Hydrobiologia **337**: 93–106, 1996.

Existence of a macrophyte-dominated clear water state over a very wide range of nutrient concentrations in a small shallow lake

Meryem Beklioglu[1,2] & Brian Moss[1]
[1] *Department of Environmental and Evolutionary Biology, The University of Liverpool L69 3BX, UK*
[2] *Department of Biology, Middle East Technical University, Ankara, 06531, Turkey*

Received 18 October 1995; in revised form 13 August 1996; accepted 20 August 1996

Key words: sewage effluent, *Daphnia*, grazing, macrophytes, clear water, alternative stable states

Abstract

Little Mere, a small shallow lake, has been monitored for four years, since its main source of nutrients (sewage effluent) was diverted. The lake has provided strong evidence for the persistence of a clear water state over a wide range of nutrient concentrations. It had clear water at extremely high nutrient concentrations prior to effluent diversion, associated with high densities of the large body-sized grazer, *Daphnia magna*, associated with low fish densities and fish predation. Following sewage effluent diversion in 1991, the nutrient concentrations significantly declined, the oxygen concentrations rose, and fish predation increased. The dominance of large body-sized grazers shifted to one of relatively smaller body-sized animals but the clear water state has been maintained. This is probably due to provision of refuges for grazers by large nymphaeid stands (also found prior to diversion). There has been a continued decrease in nutrient concentrations and expansion of the total macrophyte coverage, largely by submerged plants, following effluent diversion. The grazer community of Little Mere has also responded to this latter change with a decline in daphnids and increase in densities of weed-associated grazers. The presence of large densities of such open water grazers was the apparent main buffer mechanisms of the clear water state until 1994. The lake has, so far, maintained its clear water in the absence of such grazers. Thus, new buffer mechanisms appear to operate to stabilize the ecosystem. Little Mere appears to have shifted from previous top-down controlled clear water state to a bottom-up controlled clear water state.

Introduction

Restoration of shallow eutrophic lakes by means of external nutrient control has often resulted in only short-term recovery or complete failure (Bengtsson et al., 1975; Sas, 1989). The potential of external nutrient control seems thus to be lower for many lakes than formerly anticipated, and other techniques need to be used, often in addition to nutrient control, to ensure water quality improvement. There has been much debate about the relative importance of determination of phytoplankton crops by nutrients (bottom-up control) or by zooplankton grazing (top-down control) (DeMelo et al., 1992; Carpenter & Kitchell, 1992). It has become generally accepted that both influences may operate depending on the circumstances (McQueen, 1990). Top-down control or food web manipulation may therefore offer some help in restoration. A variety of examples shows the success of top-down control of phytoplankton crops by large Cladocera, especially *Daphnia* (van Donk et al., 1990; Gulati, 1989; Moss et al., 1994). The short-term results of these food web manipulations are encouraging, but there is still much controversy about the long-term stability of the clear-water state. Signs of deterioration of water quality of manipulated shallow lakes have already been recorded (Perrow et al., 1994; Meijer et al., 1994), hinting at a possible return to a turbid-water state. These signs are often associated with a lack of macrophytes and the significant key-role they may play in maintaining clear water in shallow lakes.

Turbid water with phytoplankton dominance (or suspended sediment) and a clear water state with strong macrophyte dominance seem to be alternative stable states in shallow eutrophic lakes (Scheffer, 1990; Moss, 1990; 1991; Scheffer et al., 1993). The macrophyte-dominated clear water state possesses a number of feedback mechanisms for stabilizing the clear water state by provision of refuges for phytoplankton grazers against fish predation (Timms & Moss, 1984), similar linkages for periphyton grazers (Leah et al., 1978), allelopathy (Wium-Anderson, 1987), reduction of resuspension of bottom material (Boström et al., 1982), and nutrient limitation of phytoplankton through nitrogen uptake by the plants or denitrification by the microorganisms associated with them (Ozimek et al., 1990; van Donk et al., 1993). Macrophytes also provide spawning grounds and refuge against cannibalization for piscivorous fish like pike, which in turn decrease zooplanktivorous and benthivorous fish density (Grimm, 1989). The role of aquatic vegetation in lake restoration is therefore predominantly a stabilizing one. Thus, success of these techniques, which have been used to improve water quality, may depend on establishment of strong and diverse macrophyte stands. In turn the effectiveness of these stands may depend on the nutrient status of the lake water. There is little precise information in these relationships but a picture is being built up from the collective experience of individual lake studies. This investigation of Little Mere, in Cheshire, is part of that experience.

Lake description

Little Mere is a small shallow (area 2.8 ha, z_{max} 2.6 m, z_{mean} 0.7 m) lake in Cheshire, England. Until June 1991, a sewage- treatment works, situated on its bank, discharged effluent into Little Mere, whose water was heavily nutrient-enriched. The algal growth potential of the water was very high with of 2484 $\mu g\ l^{-1}$ total phosphate (TP) and 4.6 mg l^{-1} ammonium (NH_4-N) mean summer pre-diversion concentrations and pH values in the range 7.3 to 9.0 (Carvalho, 1994). There was a negligible fish population because of very low dissolved oxygen concentration (less than 4 mg l^{-1} around mid-day over the summer months with a recorded minimum of 0.7 mg l^{-1}) and probable complete deoxygenation at night. Although fish could move into the lake, there was evidently little fish predation on the zooplankton community which was dominated by very large body-sized *Daphnia magna* Straus. The phytoplankton population in summer was negligible with a mean concentration of 6 mg l^{-1} chlorophyll *a* in summer 1990 (Carvalho, 1994). The lake had large stands of water-lilies (*Nuphar lutea* (L.) Smith and *Nymphaea alba* L.) and clumps of submerged plants (*Potamogeton berchtoldii* Fieber, *Elodea canadensis* Michaux).

After June 1991, when the sewage effluent was diverted, the lake began to change. Dissolved oxygen concentration rose and fish (predominantly perch, *Perca fluviatilis* L.), moved in from upstream. TP and NH_4-N concentrations fell markedly (with annual means 185 $\mu g\ l^{-1}$ and 80 $\mu g l^{-1}$, respectively). However, although nutrient concentrations remained high enough to support considerable algal growth, the chlorophyll *a* concentrations did not increase and the water stayed clear (Carvalho et al., 1995). A long period of resilience in phosphorus concentrations was anticipated in Little Mere, from previous studies on shallow eutrophic lakes which have shown small response to reduction of external nutrient loading due to internal nutrient loading. Mass balance studies of TP and dissolved inorganic nitrogen (DIN) have shown insignificant internal loading of N and P three years after effluent diversion (Beklioglu, 1995).

In this study we took advantage of the opportunity given by sewage effluent diversion to observe whether the pre-diversion macrophyte-dominated clear water state of the lake would be maintained as fish recolonized. We were also able to observe how top-down and bottom-up mechanisms might operate in the ecosystem in controlling algal growth following recolonization of fish and decline of the nutrient concentrations.

Methods

Phytoplankton and zooplankton

Water samples for chlorophyll *a*, phytoplankton and zooplankton were collected at fortnightly intervals from a central station in Little Mere from October 1990 to April 1994 using a 1-m plastic tube sampler. Chlorophyll a was extracted in 90% acetone, and concentration was calculated from the absorbance reading at 663 nm (Talling & Driver, 1961) to precision of ± 5%. Phytoplankton samples were preserved with Lugol's solution immediately after sampling and counted to a precision of ± 20% with an inverted microscope (Wilds M40) at a magnification of 400 ×. Biovolumes were determined from measurement of the linear dimensions of ten preserved cells of each taxon, using formulae for the appropriate geometric shapes (Wetzel & Likens, 1991). Biovolume density of each species (μm^3 l^{-1}) was determined by multiplying average cell volume by cell population density. Community biovolume density was obtained by summing values for all species. For zooplankton samples 10 l of water were taken from the entire water column and filtered through plankton net (mesh size 67 μm). The zooplankton samples were narcotized with a chloroform (Gannon & Gannon, 1975) and preserved in 4% formaldehyde solution. Samples were subsampled, and counted under a Kyowa steremicroscope. When samples were subsampled, at least 100 of the commonest species were counted (Bottrell et al., 1976).

Throughout summer 1992 and 1993, ancillary zooplankton samples were collected from different habitats at the same times as the regular samples for phytoplankton and zooplankton.

Fish

The lake was fished three different areas on three occasions: January 1993, June 1993 and November 1993 by using a micro- mesh seine net (25 m long, 2 m deep, 2.5 mm mesh-size). Fish were caught in three sweeps of micromesh seine net on each occasion. Fish length was measured from snout to the base of the tail fork.

Aquatic plant survey

Plant occurrence was plotted along multiple measured transects on detailed maps (1:2500) of bathymetry and vegetation made at scale of in August 1993. Plant samples were taken from a boat using a grapnel and a Petersen grab. Aquatic plants were identified using Haslam et al. (1975). Percentage cover of submerged and floating-leaved communities was estimated from a weighed photocopied image of the vegetation map.

Results

Phytoplankton and zooplankton

The lake showed a significant declining trend of annual mean chlorophyll *a* concentrations over the study period from 59 μg l^{-1} in 1990 to 6 μg l^{-1} in 1992, increasing slightly to 17 μg l^{-1} in 1993. The Secchi disc transparency reached to the lake bottom throughout the study (Carvalho et al., 1995). Mean chlorophyll *a* concentrations were mostly due to the spring increase in phytoplankton community and the spring increases were much lower and with different species contributions after sewage effluent diversion. In spring 1990 (before diversion), a huge phytoplankton biomass developed, with the diatom *Stephanodiscus hantzschii* Grun, the cryptomonads *Cryptomonas* spp. (Figure 1a & 1c) and the cyanophytes *Planktothrix agardhii* (Gom.) Anagn. et Kom. and *Coelosphaerium naegelianum* Unger (Figure 1b). In 1990 there was an increase in green algae (*Planktosphaeria* sp.) (Figure 1c). The spring increase in phytoplankton biomass developed later, and to a lesser extent, in 1991, 1992 and 1993 compared with 1990. In spring 1993 there was a shift in the dominant diatom species from *S. hantzschii* to *Aulacoseira* sp. which was also recorded in spring 1994 (Figure 1a). There was a large increase in Cryptomonas biomass in 1993 (Figure 1c).

The phytoplankton biovolumes in the summers of the various years were similar and very low. The only alga of any importance during the 1990 and 1991 summers was the large, grazer-resistant, *Volvox* sp. which was visibly present in late summer (Carvalho, 1994), but had little impact on chlorophyll *a* concentrations or algal biovolumes. Cryptomonads, (*Cryptomonas* spp.) were present with varying biovolumes in the summer phytoplankton community throughout the study period. Percentage contribution to the community biovolume are shown in Figure 2.

The zooplankton grazers included *Daphnia magna*, *Daphnia longispina* aggregate (Figure 3a), *D. hyalina* Leydig, *Bosmina longirostris* (O. F Müll) (Figure 3b), *Eurycercus lamellatus* (O. F Müll) and *Diaptomus gracilis* Sars (Figure 3c). Throughout the study period, contributions of *Cyclops* and rotifers were insignificant. In 1990 and 1991 *D. magna* and *D. longispina* dominated the crustacean zooplankton though the densities of the grazers were lower in 1991 than the previous year (Figure 3a). In both years *D. magna* was unusually bright red and because of its large size (growing up to 5 mm) it was clearly visible in the water (Carvalho, 1994; Beklioglu, 1995). Both in 1990 and 1991, *D. magna* and *D. longispina* made the highest contribution to total zooplankton density (in 1990, 56.3% and 41.9% respectively and in 1991, 72.9% and 13.3% respectively) (Figures 4a & 4b). In 1992, the contributions of *D. magna* (21.5%) and *D. longispina* (6.9%) were lower than in the previous years. *D. hyalina* was observed in the zooplankton community for the first time with a contribution of 10.8% to the total numbers (Figures 3b & 4c). There was also an increase in contribution of *Bosmina longirostris* to 13.8% (Figure 4c). In 1993, the shift from *D. magna*

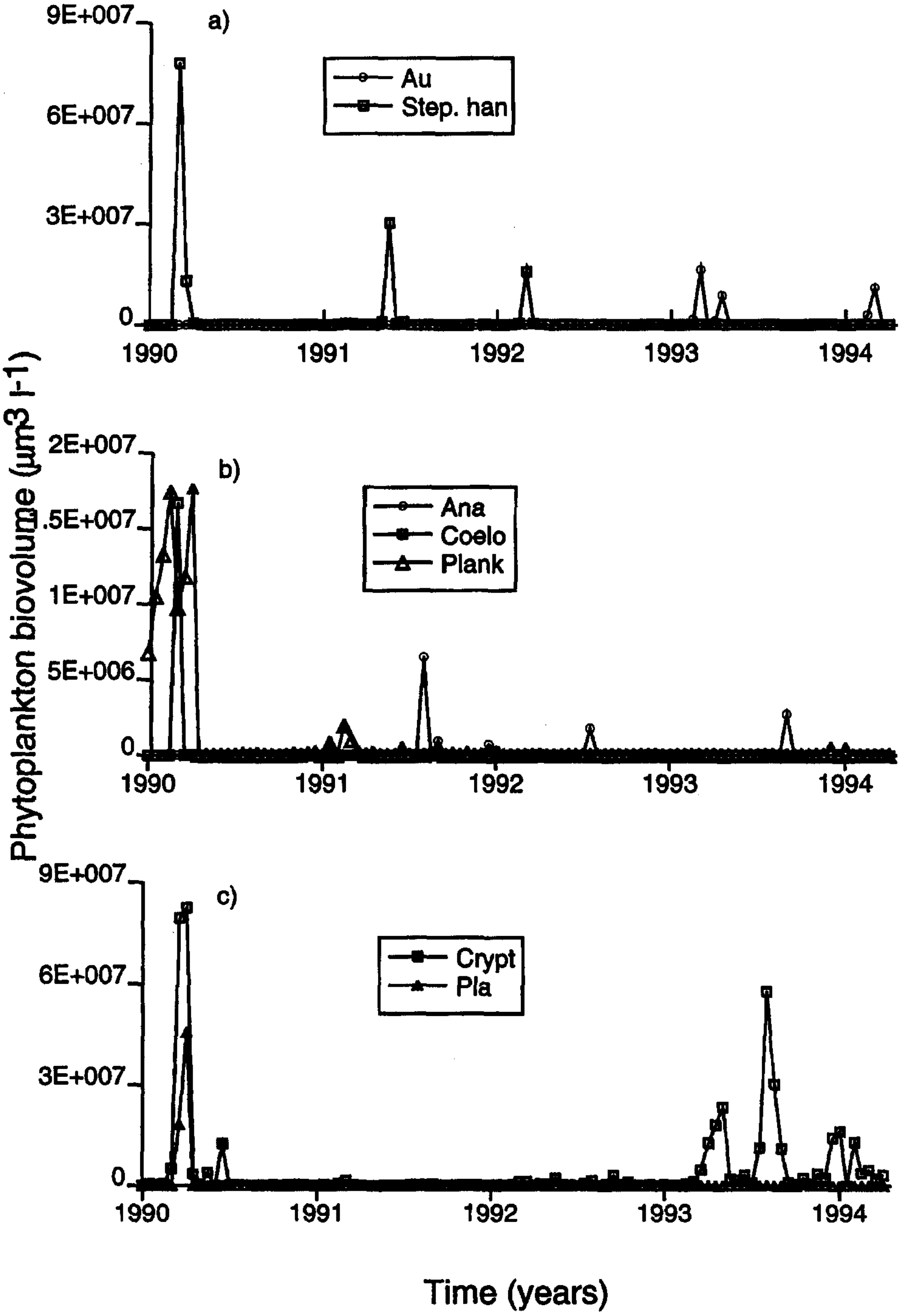


Figure 1. Changes in biovolume of (a) Step.han: *Stephanodiscus hantzchii* and Au: *Aulacoseira* sp. (b) Ana: *Anabaena* sp., Coelo: *Coelosphaerium naegelianum* and Plank: *Planktothrix agardhii* (c) Crypt: *Cryptomonas* spp., Pla: *Planktosphaeria* sp. in Little Mere between 1990 and 1994 (first three months data of 1994 shown).

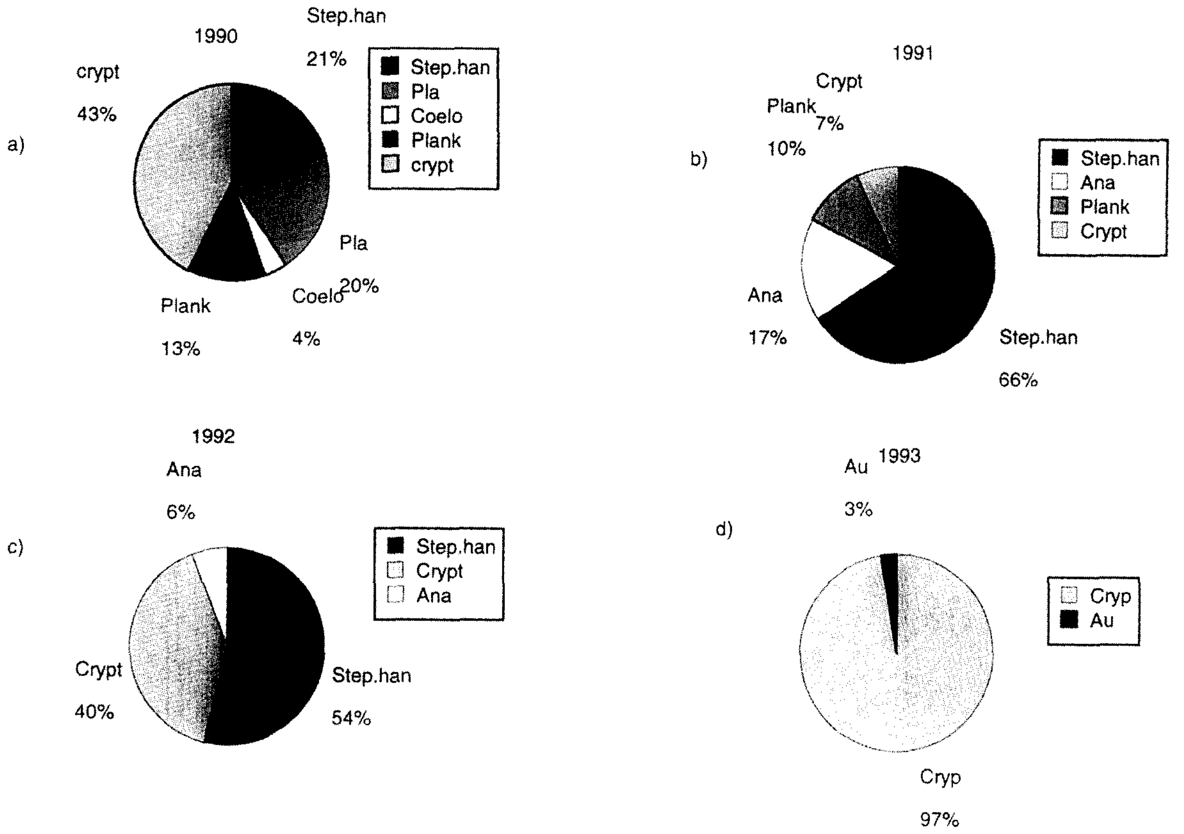


Figure 2. Changes in percentage contribution to phytoplankton biovolume in the growing seasons (March to October) of (a) 1990, (b) 1991, (c) 1992 and (d) 1993 in Little Mere.

and *D. longispina* to *D. hyalina* was much more prominent than in 1992 (Figures 3a & 3b) and *D. hyalina* made 45.3% contribution to the total zooplanton density (Figure 4d); *D. magna* was not recorded and density of *D. longispina* was very low (Figures 3a & 3b). There was also an increase in contribution of *Diaptomus gracilis*, which co-dominated along with *D. hyalina* (Figures 4c & 4d). Weed-bed associated Cladocera, including *Eurycercus lamellatus* were recorded for the first time with an important contribution to the community (12.9%) (Figure 4d).

Linear regression analysis between chlorophyll *a* and *Daphnia* density showed no significant relationship (Figures 5a & 5b), though for much of the summer the water was clear and nutrient rich and *Daphnia* was abundant. This implies availability of alternative food sources for *Daphnia* to maintain high density.

Fish

Perch, *Perca fluviatilis* L., dominated the fish community of Little Mere with 17, 99 and 19 perch caught (in January, July and November 1993, respectively) (Table 1). Numbers of roach (*Rutilis rutilis* L.) were higher in January 1993 than in July and November 1993 (11, 1 and 1 respectively) (Table 1). Populations of tench (*Tinca tinca* L.) and pike (*Esox lucius* L.) were detected but in low numbers.

Aquatic plants

The aquatic plant community in 1993 (Figure 6) was well developed in the clear water and included extensive beds of floating-leaved water lilies (*Nuphar lutea* (L.) Smith and *Nymphaea alba* L.) which covered about 33% of the lake area. There was increased spread of the submerged plant, *Potamogeton berchtoldii* Fiber between 1992 and 1993 when it covered 44% of the

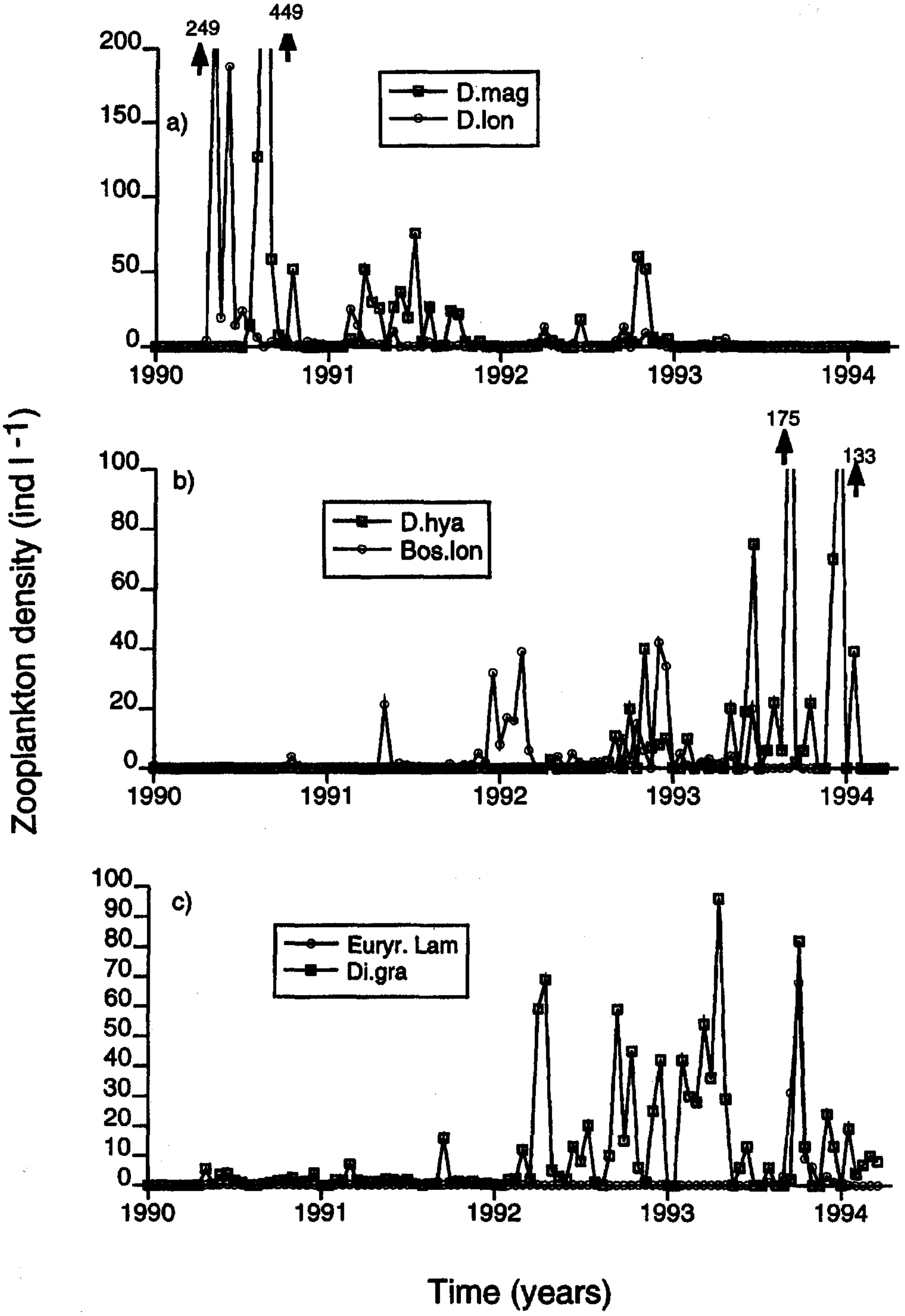


Figure 3. Changes in density of (a) *Daphnia magna* and *D. longispina* (b) *D. hyalina* and *Bosmina longispina* (c) *Diaptomus gracilis* and *Eurycercus lamellatus* in Little Mere between 1990 and 1994 (first three months data of 1994 shown).

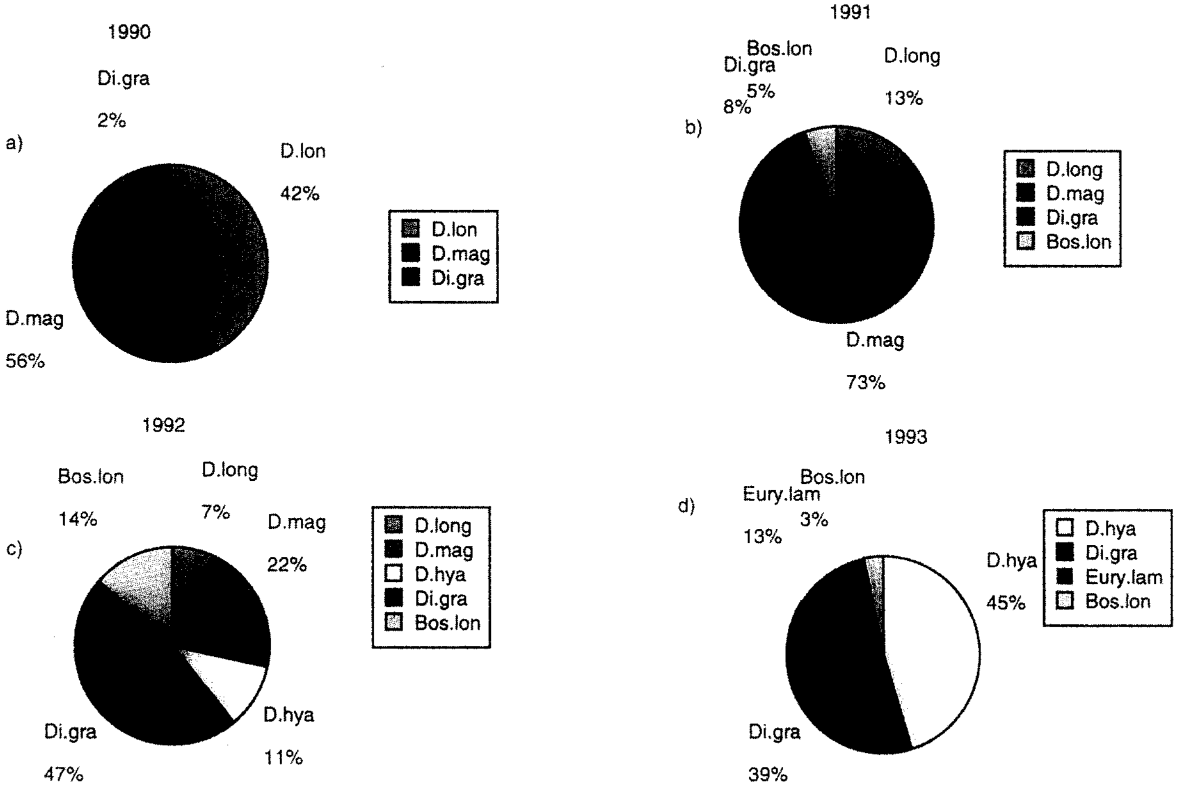


Figure 4. Changes in total zooplankton density in the growing season (March to October) of (a) 1990, (b) 1991, (c) 1992 and (d) 1993 in Little Mere.

Table 1. Details of fish caught on three occasions in 1993 in Little Mere (mean body lengths ±SD and are given in cm).

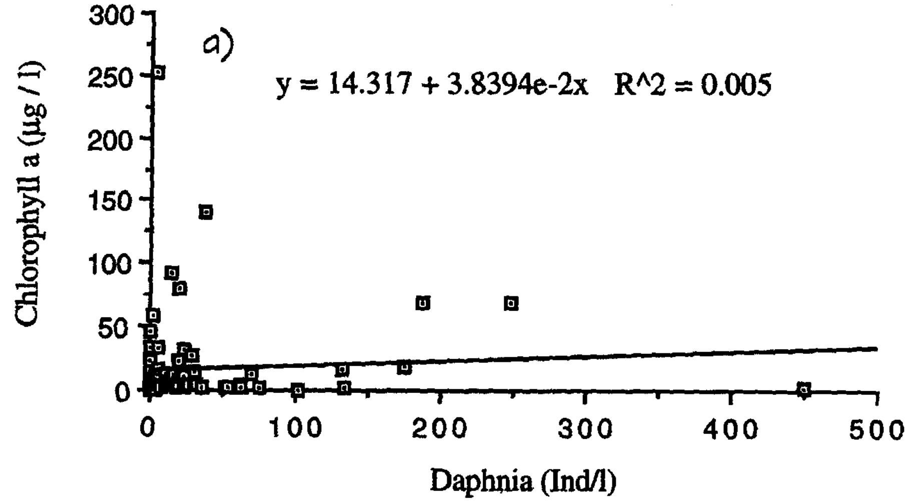
	Roach	Perch	Tench	Pike
(*Rutilis rutilis* L.)	(*Perca fluvialitis* L.)	(*Tinca tinca* L.)	(*Esox lucius* L.)	
January 1993 ∗	11	17	2	2
	(7.06±0.3)	(18±0.3)	(3.15±0.2)	(51.5±4)
July 1993	1	99	–	–
	(15.3)	(14.9±0.1)		
November 1993	1	19	–	1
	(18.5)	(17.1±0.3)		(22)

∗ Fish were caught in three sweeps of a micromesh seine net on each occasion.

lake area. The other dominant submerged species was *Elodea canadensis* Michaux. Small patches of *Nitella* sp. and *Callitriche* sp. were recorded.

Ancillary data on the zooplankton community of the lake in different habitats

D. magna densities in the summer of 1992 ($n = 12$) were significantly higher ($P < 0.001$) in water-lily beds (67 ± 27 SD ind. l^{-1}) than in open water (6 ± 10 ind. l^{-1}). Densities of *D. hyalina*, *Bosmina longirostris*, *Ceriodaphnia* spp. *Eurycercus lamellatus* and *Chy-*



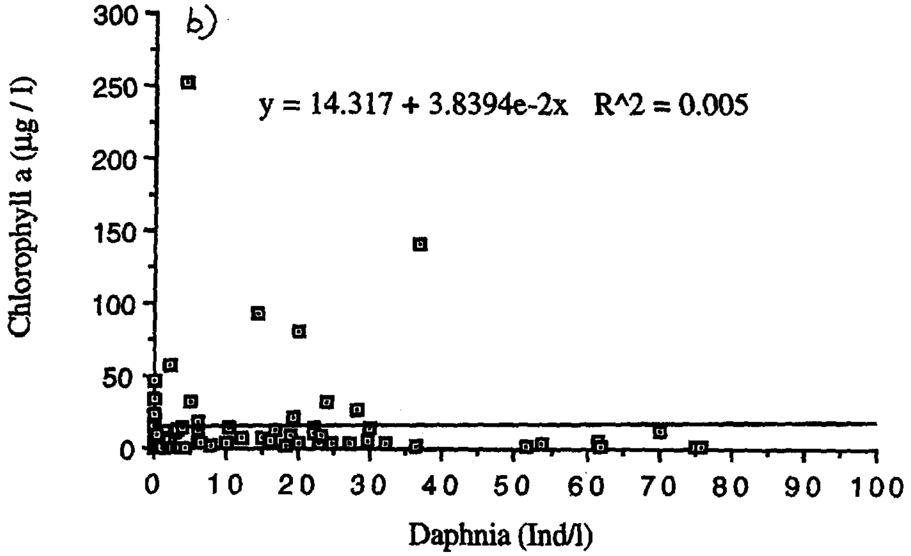


Figure 5. (a) and (b) The relationship between *Daphnia* and chlorophyll *a* in Little Mere between 1990 and 1994 (first three months data of 1994 shown).

dorus ovalis in open water, within *Nuphar lutea* beds and in *Potamogeton berchtoldii* beds in summer 1993, differed significantly (Table 2). The highest densities of *D. hyalina* were found in *Nuphar lutea* beds. Open water favoured *Bosmina longirostris*. The densities of *Ceriodaphnia* spp. were significantly lower in *Nuphar lutea* beds than in the other habitats. The densities of *Chydorus ovalis* did not differ among the plant beds. *Potamogeton berchtoldii* beds favoured *Eurycercus lamellatus*.

Discussion

According to observed relationships between lake phosphorus concentrations and chlorophyll *a* concentrations (Dillon & Rigler, 1974), Little Mere showed a huge potential for phytoplankton growth, though to a lesser but still considerable extent following the sewage effluent diversion (Carvalho et al., 1995). The lake had a brief spring increase in diatoms, small flagellates, and cyanophytes in 1990 (Carvalho, 1994), as is common in many temperate lakes (Hutchinson, 1967). This is often followed by a spring 'clear water' phase

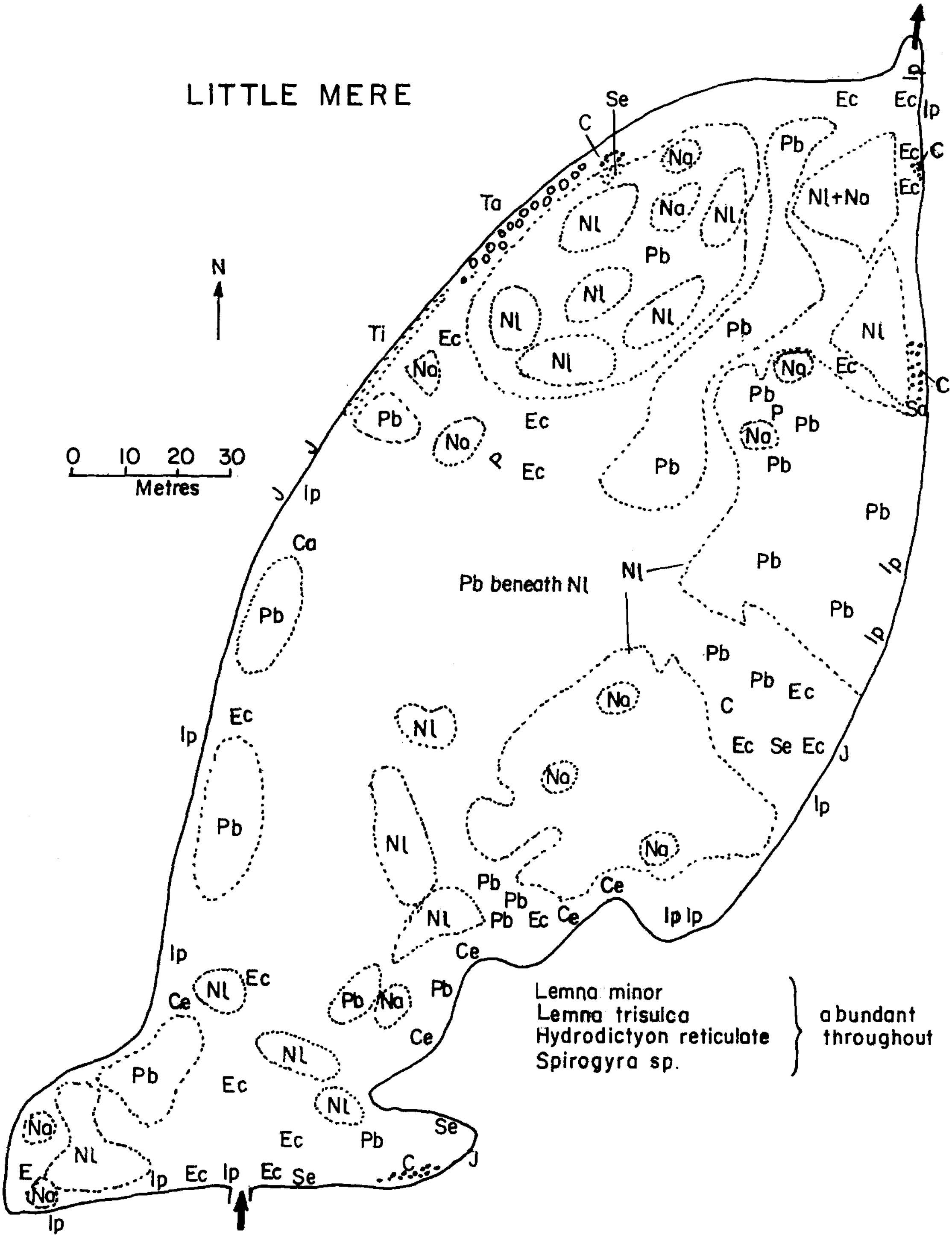


Figure 6. Aquatic plant survey of Little Mere (carried out in July 1993). Ec, *Elodea canadensis*; Ca, *Callitriche hermaphroditica*; Pb, *Potamogeton berchtoldii*; Nl, *Nuphar lutea*; Na, *Nymphaea alba*; Ip, *Iris pseudacorus*; J, *Juncus* spp.; Ta, *Typha angustifolia*; TI, *Typha latifolia*; Se, *Sparganium erectum*; C, *Carex* spp..

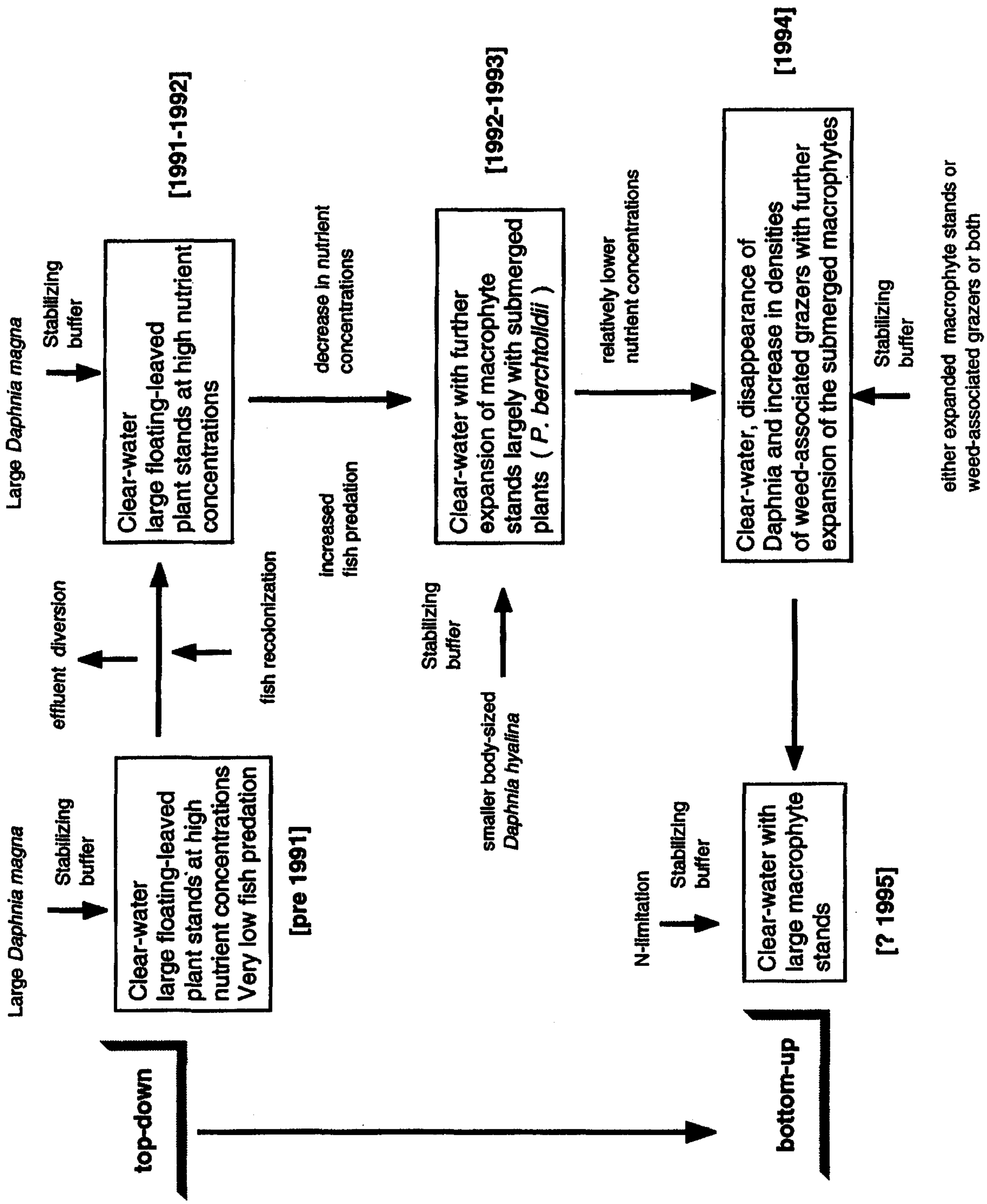


Figure 6. Ecosystem development in Little Mere between 1990 and 1994.

Table 2. Comparision of densities (Ind. l^{-1}) of *Daphnia hyalina, Bosmina longirostris, Ceriodaphnia* spp., *Chydorus ovalis* and *Eurycercus lamellatus* in open water, and within *Nuphar lutea* and *Potamogeton berchtoldii* beds in Little Mere in summer 1993. Results of Fisher's multiple comparisons (based on pairwise differences between level means): O, open water; N, *Nuphar lutea*; P, *Potamogeton berchtoldii.* The habitat values are arranged in order of increasing densities from left to right. A common line beneath letters denotes that densities in these habitats were not significantly different ($\alpha = 0.05$) from each other.

	Open water	Nuphar lutea	Potamogeton berchtoldii	One-way ANOVA	Habitats comparisons
D. hyalina	4.7±4.5	38±8	7.5±9.9	***	$\underline{\text{O}\quad\text{P}}\quad\text{N}$
B. longirostris	28±54	0.25±0.5	1±2	NS	$\underline{\text{N}\quad\text{P}}\quad\text{O}$
Ceriodaphnia spp	90±82	8.8±6.8	65±47	NS	$\text{N}\quad\underline{\text{P}\quad\text{O}}$
Chydorus ovalis	0.25±0.50	31±16	54±69	NS	$\text{O}\quad\underline{\text{N}\quad\text{P}}$
E. lamellatus	1.5±1.9	4.2±5	29±29	*	$\underline{\text{O}\quad\text{N}}\quad\text{P}$

* $P < 0.05$
*** $P < 0.01$
NS: no significance

because of large densities of filter feeders (Lampert et al., 1986). In Little Mere, the clear water phase extended throughout the summers of the study period. The summer clear water phase was almost certainly due to high densities of grazers, in particular the large bodied *Daphnia magna* (Carvalho, 1994; Beklioglu, 1995) and later *D. hyalina.*

In Little Mere, there has been a considerable change in water chemistry following sewage effluent diversion in June 1991 (Carvalho et al., 1995), which in turn has been associated with great changes in both the phytoplankton community and the zooplankton community. Although the lake had very clear water in the summers of the study period, there was an increase in summer in the biomass of *Cryptomonas* spp., in 1993, despite the presence of high densities of *D. hyalina.* The apparent lack of grazer effect on *Cryptomonas* spp. might be due to high growth rates of the algae. In 1993/4, a shift from *Stephanodiscus hantzchii* to *Aulacoseira* sp. might be a response to reduced phosphorus concentration (Anderson et al., 1990) and increased Si:P ratios (Tilman et al., 1982). Following sewage effluent diversion, TP concentrations decreased over ten fold (from 2245 mg l^{-1} in 1990 to 185 mg l^{-1} in 1993) (Carvalho et al., 1995); in turn Si:P ratio increased from 1.97 to 11.27. *Aulacoseira* sp. is a mesotrophic plankton form (Anderson, 1990) associated with high Si:P ratios (Tilman et al., 1982). However, a similar shift in diatom species occurred in the upstream Mere Mere, where there has been no input of sewage effluent nor major change following diversion of it which would appear to negate simple explanations. It is possible that year to year weather and hyrological effects may have been involved.

Cyanophytes were nearly absent from Little Mere throughout the study period, except in spring 1990. The cyanophytes disappeared in the spring at the same time as *Daphnia magna* density increased. Throughout summer the *D. magna* densities were very high and the biovolume of cyanophytes was very low. Though controversy surrounds the suitability of Cyanophyta as a food source for zooplankton (Nizan et al., 1986; Arnold, 1971; Gliwicz, 1990), a wide range of examples is available confirming a general pattern of cyanophyte reduction after fish removal and the consequent increase in filter-feeding zooplankton (van Donk et al., 1989; Jeppesen et al., 1990). The presence of inocula from the upstream Mere Mere and Little Mere's very low flushing rate in summer might be expected to favour them. However, the presence of high free-CO_2 concentration and low pH due to a large contact area with organic sediments enriched with organic matter from the sewage effluent prior to diversion, may have mitigated against cyanophytes (Shapiro, 1990). The role of CO_2 for cyanophytes in Little Mere was checked in experimental enclosures with increasing pH values (giving low free-CO_2 concentrations). Lack of cyanophytes in the lake does not seem to be function CO_2 or pH (Beklioglu & Moss, 1995).

Individuals of *D. magna* were bright red (Carvalho, 1994) due to the presence of haemoglobin, which is produced in response to low levels of dissolved oxygen (Carvalho, 1984). The pigmentation increases their vulnerability to visual predation by fish (Kerfoot,

1980) and because of their large size (up to 5 mm) and the clear water conditions, *D. magna* would have been very susceptible to fish predation. Evidently there was little fish predation on the zooplankton community since no fish were caught in three sweeps of the micromesh seine netting in 1991. The same year, gill-netting caught ten fish: six roach (21–27 cm long) and four pike (44–53 cm long) (Carvalho, 1994). The quality of the sewage effluent was such as to deoxygenate the water to near anoxia (Carvalho, 1994; Carvalho et al., 1995), which might have resulted in very brief survival of fish entering from upstream. Thus, the large body-sized *D. magna* thrived under probably very low predation pressure.

Following the sewage effluent diversion, fish, predominantly perch, *Perca fluviatilis* L., moved in from upstream (Table 1). Although the density of the large grazers, *D. magna*, decreased, clear-water was maintained despite the presence of mainly juvenile perch, probably because of the presence of large stands of macrophytes including nymphaeids, *Potamogeton berchtoldii* Fieber and *Elodea canadensis* Michaux. The importance of aquatic plants as refuges for high populations of *Daphnia* was shown in Little Mere by significantly higher numbers of *Daphnia magna* in water lily beds (67 ind l^{-1}) than open water (6 ind l^{-1}). In 1993 there was a switch from *Daphnia magna* to *Daphnia hyalina*, probably due to increased predation pressure of fish or less available food for *Daphnia magna*. *Daphnia hyalina* was prominent. Because of the increase in the aquatic plant stand, weed-bed associated zooplankters, largely *Eurycercus lamellatus*, with lesser densities of *Simocephalus* spp. and *Sida crystallina* (O.F. Müller) became more prominent. The low densities of weed-bed associated cladocerans might be due to the nature of the sampling station which was an open water. Samples taken from the weed- bed in summer 1993, at the same time as those for phytoplankton and zooplankton, contained higher densities of *Eurycercus lamellatus* in *Potamogeton berchtoldii* beds (Table 2). The density of *Daphnia hyalina* was subsequently found to be negligible during diurnal sampling in summer 1994 (Beklioglu, 1995) and this was consistent with its general density in the lake throughout summer 1994 (D. Stephen, unpublished data). Experiments with changed plant densities in enclosures in Little Mere have shown reduction in numbers of *D. hyalina* at high plant densities in the presence or absence of perch (B. Moss & R. Kornijow, unpublished data). Thus, further expansion of the macrophyte stands largely with *Potamogeton berchtoldii* might have mitigated against open water grazers such as *D. hyalina*, as significantly lower densities of it were found in *Potamogeton berchtoldii* beds in summer 1993 (Table 2).

Experiments in mesocosms, in 1992 and 1993 (Beklioglu & Moss, 1996) have shown strong effects of *Daphnia* grazing in controlling phytoplankton crops. But linear regression analysis between the density of *Daphnia* and chlorophyll *a* in Little Mere showed no significant relationship. The phytoplankton community of Little Mere was probably not nutrient-limited because the concentrations of SRP and DIN were extremely high prior to the effluent diversion and though their concentrations significantly decreased following the effluent diversion they remained substantial (Carvalho et al., 1995) and were high enough to give a large growth potential for algae. The explanation for the low phytoplankton crop was more likely related to the huge *Daphnia* density. The scatter graph (Figures 5a & 5b) showed a cluster of points around the origin because throughout the study chlorophyll *a* concentrations were near zero at very high *Daphnia* densities. This might have masked the significance of the grazing pressure of *Daphnia*. Maintenance of high *Daphnia* densities at low phytoplankton crops was most likely due to availability of alternative food sources. Some *Daphnia* species, with fine-mesh filters, like *D. magna* and *D. hyalina* are capable of utilizing bacteria and small detritus particles as a food source (Geller & Muller, 1981; Brendelberger, 1991).

Significance of Little Mere in providing evidence for the alternative stable state hypothesis

Following sewage diversion, Little Mere has so far maintained clear water, and the macrophyte-dominated clear water state found prior to diversion. Though even after effluent diversion, nutrient concentrations remained abundant, the water was clear and macrophytes flourished. If the sewage effluent had not deoxygenated the water to near anoxia and prevented much fish survival, could Little Mere have had turbid water? The answer to this question is likely to be no, because of the existence of large stands of water lilies and their buffering mechanisms. Provision of refuges to the large grazers, by macrophytes in Little Mere, may have been very important in retaining the high densities of *D. hyalina* at high fish predation following fish recolonization. Sewage effluent diversion did not increase the water clarity through reduction of phytoplankton growth in the lake because that the water was already clear prior to diversion. The results, therefore, suggest that a macrophyte dominated clear water state in summer can exist over a very wide range of nutrient concentrations, as Moss (1991) and Scheffer et al. (1993) suggest. Turbid-water with phytoplankton dominance and clear water with macrophyte dominance seem to be alternative stable states in shallow eutrophic lakes.

New model for the role of Daphnia

Biomanipulation of shallow lakes has focused on increasing daphnid density to bring water clarity through increased grazing pressure on phytoplankton crops (Shapiro & Wright, 1984; Gulati, 1990; Hosper & Meijer, 1993). In Little Mere, the presence of large densities of *Daphnia* was apparently the main buffer mechanism to stabilize macrophyte-dominated clear-water until 1994. With a mashed decline in *Daphnia*, the lake has maintained its previous clear-water state. It appears that new buffer mechanisms are now in operation for stabilizing the macrophyte-dominated clear water. Though little is known about the grazing efficiency of weed-bed associated cladocerans on phytoplankton crops, they may have played an important role in maintaining clear-water in the lake. The expansion of rooted macrophyte stands (largely *Potamogeton berchtoldii*) might also have been important for the low chlorophyll *a* concentrations as well. Rooted plants have access to sedimentary nutrients through their roots (Denny, 1972). *Elodea nuttallii* (Planchon) St. John, for example, stored 86% of the available N and 80% of the available P and acted as sink both for N and P and maintained a clear water state in Lake Zwemlust (van Donk et al., 1993). Despite the marked reduction in total phosphorus concentrations, substantial concentrations of available soluble reactive phosphorus still remain but ammonium has declined (Carvalho et al., 1995) and recently both ammonium and nitrate have been close to undetectable in Little Mere for much of the summer (Moss et al., 1996). From the nutrient concentrations of the lake for 1993/1994, the N:P ratio (7.3:1 by weight) hints at possible nitrogen-limitation of the phytoplankton community (Beklioglu, et al., submitted). Dense stands of macrophytes can cause deficiencies of nutrients in a water body (Boyd, 1971). If the expanded macrophyte stands of the lake remain high or expand further, the lake might become nitrogen-limited. Thus, Little Mere may shift from its previous and probably presently top-down controlled clear water state to a bottom-up controlled clear water state (Figure 7).

High densities of large-bodied grazers, like *Daphnia* appear to have a very important function at low or intermediate macrophyte densities in bringing about water clarity improvement or maintaining it in shallow lakes. Under high macrophyte stands, grazing pressure appears to be less significant than other buffer mechanisms of macrophytes, such as luxury uptake of nitrogen, or denitrification in stabilizing the system. Thus, biomanipulation as a restoration measure ought to aim at redevelopment of substantial aquatic plants not just establishment of high grazing pressure to achieve stable recovery.

Acknowledgments

We would like to thank Mere Golf & Country Club who gave permission to work on Little Mere, and the Higher Education Council of Turkey that gave a studentship to Meryem Beklioglu.

References

Anderson, N. J., 1990. Variability of diatom concentrations and accumulation rates in sediments of a small lake basin. Limnol. Oceanogr. 35: 497–508.

Anderson, N. J., B. Rippey & A. C. Stevenson, 1990. Change in diatom assemblage in a eutrophic lake following point source nutrient re-direction: a palaeolimnological approach. Freshwat. Biol. 23: 205–217.

Arnold, D. E., 1971. Ingestion, assimilation, survival and reproduction by *Daphnia pulex* fed seven species of blue-green algae. Limnol. Oceanogr. 16: 906–920.

Beklioglu, M., 1995. Whole lake and mesocosm studies on the roles of nutrients and grazing in determining phytoplankton crops in a system of shallow and deep lakes. Ph.D. Thesis, University of Liverpool.

Beklioglu, M. & B. Moss, 1995. The impact of pH on interactions among phytoplankton algae, zooplankton and perch (*Perca fluviatilis* L.) in a shallow, fertile lake. Freshwat. Biol. 33: 497–509.

Beklioglu, M. & B. Moss, 1996. Mesocosm experiments on the interaction of sediment influence, fish predation and aquatic plants on the structure of phytoplankton and zooplankton communities. Freshwat. Biol. (in press)

Bengtsson, L., S. Fleischer, G. Lindmark & W. Ripl, 1975. Lake Trummen restoration project I. Water and sediment chemistry. Verh. int. Ver. theor. angew. Limnol. 19: 1080–1087.

Boyd, C. E., 1971. The limonlogical role of aquatic macrophytes and their relationship to reservoir management. Reserv. Fish. Limnol. 8: 129–135.

Boström, B., M. Jannson & C. Forsberg, 1982. Phosphorus release from sediments. Arch. Hydrobiol. Beih. Ergebn. Limnol. 18: 5–31.

Brendelbelger, H., 1991. Filter mesh size of cladocerans predicts retention efficiency for bacteria. Limnol. Oceanogr. 36: 884–894.

Carpenter, S. R. & J. F. Kitchell, 1992. Trophic cascade & biomanipulation: interface of research and management – A reply to comment by DeMelo et al., Limnol. Oceanogr. 37: 208–213.

Carvalho, G. R., 1984. Hemoglobin synthesis in *Daphnia magna* Straus (Crustacea:Cladocera): ecological differentiation between neighbouring populations. Freshwat. Biol. 14: 501–506.

Carvalho, L., 1994. Top-down control of phytoplankton in a shallow hypertrophic lake: Little Mere, England. Hydrobiologia 275/276: 53–63.

Carvalho, L., M. Beklioglu & B. Moss, 1995. Changes in a deep lake following sewage diversion – a challenge to the orthodoxy of external phosphorus control as a restoration strategy. Freshwat. Biol. 34: 399–410.

DeMelo, R., R. France & D. J. McQueen, 1992. Biomanipulation: Hit or myth. Limnol. Oceanogr. 37: 192–207.

Denny, P., 1972. Sites of nutrient absorption in aquatic macrophytes. J. Ecol. 60: 819–829.

Dillon, P. J. & F. H. Rigler, 1974. The phosphorus-chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767–773.

Geller, W. & H. Muller, 1981. The filtration apparatus of Cladocera: Filter mesh-sizes and their implications on food selectivity. Oecologia 49: 316–321.

Gliwicz, Z. M., 1990. Why do cladocerans fail to control algal blooms. Hydrobiologia 200/201: 83–97.

Grimm, M. P., 1989. Northern pike (*Esox lucius* L.) and aquatic vegetation, tools in the management of fisheries and water quality in shallow waters. Hydrobiol. Bull. 23: 59–67.

Gulati, R. D., 1989. Structure and feeding activities of zooplankton community in lake Zwemlust, in the two years after biomanipulation. Hydrobiol. Bull. 23: 35–48.

Gulati, R. D., 1990. Structural and grazing response of zooplankton community to biomanipulation of some Dutch water bodies. Hydorobiologia 200–201/Dev. Hydrobiol. 61: 99–118.

Haslam, S. M., C. A. Sinker & P. A. Wolseley, 1975. British water plants. Field Studies 4: 243–351.

Hosper, H. S. & M.-L. Meijer, 1993. Biomanipulation, will it work for your lake?. A simple test for assessment of chances for clear water, following drastic fish stock reduction in shallow, eutrophic lakes. Ecol. Engineer. 2: 63–71.

Hutchinson, G. E., 1967. A Treatise on Limnology, 2. J. Wiley & Sons, N.Y., 1115 pp.

Jeppesen, E., M. Søndergaard, O. Sortkjaer, E. Mortensen & P. Kristensen, 1990. Interaction between phytoplankton, zooplankton and fish in a shallow, hypertrophic lake: a study of phytoplankton collapses in lake Sobygard, Denmark. Hydrobiologia 191: 149–164.

Kerfoot, W. C., 1980. Commentary: transparency, body size, and prey conspicuousness. In W. C. Kerfoot (ed), Evolution and Ecology of Zooplankton communities. The University Press of New England, Hanover (N.H.); Lond.: 609–617.

Lampert, W., W. Fleckner, R. Hakumat & B. E. Taylor, 1986. Phytoplankton control by grazing zooplankton: A study on the spring clear-water phase. Limnol. Oceanogr. 3: 478–490.

Leah, R. T., B. Moss & D. E. Forrest, 1978. Experiments with large enclosures in a fertile, shallow, brackish lake, Hickling Broad, United Kingdom. Int. Revue ges. Hydrobiol. 63: 291–310.

McQueen, D. J., 1990. Manipulation of lake community structure: Where do we go from here. Freshwat. Biol. 23: 613–620.

Meijer, M.-L., E. Jeppesen, E. van Donk, B. Moss, M. Scheffer, V. E. Nes, V. J. A. Berkum, G. I. Jong de, B. A. Faafeng & J. P. Jensen, 1994. Long-term responses to fish-stock reduction in small shallow lakes: interpretation of five-year results of four biomanipulation cases in The Netherlands and Denmark. Hydrobiologia 275/276: 457–466.

Moss, B., 1990. Engineering & biological approaches to restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200/201 (Dev. Hydrobiol. 61): 367–377.

Moss, B., 1991. The role of nutrients in determining the structure of lake ecosystems and implications for the restoring of submerged plant communities to lakes which have lost them. International Conference on N, P, and organic matter. Contributions by invited International Experts. 75–85. National Agency for Environmental Protection, Copenhagen, Denmark.

Moss, B., M. Beklioglu, L. Carvalho, S. Kilinc, S. McGowan & D. Stephen. Vertically-challenged limnology; contrasts between deep and shallow lakes. Hydrobiologia (in press).

Moss, B., S. McGowan & L. Carvalho, 1994. Determination of phytoplankton crops by top-down and bottom-up mechanisms in a group of English lakes, the West Midland Meres. Limnol. Oceanogr. 39: 1020–1029.

Nizan, S., C. Dimentman & M. Shilo, 1986. Acute toxic effects of the cyanobacterium *Microcystis aerginosa* on *Daphnia magna*. Limnol. Oceanogr. 31: 497–502.

Ozimek, T., R. D. Gulati & E. van Donk, 1990. Can macrophytes be useful in biomanipulation of lakes? The lake Zwemlust example. Hydrobiologia 200/201: 399–407.

Perrow, R. M., B. Moss & J. Stansfield, 1994. Trophic interactions in a shallow lake following a reduction in nutrient loading: a long-term study. Hydrobiologia 275/276: 43–52.

Sas, H., 1989. Lake Restoration by Reduction of Nutrient Loadings: Expectations, Experiences, Extrapolations. Academia Verlag Richarz, Sant Augustin.

Scheffer, M., 1990. Multiplicity of stable states in freshwater systems. Hydrobiologia 200/201 (Dev. Hydrobiol. 61): 475–486.

Scheffer, M., S. H. Hosper, M.-L. Meijer, B. Moss & E. Jeppesen, 1993. Alternative equilibria in shallow lakes. TREE 8: 275–279.

Shapiro, J. & D. I. Wright, 1984. Lake restoration by biomanipulation: Round lake, Minnesota, the first two years. Freshwat. Biol. 14: 371–383.

Tilman, D., S. S. Kilham & P. Kilham, 1982. Phytoplankton community ecology: role of limiting nutrients. Ann. Rev. Ecol. Syst. 13: 349–372.

Timms, R. M. & B. Moss, 1984. Prevention of growth of potentially dense phytoplankton by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. Limnol. Oceanogr. 29: 472–486.

van Donk, E., M. P. Grimm, R. D. Gulati & J. P. G. Klein Breteler, 1990. Whole-lake food-web manipulation as means to study community interactions in a small ecosystem. Hydrobiologia 200/201 (Dev. Hydrobiol. 61): 275–289.

van Donk, E., R. D. Gulati & M. P. Grimm, 1989. Food web manipulation in Lake Zwemlust: positive and negative effects during the first two years. Hydrobiol. Bull. 23: 19–34.

van Donk, E., R. D. Gulati, A. Iedema & J. T. Meulemans, 1993. Macrophyte-releated shifts in the nitrogen and phosphorus contents of the different trophic levels in a biomanipulated shallow lake. Hydrobiologia 251: 19–26.

Wium-Anderson, S., 1987. Allelopathy among aquatic plants. Arch. Hydrobiol. Beih. 27: 167–172.