

APPLIED ISSUES

A multivariate analysis of phytoplankton and food web changes in a shallow biomanipulated lake

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SUMMARY

1. Phytoplankton dynamics, food chain changes and resilience in Lake Zwemlust, a shallow lake in The Netherlands, are described for the period 1986–94.
2. After biomanipulation in 1987, the lake moved through two alternative states, while the external nutrient loadings were maintained. A clear-water phase, mostly dominated by macrophytes, persisted from 1987 to 1991, and a rather turbid state, dominated by algae, occurred in the summers of 1992–94, after several consecutive and sustained perturbations affecting different parts of the food web in the lake. These two periods were characterized by different community structures.
3. The phytoplankton assemblage gradually changed in a pattern that reverted in later years towards that of the pre-biomanipulation stage, although the same species composition was not regained. This agrees with some mathematical models. During the clear-water phase, nutrient shortage, light climate and zooplankton feeding selected in favour of small, high surface : volume ratio and rapidly reproducing algae. However, in mid-summer of 1992–94, nutrient availability and cladoceran grazing on edible algae favoured cyanophytes.
4. Nutrients were transferred to higher trophic levels or lost from the system at relatively high rates when the lake was in a piscivore–macrophyte-dominated state, while they tended to accumulate in the algae in a planktivore-dominated chain without macrophytes. The role of weed beds was central for nutrient competition (mostly nitrogen) with algae, as well as a refuge and a base for alternative food sources to grazers. Weed beds seemed to have a strong effect in increasing connectedness, resilience and stability of the lake community.
5. The complete return of Zwemlust to a turbid state dominated by phytoplankton seems to have depended upon turnover of the limiting nutrient, which was retarded by macrophytes and stimulated by planktivorous fish and waterfowl.

Introduction

Since the term biomanipulation was first introduced by Shapiro, Lamarra & Lynch (1975), studies on food web manipulation have been documented in about

thirty-six freshwater bodies, among which twenty are shallow lakes (Phillips & Moss, 1993). This is probably because in shallow lakes fish population management

is easier and the cost of manipulation is lower. In shallow lakes, there is growing evidence for the existence of alternative stable states, in which either phytoplankton or aquatic vegetation can exist within the same intermediate range of nutrient supply (Uhlmann, 1980; Scheffer *et al.*, 1993). The alternative stable state model implies that the states when in equilibrium are preserved by a number of buffering mechanisms, and only disturbances large enough to override these self-stabilizing capacities may cause a shift from one state to the other (Scheffer *et al.*, 1993). This disturbance can affect different parts of the ecosystem.

However, some questions remain concerning the alternative stable state model. For instance, will the system return to exactly the same steady state (species composition) after conditions revert, or will it move to only a similar equilibrium point? Although there is theoretical support for this latter approach (Scheffer, 1991), which implies the acceptance of a high degree of ecosystem unpredictability, there is a lack of experimental and field evidence.

Natural examples of alternative stable states in shallow lakes are rare, since these require long-term records (Blindow *et al.*, 1993), and in small water bodies only eight studies have extended for more than 3 years (Phillips & Moss, 1993). In addition, our knowledge of buffering mechanisms and food web interactions between pelagic and littoral systems in these lakes is limited. In pelagic systems, body size and generation times (and potentially turnover time) are often greater at higher trophic levels, while in terrestrial systems the reverse is often true. In this sense, the littoral ecosystem of a shallow lake dominated by macrophytes is expected to be intermediate. Any attempt to produce complete pelagic models (Sommer *et al.*, 1986; Carpenter & Kitchell, 1992) should include a deeper insight into these interactions. One of the theoretical criticisms of the long-term success of biomanipulation is the mismatch of the turnover times of the different trophic levels involved, which seems to be more important in deep than in shallow lakes (Phillips & Moss, 1993). Although it is generally accepted that the biotic structure of a lake ecosystem is influenced by both bottom-up and top-down mechanisms (Carpenter & Kitchell, 1992), there has been great controversy about the relative importance of each of these processes in affecting phytoplankton crops (De Melo *et al.*, 1992; Evans, 1992). The clearest outcome from biomanipulation experience is

that a lake trophic model is not as simple as formerly believed (Carpenter, Kitchell & Hodgson, 1985), since trophic links have been shown to be unequal in strength and sometimes variable (McQueen *et al.*, 1989; Novales-Flamarique *et al.*, 1993).

In this paper, we present results from a shallow lake, Lake Zwemlust (The Netherlands), in which the effects of food web manipulation have been studied for almost a decade (1986–94). Results concerning nutrient balance, and changes in zooplankton, zoobenthos and macrophytes for some years have been reported, respectively, by Van Donk & Gulati (1989, 1996), Kornijów & Gulati (1992a,b) and Van Donk *et al.* (1993, 1994).

In the present work we aim to:

- 1 characterize phytoplankton dynamics of the lake in relation to abiotic and biotic variables for the period 1986–94;
- 2 reveal some of the relevant mechanisms structuring the lake food chain, contributing with field data to help clarify some theoretical models on shallow lakes;
- 3 document the resilience and stability of the lake community.

We will use a multivariate approach since this kind of analysis has proved to be a valuable tool in determining ecological factors influencing plankton communities and visualizing trends in species (Varis, Sirvio & Kettunen, 1989; Van Tongeren *et al.*, 1992; Romo & Tongeren, 1995). Among them, canonical analysis has the advantage of combining the simplicity of regression models with the power of ordination techniques; it has low sensitivity to the multinormality assumption and is not restrictive in the upper limit of species that can be analysed in combination with other variables (Ter Braak & Verdonschot, 1995).

Materials and methods

Study area

Lake Zwemlust is a shallow (mean depth 1.5 m, maximum 2.8 m), small (1.5 ha), sheltered eutrophic lake located in the central part of the Netherlands. After 19 years of algal blooms and absence of submerged macrophytes, a biomanipulation programme was started in 1987 (Van Donk, Gulati & Grimm, 1989). Other restoration measures, such as reduction of the external nutrient loadings, were not feasible due to the nutrient-rich seepage received from the

River Vecht. This is the main source of water input apart from precipitation. The biomanipulation programme basically consisted of removing fish populations (mostly bream, *Abramis brama*) after emptying the lake and subsequent introduction of pike (*Esox lucius*) and macrophytes. A more detailed description of the restoration programme, and the lake hydrology and limnology is reported in Van Donk *et al.* (1989, 1990).

Methods

Sampling techniques used in the lake to measure different limnological parameters (nutrient concentrations, Secchi depth, chlorophyll *a*, zooplankton and phytoplankton identification and abundances) are outlined in Van Donk *et al.* (1989). Zooplankton grazing and primary production were measured between 1987 and 1992 using techniques described in Gulati (1989). Algae of size $\leq 35 \mu\text{m}$ were considered edible for zooplankton (Carpenter & Kitchell, 1992).

In order to detect trends in phytoplankton species, the matrix of algal abundance for the period 1986–94 was subjected to a correspondence analysis (Ter Braak, 1987) using the program CANOCO 3.1 (Ter Braak, 1990). Similarly, the matrices of phytoplankton and environmental variables for 1986–94, and those of phytoplankton and zooplankton and macrophytes for 1987–94, were subjected to respective canonical correspondence analyses (CCA) to ascertain relationships between them. CCA extracts from the measured environmental and biotic variables, synthetic gradients (ordination axes) that maximize the niche separation among species. These gradients are a linear combination of variables, quantitatively represented by arrows (Ter Braak, 1987). A positive correlation is expressed by relatively long vectors pointing approximately in the same direction, whereas a negative correlation is indicated by arrows pointing in opposite directions. The higher the correlation, the longer the arrow in the diagram. Missing values were estimated by linear interpolation. Plankton abundances were logarithmically transformed and centred prior to the analyses. Forward selection of the variables, using Monte Carlo permutation test (Ter Braak, 1987), was used to obtain those maximally related to phytoplankton (active variables). The results from the CCA are presented as biplots, in which the correlations with the ordination

axes for both the dependent and independent variables are plotted (Ter Braak, 1987).

Results

Phytoplankton

The correspondence analysis of algal samples revealed a gradual trend of change in species composition from 1986 to 1994, in a pattern that reverted in later years toward that of the pre-biomanipulation stage, although the same point was not attained (Fig. 1). In the CCA multivariate analyses, the variable time (years) explained 24% of the phytoplankton variance, while season explained only 10% (Table 1).

In 1986 and early 1987, before food web management, phytoplankton was mainly composed of *Scenedesmus* spp. and *Microcystis aeruginosa* Kützing, this latter encountered during summer (Fig. 2). In winter, the centric diatom *Stephanodiscus hantzschii* Grunow and *Pteromonas* sp. also developed (Fig. 3).

After biomanipulation and refilling of the lake in March 1987, phytoplankton was quickly colonized by small and rapidly growing species, such as *Cryptomonas* spp. and chlorophytes (rounded cells 2–8 μm in diameter, called small chlorophytes in Fig. 2). In addition, several small *Nitzschia* spp. and *N. acicularis* also appeared in the plankton (Figs 2 and 3), probably inoculated from sediment and macrophytes.

In mid-March 1988, there was an almost monoalgal peak of *Ankyra ankora* (G.M. Smith) Fott (chlorophyll *a* 146 mg m^{-3}), but afterwards the algal dominance returned to *Nitzschia* spp. in summer and small chlorophytes and cryptophytes (mostly *Rhodomonas lacustris* var. *nannoplanctica* Javornicky) in autumn (Figs 2 and 3). This latter composition was maintained throughout 1989, at the time that algal biomass and production were markedly reduced (Fig. 4).

In 1990, although algal biomass and primary production increased (Figs 2 and 4), the phytoplankton was still dominated by small edible forms: *Stephanodiscus hantzschii* in early spring, followed by *Oocystis* sp. in late May and *Rhodomonas lacustris* var. *nannoplanctica* and *Cryptomonas* spp. in September (Fig. 2). In 1991, there were no major algal increases during the year and phytoplankton was composed mostly of small taxa, although a gelatinous colonial chlorophyte, *Eutetramorus* cf. *fottii* (Hindak) Komárek, appeared in

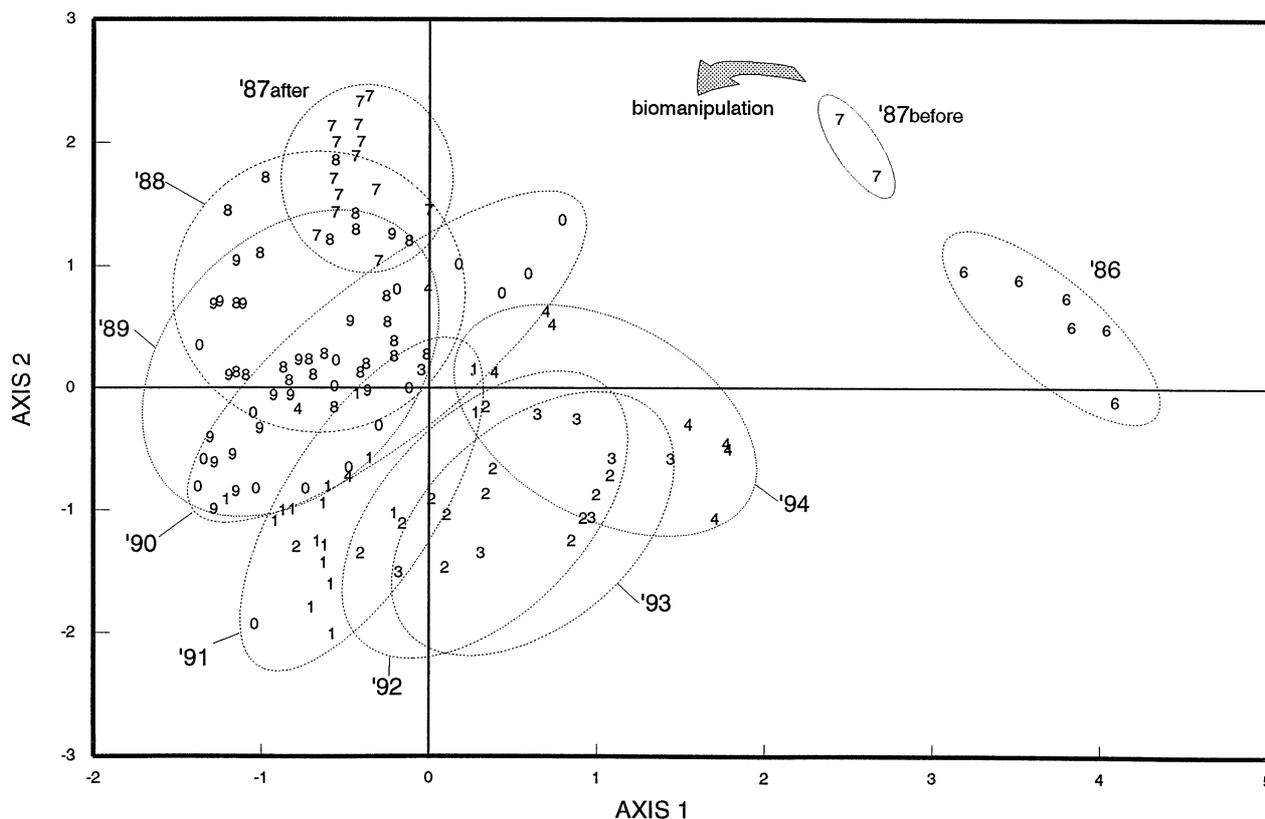


Fig. 1 (a) Correspondence analysis ordination diagram of phytoplankton samples for Lake Zwemlust during 1986–94. Algal changes in time can be followed by the encircled set of samples corresponding to each year.

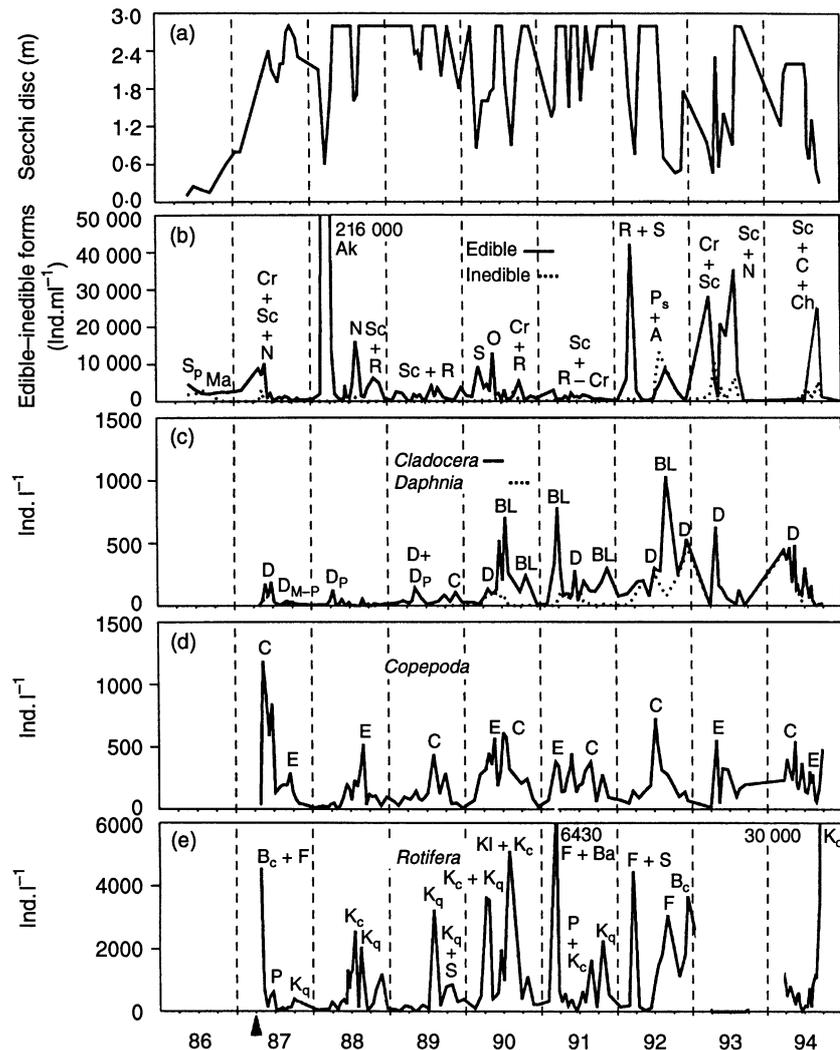
Table 1 Summary of CCA analyses between phytoplankton and different variables for 1987–94. *The total variance explained by the two first axes is calculated as the product of the cumulative percentage variance of the species–variable correlation at the second axis and the sum of all canonical eigenvalues. **During summer (June–September)

Variable	Year		Season		Abiotic		Zooplankton		Macrophytes and nutrients**	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.140	0.096	0.054	0.045	0.103	0.070	0.117	0.073	0.312	0.210
Species–variable correlations	0.886	0.770	0.739	0.647	0.755	0.752	0.806	0.689	0.970	0.967
Cumulative percentage variance										
of species data	5.7	9.6	2.2	4.1	4.2	7.1	4.8	7.8	15.6	26.2
of species–variable relation	31.7	53.6	45.2	83.3	35.9	60.3	22.1	35.9	28.8	48.2
Sum of all unconstrained eigenvalues		2.44		2.41		2.44		2.45		2.00
Sum of all canonical eigenvalues		0.44		0.12		0.29		0.53		1.08
Variance explained (%)*		24		10		17		19		52

spring (Fig. 3). However, the whole algal assemblage differed from other years, due to the incorporation of tycho planktonic taxa (filamentous chlorophytes, diatoms, desmids; Fig. 3), perhaps from the periphyton. From 1991 onwards, some periphytic species were often present in the plankton during the macrophyte growth season.

For 1992–93, the vernal peaks, as in previous years, were mostly composed of edible algae (Fig. 2), although in 1993 an alternation in dominance between small species and *Anabaena* sp. was also observed (Fig. 3). In summer, phytoplankton dominance, as in 1992, shifted to cyanophytes and *Eutetramorus* cf. *fottii* (Fig. 3), or as in 1993–94, to an alternation of edible

Fig. 2 Variations in Lake Zwemlust between 1986 and 1994 of: (a) Secchi disc; (b) total abundance of edible and inedible species. Dominant algae: Sp = *Scenedesmus* spp., Ma = *Microcystis aeruginosa*, Cr = *Cryptomonas* spp., Sc = small chlorophytes, N = *Nitzschia* spp., AK = *Ankyra ankora*, R = *Rhodomonas lacustris* var. *nannoplanctica*, S = *Stephanodiscus hantzschii*, O = *Oocystis* spp., Ps = *Pseudanabaena* sp., A = *Anabaena* sp., C = *Cyclotella* sp., Ch = *Chlamydomonas* spp.; (c) total abundance of Cladocera, specifying also that of *Daphnia* (D = *Daphnia* spp. (*D. galeata/cucullata*/hybrids), Dm = *D. magna*, Dp = *D. pulex*, C = *Chydorus sphaericus*, Bl = *Bosmina longirostris*); (d) total abundance of copepods species (C = *Cyclops* sp., E = *Eudiaptomus gracilis*); nauplii were also abundant overall; and (e) total abundance of rotifers (Bc = *Brachionus calcyflorus*, Ba = *Brachionus angularis*, F = *Filinia* sp., P = *Polyarthra* sp., Kq = *Keratella quadrata*, Kc = *Keratella cochlearis*, S = *Synchaeta* sp., Kl = *Kellicottia longispina*). The arrow indicates the beginning of biomanipulation measures in the lake in March 1987.



and inedible forms (Fig. 2). Among cyanophytes there were also differences. Thus, whereas in 1992–93 the main blue-greens were filamentous and N_2 -fixing species (*Pseudanabaena* sp., *Anabaena* sp. and *Aphanizomenon* cf. *flos-aquae* Ralfs), in July and autumn 1994 the presence of *Microcystis aeruginosa* increased, concomitant with a rise in the N:P ratio (Figs 3 and 5). Its population numbers in July were about 3×10^3 col. ml^{-1} , similar to those of pre-biomanipulation.

During the whole study period, we observed that centric diatoms mainly appeared in spring and pennate species mostly in summer (Fig. 3).

Environmental variables and macrophytes

The biplot of species and environmental variables displays fairly strong relationships, explaining 17% of

phytoplankton variance (Table 1). Secchi disc depth had the greatest correlation with phytoplankton ($P < 0.01$), being negatively related to chlorophyll *a* (Fig. 6). Other variables maximally related to phytoplankton are underlined in Fig. 6. Two main periods can be observed: one with the highest transparency, and lowest chlorophyll *a* and nutrient levels, occurring after biomanipulation, from mid-1987 to 1989 and in 1991 (left side, Fig. 6); and the other with an opposite trend for 1990 and 1992–94 (right side, Fig. 6). Chlorophyll *a* was markedly reduced after biomanipulation (from 215 to 50 mg m^{-3}), and Secchi disc transparency reached almost to the bottom (Figs 2 and 5), but decreased again to about 1 and 0.5 m in 1990 and during the summers of 1992–94, respectively (Fig. 2). During the whole study period, chlorophyll *a* and phytoplankton abundance were coupled, although in periods where cyanophytes were abundant (1986 and

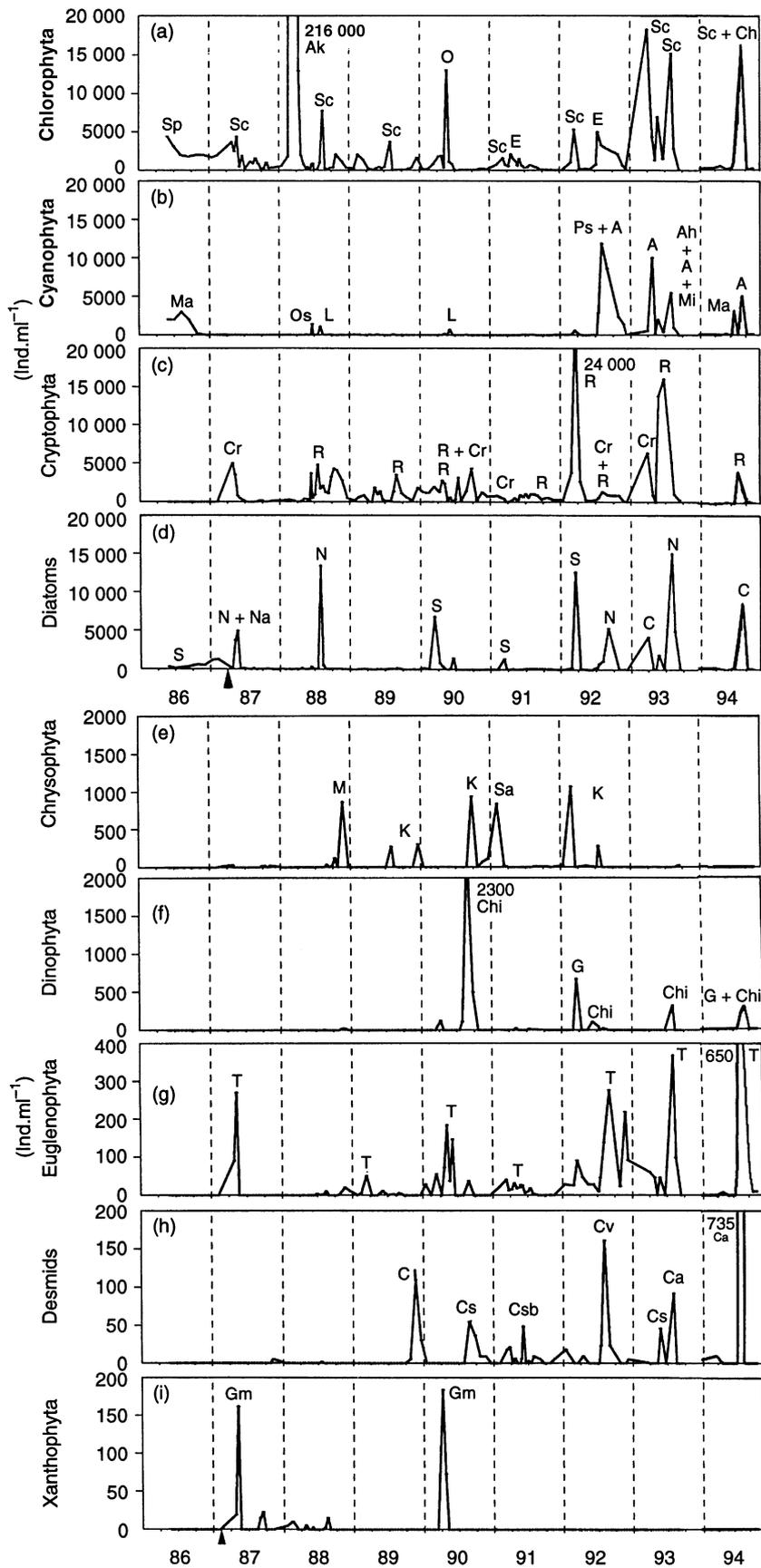


Fig. 3 Time course of the total abundance of the main phytoplankton groups in lake Zwemlust for 1986–94. Notice the change of scale on the y-axis in graphs e–i for the minor groups. Dominant species: Sp = *Scenedesmus* spp., Sc = small chlorophytes, Ak = *Ankyra ankora*, O = *Oocystis* spp., E = *Eutetramorus* cf. *fottii*, Ch = *Chamydomonas* spp., Ma = *Microcystis aeruginosa*, Os = *Oscillatoria* spp., L = *Limnothrix redekeii*, Ps = *Pseudanabaena* sp., A = *Anabaena* sp., Ah = *Aphanizomenon flos-aquae*, Mi = *Microcystis* cf. *incerta*, Cr = *Cryptomonas* spp., R = *Rhodomonas lacustris* var. *nannoplantica*, S = *Stephanodiscus hantzschii*, N = *Nitzschia* spp., Na = *Nitzschia acicularis*, C = *Cyclotella* sp., M = *Mallomonas* sp., K = *Kephyrion* sp., Sa = *Salpingoeca* sp., Chi = *Ceratium hirundinella*, G = *Gymnodinium* sp., T = *Trachelomonas* spp., Cl = *Closterium* sp., Cs = *Cosmarium* sp., Csb = *Cosmarium botrytis*, Cv = *Closterium variabile*, Ca = *Closterium acutum*, Gm = *Goniocloris mutica*.

summer of 1992), chlorophyll concentrations were relatively higher (Fig. 5).

Macrophytes and nutrients together explained 52% of total phytoplankton variance during summer (Table 1). From CCA between phytoplankton and macrophytes, we can infer that macrophyte biomass was positively related to Secchi disc depth and nutrients, especially to nitrogen forms, and negatively related to algae (Fig. 7). Therefore, clear-water phases

were linked to the expansion of macrophytes, and their decline from 1990 onwards stimulated a rise on average in nitrogen and phosphate and algal abundance (Figs 5 and 7). Concomitantly with nutrient availability, a greater species richness in the phytoplankton was observed, especially during summer (Fig. 3). The seasonal pattern of nitrogen and phosphorus (both dissolved or total forms) had in general minimum values during spring–summer (algal and macrophyte growth seasons) and a maximum in winter, except in 1987 after biomanipulation caused sediment resuspension, and during the summers of 1992–94 (Fig. 5). In 1994, mean concentrations of both nutrients markedly decreased, although phosphate still peaked in summer (Figs 5 and 7).

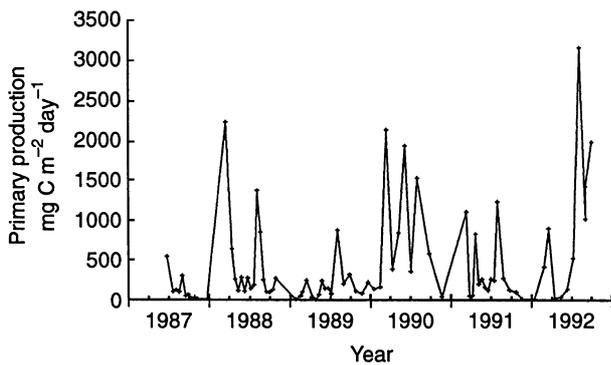
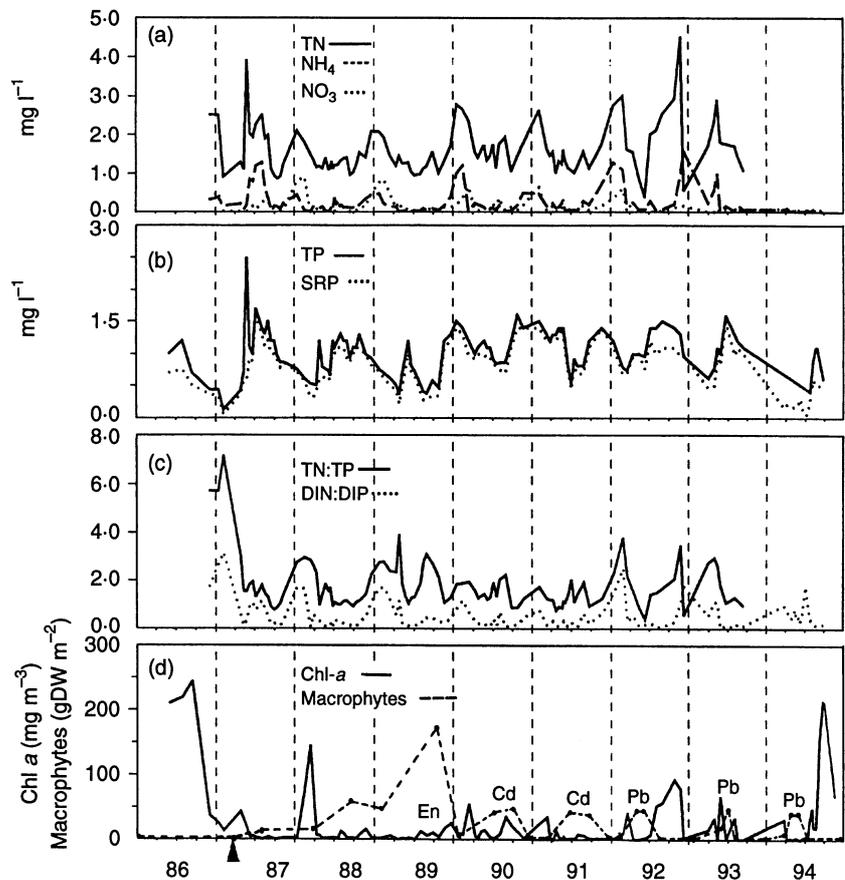


Fig. 4 Seasonal variation of phytoplankton primary production in Lake Zwemlust after biomanipulation, for 1987–92.

Zooplankton

Zooplankton explained 19% of phytoplankton variance (Table 1) and their populations in general followed phytoplankton increases (Fig. 2). The CCA

Fig. 5 Dynamics in Lake Zwemlust during 1986 and 1994 of: (a) total nitrogen (TN), dissolved ammonia and nitrate; (b) total (TP) and soluble reactive phosphorus (SRP); (c) nitrogen to phosphate ratios by weight; and (d) chlorophyll *a* and macrophytes biomass. Dominant macrophyte species: En = *Elodea nuttallii*, Cd = *Ceratophyllum demersum*, Pb = *Potamogeton berchtoldii*. The arrow indicates the beginning of biomanipulation measures in the lake in March 1987.



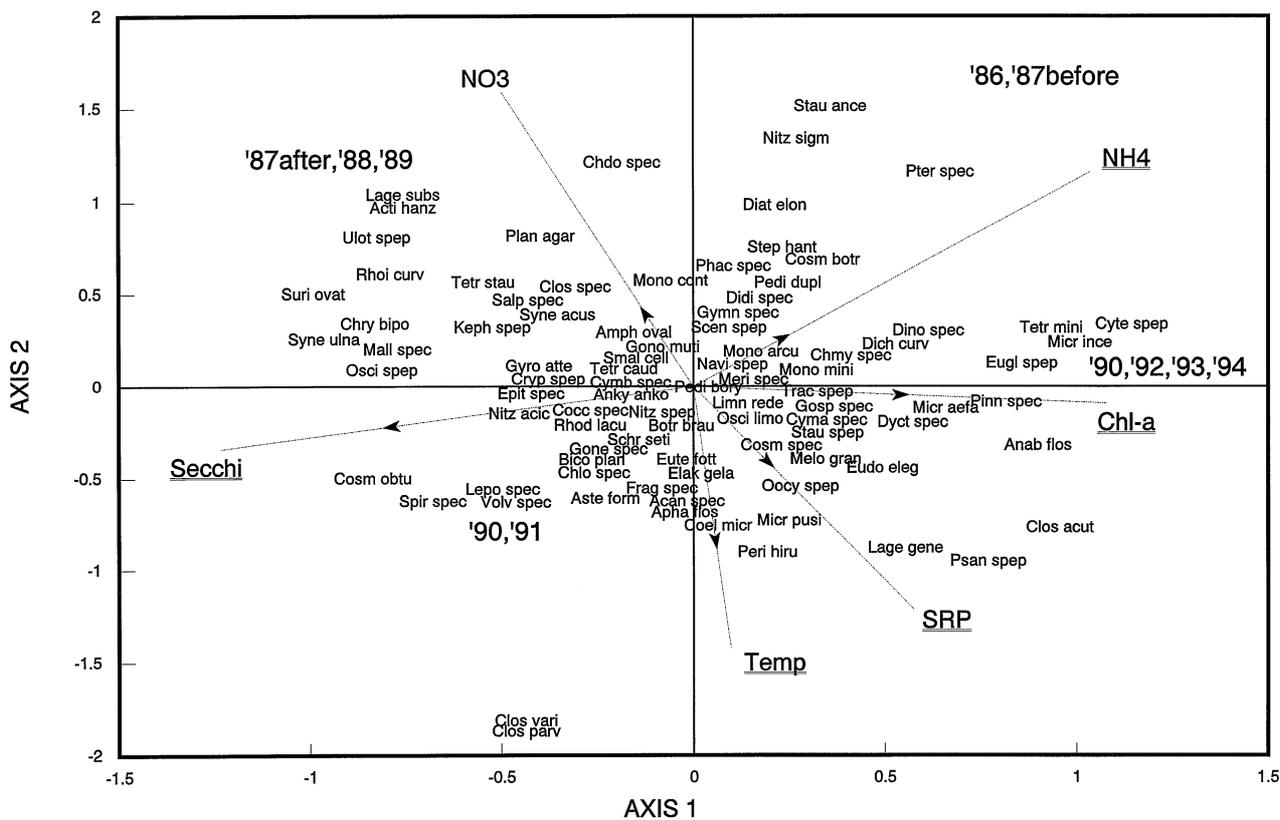


Fig. 6 CCA biplot of phytoplankton species and environmental variables scores for 1986–94. Active variables selected by the analysis ($P < 0.01$) are underlined. A positive correlation is expressed by relatively long vectors pointing approximately in the same direction, and a negative correlation is indicated by arrows pointing in opposite directions. The higher the correlation, the longer the arrow in the diagram. The variable year is also represented.

analysis between phytoplankton and zooplankton species showed daphnids to be the group with the largest correlation with phytoplankton (Fig. 8a), although in 1990 and 1994 *Keratella cochlearis* Gosse and *Eudiaptomus* sp. also had significant relationships ($P < 0.01$; Fig. 8a). Other abundant rotifers were *Filinia* spp. and *Brachionus calcyflorus* Pallas (Figs 2 and 8a). During the study period, rotifers and copepods mainly developed in summer and autumn (Fig. 2), the former having a general trend of increase from 1990 onwards, paralleling an algal rise in biomass (Figs 2 and 8b).

Among cladocerans there was a segregation of species between years, with *Daphnia magna* Straus and *D. pulex* (Leydig) Scourfield appearing chiefly in spring of 1987 and 1988–89, respectively (Fig. 2), concomitant with the greatest Secchi depths and lowest chlorophyll *a* values (Fig. 8b), whereas *Daphnia* spp. (composed of *D. cucullata*, *D. galeata* and their hybrids) and *Bosmina longirostris* O.F. Müller were the main cladocerans influencing phytoplankton during the following years

(Figs 2 and 8a). Parallel to this species shift grazing rates decreased, especially in 1990 (Fig. 9). Grazing and transparency recovered in spring 1991, due mostly to *Bosmina longirostris* in March and *Daphnia* spp. in April and June (Figs 2 and 9).

Intense zooplankton grazing periods were followed by the presence of inedible algae. Therefore, in 1992 high numbers of cladocerans in summer favoured gelatinous colonial algae and cyanophytes, whereas lower grazing pressure in the summers of 1993 and 1994 led to a co-dominance of both grazable and inedible species (Fig. 2). Apparently, the tolerance to cyanophytes among cladocerans was also different. Therefore, *Bosmina longirostris* replaced *Daphnia* spp. when blue-greens dominated phytoplankton in summer 1992 (Fig. 2). *Daphnia* spp. only increased again at the end of the year, following a greater abundance of edible algae (mostly cryptophytes, small chlorophytes and *Trachelomonas* spp., Figs 2 and 3) and probably under lower fish predation, caused by reduced activity

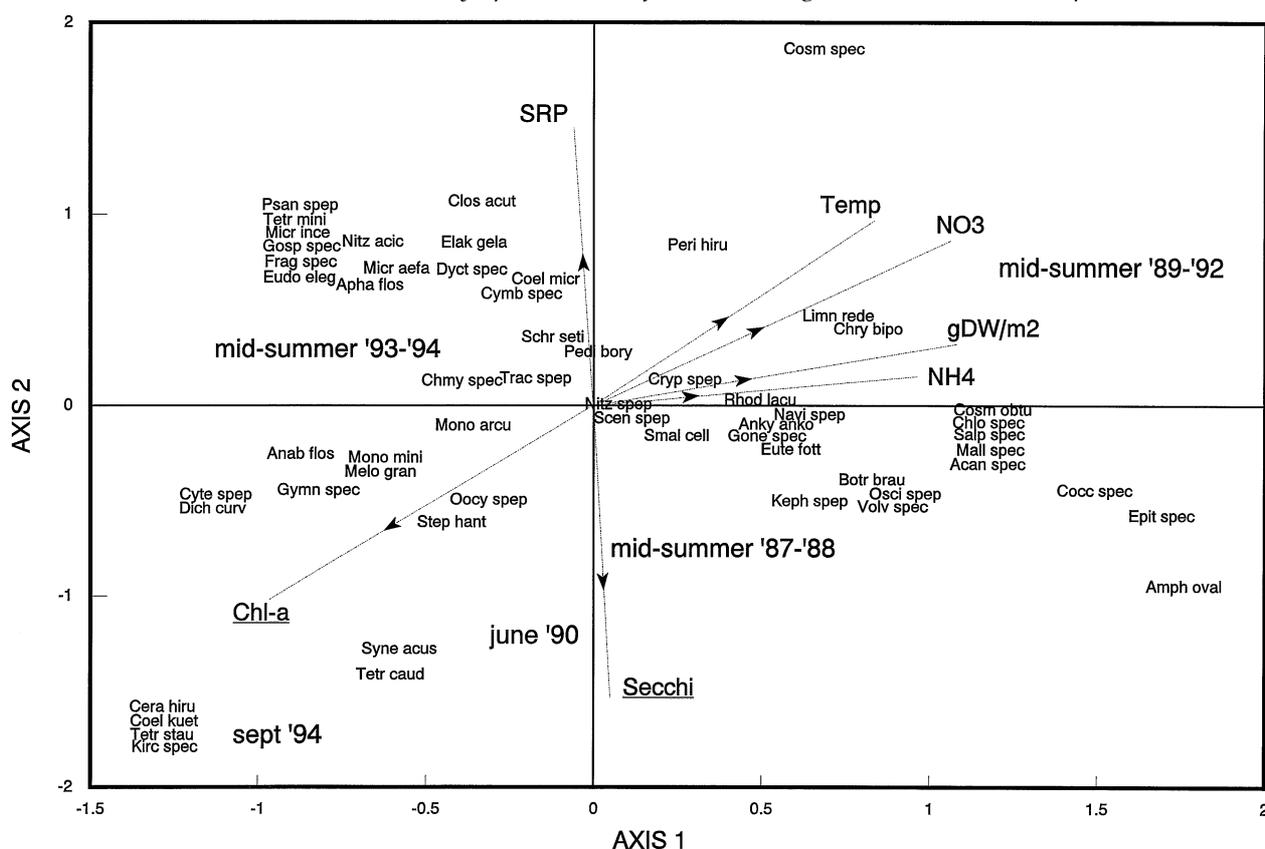


Fig. 7 CCA biplot of phytoplankton species, macrophyte biomass and environmental variables scores, during the summers (June–September) of 1987–94. Active variables ($P < 0.01$) are underlined. The variable year is also represented.

under low temperatures. Inedible forms of algae appeared even during periods of low algal density, such as in late August 1990 when *Ceratium hirundinella* (O.F. Müller) Schrank increased after a *Bosmina longirostris* peak, and in spring 1991 when *Eutetramorus cf. fottii* (Hindak) Komárek appeared after *Daphnia* spp. populations (Figs 2 and 3).

Discussion

Bottom-up effects

Our data support the idea that nitrogen and light could act as the main bottom-up factors structuring phytoplankton in Lake Zwemlust. Both variables were closely related to macrophytes. As was most evident in 1990 and 1992–94, the winter supply of the algal-limiting nutrient nitrogen (Van Donk *et al.*, 1993) conditioned the total early spring algal biomass. During the period 1988–91, nutrient shortage and underwater light climate (Van Donk 1991) probably contributed to select an algal assemblage constituted by small,

high surface : volume ratio and fast reproducing algae, such as cryptophytes and small chlorophytes (Reynolds, 1984). In the summers of 1992–94, reduction of light and nutrient availability favoured cyanophytes and some N_2 -fixing species (Reynolds, 1984; Romo & Miracle, 1995). Phytoplankton moved towards an assemblage similar to that of pre-biomanipulation, although the same equilibrium point (species composition) was not attained and it seems likely that only the dominant species (e.g. *Microcystis aeruginosa*) will resume its presence. This result agrees with and gives empirical support to some mathematical models on the nature of stable equilibrium in planktonic systems (Scheffer, 1991). The fact that subdominant species can differ greatly with small differences in the rate of resource supply and predation (Sommer, 1988) also seems consistent with this idea.

Top-down effect

Our results agree with those of McQueen *et al.* (1989), indicating that nutrient availability seems to determine

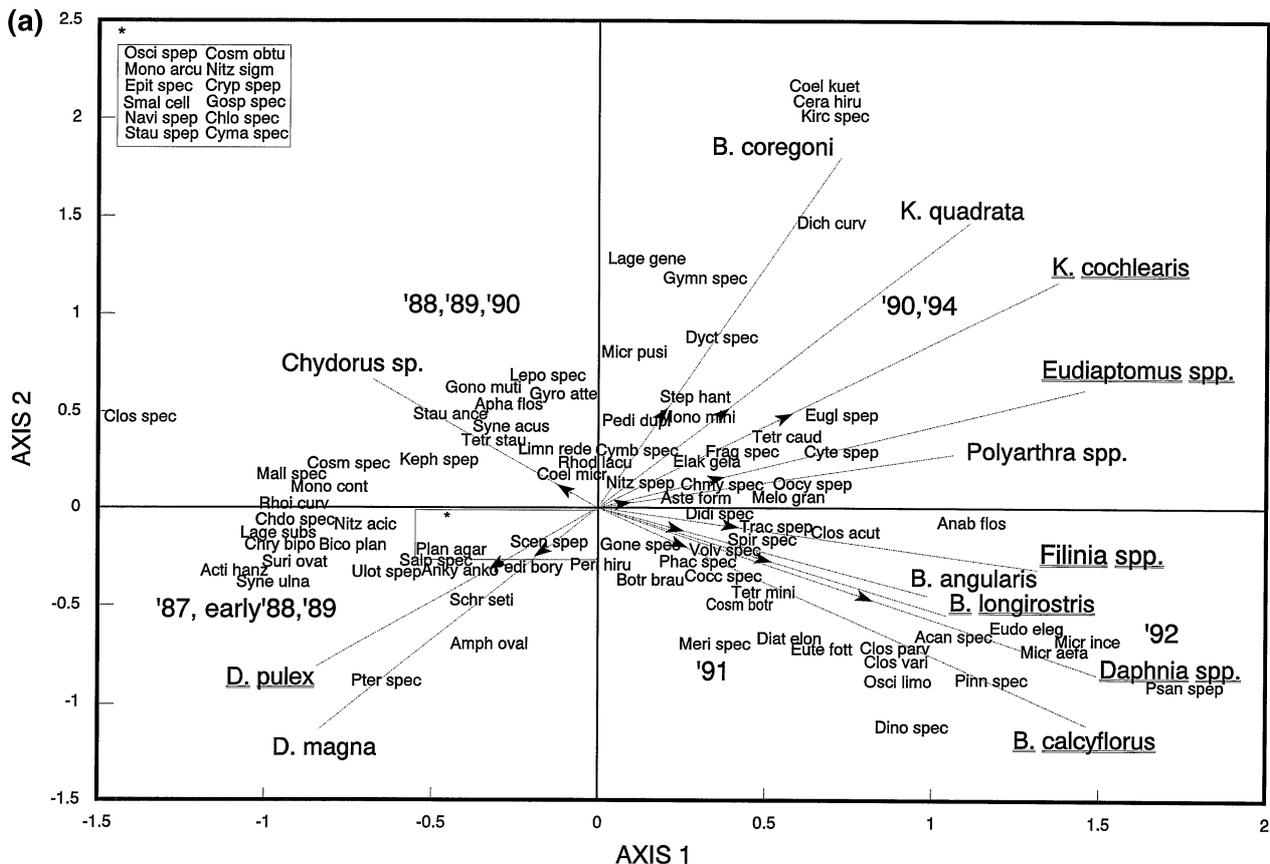


Fig. 8 (a) CCA biplot of phytoplankton in relation to zooplankton species, during the period 1987–94 (1993 was excluded due to lack of data on rotifers in this year). (b) CCA analysis between zooplankton and abiotic variables. Active variables selected by the analysis ($P < 0.01$) are underlined. The variable year is also represented.

long-term potential biomass, while predation determines the realized one. Despite the relatively clear relationship in Lake Zwemlust between *Daphnia* and algal grazing, this top-down control was only sustained for short periods. In 1987–88, large-bodied daphnids controlled algal biomass; the improved light conditions allowed macrophytes to establish, but thereafter and until 1991 nitrogen was mainly incorporated into macrophytes (Van Donk *et al.*, 1993), which limited phytoplankton growth during summer. As a result, both zooplankton grazing and water plants restricted phytoplankton to a single annual vernal standing crop for 1988–91. This pattern changed as soon as macrophytes declined, stimulating a summer algal crop. According to Kitchell (1992) this summer peak should be dominated by inedible algal forms, but we observed that the relative abundance of edible and inedible algae was partly dependent upon zooplankton grazing.

During the study in Lake Zwemlust, increases in primary producers were followed by increases in zooplankton, but the impact of zooplankton feeding rates decreased due to dominance of smaller cladoceran species, replacing large ones. This was probably the result of both fish predation on larger microcrustaceans and food limitation during 1989–91 (Gulati, 1996). Among the smaller forms, *Bosmina longirostris*, although a less efficient grazer than *Daphnia* spp. (see e.g. 1990, Fig. 9), was less affected in 1992 by the presence of cyanophytes, although unfilterable algae could have also interfered and depressed its grazing rates (Gliwicz, 1990). Although the K-strategies of cyanophytes may allow them to extend their dominance from summer to other seasons in later years (Reynolds, 1984; Romo & Miracle, 1995), at present edible forms in the lake seem abundant enough to sustain cladoceran growth.

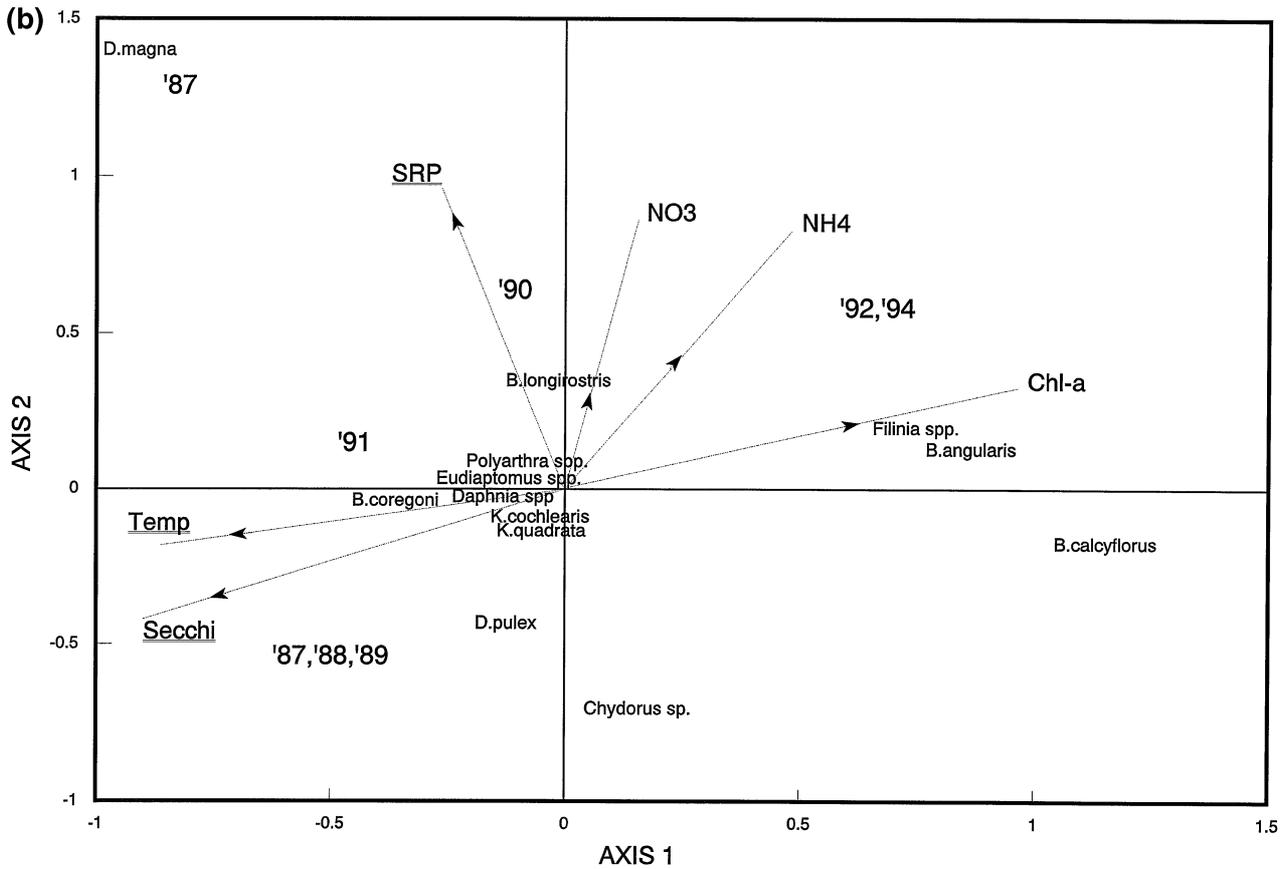


Fig. 8 Continued

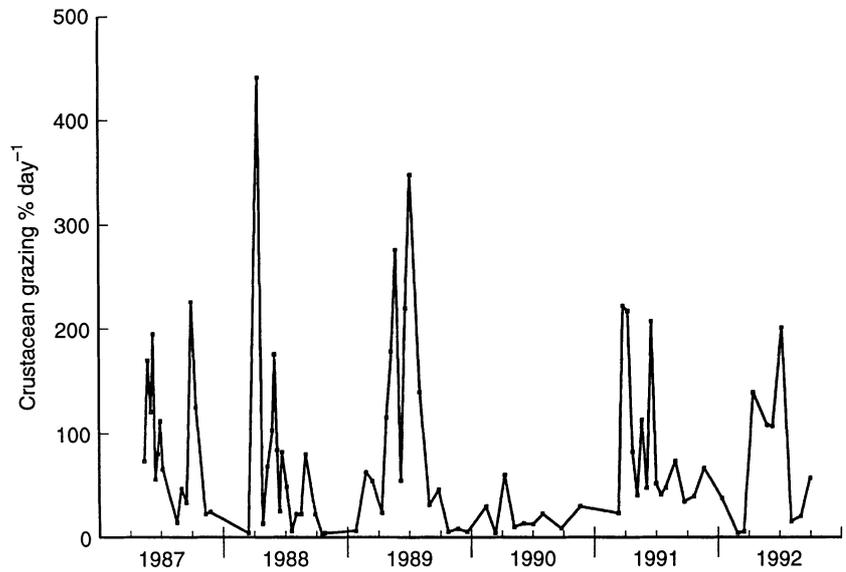


Fig. 9 Temporal variation in Lake Zwemlust of crustacean grazing, for 1987–92.

Buffering mechanisms and macrophytes

Our observations in Lake Zwemlust lend support to the model of Scheffer *et al.* (1993) and show some of

the feedback and buffering mechanisms that tend to stabilize each steady state. Lake Zwemlust is now in a transitional stage, in which both states, vegetation with clear water and phytoplankton with turbid water,

alternate during the year. Theory suggests that a large perturbation could lead the biotic community to a new steady state (Scheffer *et al.*, 1993). In Zwemlust, the disappearance of macrophytes due to grazing by rudd (*Scardinius erythrophthalmus*) and coot (*Fulica atra*) (Van Donk *et al.*, 1994) is a leading factor causing this change. However, at least several consecutive and sustained perturbations affecting different parts of the lake ecosystem were needed to bring the lake back to a turbid state during summer. The process started in 1990 as the result of a top-down perturbation, but some feedback mechanisms resisted this change. In this year, the increase in planktivorous fish (from 50 to 398 kg ha⁻¹ of rudd between 1988 and 1990; Gulati, 1996) caused changes in zooplankton, but the effect on algae was damped by macrophyte-induced nitrogen limitation. In the following year, the system re-established a clear-water phase, because zooplankton grazing on algae increased, probably as a result of food availability. These buffering mechanisms were no longer sustained after macrophyte changes. Furthermore, loss of refuges for cladocerans among water plants could also have led to *Daphnia* spp. decline by planktivore predation, which favoured rotifers.

Overall, the role of weed beds was central in resource competition with algae, in allowing refuges for cladocerans and extending grazing from spring throughout summer. They might also provide grazers with an alternative food source, since they act as traps for fine solid material (organic particles, bacteria) and as support for periphyton, and provide complex carbon at every stage of break down (Reynolds, 1994).

Lake stability

The introduction to the food web of macrophytes, which act as an alternative and persistent resource base as defined by Paine (1980), seems to stabilize and strengthen trophic linkages in the lake, increasing connectedness between different trophic levels (phytoplankton, zooplankton, fish, detritivore). According to Pimm (1984), the more connected a community is, the more resilient are its populations and the more persistent is its composition. Our phytoplankton results in Lake Zwemlust during the years of clear water and macrophyte dominance (1988–91) corroborate these assumptions. Furthermore, phytoplankton control by grazers was more efficient and the food web more stabilized when the system was nutrient

limited (DeAngelis *et al.*, 1989). However, when the food web was extended to secondary consumers, such as waterfowl, the data seem consistent with the conjecture of Pimm & Lawton (1977) that longer food chains become less resilient.

The resilience of an ecosystem is closely related to recycling of the limiting nutrient (DeAngelis *et al.*, 1989; Carpenter *et al.*, 1994), and in this respect morphology of lakes seems a determinant for trophic and abiotic responses (Moss, McGowan & Carvalho, 1994). In shallow lakes nutrient recycling is usually faster than in deeper lakes, and mechanisms that delay turnover of the limiting nutrient or reduce it (Jeppesen *et al.*, 1990) should enhance algal control. In Lake Zwemlust, with relatively low levels of sediment resuspension by wind, the total nutrient balance approaches a closed system, where trophic effects become rapidly manifest.

Comparing the periods of pelagic phases in the lake (mainly after biomanipulation in 1987 and the summers of 1992–94), algae seem more resistant to changes in nutrient inputs in food chains with four rather than three trophic levels (Carpenter & Kitchell, 1992). However, when turnover of the limiting nutrient was retarded by uptake into macrophytes, a similar response was observable even with three trophic levels (during 1990–91). In some other shallow lakes dominated by macrophytes, clear-water phases also appeared even with a high presence of zooplanktivorous fish (Timms & Moss, 1984; Moss, 1990), although they seem to persist longer if their abundance is kept low (Meijer *et al.*, 1994). In Lake Zwemlust, this is in part due to the fact that planktivorous fish also predate on macrophytes (Van Donk *et al.*, 1994).

Nutrient enrichment after macrophyte decline and temporal reduction of piscivores could be the main trophic factors pushing Lake Zwemlust between the two steady alternatives. The complete return of the lake to a turbid state dominated by phytoplankton seems now to depend upon macrophyte dynamics. If coot and fish weaken predation on macrophytes, a new clear-water phase might return. In this way, management of rudd in the lake or the introduction of an alternative food resource for birds could accelerate this response. The extent of clear and turbid phases in shallow lakes is unequal (Blindow *et al.*, 1993; Meijer *et al.*, 1994) and this, together with our limited knowledge of food web interactions between

littoral and pelagic habitats, makes the response of these systems unpredictable.

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