

An evaluation of the role of daphnids in controlling phytoplankton biomass in clear water versus turbid shallow lakes

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Abstract

Phytoplankton and zooplankton were monitored during 2 years in four eutrophic shallow lakes (two turbid and two clear water) from two wetland reserves in Belgium. In each wetland, phytoplankton biomass was significantly higher in the turbid lake than in the clear water lake. Although total macrozooplankton biomass and the contribution of daphnids to total zooplankton biomass was comparable in the clear water and the turbid lakes, the grazing pressure of macrozooplankton on phytoplankton as estimated from zooplankton to phytoplankton biomass ratios was higher in the clear water lakes. Estimated grazing by daphnids in the clear water lakes was always high in spring. In summer, however, daphnid biomass was low or daphnids were even absent during prolonged periods. During those periods phytoplankton was probably controlled by smaller macrozooplankton or by submerged macrophytes through nutrient competition, allelopathic effects or increased sedimentation rates in the macrophyte vegetation.

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Introduction

The alternative stable states theory predicts that meso- to eutrophic shallow lakes can have two alternative equilibrium states at a given nutrient loading: a clear water or a turbid state (Scheffer, Carpenter, Foley, Folke, & Walker, 2001; Scheffer, Hosper, Meijer, Moss, & Jeppesen, 1993). The clear water state is characterized

by a low phytoplankton biomass and a dense submerged macrophyte vegetation while the turbid state has a high phytoplankton biomass and usually lacks submerged macrophytes. These two alternative stable equilibrium states are stabilized by ecological feedback mechanisms. Large zooplankton like daphnids (*Daphnia* or *Ceriodaphnia*) are considered to play a central role in stabilizing the clear water and turbid states (e.g. Jeppesen et al., 1997; Scheffer, 1999). These daphnids are slow swimmers that are sensitive to fish predation (Brooks & Dodson, 1965; Pace, 1984). Daphnids are also efficient in controlling phytoplankton as they graze on a broad size-range of phytoplankton (Hall, Threlkeld, Burns, & Crowley, 1976). In clear water lakes,

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daphnids can attain a high biomass and can control phytoplankton because the submerged macrophytes provide them with a refuge from fish predation (Burks, Jeppesen, & Lodge, 2001; Timms & Moss, 1984). In turbid lakes, daphnids have no shelter from fish predation and cannot attain a sufficiently high biomass to control phytoplankton.

In 1998 and 1999, two pairs of connected shallow lakes were monitored in two wetlands in Belgium. The two lakes in both wetlands fitted each well into one of the alternative stable states categories. In each wetland, the clear lake had a significantly higher phytoplankton biomass than the turbid lake and, in the clear lake, submerged macrophytes covered about half of the lake surface while macrophytes were absent in the turbid lake (Muylaert et al., 2003). In this paper, we evaluate the importance of daphnids in regulating phytoplankton biomass in the clear water versus turbid lakes of the two wetlands.

Materials and methods

Study site

Two lakes were located in the Blankaart reserve, a wetland of international importance situated in the western part of Belgium, close to the coast (Fig. 1). The lakes in this wetland were created by peat digging and are on average about 1 m deep. The lakes are situated in an area characterized by intensive agriculture and livestock farming, which results in high inputs of nutrients to the lakes. The turbid lake, Lake Blankaart, is relatively large (32 ha) and receives surface water inputs through several rivulets. The clear water lake, Lake Visvijver, is small (0.6 ha) and receives no direct surface water inputs. During periods of high rainfall in winter, flooding connects the two lakes, resulting in an exchange of water and dissolved nutrients. In Lake Visvijver, submerged macrophytes cover about half of the lake surface. During the study period, *Chara*

globularis was the dominant macrophyte in spring but it was replaced by floating beds of filamentous green algae towards the end of summer. Fish were absent from Lake Visvijver during the study period because of a summer fish kill in 1997. In Lake Blankaart, benthivorous and planktivorous fish species like white bream (*Blicca bjoerkna*), roach (*Rutilus rutilus*) and bream (*Abramis brama*) attain high biomass, while piscivorous species are virtually absent (Muylaert et al., 2003).

The two other lakes were located in the De Maten wetland, which is situated in the northeastern part of Belgium (Fig. 1). The De Maten wetland consists of 32 small lakes that are all interconnected by a system of overflows and receive surface water inputs by two main rivulets (Cottenie, Nuytten, Michels, & De Meester, 2001; Michels, Cottenie, Neys, & De Meester, 2001). Like the lakes in the Blankaart wetland, the De Maten lakes were created by peat digging and are about 1 m deep. The two lakes studied, Lake Maten 12 and Lake Maten 13, are situated next to each other and have a similar size (Lake Maten 12: 3.2 ha, Lake Maten 13: 3.3 ha). Both lakes are fed by the same rivulet and Lake Maten 13 flows into Lake Maten 12. In Lake Maten 13, macrophytes cover about half of the lake surface while submerged macrophytes are virtually absent in Lake Maten 12. The dominant macrophytes in Lake Maten 13 during the study period were *Drepanocladus fluitans*, *Polygonum amphibium* and *Nitella translucens*. Fish biomass as measured by fyke nets in 2000 was higher in Lake Maten 12 when compared to Lake Maten 13 (Muylaert et al., 2003). Brown bullhead (*Ameiurus nebulosus*), roach and rudd (*Scardinius erythrophthalmus*) dominated the fish community in Lake Maten 12, while rudd and tench (*Tinca tinca*) were the dominant fish species in Lake Maten 13.

Sampling and analyses

The four lakes were sampled monthly during winter and biweekly during summer during two consecutive years (1998–1999). The two lakes in each wetland reserve were always sampled on the same day. Samples were collected during daytime at a fixed location in each lake. Before taking samples, Secchi depth was measured at the sampling location using a black and white disc. Subsurface samples for phytoplankton were fixed in the field using Lugol's solution. Macrozooplankton was sampled using a Schindler-Patalas trap. The trap was deployed at two depths to sample the entire water column. Macrozooplankton samples were fixed in the field with sucrose-saturated formalin (Haney & Hall, 1973). A water sample was kept refrigerated in the dark and transported to the lab to be subsampled for nutrients and suspended particulate matter (SPM). Samples for dissolved nutrients (nitrite, nitrate,

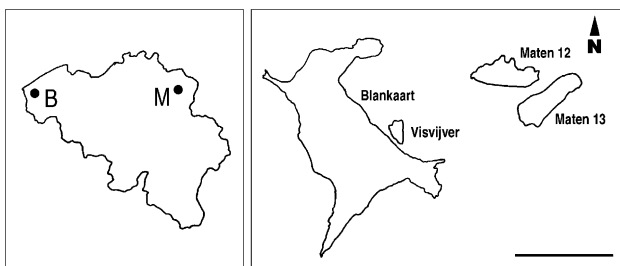


Fig. 1. The location of the 'De Blankaart' (B) and 'De Maten' (M) wetland reserves in Belgium (left) and detailed maps at identical scale of the four lakes studied (right). Scale bar is 500 m.

ammonium and orthophosphate) were first filtered over a GF/F filter and stored frozen until analysis using a Skalar autoanalyser according to standard methods (Grasshof, 1976). Only dissolved nutrients were measured. Concentrations of ammonia, nitrite and nitrate were summed to yield total dissolved inorganic nitrogen concentration. During interpretation of the data, dissolved inorganic nitrogen concentrations and orthophosphate concentrations below $10 \mu\text{g L}^{-1}$ were considered to be potentially limiting for phytoplankton (Reynolds, 1984). SPM concentrations were determined gravimetrically after filtration of a known volume of water onto a preweighed GF/F filter. Phytoplankton was identified up to genus level and also enumerated using inverted microscopy. For each genus, 25–50 cells were measured and biovolume was converted to biomass using published conversion factors (Menden-Deuer & Lessard, 2000). Macrozooplankton was enumerated using a dissection microscope. Cladocerans were identified up to species level, while copepods were identified to the order level. For each taxon in each sample, 30 individuals were measured to convert abundances to biomass using published length–weight regressions (Bottrell et al., 1976).

Data analyses

We used a method based on zooplankton to phytoplankton biomass ratios to estimate the grazing pressure exerted by macrozooplankton on phytoplankton (Blindow, Hargeby, Wagner, & Andersson, 2000; Jeppesen et al., 1994). This method assumes that cladocera graze 100% of their biomass per day, while copepods graze 50% of their biomass per day. Most phytoplankton species have growth rates in the order of 1 cell division per day. Therefore, a grazing pressure exceeding 100% of phytoplankton standing stock removed per day was considered to be of significant

influence on phytoplankton populations. Because relatively large filter-feeding cladocerans like *Daphnia* and *Ceriodaphnia* (referred to as ‘daphnids’ in the remainder of the text) feed on a wide size-range of phytoplankton and are therefore better capable of controlling phytoplankton than other zooplankton, grazing pressure exerted by these species was calculated separately from that of other macrozooplankton (mainly *Bosmina* and copepods).

Because of the connection between the two lakes in each wetland, our null hypothesis was that both lakes in each wetland were similar with respect to all variables. Therefore, paired *t*-tests were used to compare averages of variables between the two lakes in each wetland. The data were $\log(x+1)$ -transformed to reduce skewness in the data and to approximate normal distribution. A *p*-level below 0.05 was considered to be significant.

Results

Average SPM concentrations were higher in turbid lakes Blankaart and Maten 12 when compared to clear water lakes Visvijver and Maten 13 (Tables 1 and 2). The difference in average SPM concentrations was larger in the lakes of the Blankaart wetland than in the lakes of the De Maten wetland. Secchi depth was on average only about 35 cm in lakes Blankaart and Maten 12, while the lake bottom was nearly always visible in Lake Visvijver and Lake Maten 13 (data not shown). Dissolved nutrient concentrations were on average higher in the lakes of the Blankaart wetland compared to those of the De Maten wetland. In the Blankaart wetland, dissolved inorganic nitrogen concentrations were significantly higher in the turbid Lake Blankaart, while orthophosphate concentrations were significantly higher in the clear water Lake Visvijver (Tables 1 and 2, Figs. 2 and 3). In the De Maten wetland, no significant

Table 1. Averages \pm standard deviation of some important parameters measured or estimated in the two lakes from the Blankaart wetland reserve

Variable		Blankaart		Visvijver	<i>p</i> -level
Suspended particulate matter	mg L^{-1}	38 ± 27	>	5 ± 5	<0.0001
Dissolved inorganic nitrogen	$\mu\text{g N L}^{-1}$	6000 ± 6290	>	770 ± 1160	<0.0001
Orthophosphate	$\mu\text{g P L}^{-1}$	177 ± 154	<	465 ± 273	0.0002
Phytoplankton biomass	$\mu\text{g C L}^{-1}$	1192 ± 1180	>	163 ± 222	<0.0001
Fraction <20 μm	%	32 ± 21	<	76 ± 20	<0.0001
Macrozooplankton biomass	$\mu\text{g C L}^{-1}$	1490 ± 1500	>	534 ± 940	0.002
Fraction daphnids	%	13 ± 15		27 ± 51	0.086
Grazing pressure daphnids	$\% \text{ day}^{-1}$	15 ± 20	<	240 ± 533	0.0006
Grazing pressure other macrozooplankton	$\% \text{ day}^{-1}$	101 ± 113	<	227 ± 309	0.011

Paired *t*-tests were used to evaluate differences between the two lakes; when a significant difference was found, this is indicated by < or > between the columns, while the *p*-level for the test is given in the column on the right.

Table 2. Averages \pm standard deviation of some important parameters measured or estimated in the two lakes from the De Maten wetland reserve

Variable		Maten 12		Maten 13	<i>p</i> -level
Suspended particulate matter	mg L ⁻¹	19 \pm 12	>	7 \pm 10	<0.0001
Dissolved inorganic nitrogen	μ g N L ⁻¹	138 \pm 141		100 \pm 119	0.360
Orthophosphate	μ g P L ⁻¹	43 \pm 26	>	18 \pm 22	0.0004
Phytoplankton biomass	μ g C L ⁻¹	442 \pm 320	>	179 \pm 220	<0.0001
Fraction <20 μ m	%	30 \pm 21		50 \pm 31	0.091
Macrozooplankton biomass	μ g C L ⁻¹	344 \pm 370		241 \pm 359	0.059
Fraction daphnids	%	10 \pm 20		15 \pm 18	0.875
Grazing pressure daphnids	% day ⁻¹	10 \pm 13	<	288 \pm 881	0.032
Grazing pressure other macrozooplankton	% day ⁻¹	49 \pm 58	<	170 \pm 360	0.020

Paired *t*-tests were used to evaluate differences between the two lakes; when a significant difference was found, this is indicated by < or > between the columns, while the *p*-level for the test is given in the column on the right.

difference between the two lakes was found for dissolved inorganic nitrogen, while orthophosphate concentrations were significantly higher in the turbid Lake Maten 12 than in the clear water Lake Maten 13. In both Blankaart lakes, dissolved inorganic nitrogen concentrations were maximal in winter and decreased strongly during summer (Fig. 2). In the De Maten lakes, dissolved inorganic nitrogen concentrations did not display a clear seasonal pattern. Orthophosphate concentrations in both Blankaart lakes increased during summer. Orthophosphate concentrations in Lake Maten 12 did not display a clear seasonal pattern, while in Lake Maten 13, lowest orthophosphate concentrations were observed during summer. Potentially limiting dissolved inorganic nitrogen concentrations were observed on some occasions in Lake Blankaart but never in the other lakes. Potentially limiting concentrations of orthophosphate were observed on three occasions in the turbid lakes Blankaart and Maten 12 but never in the clear water Lake Visvijver. In the clear water Lake Maten 13, however, orthophosphate concentrations were frequently below the potentially limiting level.

In both wetlands, phytoplankton biomass was significantly higher in the turbid lake when compared to the clear water lake (Tables 1 and 2, Figs. 2 and 3). This difference was most pronounced in the Blankaart wetland. In the turbid lakes, phytoplankton biomass increased gradually from spring to summer and decreased again in autumn. In Lake Maten 12 in 1999, this increase was interrupted by a decrease during the period May–July. In the clear water lakes, the seasonal development of phytoplankton was much more irregular than in the turbid lakes. In Lake Visvijver, a first peak in phytoplankton biomass occurred in spring (March in 1998 and April in 1999). After this peak, phytoplankton biomass was low and increased again in summer, after the collapse of the submerged macrophyte vegetation. In

Lake Maten 13 in 1998, a small phytoplankton peak in March was followed by a long period of very low phytoplankton biomass. Phytoplankton biomass remained low until November, when a large increase in phytoplankton biomass was observed. In 1999, phytoplankton biomass in Lake Maten 13 fluctuated between 50 and 600 μ g C L⁻¹ from late March to early September.

The dominant phytoplankton groups (Table 3) in the clear water lakes were cryptophytes like *Cryptomonas* (Lake Visvijver) or *Rhodomonas* (Lake Maten 13). In addition to cryptophytes, small coccoid unicells <5 μ m (ultraplankton) were an important component of the phytoplankton community in the clear water lakes, together with *Peridinium* in Lake Maten 13. In turbid Lake Blankaart, the dominant phytoplankton groups were coenobial chlorophytes (*Pediastrum*, *Oocystis* and *Scenedesmus*). During spring, however, *Stephanodiscus* dominated phytoplankton biomass, while the cyanobacterium *Planktothrix* was important in late summer 1999. In turbid Lake Maten 12, the dominant phytoplankton groups were euglenophytes like *Trachelomonas* and *Phacus* together with the coenobial chlorophyte *Scenedesmus*. In both wetlands, phytoplankton <20 μ m (Tables 1 and 2, Figs. 2 and 3) represented on average a higher fraction of total phytoplankton biomass in the clear water lakes when compared to the turbid lakes but this difference was only significant in the Blankaart wetland.

Average total macrozooplankton biomass was higher in the turbid than in the clear water lakes (Tables 1 and 2, Figs 2 and 3) although this difference was only significant in the De Maten wetland. The contribution of the daphnids *Daphnia* or *Ceriodaphnia* to total macrozooplankton biomass was slightly higher in the clear water lakes but this difference was not significant in both wetlands. In the turbid lakes, daphnids as well as

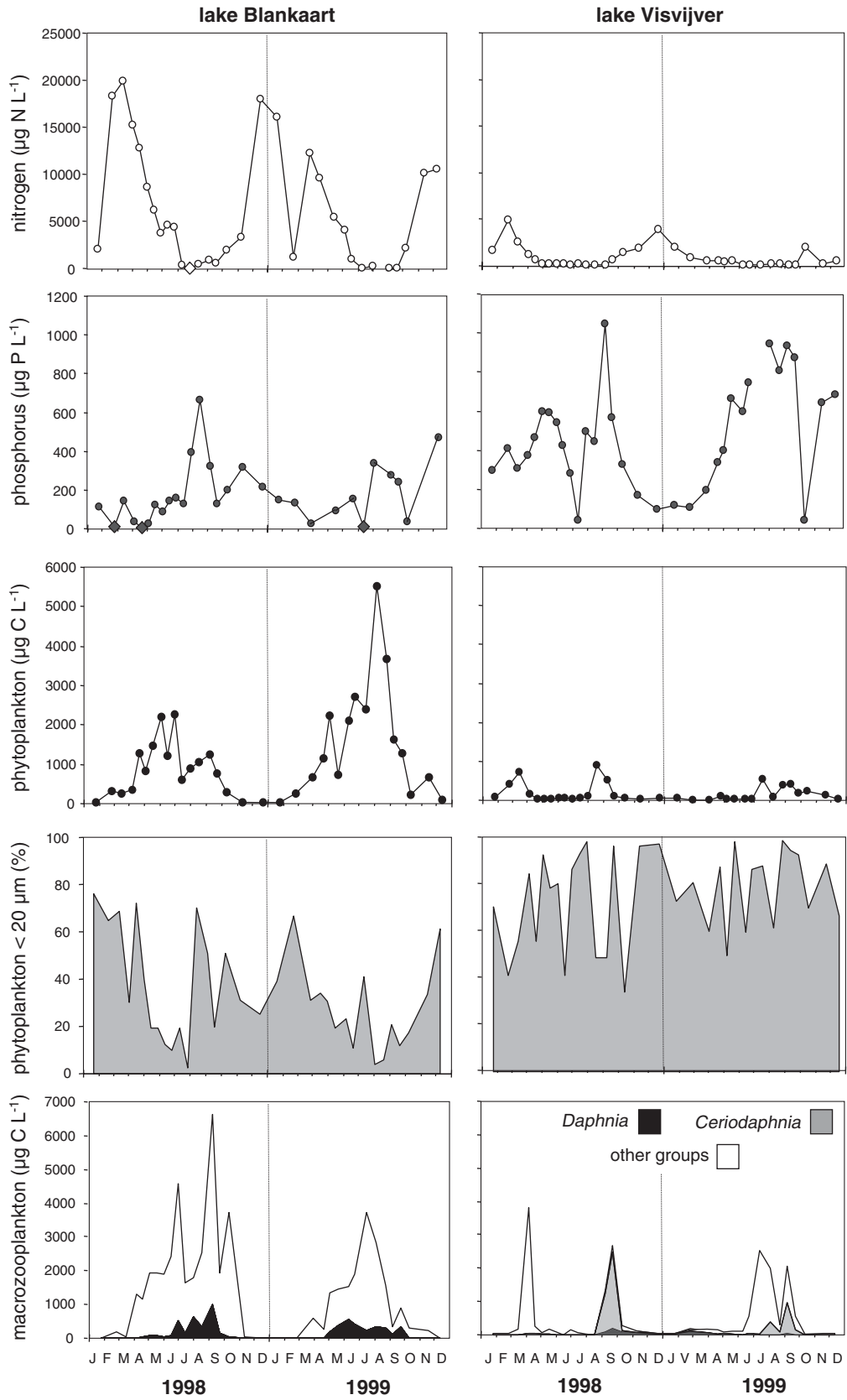


Fig. 2. Temporal variation of dissolved inorganic nitrogen and orthophosphate concentrations, phytoplankton biomass, the contribution of small (<20 μm) phytoplankton to total biomass, and biomass of macrozooplankton in the two lakes from the Blankaart wetland. When dissolved nutrient concentrations were potentially limiting (< 10 μg L⁻¹), this is indicated by a diamond in the graphs.

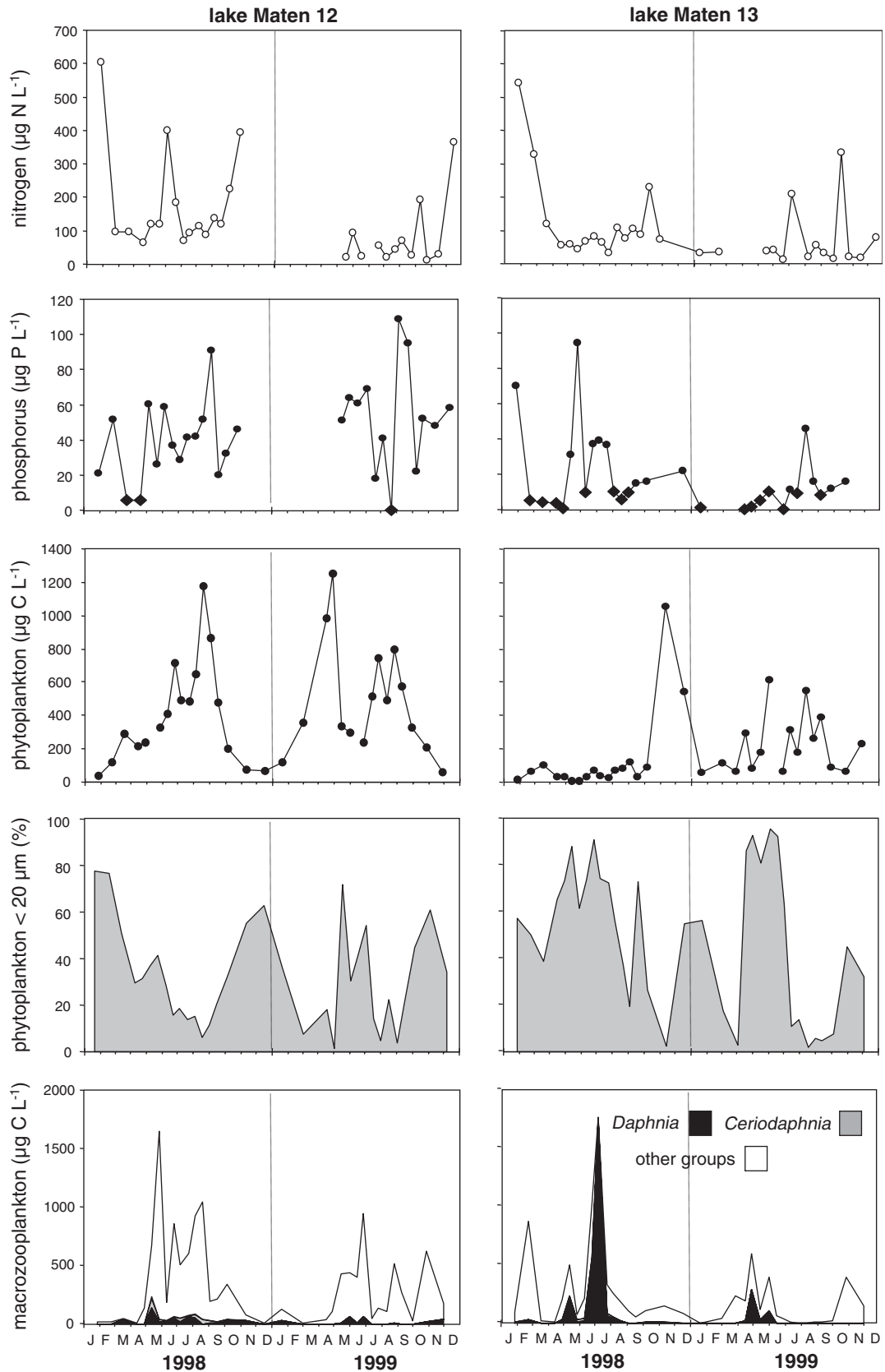


Fig. 3. Temporal variation of dissolved inorganic nitrogen and orthophosphate concentrations, phytoplankton biomass, the contribution of small (<20 μm) phytoplankton to total biomass, and biomass of macrozooplankton in the two lakes from the De Maten wetland. When dissolved nutrient concentrations were potentially limiting ($< 10 \mu\text{g L}^{-1}$), this is indicated by a diamond in the graphs.

Table 3. Percentage contribution to annual average phytoplankton biomass of the 10 dominant genera in the four lakes studied

'De Blankaart'		'De Maten'					
Blankaart		Visvijver		Maten 12		Maten 13	
<i>Pediastrum</i>	31	<i>Cryptomonas</i>	45	<i>Trachelomonas</i>	19	<i>Rhodomonas</i>	29
<i>Oocystis</i>	11	Ultraplankton	22	<i>Scenedesmus</i>	14	<i>Peridinium</i>	10
<i>Scenedesmus</i>	10	<i>Rhodomonas</i>	7	<i>Phacus</i>	11	Cocoid < 5 µm	7
<i>Cryptomonas</i>	10	<i>Microcystis</i>	4	Cocoid < 5 µm	8	<i>Cryptomonas</i>	6
<i>Stephanodiscus</i>	6	<i>Kirchneriella</i>	2	<i>Cryptomonas</i>	6	<i>Desmidium</i>	6
<i>Planktothrix</i>	5	<i>Anabaena</i>	2	<i>Chroococcus</i>	5	<i>Trachelomonas</i>	5
<i>Staurastrum</i>	3	<i>Stephanodiscus</i>	2	<i>Euglena</i>	3	<i>Euglena</i>	5
<i>Lepocynclis</i>	3	<i>Peridinium</i>	1	<i>Pediastrum</i>	3	<i>Scenedesmus</i>	5
<i>Coelastrum</i>	2	<i>Euglena</i>	1	<i>Staurastrum</i>	3	<i>Pediastrum</i>	2
<i>Phacus</i>	2	<i>Volvox</i>	1	<i>Rhodomonas</i>	3	<i>Staurastrum</i>	2

other macrozooplankton attained their maximal biomass during summer. In the clear water lakes, macrozooplankton biomass peaks occurred irregularly throughout the year. The grazing pressure exerted on phytoplankton by daphnids as well as other macrozooplankton groups was significantly higher in the clear water than in the turbid lakes (Tables 1 and 2, Fig. 4). In the turbid lakes, grazing pressure by daphnids never exceeded a 100% removal of phytoplankton standing stock per day. Other macrozooplankton groups sometimes grazed more than 100% of phytoplankton biomass per day in the turbid lakes, especially in Lake Blankaart in 1998 and in Lake Maten 12 during spring and early summer, but in general the grazing impact of other macrozooplankton was low. In both clear water lakes, grazing by daphnids frequently exceeded 100% of phytoplankton biomass removed per day. Grazing by daphnids was high on at least one sampling occasion during spring. In 1999 in Lake Visvijver and in 1998 in Lake Maten 13, daphnids continued to exert a high grazing pressure during most of the summer. In the other years, on the contrary, grazing by daphnids was low or daphnids were even absent during prolonged periods in summer.

Discussion

In both wetlands, biomass of daphnids as well as other macrozooplankton was comparable in the turbid and the clear water lake, despite the fact that the turbid lakes had a higher biomass of planktivorous fish and lacked submerged macrophytes that could protect macrozooplankton from fish predation (Muylaert et al., 2003). The contribution of daphnids to total macrozooplankton biomass was also not significantly different between the clear water and turbid lakes. This suggests that macrozooplankton in general and daph-

nids in particular can compensate for the high fish predation pressure present in turbid lakes. In turbid lakes, high predation losses may be partially counterbalanced by high population growth rates resulting from high food levels. The success of macrozooplankton in the turbid lakes may also be related to their small size. This is illustrated by the fact that the daphnids in the turbid lakes were mainly small species like *Daphnia galeata*, *D. cucullata* and their hybrids, which are relatively insensitive to fish predation (Declerck & De Meester, 2003).

Although daphnids attained a similar biomass in the turbid than in the clear water lakes, their estimated grazing pressure on phytoplankton was significantly lower in the turbid lakes, mainly because phytoplankton biomass was higher in the turbid lakes. In the turbid lakes, the estimated grazing pressure of daphnids never exceeded more than 100% of phytoplankton biomass per day. Other macrozooplankton (predominantly *Bosmina* and cyclopoid copepods) on some occasions had the capacity to graze a significant fraction of phytoplankton standing stock per day. However, these taxa graze only on small phytoplankton species (Hall et al., 1976), whereas large phytoplankton species like coenobial chlorophytes, euglenophytes or cyanobacteria dominated the phytoplankton community in the turbid lakes. This probably explains why phytoplankton biomass in the turbid lakes increased continuously from spring to summer and why a concomitant increase in biomass of daphnids and other macrozooplankton failed to result in a decline in phytoplankton biomass.

In the clear water lakes, the estimated grazing pressure of daphnids frequently exceeded 100% of phytoplankton biomass per day. This was not due to a higher biomass of daphnids in the clear water lakes but due to a lower biomass of phytoplankton. In both years in the clear water lakes, the estimated grazing pressure of daphnids was maximal during spring. Grazing by daphnids in spring probably contributed to the

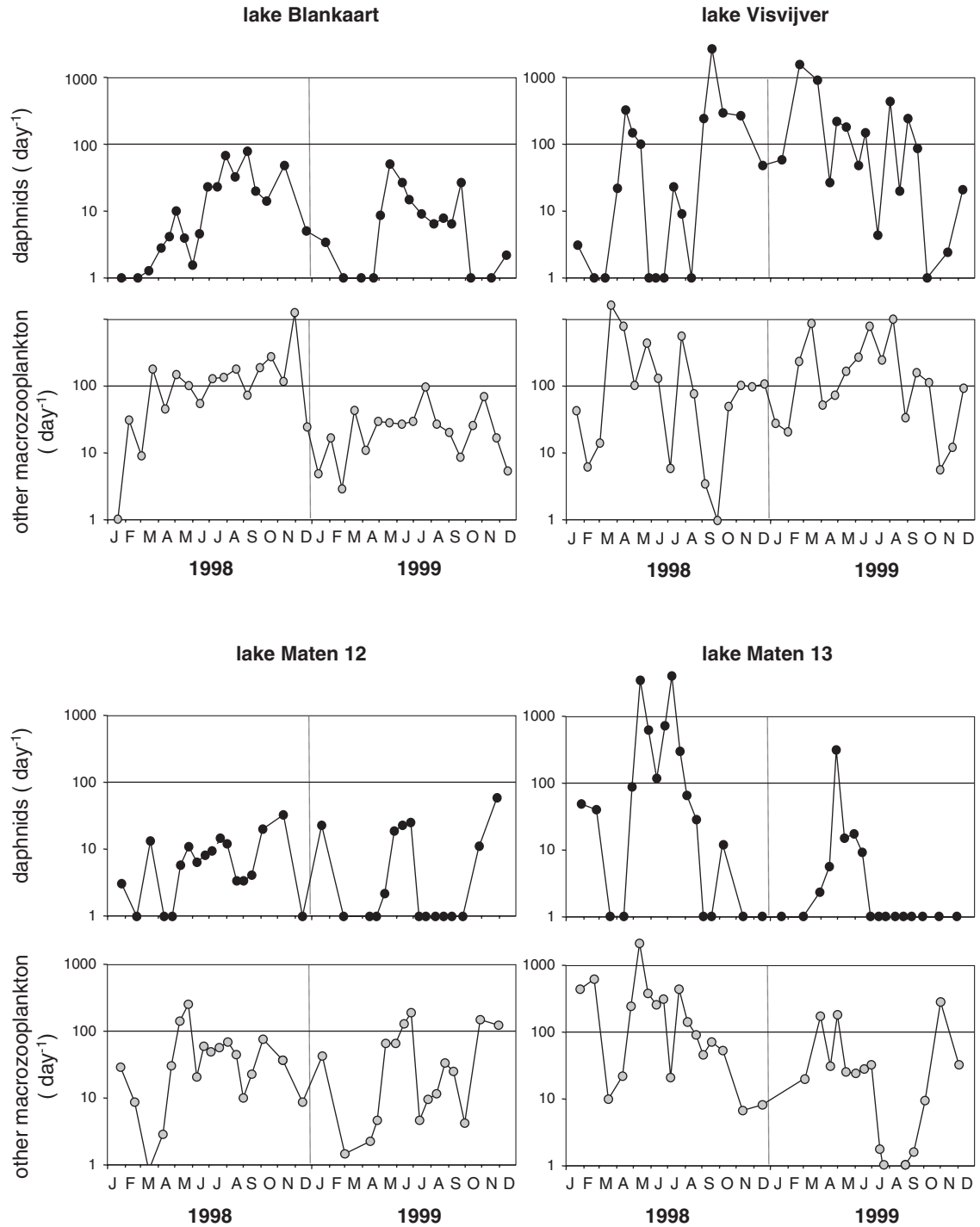


Fig. 4. Estimated grazing pressure (in % of phytoplankton standing stock removed day^{-1}) exerted by daphnids and other macrozooplankton on phytoplankton in the studied lakes. Note the logarithmic scale on the vertical axis. The horizontal line corresponds to an estimated grazing pressure of 100% of phytoplankton biomass removed daily.

establishment of a spring clear water phase in the clear water lakes, a well-known phenomenon that occurs in many lakes with low fish predation pressure (Deneke & Nixdorf, 1999; Lampert, Fleckner, Rai, & Taylor, 1986; Sommer, Gliwicz, Lampert, & Duncan, 1986). During summer, however, the grazing pressure of daphnids was

relatively low. During the summer of 1998 in Lake Visvijver and during the summer of 1999 in Lake Maten 13, daphnids were present at low biomass or were even absent during prolonged periods. The reason why biomass of daphnids was low during summer in the clear water lakes remains unclear. Midsummer declines

of daphnid populations are a common phenomenon in lakes (Hülsmann, 2003; Luecke, Vanni, Magnuson, Kitchell, & Jacobson, 1990; Sommer et al., 1986). Midsummer declines of daphnids are often ascribed to predation by new cohorts of age-0 fish (Cryer, Peirson, & Townsend, 1986). Predation by age-0 fish may explain the disappearance of daphnids in Lake Maten 13 but not in Lake Visvijver, as this latter lake is free of fish due to a period of anoxia caused by massive mortality of macrophytes in the year before the start of this study. Another possible explanation for the often low biomass of daphnids during summer in the clear water lakes may be predation by macroinvertebrates associated with the submerged macrophyte vegetation. The biomass of daphnids may also have been low because of the low food levels in the clear water lakes during summer.

A low grazing pressure of daphnids on phytoplankton during summer has been observed in previous studies of clear water shallow lakes (Blindow et al., 2000; Tonno, Kunnapp, & Noges, 2003), suggesting that other factors than daphnids are responsible for the low phytoplankton biomass in summer in clear water shallow lakes. In the clear water lakes Visvijver and Maten 13, grazing by macrozooplankton other than daphnids was often high when grazing by daphnids was low in summer. In contrast to the turbid lakes, where these inefficient grazers failed to control phytoplankton, these smaller zooplankton groups may have been more efficient in the clear water lakes, where small and therefore easily ingestible phytoplankton was a more important component of the phytoplankton community. Like in many clear water lakes (e.g. Godmaire & Planas, 1986; Schriver, Bøgestrand, Jeppesen, & Søndergaard, 1995; Søndergaard & Moss, 1998), small cryptophytes and coccoid phytoplankton species dominated the phytoplankton community in lakes Visvijver and Maten 13. The low phytoplankton biomass in the clear water lakes during summer may also be due to direct effects of the submerged macrophyte vegetation on phytoplankton. Macrophytes may take up a large part of nutrients in clear water lakes, resulting in nutrient limitation of phytoplankton (Kufel & Ozimek, 1994; Van Donk, Gulati, Iedema, & Meulemans, 1993). Indeed, in Lake Visvijver, N concentrations declined strongly during the vegetated period, resulting in a very low N:P ratio (< 1) and in Lake Maten 13, orthophosphate concentrations were frequently below the level that is potentially limiting phytoplankton growth. Macrophytes also produce allelopathic substances that inhibit the growth of phytoplankton (Gross, 2003) and reduce water column turbulence, resulting in increased sedimentation losses of phytoplankton (Jones, 1990). The low phytoplankton biomass in the clear water lakes during summer may also be the result of a synergetic effect of macrophytes and zooplankton other than daphnids. By reducing

nutrient levels and turbulence in the water column, macrophytes may create an environment that favours small phytoplankton taxa that are easily grazed by zooplankton. Small phytoplankton taxa have lower sedimentation rates and are more efficient in taking up nutrients than large taxa and tend to dominate in environments characterized by low nutrient level and/or low turbulence (Reynolds, 1988).

In conclusion, our results suggest that the higher predation pressure of fish in turbid lakes does not influence total macrozooplankton biomass and the contribution of daphnids to zooplankton biomass, but the ability of zooplankton to attain a sufficiently high biomass to control phytoplankton. The grazing pressure of daphnids on phytoplankton (estimated from zooplankton to phytoplankton biomass ratios) was higher in the clear water lakes than in the turbid lakes. During summer, however, grazing pressure by daphnids was often low in the clear water lakes. During summer, the submerged macrophyte vegetation as well as other zooplankton probably played a more important role in controlling phytoplankton than daphnids.

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References

- Blindow, I., Hargeby, A., Wagner, B. M. A., & Andersson, G. (2000). How important is the crustacean zooplankton for maintenance of water clarity in shallow lakes with abundant submerged vegetation? *Freshwater Biology*, *44*, 185–197.
- Bottrell, H. H., Duncan, A., Gliwicz, Z. M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., et al. (1976). A review of some problems in zooplankton production studies: Contribution from the Plankton Ecology Group (IBP). *Norwegian Journal of Zoology*, *24*, 419–456.
- Brooks, D., & Dodson, S. L. (1965). Predation, body size, and composition of plankton. *Science*, *150*, 28–35.

- Burks, R. L., Jeppesen, E., & Lodge, D. M. (2001). Littoral zone structures as *Daphnia refugia* against fish predators. *Limnology & Oceanography*, 46, 230–237.
- Cottenie, K., Nuytten, N., Michels, E., & De Meester, L. (2001). Zooplankton community structure and environmental conditions in a set of interconnected ponds. *Hydrobiologia*, 442, 339–350.
- Cryer, M., Peirson, G., & Townsend, C. R. (1986). Reciprocal interactions between roach, *Rutilus rutilus*, and zooplankton in a small lake: Prey dynamics and fish growth and recruitment. *Limnology & Oceanography*, 31, 1022–1038.
- Declercq, S., & De Meester, L. (2003). Impact of fish predation on coexisting *Daphnia* taxa: A partial test of the temporal hybrid superiority hypothesis. *Hydrobiologia*, 500, 83–94.
- Deneke, R., & Nixdorf, B. (1999). On the occurrence of clear-water phases in relation to shallowness and trophic state: A comparative study. *Hydrobiologia*, 409, 251–262.
- Godmaire, H., & Planas, D. (1986). Influence of *Myriophyllum spicatum* L. on the species composition, biomass and primary productivity of phytoplankton. *Aquatic Botany*, 23, 299–308.
- Grasshof, K. (1976). *Methods of seawater analysis*. New York: Verlag Chemie.
- Gross, E. M. (2003). Allelopathy of aquatic autotrophs. *Critical Reviews in Plant Sciences*, 22, 313–339.
- Hall, D. J., Threlkeld, S. T., Burns, C. W., & Crowley, P. H. (1976). Size-efficiency hypothesis and size structure of zooplankton communities. *Annual Review of Ecology & Systematics*, 7, 177–208.
- Haney, J. F., & Hall, D. J. (1973). Sugar coated *Daphnia*: A technique for cladocera. *Limnology & Oceanography*, 18, 331–333.
- Hülsmann, S. (2003). Recruitment patterns of *Daphnia*: A key for understanding midsummer declines? *Hydrobiologia*, 491, 35–46.
- Jeppesen, E., Jensen, J. P., Søndergaard, M., Lauridsen, T., Pedersen, L. J., & Jensen, L. (1997). Top-down control in freshwater lakes: The role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia*, 342/343, 151–164.
- Jeppesen, E., Søndergaard, M., Kanstrup, E., Petersen, B., Eriksen, R. B., Hammerhøj, M., et al. (1994). Does the impact of nutrients on the biological structure and function of freshwater and brackish lakes differ? *Hydrobiologia*, 275/276, 15–30.
- Jones, R. C. (1990). The effect of submersed aquatic vegetation on phytoplankton and water quality in the tidal Potomac river. *Journal of Freshwater Ecology*, 5, 279–288.
- Kufel, L., & Ozimek, T. (1994). Can *Chara* control phosphorus cycling in Lake Lukajno (Poland)? *Hydrobiologia*, 275/276, 277–283.
- Lampert, W., Fleckner, W., Rai, H., & Taylor, B. E. (1986). Phytoplankton control by grazing zooplankton – A study on the spring clear-water phase. *Limnology & Oceanography*, 31, 478–490.
- Luecke, C., Vanni, M. J., Magnuson, J. J., Kitchell, J. F., & Jacobson, P. T. (1990). Seasonal regulation of *Daphnia* populations by planktivorous fish – Implications for the spring clear-water phase. *Limnology & Oceanography*, 35, 1718–1733.
- Menden-Deuer, S., & Lessard, E. J. (2000). Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnology & Oceanography*, 45, 569–579.
- Michels, E., Cottenie, C., Neys, L., & De Meester, L. (2001). Zooplankton on the move: First results on the quantification of dispersal of zooplankton in a set of interconnected ponds. *Hydrobiologia*, 442, 117–126.
- Muylaert, K., Declercq, S., Geenens, V., Van Wichelen, J., Degans, H., Vandekerckhove, J., et al. (2003). Zooplankton, phytoplankton and the microbial food web in two turbid and two clearwater shallow lakes in Belgium. *Aquatic Ecology*, 37, 137–150.
- Pace, M. L. (1984). Zooplankton community structure, but not biomass, influences the phosphorus chlorophyll a relationship. *Canadian Journal of Fisheries & Aquatic Sciences*, 41, 1089–1096.
- Reynolds, C. S. (1984). *Freshwater phytoplankton* (384pp.). Cambridge: Cambridge University Press.
- Reynolds, C. S. (1988). Functional morphology and the adaptive strategies of freshwater phytoplankton. In C. D. Sandgren (Ed.), *Growth and reproductive strategies of freshwater phytoplankton* (pp. 388–433). Cambridge: Cambridge University Press.
- Scheffer, M. (1999). The effect of aquatic vegetation on turbidity: How important are the filter feeders? *Hydrobiologia*, 409, 307–316.
- Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413, 591–596.
- Scheffer, M., Hosper, S. H., Meijer, M.-L., Moss, B., & Jeppesen, E. (1993). Alternative equilibria in shallow lakes. *Trends in Ecology & Evolution*, 8, 275–278.
- Schriver, P., Bøgestrand, J., Jeppesen, E., & Søndergaard, M. (1995). Impact of submerged macrophytes on fish–zooplankton–phytoplankton interactions – Large-scale enclosure experiments in a shallow eutrophic lake. *Freshwater Biology*, 33, 255–270.
- Sommer, U., Gliwicz, Z. M., Lampert, W., & Duncan, A. (1986). The PEG-model of seasonal succession of planktonic events in fresh waters. *Archiv für Hydrobiologie*, 106, 433–471.
- Søndergaard, M., & Moss, B. (1998). Impact of submerged macrophytes on phytoplankton in shallow freshwater lakes. In E. Jeppesen, M. Søndergaard, & K. Christoffersen (Eds.), *The structuring role of submerged macrophytes in lakes* (pp. 115–132). New York: Springer.
- Timms, R. M., & Moss, B. (1984). Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. *Limnology & Oceanography*, 29, 472–486.
- Tonno, I., Kunnapp, H., & Noges, T. (2003). The role of zooplankton grazing in the formation of ‘clear water phase’ in a shallow charophyte-dominated lake. *Hydrobiologia*, 506, 353–358.
- Van Donk, E., Gulati, R. D., Iedema, A., & Meulemans, J. T. (1993). Macrophyte-related shifts in the nitrogen and phosphorus contents of the different trophic levels in a biomanipulated shallow lake. *Hydrobiologia*, 251, 19–26.