesen, E., Kairesalo, T., Luokkanen, E., Nilsson, P., Søndergaard, M., Strand, J., 1998. Biomanipulation as an application of food-chain theory: constraints, synthesis, and recommendations for temperate lakes. Ecosystems 1, 558–574.
Hosper, S.H., 1997. Clearing lakes: an ecosystem approach to the restoration and management of shallow lakes in The Netherlands, Ministry of Transport, Public Works and Water Management, Institute for Inland Water Management and Wastewater Treatment. Lelystad, The Netherlands.
James, W.F., Barko, J.W., 1990. Macrophyte influences on the zonation of sediment accretion and composition in a north-temperate reservoir. Arch. Hydrobiol. 120, 129–142.
Jeppesen, E., Jensen, J., Søndergaard, M., Lauridsen, T., Pedersen, L., Jensen, L., 1997. Top–down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. Hydrobiologia 342–343, 151–164.
Jessen, B., Lound, R., 1962. An Evaluation of a Survey Technique for Submerged Aquatic Plants. Game Investigational Report No. 6, Minnesota Department of Conservation, St. Paul, MN.
Jupp, B., Spence, D., 1977. Limitations of macrophytes in a eutrophic lake, Lock Leven. II. Wave action, sediments and waterfowl grazing. J. Ecol. 65, 431–446.
Kantrud, H.A., 1990. Sago Pondweed (*Potamogeton pectinatus* L.): A Literature Review. US Fish and Wildlife Service, Fish and Wildlife Resource Publication No. 176.
Kowalczewski, A., Ozimek, T., 1993. Further long-term changes in the submerged macrophyte vegetation of the eutrophic Lake Mikolajskie (north Poland). Aquat. Bot. 46, 341–345.
Lauridsen, T., Jeppesen, E., Andersen, F.O., 1993. Colonization of submerged macrophytes in shallow fish manipulated Lake Væng: impact of sediment composition and waterfowl grazing. Aquat. Bot. 46, 1–15.
Lauridsen, T., Jeppesen, E., Søndergaard, M., 1994. Colonization and succession of submerged macrophytes in shallow Lake Væng during the first five years following fish manipulation. Hydrobiologia 275–276, 233–242.
Lodge, D.M., Cronin, G., Van Donk, E., Froelich, A.J., 1998. Impact of herbivory on plant standing crop: comparisons among biomes, between vascular and non-vascular plants and among freshwater herbivore taxa. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), The Structuring Role of Submerged Macrophytes in Lakes. Springer, New York, pp. 149–174.
McCune, B., Medford, M.J., 1997. PC-ORD, Multivariate Analysis of Ecological Data, Version 3.0. MjM Software Design, Gleneden Beach, OR.
McQueen, D., Mark, J., Johannes, R.S., Lafontaine, N.R., Young, A.S., Longbotham, E., Lean, D.R.S., 1990. Effects of planktivore abundance on chlorophyll-*a* and Secchi depth. Hydrobiologia 200–201, 337–341.
Middleboe, A.L., Markager, S., 1997. Depth limits and minimum light requirements of freshwater macrophytes. Freshwater Biol. 37, 553–568.
Moss, B., 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200–201, 367–377.
Moss, B., Stansfield, J., Irvine, K., Perrows, M., Phillips, G., 1996. Progressive restoration of a shallow lake: a 12-year experiment in isolation, sediment removal and biomanipulation. J. Appl. Ecol. 33, 71–86.
Okland, R., 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? J. Veg. Sci. 7, 289–292.
Ozimek, T., Gulati, R.D., Van Donk, E., 1990. Can macrophytes be useful in biomanipulation of lakes? The Lake Zwemlust example. Hydrobiologia 200–201, 399–407.
Ozimek, T., Pieczynska, E., Hankiewicz, A., 1991. Effects of filamentous algae on submerged macrophyte growth: a laboratory experiment. Aquat. Bot. 41, 309–315.
Palmer, M.W., 1993. Putting things in even better order: the advantages of canonical correspondence analysis. J. Ecol. 74, 2215–2230.

Perrow, M.R., Meijer, M.-L., Dawidowicz, P., Coops, H., 1997a. Biomanipulation in shallow lakes: state of the art. Hydrobiologia 342–343, 355–365.
Perrow, M.R., Schutten, J., Howes, J.R., Holzer, T., Madgwick, F.J., Jowitt, A.J.D., 1997b. Interactions between coot (*Fulica atra*) and submerged macrophytes: the role of birds in the restoration process. Hydrobiologia 342–343, 214–225.
Petticrew, E., Kalff, J., 1992. Water flow and clay retention in submerged macrophyte beds. Can. J. Fish. Aquat. Sci. 49, 2483–2489.
Rice, W.R., 1990. A consensus combined P-value test and family-wide significance of component tests. Biometrics 46, 303–308.
Sand-Jensen, K., Vindbæk Madsen, T., 1991. Minimum light requirements of submerged freshwater macrophytes in laboratory experiments. J. Ecol. 79, 749–764.
Scheffer, M., 1998. Ecology of shallow lakes. Chapman & Hall, London.
Scheffer, M., Hosper, S.H., Meijer, M.-L., Moss, B., Jeppesen, E., 1993. Alternative equilibria in shallow lakes. Trends Ecol. Evol. 8, 275–279.
Scheffer, M., de Redelijkheid, M.R., Noppert, F., 1992. Distribution and dynamics of submerged vegetation in a chain of shallow eutrophic lakes. Aquat. Bot. 42, 199–216.
Schriver, P., Bogestrand, J., Jeppesen, E., Sondergaard, M., 1995. Impact of submerged macrophytes on fish–zooplankton–phytoplankton interactions: large-scale enclosure experiments in a shallow eutrophic lake. Freshwater Biol. 33, 255–270.
Shapiro, J., 1990. Biomanipulation: the next phase-making it stable. Hydrobiologia 200–201, 13–27.
Simons, J., Nat, E., 1996. Past and present distribution of stoneworts (Characeae) in The Netherlands. Hydrobiologia 340, 127–135.
Simons, J., Ohm, M., Daalder, R., Boers, P., Rip, W., 1994. Restoration of Botshol (The Netherlands) by reduction of external nutrient load: recovery of a Characean community, dominated by *Chara connivens*. Hydrobiologia 275–276, 243–253.
Søndergaard, M., Bruun, L., Lauridsen, T., Jeppesen, E., Vindbæk Madsen, T., 1996. The impact of grazing waterfowl on submerged macrophytes: in situ experiments in a shallow eutrophic lake. Aquat. Bot. 53, 73–84.
Strand, J., 1999. The development of submerged macrophytes in Lake Ringsjön after biomanipulation. Hydrobiologia 404, 113–121.
Ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. J. Ecol. 67, 1167–1179.
Ter Braak, C.J.F., 1994. Canonical community ordination. I. Basic theory and linear methods. Ecoscience 1, 127–140.
Ter Braak, C.J.F., 1995. Ordination. In: Jongman, R.H.G., Ter Braak, C.J.F., Van Tongeren, O.F.R. (Eds.), Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge, UK, pp. 91–169.
Ter Braak, C.J.F., Verdonschot, P.F.M., 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquat. Sci. 57, 254–289.
Timms, R., Moss, B., 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplantivorous fish, in a shallow wetland ecosystem. Limnol. Oceanogr. 29, 472–486.
Van den Berg, M.S., Coops, H., Meijer, M.-L., Scheffer, M., Simons, J., 1998a. Clear water associated with a dense *Chara* vegetation in the shallow and turbid Lake Veluwemeer, The Netherlands. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), The Structuring Role of Submerged Macrophytes in Lakes. Springer, New York, pp. 339–352.
Van den Berg, M.S., Coops, H., Simons, J., De Keizer, A., 1998b. Competition between *Chara aspera* and *Potamogeton pectinatus* as a function of temperature and light. Aquat. Bot. 60, 241–250.
Van Dijk, G.M., Van Vierssen, W., 1991. Survival of a *Potamogeton pectinatus* L. population under various light conditions in a shallow eutrophic lake (Lake Veluwe) in The Netherlands. Aquat. Bot. 39, 121–129.
Van Donk, E., Gulati, R.D., 1995. Transition of a lake to turbid state six years after biomanipulation: mechanisms and pathways. Water Sci. Tech. 32, 197–206.
Van Donk, E., Gulati, R.D., Grimm, M., 1989. Food-web manipulation in Lake Zwemlust: positive and negative effects during the first two years. Hydrobiol. Bull. 23, 19–35.
Van Donk, E., Otte, A., 1996. Effects of grazing by fish and waterfowl on the biomass and species composition of submerged macrophytes. Hydrobiologia 340, 285–290.

Van Wijk, R., 1989. Ecological studies on *Potamogeton pectinatus* L. III. Reproductive strategies and germination ecology. Aquat. Bot. 33, 271–299.
Vermaat, J., Santamaria, L., Roos, P., 2000. Water flow across and sediment trapping in submerged macrophyte beds of contrasting growth form. Arch. Hydrobiol. 148, 549–562.
Weisner, S., Strand, J., Sandsten, H., 1997. Mechanisms regulating abundance of submerged vegetation in shallow eutrophic lakes. Oecologia 109, 592–599.