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Effects of zooplankton grazing and nutrients on the bloom-forming, N_2-fixing cyanobacterium *Aphanizomenon* in Lake Kinneret

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A bloom of the filamentous, N_2-fixing cyanobacterium Aphanizomenon ovalisporum Forti occurred for the first time in Lake Kinneret during late summer and fall 1994. During subsequent years (1995–1999), Aphanizomenon also appeared in late summer and fall, but did not bloom. In outdoor microcosm experiments, we examined zooplankton grazing on Lake Kinneret phytoplankton, with and without Aphanizomenon present, and the effects of N, P and N:P ratios on phytoplankton growth. In one-day feeding experiments, clearance and grazing rates of the ambient Lake Kinneret zooplankton assemblage feeding in lake water dominated by Aphanizomenon were 10-fold lower than in water without Aphanizomenon. We suspect that the low grazing rates were due to interference caused by the presence of Aphanizomenon. In 9-day nutrient addition experiments, significant enhancement effects on phytoplankton were detected with additions of either P or N; a high N:P was better for phytoplankton growth than a low N:P. After 7 days, bottles receiving low P and no N additions were dominated by Oscillatoria sp. and Closterium acutum; few Aphanizomenon were present. In contrast, bottles receiving high P and N additions had large increases of Aphanizomenon, as well as Oscillatoria and Closterium. There was a tendency for more green algae and diatoms with increasing N additions. These results provide evidence that (i) non-grazeability of Aphanizomenon enabled it to gain a competitive advantage over grazeable phytoplankton, and (ii) that nutrient limitation, but not grazing, was probably important in the eventual decline of the Aphanizomenon bloom.

INTRODUCTION

Cyanobacteria are often principal components of pelagic phytoplankton assemblages in freshwater lakes. Hence, their contribution to various aspects of ecosystem function (e.g. nutrient cycling, production and food web dynamics) has received considerable attention (Shapiro *et al.*, 1982; Pearl *et al.*, 1987; Howarth *et al.*, 1988a, b; Marino *et al.*, 1990). Particularly with regard to lakes and reservoirs serving important economic and social interests, nitrogen-fixing cyanobacteria are a major concern, given their potential importance as sources of nitrogen inputs to a lake, non-grazeability by zooplankton and production of toxic compounds (Reynolds, 1987).

Lake Kinneret serves a vital role in Israel's freshwater balance. As the principal storage and supply reservoir in the National Water Carrier System, water from Lake Kinneret flows to all reaches of the country for domestic, agricultural and industrial purposes. Lake Kinneret water is even used to replenish over-pumped aquifers in the Mediterranean coastal area of Israel. Lake Kinneret is eutrophic with annual primary production rates of ~650 g C m^{-2} day^{-1}, due mostly to the spring bloom of the dinoflagellate *Peridinium gatunense* (Berman, 1978b). Nevertheless, N_2-fixing cyanobacteria were conspicuously absent from Lake Kinneret phytoplankton prior to 1994 (Pollingher, 1978, 1986; Pollingher and Berman, 1991).

Although the reasons are presently unclear, the N_2-fixing cyanobacterium *Aphanizomenon ovalisporum* Forti (hereafter *Aphanizomenon*) appeared for the first time and bloomed during late summer 1994. Since then it has been a member of the Lake Kinneret phytoplankton summer

assemblage (Pollingher *et al.*, 1998; Hadas *et al.*, 1999). With the purpose of obtaining preliminary understanding of the role that *Aphanizomenon* may play in the Lake Kinneret food web, we conducted a series of microcosm experiments examining the separate effects of zooplankton grazing and nutrient additions on Lake Kinneret phytoplankton during the 1994 *Aphanizomenon* bloom period. Grazing results were compared with grazing estimates obtained from similar experiments conducted in the previous summer, with no *Aphanizomenon*. Our results are in agreement with the general view that non-grazeability of *Aphanizomenon* allows it to gain a competitive advantage over grazeable phytoplankton in the lake. Moreover, nutrient addition experiments revealed that nutrient limitation, but not grazing, was probably important in the eventual crash of the *Aphanizomenon* bloom.

METHOD

Zooplankton grazing

Experiments were conducted in 20 l clear, polyethylene bottles suspended between 0.5 and 1 m depth in 5 m^3 outdoor tanks filled with Lake Kinneret water. The design employed (Lehman, 1980a, b; Epp, 1996) allowed the separation of grazing effects (typically negative effects) on plankton assemblages from the positive effects of nutrient recycling from the consumers that occurred within the experimental containers. Zooplankton grazing rates on phytoplankton were determined from the changes in phytoplankton densities during the experimental period as functions of zooplankton biomass. The basic design of the experiment, as conducted in summer 1993, consisted of measuring changes in size-fractionated chlorophyll (<20 μm = nano-chlorophyll and ≥20 μm = net-chlorophyll) over a 24 h period in bottles containing lake water with varying densities of zooplankton. In summer 1994 when *Aphanizomenon* dominated, we also followed changes in taxon-specific algal abundances using direct phytoplankton counts.

Nine (1994) or 12 (1993) 20 l bottles were filled with filtered (100 μm) water pumped from the lake and stocked with various zooplankton densities (Table I). Zooplankton were collected from the lake with horizontal tows of a 1 m diameter, 250 μm mesh conical plankton net. Concentrated zooplankton were then added to the bottles at final densities equivalent to 0×, 1× and 4× the ambient densities observed for the lake during the time of the experiment. In order to saturate algal uptake rates for ammonium and phosphate, initial concentrations of dissolved inorganic nutrients were increased by additions of standard solutions of Na_2HPO_4 and NH_4Cl to final concentrations of ~50 μg PO_4-P l^{-1} and 500 μg NH_3-N l^{-1}. This was done in order to ensure that the potential for confounding indirect enhancement of phytoplankton by zooplankton excretion of these nutrients was minimal. All bottles were sampled at 0 and 24 h to determine initial and final biomass of zooplankton, net- and nano-phytoplankton chlorophyll, algal densities, and concentrations of ammonia and soluble reactive phosphorus.

Chlorophyll concentrations were determined fluorometrically on whole and filtered (20 μm) water following acetone extraction (Holm-Hansen *et al.*, 1965). Net-chlorophyll was calculated by subtraction of nano-chlorophyll from whole water chlorophyll. For comparison with biomass estimates from direct counts, net- and nano-chlorophyll were converted to wet weight biomass, assuming a chlorophyll content of 0.28 and 0.45%, respectively (Berman, 1978a; U. Pollingher, personal communication). Zooplankton biomass was determined by direct microscopical counts at the end of each experiment, followed by conversion to wet weight biomass according to Gophen (Gophen, 1992). For the *Aphanizomenon* experiment only, phytoplankton were counted with a Zeiss inverted microscope using the Utermöhl (Utermöhl, 1958) method. Cell numbers were converted to wet weight biomass according to their geometric shapes (Hillebrand *et al.*, 1999).

Zooplankton grazing rates were quantified by linear regression of r (the net intrinsic rate of change) for each chlorophyll fraction or algal taxon on zooplankton

Table I: General characteristics of grazing experiments

	1993		1994	
Treatment	Zooplankton mg l^{-1}	Grazer assemblage (%)	Zooplankton mg l^{-1}	Grazer assemblage (%)
0×	0.1	*Ceriodaphnia* (59) *Bosmina* (31)	0.1	*Bosmina* (38) *Diaphanosoma* (29)
1×	2.1	*Diaphanosoma* and *Moina* (9)	2.9	Juvenile cyclopoid copepodids (17)
4×	7.5		12.0	*Ceriodaphnia* (14)

biomass, Z (mg l^{-1}). The negative of the slope of this regression equals the clearance rate (*CR*) of the zooplankton in units of l g_Z^{-1} day^{-1}. As nutrients were added at the beginning of the experiment, phytoplankton growth was typically enhanced (i.e. $r > 0$ without grazers). However, the slope of the regression indicates zooplankton-dependent (grazing) effects. A negative slope indicates grazing; a slope of 0 indicates that no grazing occurred. Due to the initial saturation of nutrient uptake rates, we did not find any positive slopes resulting from nutrient regeneration during the short course of the experiment.

The mean biomass *A* (μg l^{-1}) of each planktonic group of interest (e.g. net-chlorophyll) in the experimental containers was calculated as

$$A = (A_0 - A_t) / (r_A \times \Delta t) \quad (1)$$

where A_0 and A_t = initial and final biomass of the particular group, Δt = 1 day. Zooplankton grazing rates, *GR*, were then calculated as the product of the mean biomass of a given taxon and the taxon-specific clearance rate ($GR = CR \times A$) and have units of μg_{chl} g_Z^{-1} day^{-1} or $mg_{wet\ wt}$ g_Z^{-1} day^{-1}.

Nutrient additions

Also during the 1994 bloom of *Aphanizomenon*, we conducted two nutrient enrichment experiments in which nitrogen and phosphorus were added to 20 l bottles containing 20 μm-filtered lake water. Two designs were used, each replicated two- or threefold. Experiment 1 consisted of manipulation of N and P concentrations in a cross-classified design consisting of two levels of P and four levels of N (Figure 1). As this design also involved different N:P ratios, we used a second design (Experiment 2) consisting of two levels of P and two levels of N:P ratios nested within the first design. Both experiments were run simultaneously using the same set of bottles for treatment combinations occurring in both experiments.

Initial ambient P and N concentrations were 0.012 mg PO_4-P l^{-1} and 0.400 mg (NO_3-N + NH_4-N) l^{-1}. Phosphorus was added to bottles using 0.028 and 0.108 μg PO_4-P l^{-1} additions as KH_2PO_4 for low and high P treatments (0.04 and 0.12 mg PO_4-P l^{-1}), respectively. Nitrogen was added to bottles using additions of 0, 0.8, 1.6 and 5.6 mg (50% NO_3-N + 50% NH_4-N) l^{-1} as NH_4Cl and $NaNO_3$, for final concentrations of 0.4, 1.2, 2.0 and 6.0 mg (NO_3-N + NH_4-N) l^{-1}. The experiment was conducted between 31 October and 8 November 1994, with samples for chlorophyll taken at ~2-day intervals.

Chlorophyll concentrations were determined as above. Rates of change of chlorophyll concentrations (r_{chl}) were analyzed using repeated-measures ANOVA on each experiment separately. We scanned bottles microscopically at the start and end of the experiment for dominant phytoplankton taxa.

RESULTS

Zooplankton grazing

Zooplankton biomass in both grazing experiments was dominated by the cladocerans *Ceriodaphnia reticulata*, *Bosmina longirostris*, *Diaphanosoma brachyurum* and *Moina rectirostris* (Table I). Cyclopoid copepods (mostly herbivorous juveniles of *Mesocyclops oogunnus* and *Thermocyclops dybowskii*) and rotifers constituted the remainder. During the 1993 grazing experiment, most (80%) of the phytoplankton biomass was in the form of diatoms (dominant genera *Anoemoneis* and *Cyclotella*), chlorophytes (*Chlamydomonas* and *Closterium*) and cryptophytes (*Rhodomonas* and

P, mg l^{-1}	N, mg l^{-1}	0.4	1.2	2.0	6.0
0.040		P = 0.04, N = 0.4 **N:P = 10** (3)	P = 0.04, N = 1.2 (3)	P = 0.04, N = 2.0 **N:P = 50** (3)	P = 0.04, N = 6.0 (3)
0.120		P = 0.12, N = 0.4 (2)	P = 0.12, N = 1.2 **N:P = 10** (2)	P = 0.12, N = 2.0 (2)	P = 0.12, N = 6.0 **N:P = 50** (2)

Fig. 1. Experimental design used for Experiments 1 and 2, showing final nutrient concentrations (i.e. after additions) and ratios in each treatment combination. Treatment combinations for Experiment 1 that also served as treatment combinations in Experiment 2 are indicated in bold type. Number of replicates for each treatment combination shown in parentheses.

Cryptomonas). In the 1994 experiment, *Aphanizomenon* constituted most (94.6%) of the algal biomass; chlorophytes and dinoflagellates (mostly *Peridiniopsis* spp.) constituted most of the remainder.

Zooplankton clearance rates for chlorophyll measured in 1994 in the presence of *Aphanizomenon* were an order of magnitude lower than clearance rates measured the previous year in which *Aphanizomenon* was absent (Figure 2). Nano-chlorophyll was grazed at approximately 94 $\mu g_{chl}\ g_Z^{-1}\ day^{-1}$ when *Aphanizomenon* was present, compared with 506 $\mu g\ g_Z^{-1}\ day^{-1}$ with no *Aphanizomenon* present (Table II). Net-chlorophyll was not grazed in the 1994 experiment, compared with 219 $\mu g_{chl}\ g_Z^{-1}\ day^{-1}$ in the 1993 experiment with typical Lake Kinneret summer phytoplankton.

Analysis of taxon-specific clearance rates in the 1994 experiment indicates no grazing on *Aphanizomenon* and little grazing on any of the dominant non-*Aphanizomenon* taxa (Table III), although small flagellated species (the cryptophytes *Cryptomonas* spp. and *Rhodomonas* spp., and the haptophyte *Erkenia* sp.) were cleared at rates similar to those measured in the 1993 experiments for nano-chlorophyll.

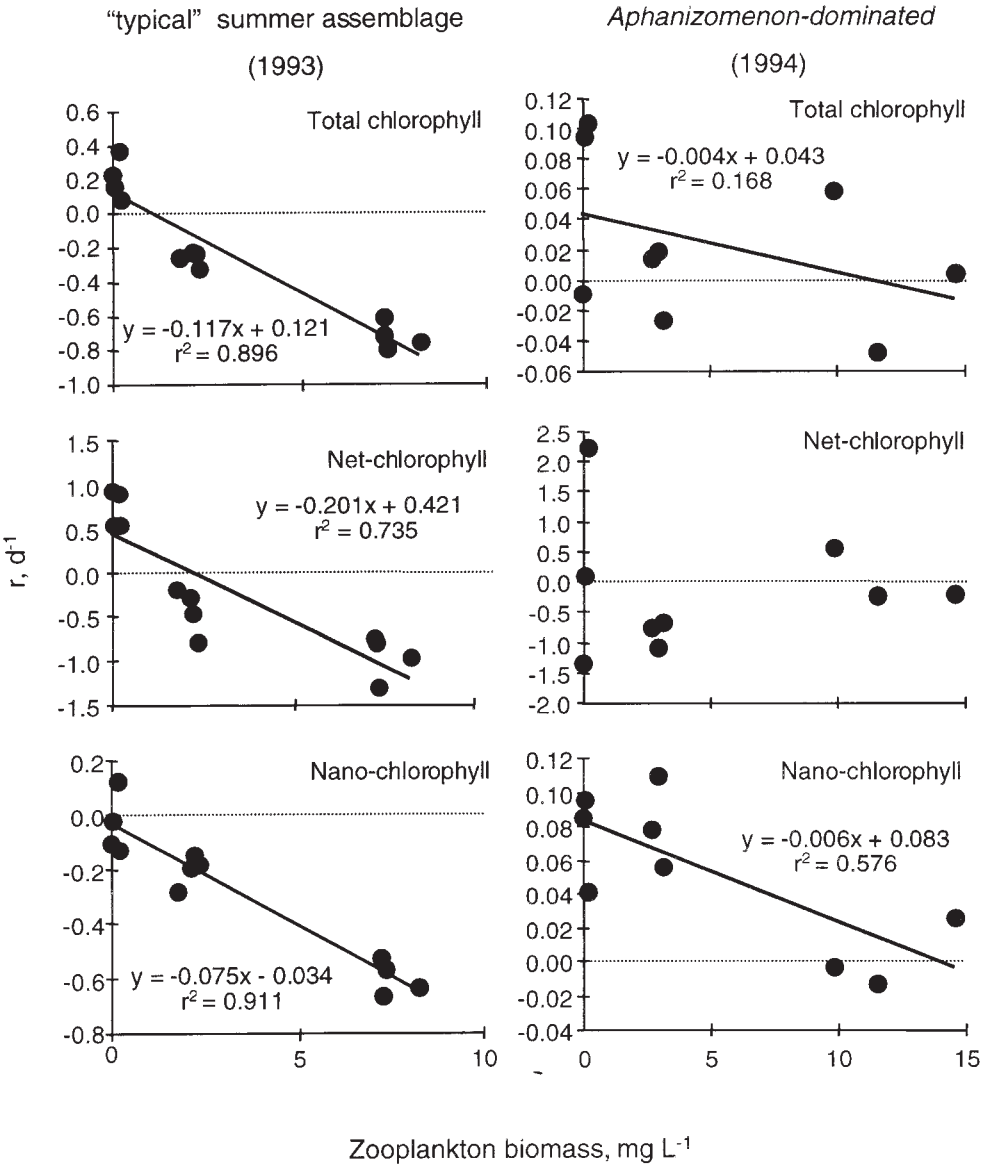

Fig. 2. Intrinsic rates of increase (*r*) of total, net- and nano-chlorophyll during one-day feeding experiments with Lake Kinneret zooplankton feeding on a typical summer phytoplankton assemblage in 1993 (**left panels**) and on an *Aphanizomenon*-dominated assemblage in 1994 (**right panels**). Regressions were fitted by least-squares and give estimates of zooplankton clearance rates as the –slope and maximum potential algal growth rates as the y-intercept.

Table II: Clearance and grazing rates by Lake Kinneret zooplankton feeding on a typical summer phytoplankton assemblage (1993) and on an Aphanizomenon-dominated assemblage (1994)

Chlorophyll size fraction	*CR* l g_Z^{-1} day^{-1}	Algal biomass µg chl l^{-1}	*GR* µg chl g_Z^{-1} day^{-1}	*GR* mg wet wt. g_Z^{-1} day^{-1}
Typical summer assemblage (1993)				
Total	117	8.5	995	221
Net	201	2.9	583	129
Nano	75	6.0	450	100
Aphanizomenon bloom (1994)				
Total	4	17.2	67	15
Net	0	1.5	0	0
Nano	6	15.7	94	21

However, these two taxa accounted for only 47 $\mu g_{wet\ wt}\ l^{-1}$, giving a grazing rate of ~5 $mg_{wet\ wt}\ g_Z^{-1}\ day^{-1}$, which is less than 2% of the grazing rates for nano-chlorophyll measured in 1993. During the course of the experiment, mean filament length of *Aphanizomenon* declined by a mean of 12.5 (±5.0) µm across all treatments and independent of grazer density.

Nutrient additions

Generally, chlorophyll concentrations responded positively to all nutrient additions, and r_{chl} declined with time in all bottles (Figures 3 and 4). In Experiment 1, the highest chlorophyll occurred in bottles containing high P and high N concentrations. Significant effects on r_{chl} were detected for both P and N, with both nutrients yielding higher growth rates with higher concentrations (Figure 3). Although N:P ratios varied from 3.3:1 to 150:1 across all treatment combinations in Experiment 1, no P × N interaction effect was detected. In Experiment 2, chlorophyll responded as in Experiment 1, with higher concentrations developing in bottles containing high P and high N:P ratios (Figure 4). Significant effects on r_{chl} were detected for both P and N:P, with high levels of P and N:P ratios being better for total algal growth. No significant P × N:P interaction effects were detected.

Aphanizomenon were dominant on day 1 in all bottles and were probably not N-limited as few heterocysts were present. By day 7 (peak of chlorophyll concentrations), many changes had occurred. Bottles receiving low P and no N additions were dominated by *Oscillatoria* and *Closterium*; few *Aphanizomenon* were present. In contrast, all other bottles, especially those receiving high P and high N additions, revealed large increases in *Aphanizomenon*, as well as *Oscillatoria* and *Closterium*. There was a tendency for more green algae and diatoms with increasing N additions. By day 9, conditions in the bottles deteriorated such that chlorophyll concentrations declined to levels similar to, or lower than initial values, except in bottles containing the highest nutrient concentrations.

DISCUSSION

Factors underlying the 1994 bloom of *Aphanizomenon* in Lake Kinneret remain speculative. Many prerequisites have been suggested, including unusually warm temperatures and calm winds, elevated concentrations of nutrients (especially P, but also trace metals and other growth factors), low N:P ratios, and long-term and recent changes in nutrient and hydrological regimes of the northern catchment of Lake Kinneret (Berman *et al.*, 1998; Hadas *et al.*, 1999). Though present ever since, the failure of *Aphanizomenon* to bloom in subsequent years, as in 1994, is more bewildering. Clearly, changes at the ecosystem level are involved, as anthropogenic stress in Lake Kinneret has increased continually throughout recent decades (Berman, 1998; Ben-Meir, 2000). Unfortunately, the number of possible factors, and the complexity with which these factors could interact to provide *Aphanizomenon* with the opportunity to invade Lake Kinneret, severely reduce the possibility of ever pinpointing an exact cause of the bloom. Our study does not address why *Aphanizomenon* appeared suddenly in 1994, nor why it bloomed as it did. Rather, our study permits us to speculate on the conditions conducive to *Aphanizomenon* proliferation in Lake Kinneret. Our results indicate that *Aphanizomenon* has at least one advantage over other typical Lake Kinneret summer phytoplankton—negligible grazing losses.

Clearly, zooplankton clearance rates were reduced in the 1994 experiment when *Aphanizomenon* was dominant.

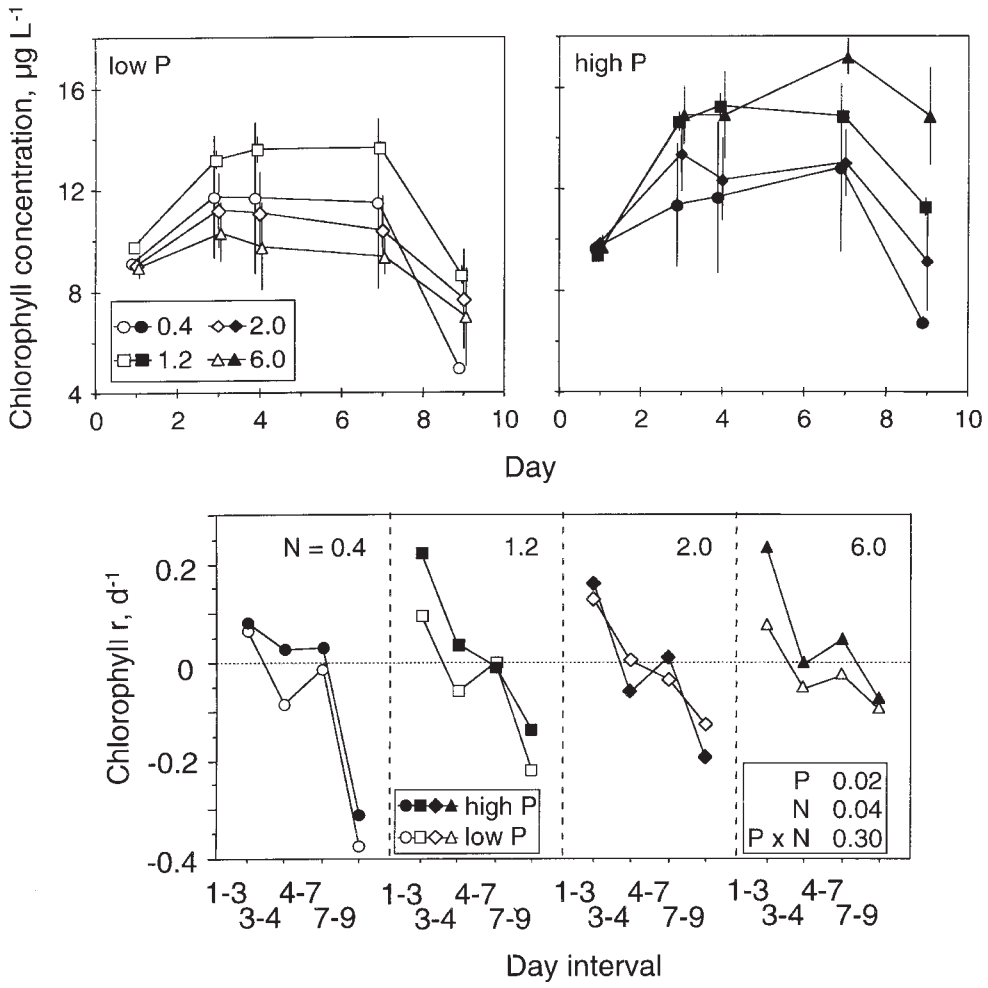

Fig. 3. (**Upper panel**) Mean (±SE) concentrations of chlorophyll during Experiment 1. P concentrations were 40 µg l^{-1} in the low P treatment and 120 µg l^{-1} in the high P treatment. Symbols represent the N concentrations (in mg l^{-1}) in each nitrogen treatment. (**Lower panel**) Mean (±SE) rates of change of chlorophyll during Experiment 1. Numbers indicate nitrogen concentrations in each nitrogen treatment. Phosphorus treatments and results of ANOVA shown in insets.

Nevertheless, there was some grazing, as indicated by nano-chlorophyll and cryptophytes. Although nano-chlorophyll was dominated by *Aphanizomenon*, we rule out significant *Aphanizomenon* grazing based on direct counts. We also rule out the 'filament clipping' phenomenon observed by Schaffner *et al.* (Schaffner *et al.*, 1994) as *Aphanizomenon* mean filament size did not change with grazer density during the grazing experiment. As such, we conclude that while low-level grazing (i.e. undetectable by our methods) was possible, we suspect that the observed nano-chlorophyll grazing rates were due to ingestion of other small phytoplankton also included in the nano-chlorophyll fraction, and that *Aphanizomenon* actually interfered with zooplankton feeding, as indicated by the extremely low grazing rates in 1994 compared with 1993, when *Aphanizomenon* was absent.

Several mechanisms, including size, taste, toxicity and nutritive value, have been identified that may result in reduced food intake by zooplankton in the presence of cyanobacteria (Burns, 1987; Haney, 1987; Lampert, 1987; de Bernardi and Giussani, 1990). However, there is no general consensus that cyanobacteria are bad food for zooplankton. Indeed, several studies have shown that in situations where grazers and cyanobacteria co-occur, there are no negative effects of the cyanobacteria on grazer food intake (Schaffner *et al.*, 1994; Epp, 1996). In contrast, in situations in which grazers are presented with cyanobacteria that are not typically associated with the grazer's normal food supply, the cyanobacteria often present obstacles to feeding, growth and survival in the grazer population (de Bernardi and Giussani, 1990). This is likely the scenario most relevant to the Lake Kinneret *Aphanizomenon* bloom.

The 1994 *Aphanizomenon* bloom represents the first ever

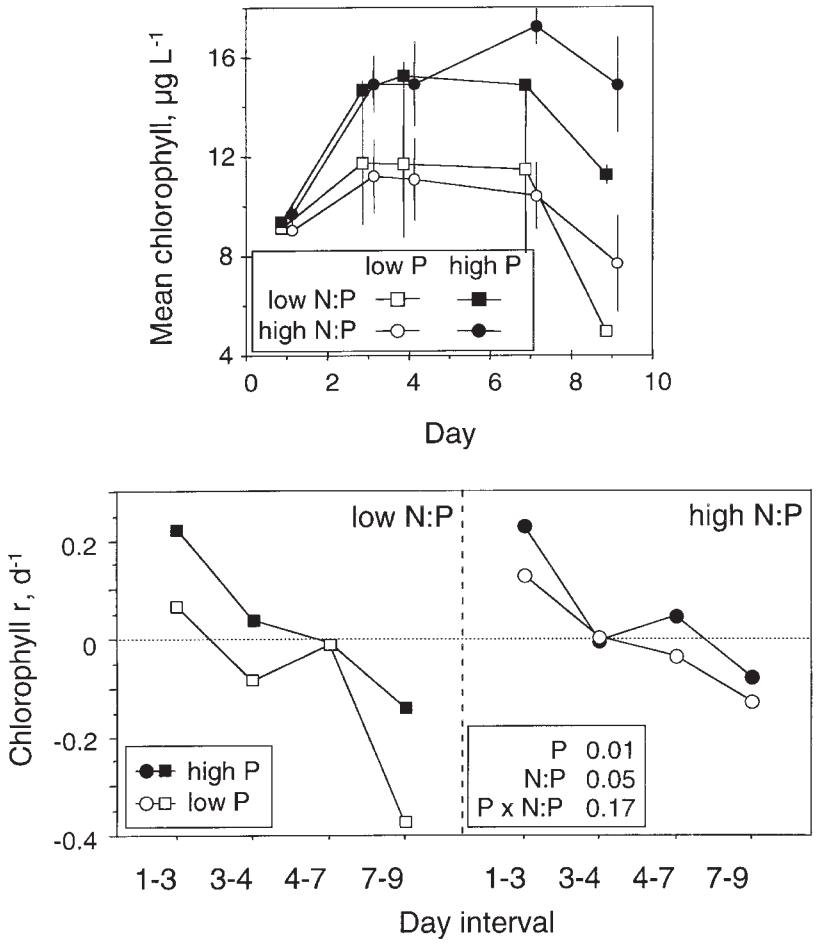

Fig. 4. (**Upper panel**) Mean (±SE) concentrations of chlorophyll during Experiment 2. Inset shows P and N:P ratio treatments. Actual concentrations of P and N are as in Figure 1. (**Lower panel**) Mean (±SE) rates of change of chlorophyll during Experiment 2. Phosphorus treatments and results of ANOVA shown in insets.

such event in the lake, although filamentous cyanobacteria have previously been reported as non-lake dwelling algae that originated outside the lake (Pollingher *et al.*, 1998). Unlike the well known *Aphanizomenon flos-aquae* that forms large 'grass-blade' bundles, trichomes of *Aphanizomenon* in Lake Kinneret remained as individual filaments and were evenly mixed throughout the epilimnetic water column (Pollingher *et al.*, 1998). Thus, the trichomes were conceivably collectible by Lake Kinneret zooplankton. Although Fulton (Fulton, 1988) and Epp (Epp, 1996) concluded that filamentous form alone was not a sufficient explanation for lack of zooplankton feeding on filamentous cyanobacteria, mechanical interference was still a likely possibility simply because of the high concentration of *Aphanizomenon* [2575 filaments l^{-1}; 6 $mg_{wet\ wt}$ l^{-1} at the peak of the 1994 bloom (Pollingher *et al.*, 1998)], as ingestion rates drop precipitously at saturating densities (de Bernardi and Giussani, 1990).

Interestingly, the high clearance rates measured for small flagellated cryptophyte and haptophyte species in the *Aphanizomenon* experiment suggest that *Aphanizomenon* did not pose an insurmountable obstacle to food collection by the grazer assemblage. Indeed, it has been shown that small grazers like *Bosmina* and *Ceriodaphnia*, that dominated our system, are better able to avoid the complications of filamentous algae compared with the larger *Daphnia* (Lampert, 1987).

Aphanizomenon ovalisporum can produce the hepatotoxin, cylindrospermopsin (Banker *et al.*, 1997), but cylindrospermopsin was not detected in the lake water during the bloom (Berman *et al.*, 1998). Moreover, studies have indicated that *Aphanizomenon* is rarely toxic to zooplankton (Lampert, 1987). Of course, other chemicals produced by *Aphanizomenon* could conceivably provide a deterrent to grazing in the form of an unfavorable taste (Demott, 1985). Unfortunately, our short-term experiments did not allow us to address such issues. Nevertheless, overall food intake was reduced in the *Aphanizomenon* experiment relative to when

Aphanizomenon was absent, suggesting that a prolonged bloom could produce the effect of starvation in the grazer assemblage.

Hadas *et al.* concluded that one factor underlying the *Aphanizomenon* bloom of 1994 was a sudden increase (by 40% over previous years) in total dissolved P concentrations following a decline in total N concentrations in the lake over about 10 years (Hadas *et al.*, 1999). They suggested that the ability to use N_2 and organic forms of dissolved P was beneficial to *Aphanizomenon*. In the early stages of bloom development, *Aphanizomenon* had a high number of heterocysts per filament and during the peak of the bloom, extraordinarily high values of alkaline phosphatase activity were measured (Hadas *et al.*, 1999), suggesting that as inorganic P became increasingly depleted, *Aphanizomenon* utilized organic P sources.

Our nutrient addition experiments were designed to shed light on the relative importance of absolute nutrient concentrations, as well as their ratios, to *Aphanizomenon*. Typically, it is assumed that high P availability and low N:P ratios are favorable for N_2-fixing cyanobacteria (Smith, 1983; Reynolds, 1987). Of course, the concept of nutrient limitation is ambiguous without appropriate definition of what exactly is being limited [e.g. growth in a specific taxon, total primary production etc. (Howarth, 1988)]. Given that *Aphanizomenon* was heterocystic and that alkaline phosphatase activity was high during the bloom peak, we assume that either P, or some third factor, was likely limiting growth in *Aphanizomenon*.

The nutrient addition experiments coincided with the peak of the *Aphanizomenon* bloom in 1994 (Pollingher *et al.*, 1998). Our results suggest that during this time, total algal biomass was limited by both N and P, as additions of either resulted in chlorophyll increases. It is not possible to determine precisely the extent of nutrient limitation in *Aphanizomenon* from our experiments, although a lack of *Aphanizomenon* response in the bottles receiving low P and no N additions, while other species increased, suggests that *Aphanizomenon* was more severely limited by P than other taxa. A complete domination by *Aphanizomenon* in bottles receiving high P (regardless of N concentrations or N:P ratios) suggests that factors other than N_2-fixation and high phosphatase activity were beneficial to *Aphanizomenon*. Hadas *et al.* suggest that a third superior competitive ability in *Aphanizomenon* could be involved—efficient uptake of carbon under extremely low concentrations (Hadas *et al.*, 1999). Hadas *et al.* noted elevated pH and alkalinity values in the lake during October that could have reduced CO_2 availability, thus giving an advantage to species with efficient inorganic carbon-concentrating mechanisms, as is common in cyanobacteria (Hadas *et al.*, 1999). Although we did not measure pH in our bottles, we suspect that pH was elevated with increased chlorophyll and that because the bottles were sealed, CO_2 could have become limiting. Nevertheless, we still conclude that N and P were important factors contributing to the success of *Aphanizomenon*, as chlorophyll concentrations declined precipitously by day 9 in all bottles except for those containing the highest levels of N and P additions.

Aphanizomenon has continued to occur in Lake Kinneret each summer since the 1994 bloom, though not in bloom proportions, suggesting that whatever was the impetus for the bloom, it has diminished in its efficacy with time. Temporal coincidence of the bloom with the completion of a major wetland construction project in Lake Kinneret's northern catchment basin provides one possible explanation—a sudden increase followed by waning

Table III: Clearance (CR) and grazing rates (GR) on various phytoplankton taxonomic groups by Lake Kinneret zooplankton feeding on an Aphanizomenon-dominated assemblage (1994)

Algal group	*CR* l g_Z^{-1} day^{-1}	Algal biomass µg wet wt l^{-1}	*GR* mg wet wt g_Z^{-1} day^{-1}
Total	0	6189	0
Aphanizomenon	0	5861	0
Chlorophyta	0	143	0
Dinophyta	0	100	0
Cryptophyta	107	38	4.1
Other Cyanobacteria	0	24	0
Bacillariophyta	0	14	0
Haptophyta	74	9	0.7

inputs of a peat-based growth factor such as organic chelators. In 1994, a portion of the extinct Lake Hula wetland upstream of Lake Kinneret was re-flooded after about 40 years of being dry (Hambright and Zohary, 1999). The resulting shift of soils from dry, oxic conditions to wet, anoxic conditions drastically altered nutrient cycling dynamics in the Hula Valley (Hambright *et al.*, 1998; Markel *et al.*, 1998). Dissolved organic matter, including various chelators, leached from the re-flooded peat soils and carried to Lake Kinneret via the Jordan River, could have contributed to the appearance and success of *Aphanizomenon* later that year. This hypothesis is supported by results from a recent outdoor bottle experiment in which, in the presence of excess N and P, the addition of the chelator EDTA to natural summer phytoplankton from Lake Kinneret enhanced the development of *Aphanizomenon* in comparison with controls to which EDTA was not added (Zohary and Berman, unpublished data). If this Hula-origin chelator hypothesis holds, then it can be further speculated that in the years that followed the 1994 initial re-flooding, the amount of leached organic matter declined, thus reducing the potential for an *Aphanizomenon* bloom.

Understanding why the *Aphanizomenon* bloom occurred, and why *Aphanizomenon* continues to be a major constituent of the summer phytoplankton assemblage of Lake Kinneret, remains a priority for the Kinneret Limnological Laboratory. Although our results cannot explicitly address these questions, they do contribute to the growing body of information on the role of this exotic phytoplankter in Lake Kinneret. *Aphanizomenon* clearly has advantages over taxa more typical of the summer Kinneret assemblage with regards to zooplankton grazing losses and nutrient acquisition. As there is no likely foreseeable manner for increasing grazing losses to *Aphanizomenon*, we can only recommend that efforts towards reducing nutrient concentration and availability in Lake Kinneret be continued in order to reduce the likelihood of future blooms of *Aphanizomenon*.

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