4 Field Observations of Daphnid Grazing

4.1 Two Different Lakes in Holland

From mesocosm studies and plankton eco-assays examining toxicant exposure, it has become clear that the grazing effectiveness of daphnids is an important factor in plankton dynamics, and that the grazing effectiveness can be reduced by toxicant loading. In this chapter, the relevance of daphnid grazing in the field situation will be demonstrated on the basis of field surveys carried out in two Dutch lakes: Lake Geestmerambacht and Lake Amstelmeer.

Lake Geestmerambacht and Lake Amstelmeer are two moderately deep, man-made lakes in the province of North-Holland in the Netherlands (see Fig. 4.1). Both lakes were studied quite intensively during the nineteen nineties, with particular attention paid to their plankton communities. Comparative eco-assay studies were performed with water from both lakes in order to acquire an improved understanding of the variation in the grazing effectiveness of daphnids, and biotic and abiotic factors that may influence it .

Morphology

Lake Geestmerambacht was created from 1967 to 1979 as a consequence of sand excavation. The lake has a surface area of 70 ha and an average depth of 11 metres, with a deep area of 20–21 metres in the center . It is an occasional reservoir (8 Mm^3) for excessive polder water. The water residence time is more than 15 years. The surrounding area is used for recreation and pasture for cattle farming. The water is mildly brackish (salinity 0.25‰). The lake is monomictic, with stratification occurring in summer during the period from May–June to September–October (WL 1996; Van Dokkum and Van der Veen, 2000).

Lake Amstelmeer is a former tidal channel (Amsteldiep) of the Wadden Sea tidal area. In 1925, a dam was constructed separating the channel from the sea, thereby creating the lake. It has a surface area of 650 ha and is moderately deep with an average depth of 4.5 metres and a central section that is 10–16 metres deep. Lake Amstelmeer is an operational reservoir (29 Mm^3) for superfluous polder water from a catchment area consisting of 24 000 ha of polders in agricultural use (flower bulb cultivation, arable land). The residence time of the water is 2–3 months. The lake has slightly brackish water (salinity: 0.5–1.5‰).

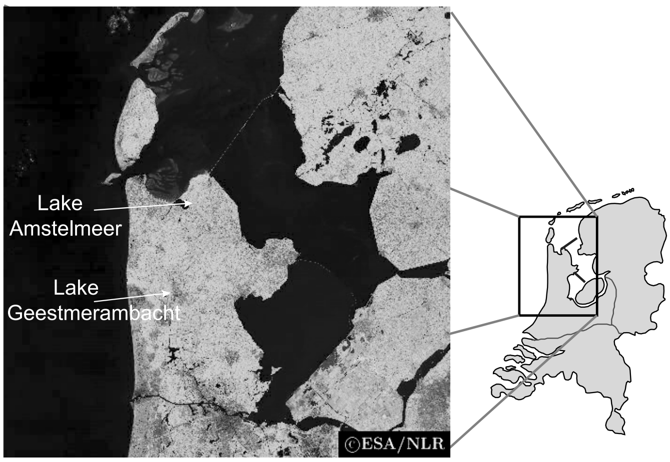

Fig. 4.1. Location of Lake Geestmerambacht and Lake Amstelmeer in the Netherlands

Water Quality

Both lakes are eutrophic: the average total P concentration is 0.45 mg/l in both lakes. The Kjeldal N concentration is higher in Lake Amstelmeer (2.3 mg/l) than in Lake Geestmerambacht (1.4 mg/l).

Lake Geestmerambacht does not have a permanent eutrophied character, and turbidity is generally low with a secchi-depth of 50–320 cm; and chlorophyll-a concentrations ranging from < 8 µg/l during the clear water phase which follows a short spring bloom of up to 185 µg/l during the cyanobacteria blooms that are regularly observed during August–September, (Van Dokkum et al. 1999; Van Dokkum and Hoornsman, 2000; Foekema and Van Dokkum, 2000; Holthaus et al. 2001).

In contrast, Lake Amstelmeer has a permanent eutrophied character (*senso lato,* see Chap. 1): a high turbidity, secchi-depth of 30–140 cm; no submerged vegetation; and a chlorophyll-a concentration typically ranging from 50 up to more than 200 µg/l (Fig. 4.2). A clear water phase is not reached.

4.2 The Plankton Dynamics in Lake Geestmerambacht

Phytoplankton

The phytoplankton dynamics in Lake Geestmerambacht show a typical seasonal pattern (see Fig. 4.3).

In winter, the chlorophyll-a concentration is low and the transparency of the lake is high. In the spring, when the water temperature and day-length increase, phytoplankton starts to develop and the spring bloom can reach chlorophyll concentrations up to 185 µg/l. Diatoms and green algae dominate the plankton (AquaSense 1996) (see Fig, 4.4). After the spring bloom has collapsed, a clear water

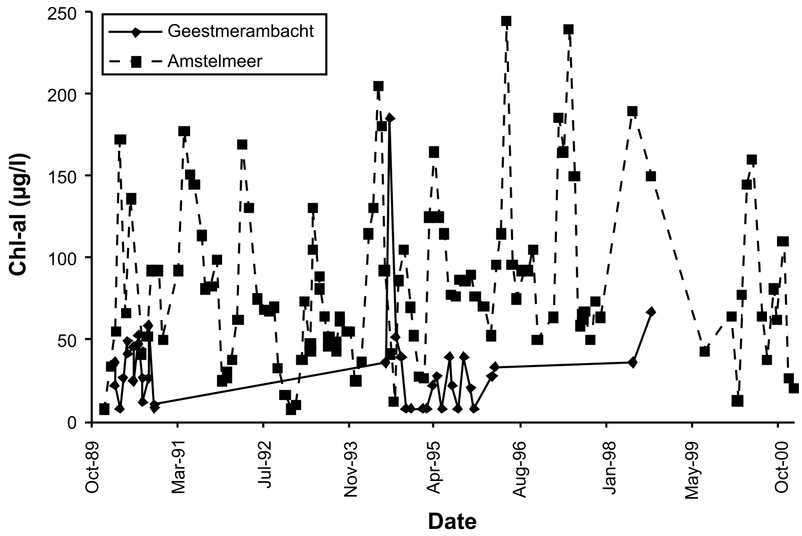

Fig. 4.2. Algal density (expressed as chlorophyll-a, in µg/l) in Lake Geestmerambacht and Lake Amstelmeer in 1990–2000

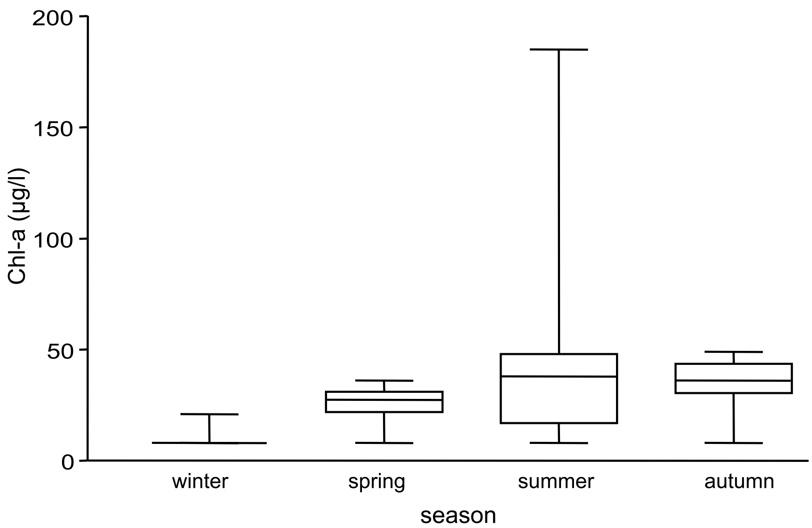

Fig. 4.3. Seasonal phytoplankton dynamics for Lake Geestmerambacht in the period 1990–2000 (box-whisker plots). See Fig. 4.10 for comparison

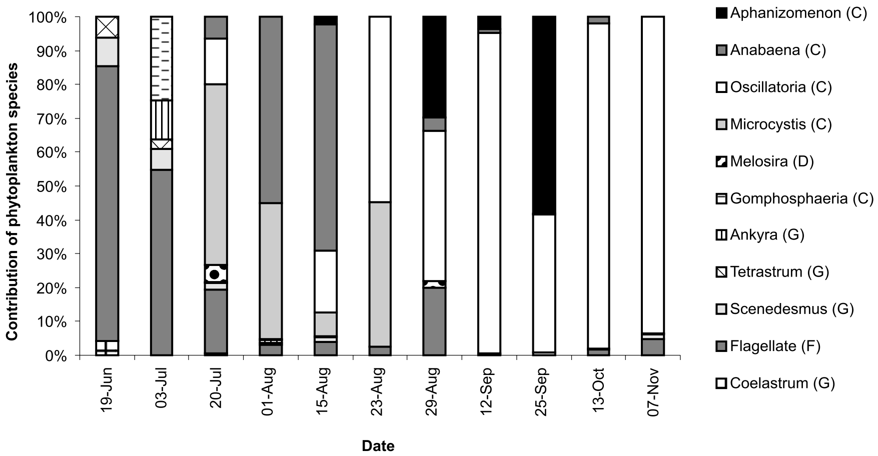

Fig. 4.4. Phytoplankton composition in Lake Geestmerambacht water in 2000. Abbreviations in the legend: (G)=green algae; (D)=Diatom; (C)=cyanobacteria; (F)= Flagellate

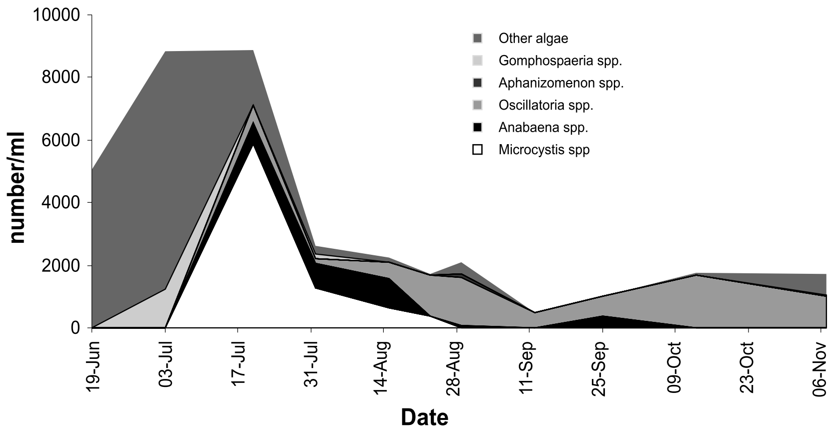

Fig. 4.5. The summer/autumn bluegreen algae bloom in Lake Geestmerambacht in 2000. In July, bluegreen algae (esp. Microcystis) began to dominate the plankton. In mid August, floating mats of Microcystis aeruginosa were observed. After this, an Oscillatoria bloom developed. Other algae: mainly flagellates and green algae. Data from Holthaus et al. 2001

phase with chlorophyll-a densities < 50 μg/l is reached. During the summer months, however, bluegreen algae begin to develop. The summer bluegreen algae bloom was monitored from 1998 to 2000 (Van Dokkum et al. 1999; Van Dokkum and Hoornsman, 2000; Foekema and Van Dokkum 2000; Holthaus et al. 2001). Bluegreen algae start to develop in June, and at the end of July/ early August the plankton is dominated by cyanobacteria (> 90%). The bloom continues to the end of October.

The morphology of the lake is probably a major reason for the dominance of cyanobacteria in the late summer and autumn. Lake Geestmerambacht is a relatively deep lake, with a depth of 20–22 meters. The lake is monomictic and becomes stratified from ca. June to October. The thermocline is located at a depth of ca. 10 meters in June, and ca. 15 meters in October (AquaSense 1996). During the period of stratification, phosphorus and nitrogen are incorporated in algal biomass in the epilimnion. Due to the death and subsequent sedimentation of the algae, the epilimnion may be depleted of nutrients. In these circumstances, bluegreen algae with the ability to control their own buoyancy have a competitive advantage over algae that cannot do so, because they can find nutrients near the thermocline at night and in the light near the water surface during the day (Chorus and Bartram 1999). *Microcystis*, the dominant cyanobacteria occurring during the summer bloom, is typical for stratified monomictic lakes (Chorus and Bartram 1999).

Zooplankton

The zooplankton in the lake is not studied on a regular basis, and therefore little information is available., An inventory of the zooplankton dynamics was made in 1994 (AquaSense 1996, see Fig. 4.6). Substantial numbers of rotifera and copepods were found from March to November. Cladocerans were present in June and August–November,. The species found in June was *Bosmina coregoni*.The cladoceran community was more diverse in the autumn with *Daphnia hyalina*, *Diaphanosoma brachyurum* and *Bosmina longirostris* also present.

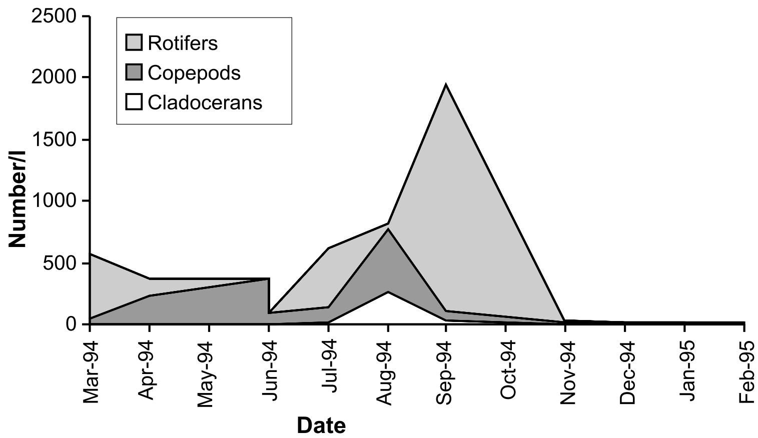

Fig. 4.6. Zooplankton dynamics at one location in Lake Geestmerambacht in 1994. Data from AquaSense 1996

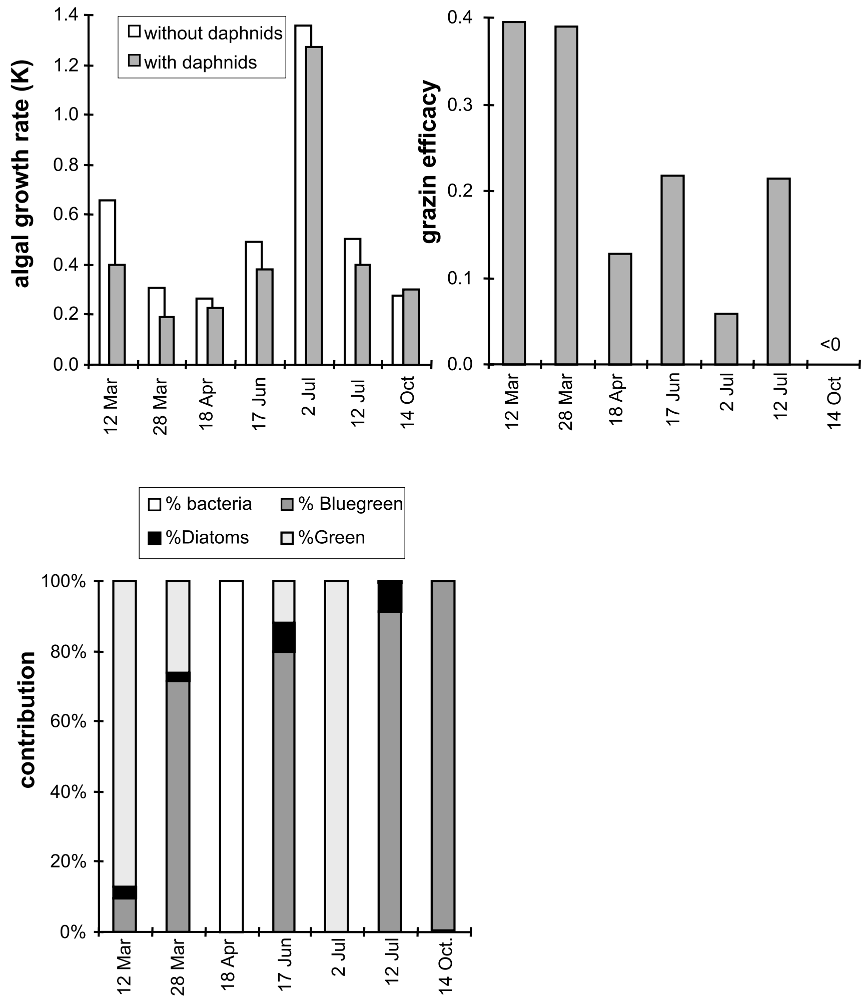

Fig. 4.7. Upper left panel: Development rates of natural algal communities from Lake Geestmerambacht in the plankton-eco-assay, sampled throughout the year. Right panel: The daphnid grazing effectiveness determined in these plankton eco-assay tests at initial daphnid densities of 8 per litre. Lower left panel: The phytoplankton composition

Zooplankton Grazing

In 1996, a series of plankton ecoassays were performed with water from Lake Geestmerambacht, in order to characterise the grazing effectiveness of daphnids in response to the seasonal change in algal composition. The grazing effectiveness (Fig. 4.7) showed a clear seasonal variation with a general reduction in the grazing effectiveness throughout the year. The highest grazing effectiveness (40%) was reached in March. In the summer period the grazing effectiveness fell to below 20%. In the test performed on July 2nd, a grazing effect capable of inhibiting the development of algal density was, apparently, completely absent. The failure of grazing was most likely caused by the extremely rapid growth of the green algae *Chlorococcus.* Moreover, *Chlorococcus* can appear in a broad size range from 10–100 µm, and it is possible that selective grazing on the edible smaller cells could cause a shift of the population towards larger, inedible cells.

This series of tests clearly revealed that the capability of daphnids to control algal growth may vary considerably throughout the year, due to the changes in algal composition. Daphnid grazing throughout the growing season may cause a shift in the algal community to less edible species partly as a result of grazing. However, it also revealed that even blue-green algae could be grazed reasonably effectively (GR% = 10–20%) in these studies with relatively low initial algal concentrations (i.e. *Anabaena sp*. dominating in June).

Daphnid grazing, however, was completely absent during the final test of this series in October. In this test, the algal community consisted entirely of a population of the blue-green *Oscillatoria,* which often exists in filamentous structures which are not easily ingested by daphnids.

It was observed in an experiment using *Oscillatoria* (see Sect. 2.2), that the grazing effectiveness on filamentous cyanobacteria is heavily dependent on the initial daphnid densities.

Daphnid grazing on *Anabaena sp*. in July was also observed as being only marginal (GR% 2–5) at initial densities of 4 or 6 *D. magna* per litre whereas, at initial densities of 8–12 individuals per litre, a grazing effectiveness of 20, to over 50%, was obtained, resulting in moderate control of the *Anabaena* population development.

Resilience of the Plankton Community to Eutrophication

From a lake management point-of-view, it is important to have information on the response of the plankton community to an increase in the nutrient load. The "resilience" of the plankton in Lake Geestmerambacht was studied in a series of three experiments, where nutrients were added to the natural water (including phyto- and zooplankton species and densities) and the response of the plankton was recorded. The results are shown in Fig. 4.8. The algal density increased when increasing amounts of nutrients were added to the water, but the zooplankton was still able to exert a certain amount of top-down control. The chlorophyll-a density was a constant < 80 µg/l.

Another experiment was performed by adding daphnids to the water from which the resident zooplankton community was excluded by sieving. The effect of zooplankton on algal density was demonstrated by carrying out experiments with and without (added) zooplankton. In the systems without daphnids, higher algal concentrations were reached at higher nutrient loads. In the systems with daphnids, however, the algal densities were controlled at much lower levels (Fig. 4.9). The results of the eco-assay strongly resemble the semi-field observations of the chlorophyll-a to P response under daphnid rich and poor conditions. Sarnelle (1992) calculated a chlorophyll to P ratio of 0.5 when few daphnids were present,

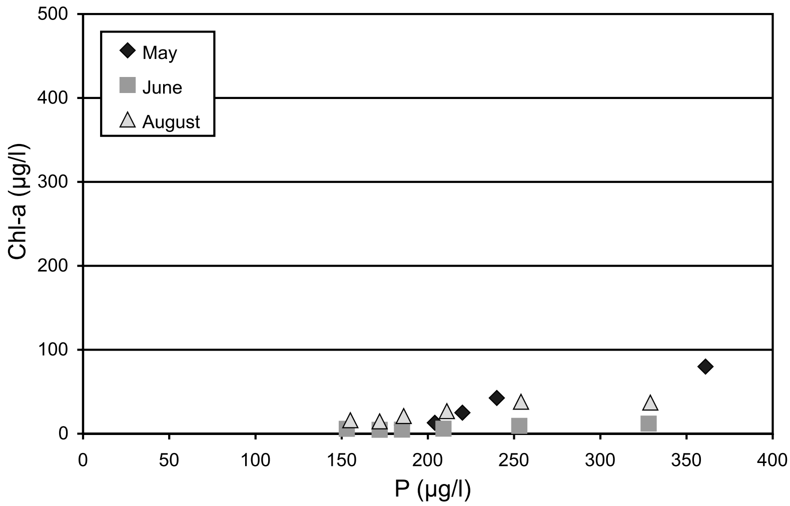

Fig. 4.8. Response of the phytoplankton (expressed as maximum chlorophyll-a concentration measured) after addition of nutrients to natural water from Lake Geestmerambacht in indoor microcosms. The experiments were carried out in 1995. Initial zooplankton densities (cladocerans – copepods) were 17–13 in the May experiment; 45–12 in the June experiment, and 5–3 in the August experiment. The nutrient concentration on the x-axis was natural P + P addition. See Fig. 4.12 for comparison

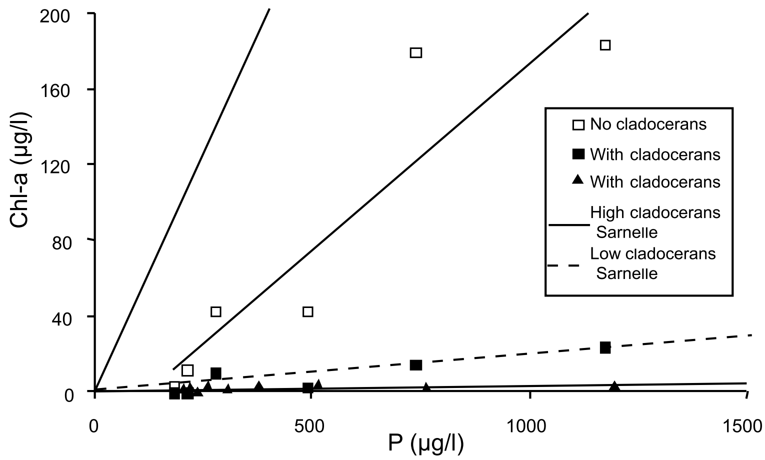

Fig. 4.9. Response of algal density (chlorophyll-a) to increased P-load in systems with and without daphnids after 9–12 days. The lines are chlorophyll to P response under Daphnid rich and Daphnid poor conditions predicted by Sarnell (1992); see text

and 0.02 when daphnid densities were high. In the eco-assay, chlorophyll to P ratio of 0.2 was recorded in the absence of daphnids, although a ratio of 0.02 was also recorded with daphnids present.

Synopsis

In Lake Geestmerambacht, a spring bloom of diatoms and green algae is usually followed by a short clear water phase, in June. During this time, cladocerans, copepods and rotifers, which are able to control algal densities at a low level, are present. Grazing is efficient during this period. Experiments have shown that the zooplankton community can control the phytoplankton production during this period, even when nutrients are added to the system. The fact that a summer/autumn bluegreen algae bloom occurs each year is probably not the result of reduced top-down control. It is rather a result of the stratification of the lake and the subsequent depletion of the nutrient pool in the epilimnion, thereby providing favourable conditions for Microcystis and other bluegreen algae. Cladocerans are present during this bloom, and have been shown to graze on some cyanobacteria (Oscillatoria). However, the zooplankton cannot prevent cyanobacteria from blooming. In late autumn, when the stratification breaks and temperatures drop, the cyanobacteria bloom collapses and a clear winter phase starts.

4.3 The Plankton Dynamics in Lake Amstelmeer

Phytoplankton

The annual dynamics of phytoplankton biomass is characterised by relatively high densities, even in winter (Fig. 4.10).

The phytoplankton is dominated by cyanobacteria, sometimes associated with green algae. Diatoms are only present in low densities during the spring bloom. Dominant cyanobacteria appear in the following order: *Oscillatoria spec.* (autumn/winter), *Microcystis aeruginosa* (spring blooms), *Gomposphaeria lacustris,*

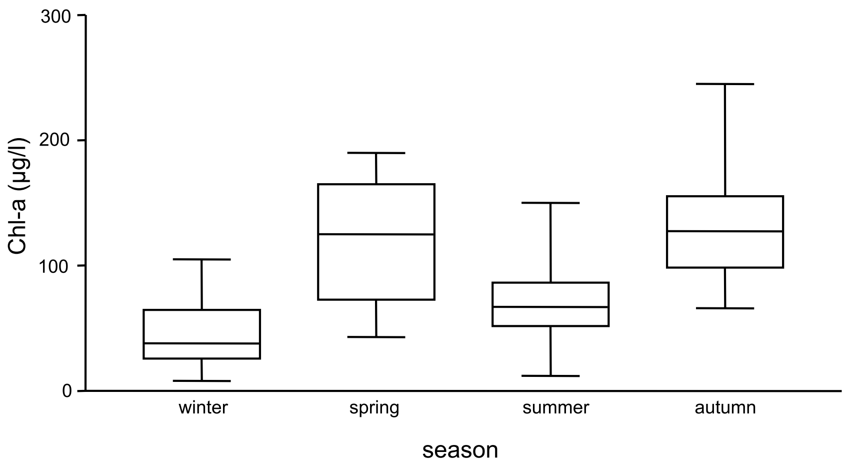

Fig.4.10. Seasonal phytoplankton dynamics for Lake Amstelmeer. Box-whisker plots for the period 1990–2000. Data from Hoogheemraadschap Hollands Noorderkwartier, unpublished. See Fig. 4.3 for comparison

Anabaena spec. (in July) and *Aphanizomenon floss-aqua* (August blooms). The algal densities are high. A clear water phase is not reached, not even in winter: On February 5th 1996, a concentration of 75 µg/l chlorophyll-a was measured under a covering of ice (*Oscillatoria spec.*) (Hogenbirk 1996).

Zooplankton

Only a limited amount of data is available pertaining to the zooplankton in the lake. In March–June 1996, the seasonal succession of the zooplankton was recorded (Hogenbirk 1996). The zooplankton was dominated by rotifers in March, while in April the dominance shifted to copepods. Cladocerans (viz. *Daphnia longispina, Bosmina spp.*) were present from the end of May onwards.

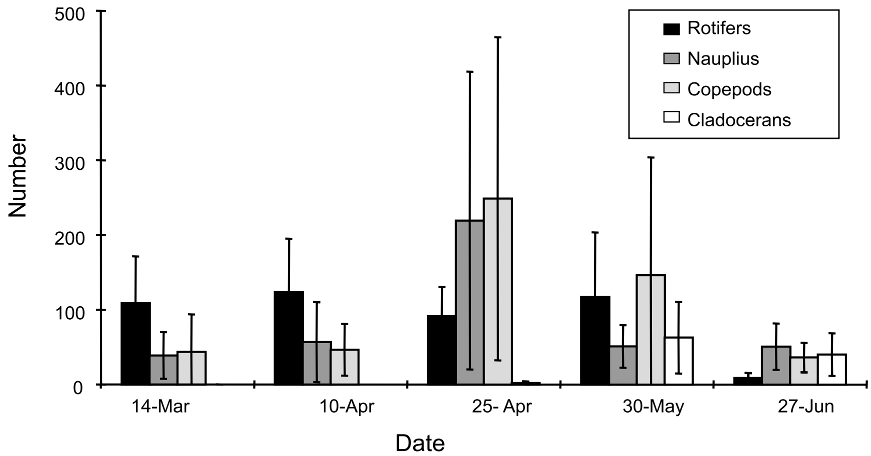

Fig. 4.11. Zooplankton community dynamics in the spring of 1996. Dates are average and standard deviations of 14 sampling sites in lake Amstelmeer (from: Hogenbirk 1996)

Resilience of the Plankton Community to Eutrophication

As for Lake Geestmerambacht, three experiments were carried out in order to test the effects of nutrient additions on the natural plankton community of the lake. The results are shown in Fig. 4.12. There was an intense response to the added nutrients by the phytoplankton.The addition of phosphorus resulted in very high chlorophyll-a concentrations (> 500 µg/l), especially in May. The zooplankton was clearly unable to control the development of the phytoplankton. This might, however, have been due to the high initial algal density.

Synopsis

Lake Amstelmeer has a continuous bloom of bluegreen and green algae throughout the year and no clear water phase. Algal densities remain high, even in winter. The reason for this is not the absence of daphnids, as daphnids are present in the

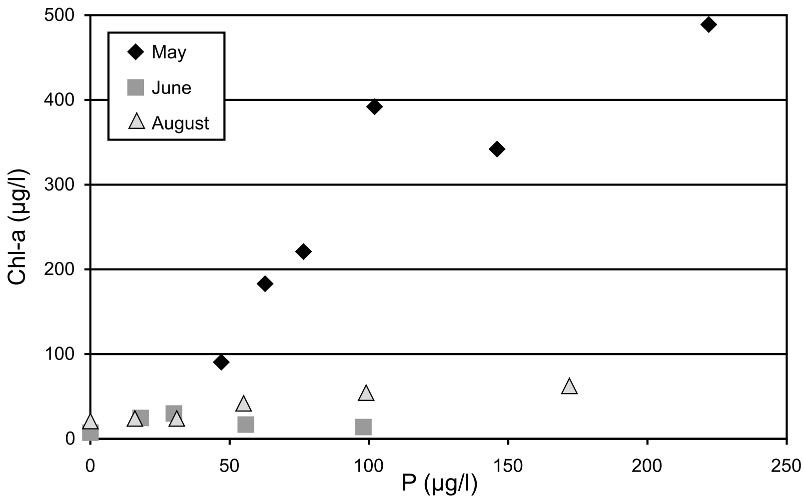

Fig. 4.12. Response of the phytoplankton (expressed as maximum chlorophyll-a concentration measured) after addition of nutrients to natural water from Lake Amstelmeer in indoor microcosms. The experiments were carried out in 1995. Initial zooplankton densities (cladocerans – copepods, in numbers per litre) were 2–9 in the May experiment; 1–5 in the June experiment, and 2–1 in the August experiment. The nutrient concentration on the x-axis is total phosphorus (background P + aditional P). See Fig. 4.8 for comparison

lake from May onwards. The robust response of algae to added nutrients in a spring microcosm experiment with natural water, suggested that the grazing by daphnids was suboptimal.

4.4 What Can Be Learned from These Lakes?

This chapter shows that two lakes with comparable nutrient levels can show very different phytoplankton dynamics. In Lake Geestmerambacht, the spring bloom was followed by a clear water phase during which the top-down control by zooplankton is very strong. Even a nutrient pulse will not lead to eutrophication phenomena during this period. On the other hand, Lake Amstelmeer shows a continuous algae bloom despite the presence of daphnids. The intense response to a nutrient pulse indicates that thegrazing capacity of the daphnid population is reduced.

In order to test this hypothesis, an experiment was executed with water from both lakes, at a point in time in which the phytoplankton communities resembled one another (Fig. 4.13). The natural zooplankton was removed and a standard community of cladocerans (*Symocephalus, Daphnia magna, D. longispina*) was added to the water. The phytoplankton community development was followed over time. At the same time, experimental systems without zooplankton were observed. The results are shown in Fig. 4.14.

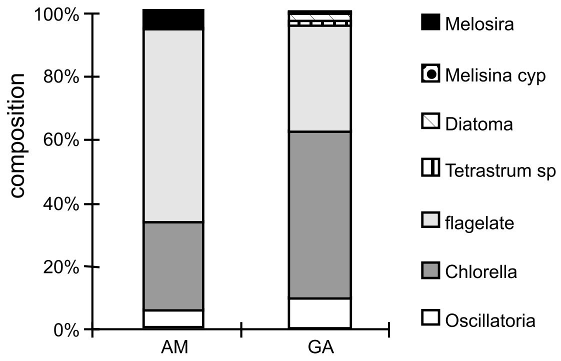

Fig. 4.13. Composition of the phytoplankton community at the start of the experiment. AM = Lake Amstelmeer; GA = Lake Geestmerambacht

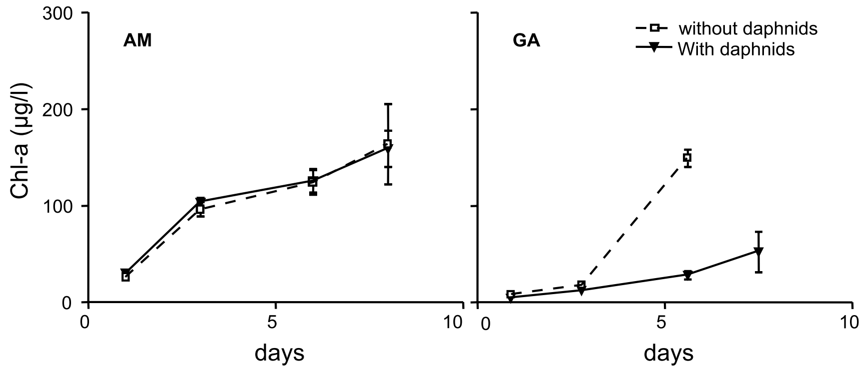

Fig. 4.14. Algal development in filtered Lake Amstelmeer water (left) and Lake Geestmerambacht water (right) with and without cladocerans

In the water from Lake Geestmerambacht, daphnid grazing resulted in a reduced chlorophyll-a density in comparison to the situation without daphnids. The grazing efficacy was 44%. In the Lake Amstelmeer water, however, a similar cladoceran community was completely unable to control the phytoplankton (grazing effectiveness of only 4%). The reproduction of daphnids (esp. *D. longispina*) resulted in an increase to the initial density of 9 individuals to a density of up to 60 per litre in the Geestmerambacht systems (see Fig. 4.15). In the Amstelmeer systems with daphnids, the final population density was 30 individuals per litre of water, which indicated some reproduction despite the extremely low grazing effectiveness.

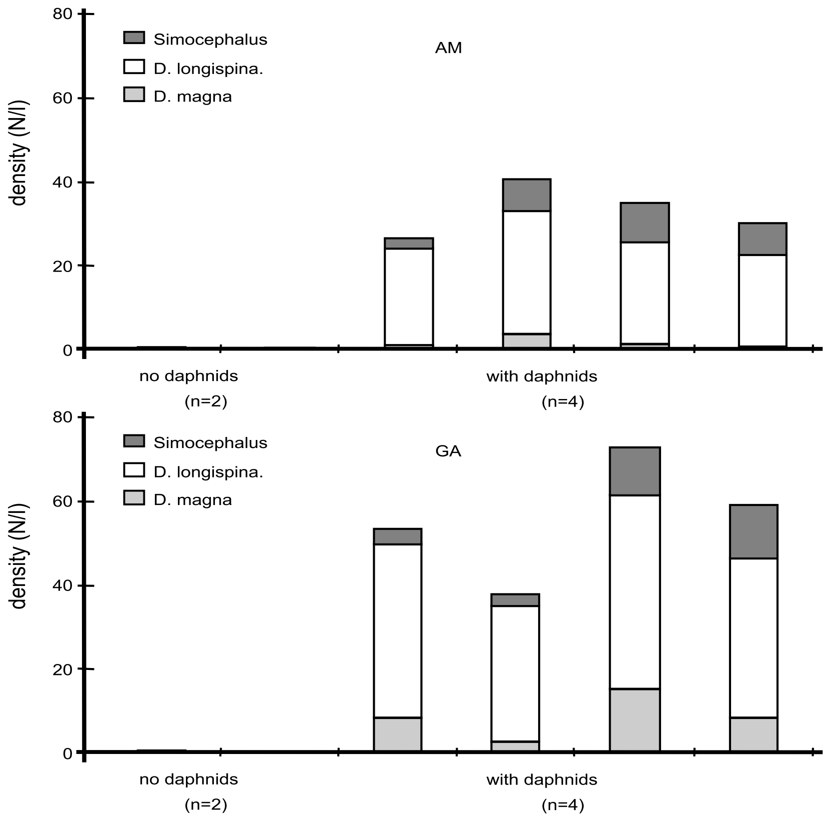

Fig. 4.15. Daphnid densities in the microcosms at the end of the experiments (after 8 days). Top: Lake Amstelmeer (AM); Bottom: Lake Geestmerambacht (GA). The initial density in the systems "with daphnids" was 9 per litre

Water Quality Is Critical

The conclusion from this experiment – where the zooplankton community is identical and the phytoplankton community almost identical – is that the reason for the significantly different grazing efficacies (44% and 4% respectively) must lie in the water quality. The water from Lake Amstelmeer was less suited to cladocerans than was the water from Lake Geestmerambacht. Reproduction could take place (which must be the case, as cladocerans are also found in the field situation) but the grazing effectiveness was reduced.

The factor responsible for this sub-optimal water quality is not easily identified (see Table 4.1). Lake Amstelmeer is influenced by many (potential) sources of pollution, such as drainage water from the surrounding agricultural areas, sewage treatment plant effluent and the dumping of dredged sediments. A recent inventory showed the presence of agricultural pesticedes in concentrations exceeding the prescribed quality standards in the canals transporting water to and from the lake (Van der Helm, 2000).

Table 4.1. Factors that may explain the difference in grazing effectiveness between the lakes

	Lake Amstelmeer	Lake Geestmerambacht
Water quality		
pH	8.5	8.6
Kjeldahl-N (mg N/l)	2.0	1.4
Total-P (mg P/l)	0.4	0.4
Salinity	0.5 – 1.5 ‰	0.25 ‰
Characteristics		
Isolation	part of a canal system; lake has a water transport and storage function	relatively isolated; used incidentally for water storage (flood control)
Land use	flower bulb culture, arable land	arable land, pastures (cattle, sheep)
Pollution sources	dumped polluted dredging materials (1982), lake received effluent of sewage treatment plant until 1996	some influence from recreation (swimming, surfing, diving, fishing)

Another factor lie in the fact that the lake is brackish, with a salinity of approx. 500–700 mg/l Cl (Hogenbirk 1996). Highest concentrations are approx. 900 mg/l in November; and concentrations are lowest in April (< 500 mg/l). In the deepest parts of the lake, the chlorine concentration can reach up to 1600 mg/l near the bottom (Anonymous 1994). Salinity is not very toxic to *Daphnia magna* (EC_{50} 48 h. for artificial sea salt 5600 mg/l; Grootelaar and Maas-Diepeveen 1988). In eco-assays, a LOEC for daphnid grazing was observed at 3000 mg/l (see Sect. 3.3), but some effects on grazing were observed at concentrations as low as 1600 mg/l (see Chap. 3). Other daphnids, such as *Ceriodaphnia dubia*, are more sensitive (EC_{50} 48h. 1189 mg/l Cl; Mount et al. 1997). This indicates that the highest concentrations in lake Amstelmeer could have affected the cladoceran community. As the maximum salinity is measured in November and it decreases during the spring, salinity could well explain the delayed cladoceran development.

An Incidental Case?

A similar difference in daphnid grazing effectiveness was observed by Madveev et al. (1994) in a comparison of two eutrophic Australian lakes: one in a dry forested area (Lake Dartmouth) and one in an agricultural area (Lake Hume).

The mean chlorophyll-a level in Lake Hume was high in comparison with Lake Dartmouth. In a bio-assay, added zooplankton had no clear effect on the algal density in water from Lake Hume. The algal concentration decreased with increasing daphnid density in water taken from Lake Darthmouth, indicating effective grazing. Nutrient enrichment resulted in enhanced algal density in Lake Hume, while in Lake Dartmouth this did not result in enhanced algal density due to daphnid grazing control (Fig. 4.16).

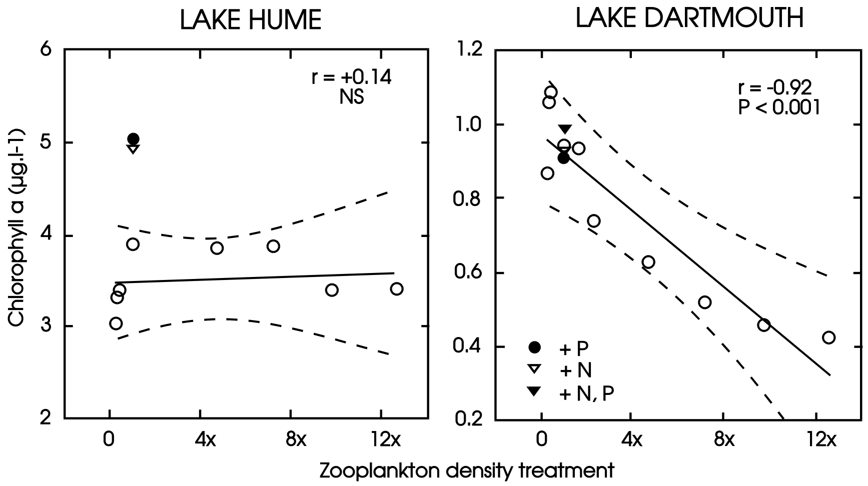

Fig. 4.16. Phytoplankton concentration (chlorophyll-a) as a function of zooplankton density in two Australian lakes. In lake Dartmouth (right panel), increasing zooplankton density reduced the algae density (grazing). In lake Hume, no grazing seemed to take place (left panel). From Matveev et al. 1994

The main zooplankton species in Lake Dartmouth was *Daphnia carinata*, which was almost completely absent in Lake Hume, where other cladoceran species and copepods dominated. Although the authors do not link these observations to differences in toxicant stress, the land use suggests that the pesticide concentration in Lake Hume may well have been higher than in Lake Dartmouth. Matveev and Madveeva (1997) estimated a grazing effectiveness for a cladoceran community dominated by *D. carinata* at up to 0.80 per day^{-1}, which is important for the development of a clear water phase. Significant grazing is predicted when the cladoceran / phytoplankton biomass ratio is greater than > 0.1.