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Experimental studies of zooplankton–phytoplankton–nutrient interactions in a large subtropical lake (Lake Okeechobee, Florida, U.S.A.)

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SUMMARY

1. Over a 1-year period, twenty controlled experiments were performed using small mesocosms (20-l clear plastic carboys) and plankton communities collected from four sites in shallow, subtropical Lake Okeechobee, Florida. In replicated treatments, macrozooplankton grazers were excluded by size fractionation (115 μm), and/or nutrients (N and P) were added, and impacts on phytoplankton biomass and productivity were measured after 3-day incubations.
2. In most experiments (fifteen out of twenty), there was no significant effect of zooplankton exclusion on phytoplankton biomass or productivity, but there were significant increases in those attributes due to nutrient additions. The magnitude of the responses was a function of light availability at the collection sites.
3. In three experiments, zooplankton exclusion led to declines in phytoplankton biomass and productivity, suggesting that animals may sometimes have net positive effects on the phytoplankton, perhaps via nutrient recycling.
4. In only two experiments was there evidence of net negative impacts of grazers on the phytoplankton. In both instances, cladocerans (*Daphnia ambigua* and *Eubosmina tubicen*) were dominant in the zooplankton. However, the increases in chlorophyll *a* due to zooplankton exclusion were small (5–20%), probably because of the small size and relatively low grazing rates of the cladocerans.
5. The results support the hypothesis that phytoplankton biomass in Lake Okeechobee is little affected by herbivorous macrozooplankton. This may be a common feature of lowland tropical and subtropical lakes.

Introduction

Zooplankton play an important role in lake ecosystems, transferring energy from primary producers to predators and suppressing the abundance of phytoplankton. When their grazing is intense, zooplankton can substantially reduce total phytoplankton biomass and productivity, producing 'clear-water phases' when phytoplankton are extremely scarce (Lampert *et al.*, 1986; Arndt & Nixdorf, 1991). Zooplankton also can affect the relative abundance of phytoplankton species, both by direct grazing and by nutrient regeneration (Carney & Elser, 1990). As first proposed by Porter (1973), and subsequently validated by many others (e.g. Lynch & Shapiro, 1981; Lehman & Sandgren, 1985; Sommer, 1988; Brett *et al.*, 1994), small edible phytoplankton are generally reduced by grazers, while large filamentous, colonial and gelatinous taxa are usually not affected, or may be enhanced by zooplankton-mediated nutrient regeneration. Zooplankton can also regulate the relative degree of nitrogen and phosphorus limitation of phytoplankton by preferentially sequestering one of those nutrients from ingested food particles (Elser *et al.*, 1988).

These complex interactions between phytoplankton and zooplankton have been elucidated through decades

of research, including: (i) multi-year observations of plankton dynamics; (ii) field and laboratory studies of zooplankton grazing and nutrient regeneration; and (iii) experimental manipulations of mesocosms and whole lakes. However, nearly all of this research has been done on temperate dimictic lakes. We still know very little about the interactions between zooplankton and phytoplankton in other geographical regions, in particular the tropics and subtropics. Tropical and subtropical lakes differ dramatically from temperate dimictic lakes in terms of basic physical, chemical and biological characteristics, including plankton community structure (Lewis, 1978; Saunders & Lewis, 1988; Crisman, 1990). Hence, there also may be fundamental differences in the nature of their trophic interactions and other ecological processes.

In the present study, we considered phytoplankton–zooplankton interactions in Lake Okeechobee, a lowland subtropical lake in Florida, U.S.A. It has been suggested that phytoplankton are not significantly impacted by zooplankton grazing in the lake (Crisman, Phlips & Beaver, 1995), and that energy flow from phytoplankton to higher trophic levels in subtropical lakes occurs primarily through planktivorous fish (e.g. *Dorosoma*) grazing directly on phytoplankton. These conclusions were based on results of a study conducted in the late 1970s by Crisman & Beaver (1990), wherein large *in situ* fishless mesocosms were placed into three shallow Florida lakes (including Lake Okeechobee), and plankton responses were compared with open-lake reference conditions. Inside the mesocosms, crustacean zooplankton abundances increased dramatically, and so did the cyanobacteria-dominated phytoplankton biomass. The authors concluded that both the zooplankton and phytoplankton were regulated by fish grazing. The experiments were restricted to shallow littoral areas, and it is uncertain whether the results can be generalized to the pelagic, which accounts for over 75% of the lake area.

The present research was conducted in order to quantify:

1 the net effects of zooplankton on biomass and productivity of natural phytoplankton assemblages in Lake Okeechobee;
2 the net effects of zooplankton on phytoplankton responses to nutrient additions;
3 seasonal and spatial variation in the zooplankton effects.

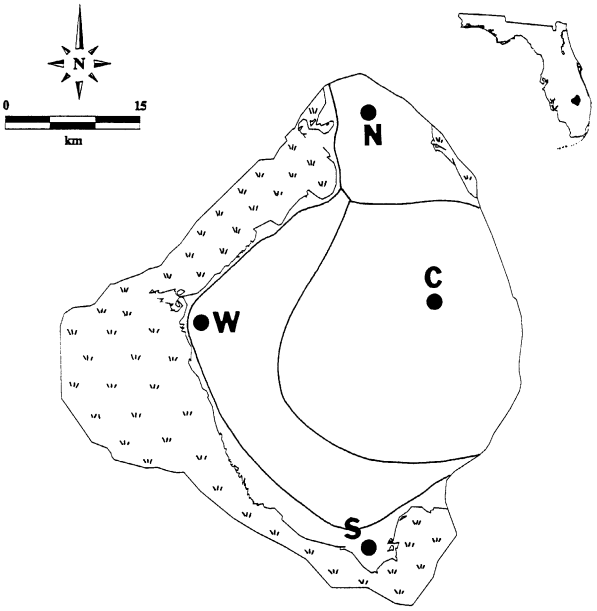

Fig. 1 Map of Lake Okeechobee, showing locations of the four sampling sites in relation to the pelagic ecological zones defined by Phlips *et al.* (1993). The shaded area along the western edge of the lake is littoral marsh, and the inset map shows the location of the lake in south Florida, U.S.A.

This was accomplished by performing twenty controlled, whole-community experiments, in four distinct lake regions, during 1994 and 1995. The results are compared with findings from studies conducted on other lowland tropical lakes, to gain insight into the processes that control zooplankton–phytoplankton interactions.

Materials and methods

Experiment locations and timing

Experiments were conducted using water and plankton obtained at four sites in Lake Okeechobee (Fig. 1). The eutrophic lake is characterized by its large size (1800 km^2), shallow depth (Z_{mean} = 2.7 m, Z_{max} = 5.0 m) and turbid water (Secchi depths < 0.5 m). The sampling sites, hereafter designated as north, central, south and west, were chosen to represent each of four pelagic 'ecological zones', regions that differ from one another in terms of nutrient concentrations, phytoplankton biomass and underwater light attenuation (Phlips *et al.*, 1993). The north site is located in a zone characterized by high concentrations of total phosphorus (TP) and high algal biomass. Light is sufficient for algal growth during much of the year because the mixed depth generally is less than the photic depth. The

central site has unconsolidated mud sediments, high TP concentrations, but low algal biomass. Resuspended sediments cause high turbidity and, in the deeper water column (5 m, compared with 3 m in the north), phytoplankton are often mixed below the critical depth for photosynthesis. The result is light limitation of phytoplankton growth (Aldridge, Phlips & Schelske, 1995). The south site is in a narrow zone bordering the littoral marsh. This water is shallow and clear, has lower TP concentrations, and the substratum is consolidated sand, rock and peat. Phytoplankton biomass is sporadically high, and peaks may be coupled to external nutrient inputs from rainfall or tributaries (Phlips, Aldridge & Hanlon, 1995). This zone displays the strongest year-round nutrient limitation (Aldridge, Phlips & Schelske, 1995). The west site is in a transitional zone with characteristics intermediate between the central and littoral margin zones.

For each site, we conducted experiments (one per week) during November 1994 and January, May, July and September 1995, in order to account for seasonal limnological variability. Detailed information on the seasonal patterns of physical, chemical and biological parameters in Lake Okeechobee may be found in Aumen & Wetzel (1995).

Field sampling methods and experimental design

The duration of each experiment was 72 h. Initial sampling occurred on Monday morning and all experiments were terminated on Thursday afternoon. Day 0 sampling in the lake included temperature, pH and dissolved oxygen profiles (with a Hydrolab water analyser), and Secchi transparencies (with a 20 cm black and white disk). Twelve 20-l carboys (Nalgene® transparent polycarbonate carboys with wide-mouth screw-cap openings and stainless steel handles) were pumped full of unfiltered lake water collected from 0.5 m depth. Immediately thereafter, the contents of six carboys were gently poured through a 115-μm Nitex screen into six empty carboys. The objective was to produce six carboys of water free of macrozooplankton (defined as cladocerans, adult copepods and copepodids). The 115-μm screen was selected because in preliminary work (using 40-, 115-, 200- and 300-μm screens) it was found to remove zooplankton most effectively, while at the same time allowing the phytoplankton to pass through. It was not possible to establish treatments free of both macro- and microzooplankton (rotifers, nauplii and protozoa). Microzooplankton grazing impacts could be important, and they are currently being quantified in a related, non-experimental study of pelagic carbon fluxes.

As soon as the twelve carboys (six untreated and six macrozooplankton-free) were filled, water samples were collected for chemical and plankton analyses. All samples were collected by siphoning water from the carboys using a clear plastic hose. For chlorophyll *a*, TP and total nitrogen (TN), whole water samples were collected. Soluble reactive P (SRP) and dissolved inorganic N (DIN) samples were field filtered through a 0.45-μm glass fibre primary filter, followed by a 0.45-μm polycarbonate secondary filter. The samples were placed into HCl-rinsed plastic bottles and stored on ice until processing.

Day 0 (ambient) macrozooplankton samples were collected from the lake by pumping three additional carboys full of water from the sampling depth, and then filtering the entire 20-l contents of each carboy through a 115-μm screen. The retained animals were placed into Whirl-pak bags, and preserved in 5% formalin–sucrose solution.

Whole-water samples were also collected and preserved with acid Lugol's solution for enumeration of phytoplankton.

After the samples were collected, three of the untreated carboys and three of the macrozooplankton-free carboys were spiked with N (as KNO_3) and P (as KH_2PO_4), in order to increase the total nutrient levels by 500 μg l^{-1} N and 50 μg l^{-1} P. This resulted in four treatments (each in triplicate): control (C): intact zooplankton assemblage, no nutrients added; zooplankton exclusion (Z): macrozooplankton removed with the 115-μm screen, no nutrients added; nutrient (N): intact zooplankton assemblage, nutrients added; and zooplankton exclusion + nutrient (NZ): macrozooplankton removed and nutrients added. Nutrient additions were based on the recommendation by Schelske (1984) that enrichments should be realistic, and not exceed twice the ambient concentrations. In this study, TN concentration was increased 1.8 times the ambient, and TP was increased 1.4 times (averages for the twenty experiments).

Incubation of the carboys and post-incubation sampling

After attempts to incubate carboys in the field we found that, due to rough weather and consequent

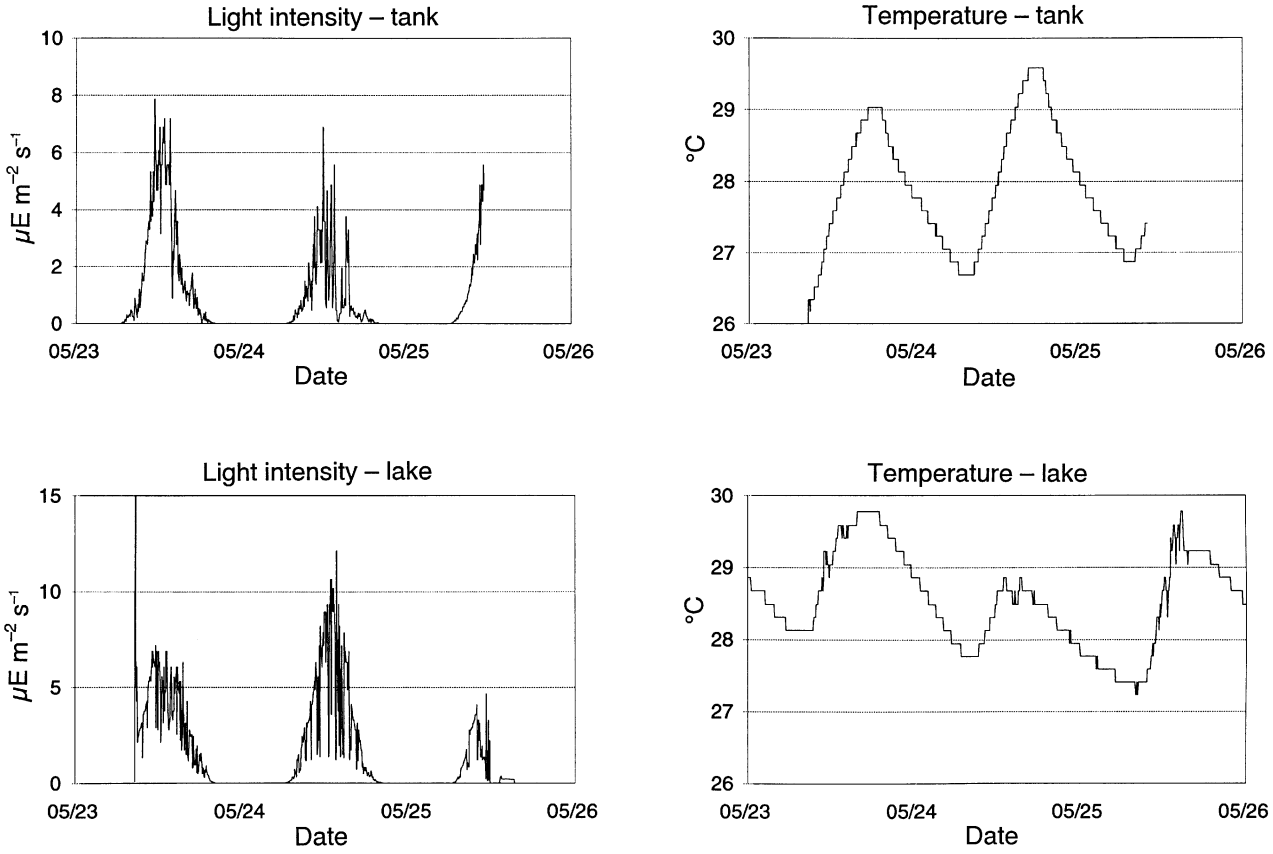

Fig. 2 Irradiance and temperature measured at Secchi depth in the lake and at incubation depth in one of the experimental tanks. The data were obtained in May 1995, when an experiment was conducted at the central lake site.

breakages, this was not feasible. We then decided to use as the incubation site two large fibreglass tanks located at the headquarters of the South Florida Water Management District, about 50 km from Lake Okeechobee. The tanks were filled with water and covered with greenhouse shade cloths in order to produce light levels at mid-water column similar to those measured at the Secchi depth of each collection site. Irradiance varied between 10 and 300 $\mu E\ m^{-2}\ s^{-1}$, depending on lake conditions. Six carboys were placed into each tank, in an inverted position with their handles attached to nylon lines and concrete anchor blocks.

To determine whether conditions in the tanks reflected conditions at the lake, we recorded temperature and irradiance (Onset Instruments Inc. StowAway miniature data loggers) concurrently during one experiment at the field site and in one tank. Irradiance at Secchi depth in the lake (Fig. 2) reached daily maxima of 7–10 $\mu E\ m^{-2}\ s^{-1}$, while in the tanks daily irradiance maxima were from 5 to 9 $\mu E\ m^{-2}\ s^{-1}$. The very low levels of irradiance on this occasion reflect the high abiotic turbidity at the lake site. Water temperatures in the lake varied dielly by about 2 °C, with maxima and minima near 29 and 27 °C, respectively. In the tank, diel variation was about 3 °C, with maxima and minima near 29 and 26 °C, respectively. Subsequent measurements also confirmed that the two tanks displayed similar diel patterns of temperature and irradiance. We conclude that conditions in the tanks were a reasonable approximation of conditions in the lake, at least in terms of the measured variables.

After 3 days incubation, the carboys were retrieved from the tanks and sampled for water chemistry and plankton as described above. In addition, samples were collected for primary productivity measurements. Unfiltered water was siphoned into 250-ml glass BOD bottles (four per carboy), which were held in a covered chest with water from the tank to maintain ambient temperature until incubation commenced in the laboratory.

Final samples of macrozooplankton were collected

by pouring the remaining contents (≈15 l) of each carboy through a 115-μm screen. The retained animals were preserved as described above.

Laboratory procedures

Phytoplankton chlorophyll *a* concentrations were determined according to standard methods (APHA, 1989), after filtering samples onto Whatman GF/C (1.2-μm) fibreglass filters buffered with $MgCO_3$, grinding with a tissue grinder and 12-h extraction in 90% acetone in a dark freezer. Total phosphorus concentrations were determined colorimetrically after persulphate digestion in an autoclave (USEPA, 1979), and SRP concentrations were determined on the undigested field-filtered samples. Total nitrogen concentrations were determined according to standard methods for flow-injection autoanalysers (USEPA, 1987). The DIN concentrations were determined as the sum of NO_3, NO_2 and NH_4, where NO_3 and NO_2 were determined using the cadmium reduction method, and NH_4 by the phenate method (APHA, 1989). All field and laboratory procedures included field blanks, equipment blanks and internal spikes, as called for in the South Florida Water Management District Comprehensive QA/QC Plan (SFWMD, 1993).

Phytoplankton primary productivity was determined by incubating the BOD bottles for 4 h in a controlled environment chamber at the temperature measured at 0.5 m in the tanks. We did not attempt to mimic light conditions in the tanks but incubated at a constant light level of 150 $\mu E\ m^{-2}\ s^{-1}$. This was necessary to produce changes in dissolved oxygen concentration that could be detected after a 4 h incubation. These rates indicate potential productivity, rather than the actual rates that were occurring in the tanks at lower irradiances.

Dissolved oxygen concentrations in the two pre-incubation 'initial' BOD bottles and two post-incubation 'light' BOD bottles were determined using an Orion 250 A meter equipped with an Orion dissolved oxygen electrode. The net amounts of oxygen produced (net primary productivity, NPP) during incubations were converted to amounts of carbon fixed as described in Wetzel & Likens (1979).

Macrozooplankton samples were counted on an inverted microscope at ×100 magnification. Sample aliquots were counted until at least 400 animals, or the entire sample volume (which ever occurred first) was obtained. For samples containing over 400 animals, this procedure results in an estimated counting accuracy of 90% (Lund, Kipling & LeCren, 1958). Population densities were determined from the counts as individuals (ind.) l^{-1}, based on carboy volumes and volumetric portions of samples counted. Total macrozooplankton densities were calculated as the sum of cladoceran, adult copepod and copepodid densities.

Phytoplankton were counted at ×400 magnification using the inverted microscope method (Lund, Kipling & Lecren, 1958).

Statistical analyses

Two response variables were considered in the analyses: chlorophyll *a* concentrations and NPP. Productivity was measured only on the final day of the experiments, but chlorophyll *a* was measured on both day 0 and the final day. We applied one-way ANOVAs to chlorophyll *a* data from day 0, and found that there were never significant differences in treatment means. On average, the coefficient of variation (mean/standard deviation) was less than 10% of the overall mean for the twelve carboys, and concentrations varied by less than 2 $\mu g\ l^{-1}$ between most carboys. This indicates that the 115-μm screening did not significantly reduce phytoplankton biomass. As a result, we considered only the final day chlorophyll *a* data (rather than some rate of change calculated from initial and final values) in the statistical analyses that follow.

Two-way ANOVAs were performed using the final day data, in order to investigate the effects of nutrient addition (two levels: ambient and enhanced), zooplankton removal (also two levels: ambient and reduced), and their interaction on the response variables. On two occasions (November at the south site and January at the central site) there was an unbalanced experimental design due to lack of replication for one of the treatments. In those cases, the inter-treatment differences in chlorophyll *a* and primary productivity were assessed using one-way ANOVA and Tukey's test as a mean separation technique. Only the replicated treatments were compared. In all cases, results were considered statistically significant where the P value associated with the F test was < 0.05. Statistical analyses were performed using the general linear models procedure of SAS (1993).

Results

Limnological conditions at the lake sites

There was considerable variation in limnological conditions at the sites where water and plankton assemblages were collected. This variation is important, for it may explain a considerable amount of the seasonal and spatial variation in phytoplankton responses to treatments (see below).

Lake water temperature (measured on day 0 of each experiment) ranged from 17 to 32 °C (Fig. 3a). The minima occurred in January, and the maxima occurred in July. There was no pronounced inter-station variation in this seasonal pattern.

Secchi depths (Fig. 3b) ranged from below 20 cm to over 90 cm. The lowest values occurred at the central site, and during November–March. As indicated, the central site overlies unconsolidated mud sediment, and during winter (the windy season in subtropical Florida) sediments are resuspended and transported over much of the open water region, including the north and west sites.

Macrozooplankton densities (Fig. 3c) were generally below 50 ind. l^{-1}, except during September at the north site, when densities were double that average value. Minimal densities occurred during March at the central site, and during January at the north and west sites. There was less seasonal variation in macrozooplankton densities at the south site.

Total phosphorus concentrations (Fig. 4a) were > 40 μg l^{-1} at all stations, reflecting the eutrophic nature of the lake. Lower values occurred at the south and north sites, and higher values occurred at the central and west sites. The latter two sites also displayed a pronounced seasonal pattern, with very high TP during January. This coincided with the low Secchi disk transparencies, and probably indicates high concentrations of P-rich inorganic seston in the water column (Havens, 1995). TN concentrations (Fig. 4b) were highly variable, both seasonally and between sampling sites.

Chlorophyll *a* concentration (Fig. 5a) was about 40 μg l^{-1} throughout the year at the south site, always below 15 μg l^{-1} at the central site, and varied over the year at the north and west sites. Annual maxima were in November at the north and west sites.

Seasonal and spatial patterns of soluble nutrients (Fig. 5b,c) reflect changes in chlorophyll *a* and, presumably, algal uptake of the nutrients. SRP and DIN were always low at the south site and high at the central site (except during summer when DIN levels were greatly reduced). At the north and west sites, DIN was below the detection level (7 μg l^{-1}) in November, when chlorophyll *a* peaked, but SRP remained relatively high. In general, the results indicate a greater depletion of DIN than SRP during periods of peak algal biomass, consistent with previous bioassay results that indicated lake-wide N limitation during summer (Aldridge *et al.*, 1995).

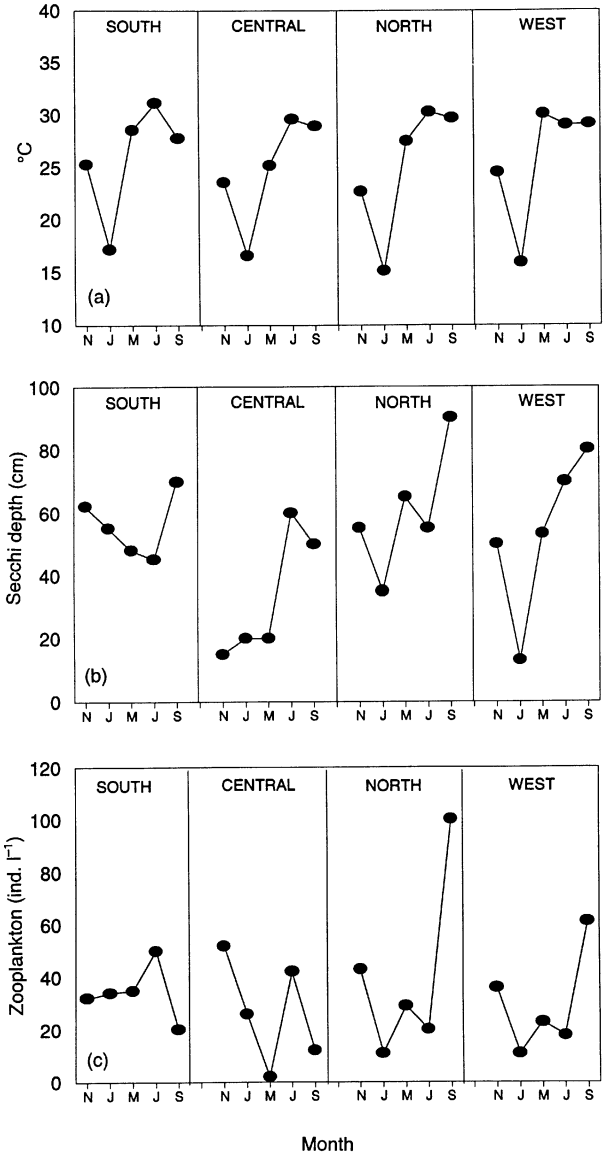

Fig. 3 Selected physical and biological conditions at the four sampling sites during the experiments: (a) lake water temperature; (b) Secchi disk transparency; and (c) total abundances of macrozooplankton (cladocerans, adult copepods, and copepodids).

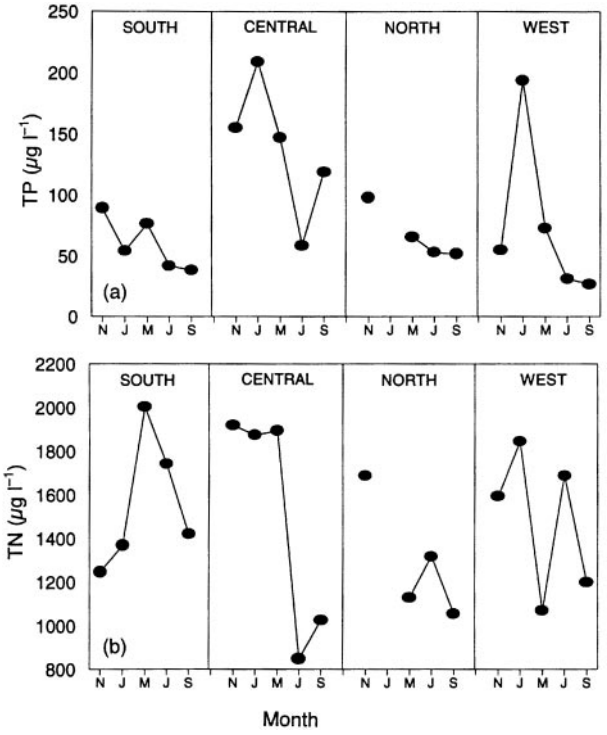

Fig. 4 Selected chemical conditions at the four sampling sites during the experiments: (a) total phosphorus (TP) concentrations; (b) total nitrogen (TN) concentrations.

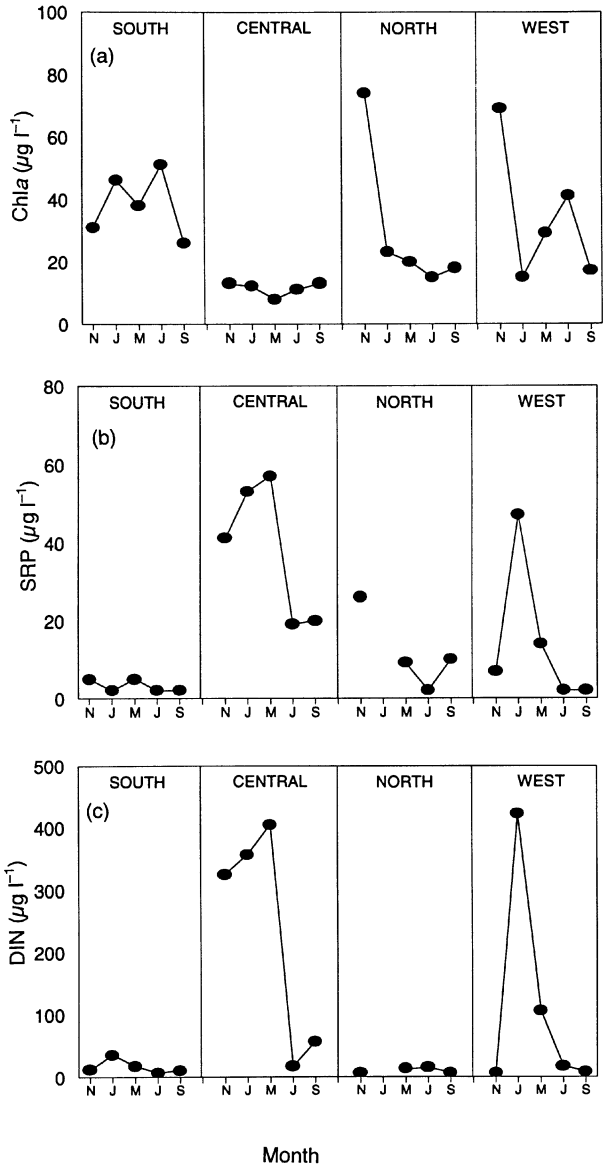

Fig. 5 Selected chemical and biological conditions at the four sampling sites during the experiments: (a) chlorophyll *a* concentrations; (b) soluble reactive phosphorus (SRP) concentrations; and (c) dissolved inorganic nitrogen (DIN) concentrations.

The lake phytoplankton was dominated numerically by cyanobacteria on all sampling dates and at all four lake sites (Table 1). The most abundant taxa were *Microcystis incerta*, *Oscillatoria* sp. and *Lyngbya limnetica*. These same taxa were reported to be dominant during 1988–90 (Cichra *et al.*, 1995). The macrozooplankton was dominated by the copepods *Diaptomus dorsalis* and *Tropocyclops prasinus*. At the west station, three small cladocerans (*Daphnia ambigua*, *Eubosmina tubicen* and *Diaphanosoma brachyurum*) were also common. The same zooplankton were reported as dominants by Crisman, Phlips & Beaver (1995), who sampled the lake from 1988 to 1992.

Total nutrient and macrozooplankton levels

The short duration of these experiments (3 days) precluded nutrient sequestering by periphyton growing on carboy walls. Thus, final TN and TP concentrations in the nutrient addition treatments were close to the calculated 500 and 50 μg l^{-1} enhancements over control levels, respectively (Table 2). The 115-μm screen was generally quite effective at removing macrozooplankton. On average, total macrozooplankton density declined by 54%, and on several occasions we removed over 80%. However, there were several experiments in which only 20–30% density reductions were achieved. This happened when the macrozooplankton was strongly dominated by *T. prasinus*. Presumably, these animals pass through the screen if their bodies are aligned perpendicularly to the filtering surface.

Algal grazing rates are a function of total zooplankton biomass, rather than density. Small cladocerans

Table 1 Numerically dominant phytoplankton and zooplankton taxa at the lake sampling stations during the twenty mesocosm experiments. The listed taxa, in order of decreasing relative density, are those that account for > 10% of the total assemblage density

Location	Month	Phytoplankton	Macrozooplankton
South	Nov.	*Oscillatoria* spp., *Lyngbya contorta* Lemmermann, *L. limnetica* Lemmermann, *Anabaena circinalis* Rabenhorst	*Tropocyclops prasinus* (Fisher), *Diaptomus dorsalis* Marsh
	Jan.	*Microcystis incerta* Lemmermann, *Merismopedia tenuissima*, Lemmermann, *Oscillatoria* spp.	*T. prasinus*, *D. dorsalis*
	May	*M. incerta*, *M. tenuissima*, *Oscillatoria* spp.	*D. dorsalis*, *T. prasinus*
	July	*Oscillatoria* spp., *L. limnetica*, *M. incerta*	*D. dorsalis*, *T. prasinus*
	Sept.	*L. limnetica*, *Oscillatoria* spp., *Aphanocapsa delicatissima* West & West	*T. prasinus*, *D. dorsalis*
Central	Nov.	*Microcystis incerta*, *L. contorta*, *L. limnetica*, *M. tenuissima*	*T. prasinus*, *D. dorsalis*
	Jan.	*M. incerta*, *L. contorta*	*D. dorsalis*, *T. prasinus*, *Acanthocyclops vernalis* (Fisher)
	May	*M. incerta*, *M. tenuissima*, *L. limnetica*	*T. prasinus*
	July	*L. limnetica*, *M. incerta*, *L. contorta*, *M. tenuissima*	*T. prasinus*, *D. dorsalis*
	Sept.	*A. delicatissima*, *M. tenuissima*, *L. limnetica*	*T. prasinus*, *D. dorsalis*, *Eubosmina tubicen* (Brehm)
North	Nov.	*Oscillatoria* sp., *Coelosphaerium* sp., *L. limnetica*	*T. prasinus*, *D. dorsalis*, *E. tubicen*
	Jan.	*M. incerta*, *M. tenuissima*, *L. contorta*	*D. dorsalis*, *T. prasinus*
	May	*M. incerta*, *M. tenuissima*	D. dorsalis, *T. prasinus*
	July	*M. incerta*, *L. limnetica*, *Oscillatoria* sp., *M. tenuissima*	*T. prasinus*, *E. tubicen*, *D. dorsalis*
	Sept.	*L. limnetica*, *Oscillatoria* sp., *A. delicatissima*	*T. prasinus*, *E. tubicen*
West	Nov.	*Oscillatoria* sp., *M. tenuissima*, *A. variabilis*	*T. prasinus*, *D. dorsalis*
	Jan.	*M. incerta*, *M. tenuissima*, *L. contorta*	*D. dorsalis*, *T. prasinus*, *Daphnia ambigua* Scourfield
	May	*Oscillatoria* sp., *M. incerta*	*T. prasinus*, *Diaphanosoma brachyurum* (Lie'ven)
	July	*L. limnetica*, *Oscillatoria* sp., *M. tenuissima*, *M. incerta*	*E. tubicen*, *T. prasinus*, *D. dorsalis*
	Sept.	*Oscillatoria* sp., *L. limnetica*	*T. prasinus*, *E. tubicen*

and copepods clear less water per unit time than do larger individuals (Paffenhofer & Knowles, 1978; Knoechel & Holtby, 1986), and small omnivorous cyclopoids consume algae at considerably lower rates than do larger cyclopoids (Adrian & Frost, 1992). Therefore, it is important to consider animal size and total assemblage biomass in those experiments where only small density reductions occurred. To accomplish this, we re-examined the macrozooplankton samples from the seven occasions with less than 40% density reductions. We measured the body lengths of the first fifty animals encountered while scanning each sample, and developed size–frequency plots. Three representative examples are given in Fig. 6. Screening clearly removed the largest animals from the population. Generally, the cut-off is near 600 μm body length, well in excess of the 115-μm mesh size. However, a 600-μm-long copepod has a width of < 200 μm, closer to the expected porosity.

The net effect of the screening was to reduce mean zooplankton body length by 100–200 μm, and mean individual biomass by 0.5–1 μg. As a result, total biomass reductions in the Z treatments were about 2-fold greater than density reductions. For example, density was reduced by 34% at the north site in November, by 30% at the same site in July, and by 32% at the west site in July (Table 2). The corresponding reductions in macrozooplankton total biomass were 75%, 60% and 61%, respectively. In conclusion, we believe that our experimental manipulations achieved substantial reductions in macrozooplankton biomass and, presumably, grazing intensity.

Chlorophyll a and net primary productivity

Responses to nutrient additions were pronounced, and they varied seasonally and spatially (Figs 7 and 8; Table 3). There were only a few instances where zooplankton appeared to affect the phytoplankton or their response to nutrient additions, and in those cases the effects were minimal.

At the south site, there were significant increases in

Table 2 Summary of nutrient increases and zooplankton reductions actually attained in the twenty experiments. Nutrient levels are given as average final day concentration and percentage concentration increases observed in the N and NZ treatments relative to the C and Z treatments. Zooplankton reductions are given as average density and percentage density reductions observed in the Z and NZ treatments relative to the C and N treatments. (C = control; Z = zooplankton exclusion; N = nutrient addition; NZ = nutrient addition and zooplankton exclusion)

		Total nitrogen		Total phosphorus		Macrozooplankton	
Location	Month	$\mu g\ l^{-1}$	%	$\mu g\ l^{-1}$	%	ind. l^{-1}	%
South	Nov.	490	37	47	53	38	53
	Jan.	525	39	46	102	39	76
	May	366	29	53	74	35	45
	July	394	19	46	112	60	45
	Sept.	384	29	39	122	38	30
Central	Nov.	583	37	44	28	40	94
	Jan.	314	16	59	42	21	88
	May	550	34	47	38	20	65
	July	416	46	51	98	51	55
	Sept.	514	58	46	128	39	28
North	Nov.	354	22	47	44	26	34
	Jan.					12	86
	May	519	53	47	77	177	53
	July	446	36	45	105	62	30
	Sept.	435	47	46	90	41	26
West	Nov.	443	26	55	117	48	76
	Jan.	316	15	26	13	11	85
	May	510	40	39	49	194	52
	July	388	32	43	139	73	32
	Sept.	400	34	37	119	16	30
Averages		+439	+34	+45	+82	–52	–54

chlorophyll *a* in response to nutrient additions during all months. The relative increase (compared with the controls) was greatest in September and least in January. In no case was there a significant response to zooplankton exclosure. In two of the experiments (May and July) there was an increase in chlorophyll *a* in the controls, compared with the lake, perhaps due to an enclosure effect. It should be recognized that the lake samples were collected at the beginning of the experiment, however, while the treatment samples were taken on day 3. Primary productivity responses to treatments at the south site were very similar to the responses in chlorophyll *a*, and indicate nutrient limitation during all months when productivity was measured.

At the central site, the most common result was no significant response to the treatments. This indicates that phytoplankton were limited by some factor other than nutrients and zooplankton, perhaps light. In a smaller number of cases, there were significant responses to nutrient additions and/or zooplankton removal. In July there was a significant increase in chlorophyll *a* due to nutrient additions, and in January there was a significant zooplankton exclusion effect. The Z treatment was not replicated in January, and therefore statistical comparison could only be made between the N and NZ treatments. There was only a slight reduction ($4\ \mu g\ l^{-1}$) of chlorophyll *a* in the NZ treatment, in which macrozooplankton density was reduced by nearly 90% compared with the N treatment (Table 2). Given that soluble N and P were present in surplus (see below), this effect cannot be reasonably attributed to reduced zooplankton nutrient recycling, as has been observed elsewhere (Elser & Goldman, 1990). It also is not due to removal of phytoplankton by filtration, because initial concentrations of chlorophyll *a* were very similar in the Z and C treatments (11 and $10\ \mu g\ l^{-1}$, respectively). One explanation is that filtration damaged some of the larger phytoplankton, leading to a decline in their population densities and chlorophyll *a* during the experiment. Primary productivity at the central site was significantly

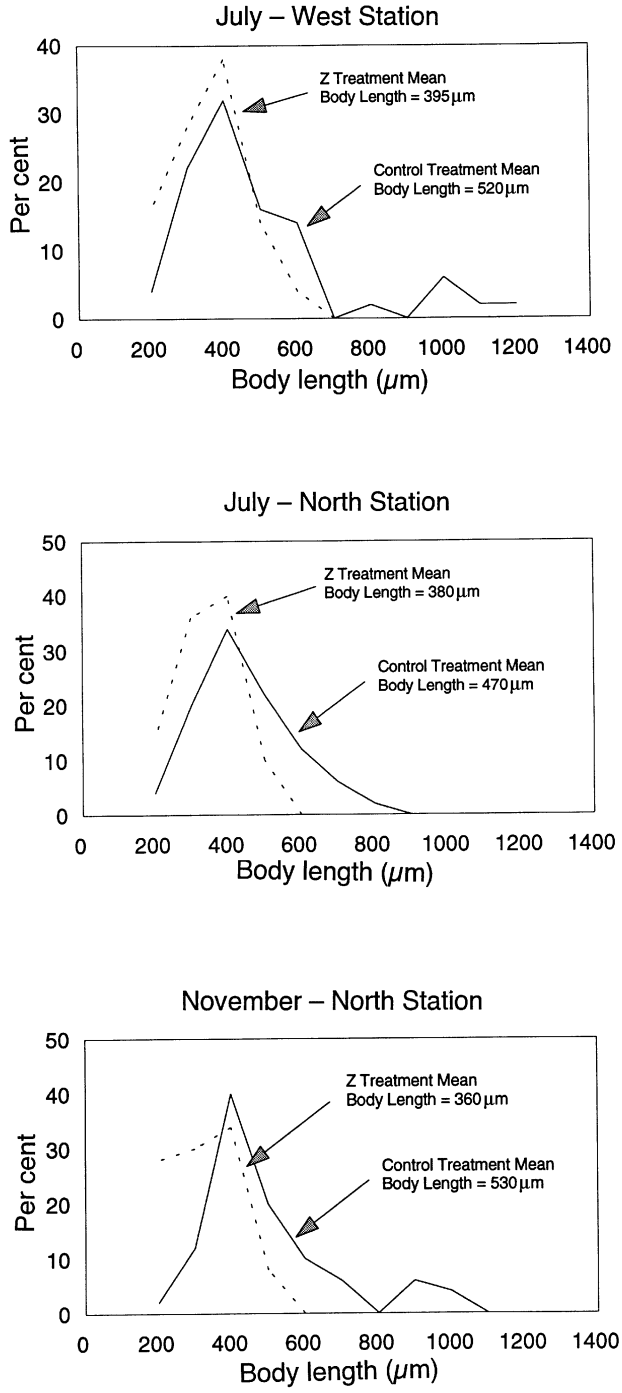

Fig. 6 Comparative size frequency distributions of the crustacean zooplankton assemblages in control and zooplankton exclusion treatments, during three experiments.

enhanced by nutrient addition in July and September, when water clarity was maximal. In January and May there were no significant nutrient effects. Zooplankton removal had significant effects on primary productivity in May and July. In May macrozooplankton removal caused a slight increase in primary productivity in the low nutrient treatments, but it reduced primary productivity in the nutrient-enhanced treatments. In July, the macrozooplankton reduction caused a slight decline in primary productivity in the NZ treatment relative to the N treatment.

At the north site, there were significant increases in chlorophyll *a* due to nutrient additions in all months except January. During that month, the ANOVA results indicate a significant interaction effect; chlorophyll *a* increased when zooplankton were excluded at the low nutrient level, but declined when zooplankton were excluded at the high nutrient level. A similar result occurred in July, although in this case there was also a significant main effect of nutrients. Chlorophyll *a* increased in the Z treatment relative to the control (indicative of a grazing impact), but decreased in the NZ treatment relative to the N treatment. The July results indicate that the magnitude of chlorophyll *a* increase was affected by the presence of macrozooplankton; when they were present the increase was more pronounced then when they were reduced in density (by 30% in this case). The macrozooplankton may have been playing a role in recycling soluble P, which was below the limit of detection (see below), even in the treatments where 50 µg l^{-1} was added. Primary productivity was stimulated by nutrient additions in May, July and September. There was no evidence of zooplankton effects.

At the west site, nutrient additions also resulted in significant increases in chlorophyll *a* on all dates. In January and July there were also significant zooplankton exclosure effects. In both months the exclusion of macrozooplankton led to slight increases in chlorophyll *a* in both the low nutrient and nutrient-enriched treatments. This is evidence of direct grazing impacts by macrozooplankton on the phytoplankton. Interestingly, the January experiment used water and plankton from the only date/site where *Daphnia* (the small-bodied *D. ambigua*) was dominant, whereas in July another small cladoceran (*Eubosmina tubicen*) was dominant. The zooplankton effect in July appears to be more pronounced in the nutrient-enriched treatment (the ANOVA interaction effect is marginally significant). This indicates that while the net effect of macrozooplankton on phytoplankton was negative, the zooplankton may have been providing dissolved nutrients to the phytoplankton under the ambient P-deficient conditions. Primary productivity at the west

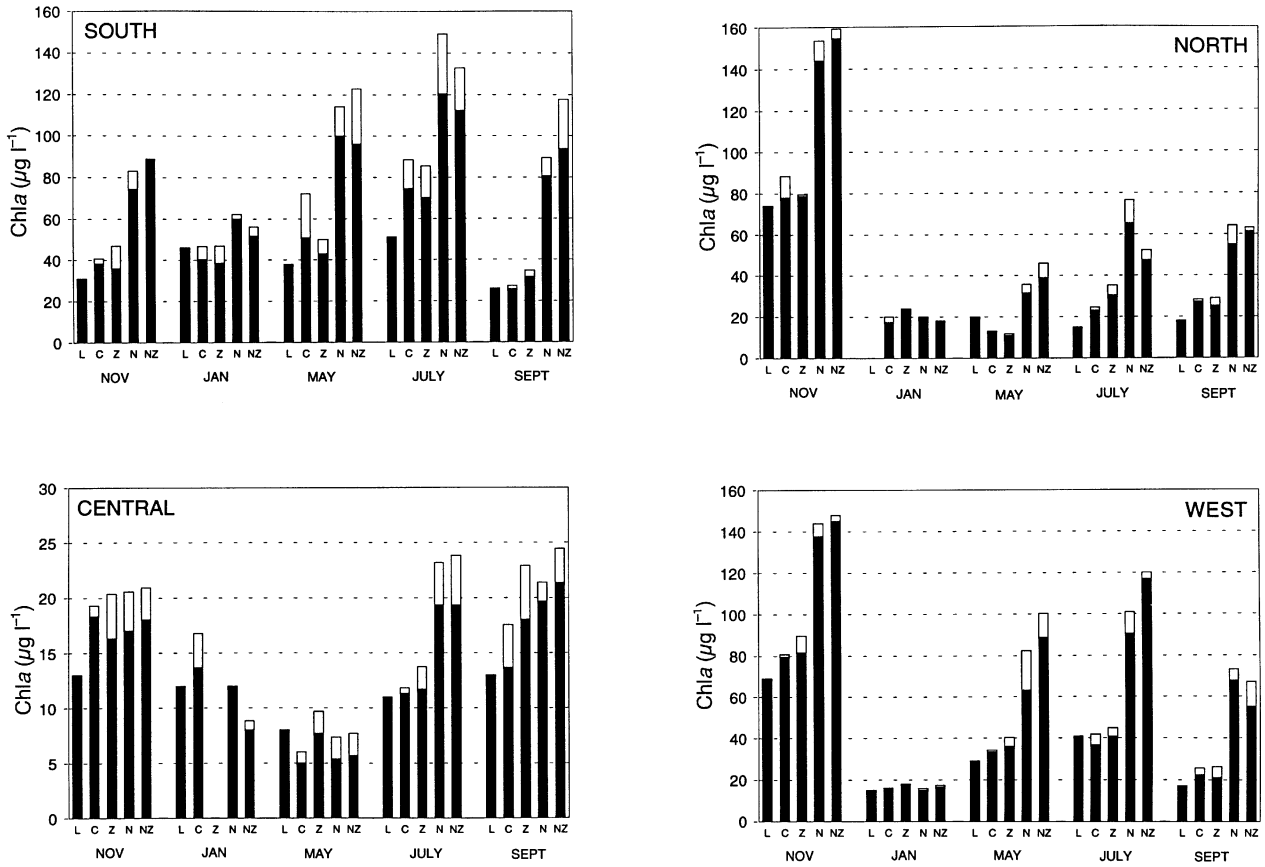

Fig. 7 Mean (± SD, shown as white bars) concentrations of chlorophyll *a* in the various treatments (C = control; Z = zooplankton exclusion; N = nutrient addition; NZ = nutrient addition and zooplankton exclusion) at the end of each experiment. Initial lake values (L, unreplicated) are shown for comparison. In January, there was no Z treatment at the central station.

site was also significantly enhanced by nutrient additions in May, July and September. In May there was also a zooplankton exclusion effect; productivity was slightly less in treatments where grazers were removed.

There was a strong correspondence between the results for DIN and SRP and the results for chlorophyll *a*. At the south station, where significant increases in chlorophyll *a* occurred on all dates, there were low levels of DIN and SRP in the water, and on most dates a large portion of the added N and P was removed from the water, presumably by the phytoplankton uptake. At the north station, the high chlorophyll *a* levels and dramatic increases observed in November coincided with low concentrations of DIN, and removal of nearly 80% of the added soluble N by the growing phytoplankton populations. Considerably less of the added N was utilized in other months, when chlorophyll *a* increases also were reduced in magnitude. The central station, which did not display significant increases in chlorophyll in November, January or May, also had high concentrations of DIN and SRP in the water at those times. Little of the added N or P was removed from the water in the treated carboys (i.e. the final concentration differences between controls and nutrient-spiked carboys were about equal to the calculated additions). In July, when a significant chlorophyll increase was observed, there were lower levels of DIN and SRP in the water, and much of the added N and P was removed during the experiment. The same general pattern was in evidence at the west site.

Phytoplankton responses v site conditions

There were striking relationships between conditions encountered in the lake at the start of each experiment and the magnitude of chlorophyll *a* responses to nutrient additions (Fig. 9). The strongest response (expressed as a percentage increase in concentration

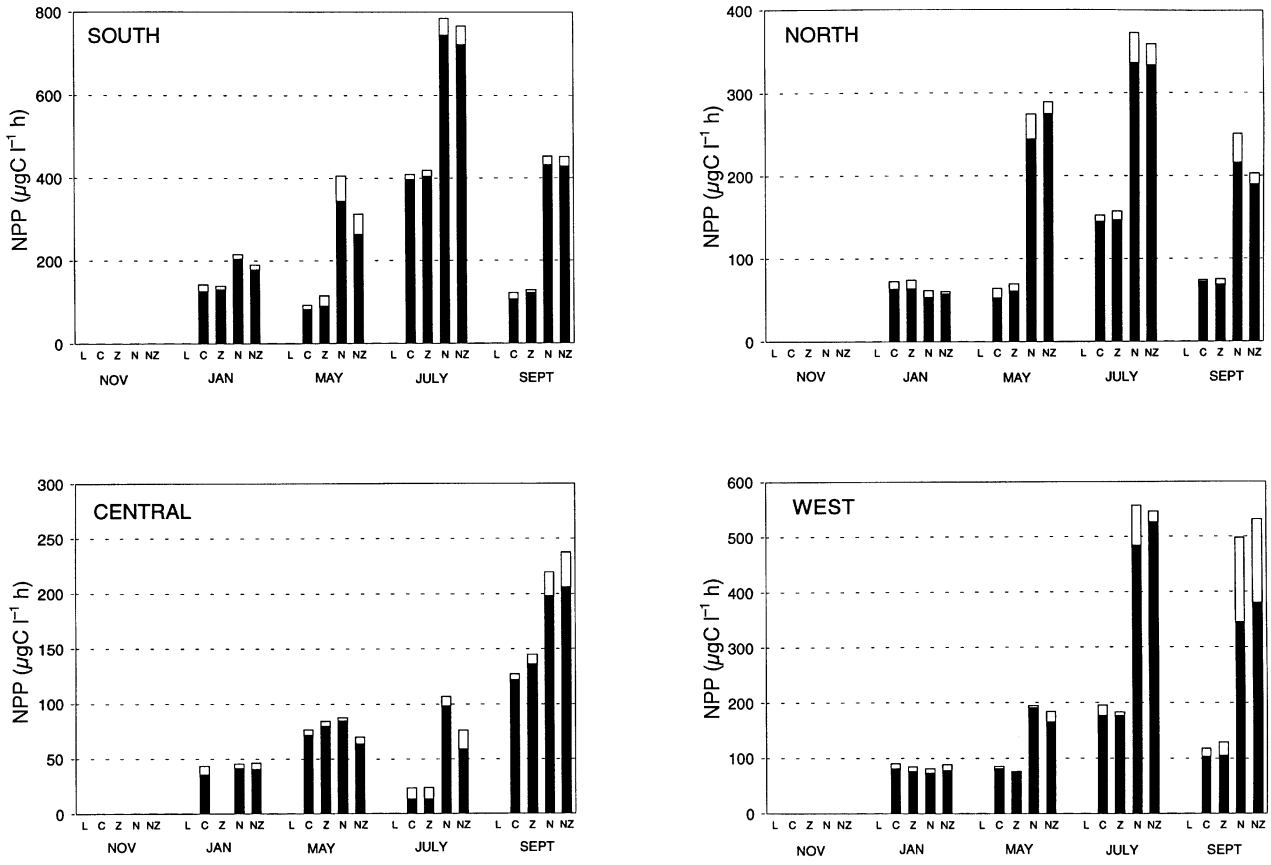

Fig. 8 Mean (± SD, shown as white bars) rates of net phytoplankton primary productivity in the various treatments (C = control; Z = zooplankton exclusion; N = nutrient addition; NZ = nutrient addition and zooplankton exclusion) at the end of each experiment. Initial lake values (L, unreplicated) are shown for comparison. Primary productivity was not measured in November.

in the nutrient-enriched treatments relative to the controls) occurred where: (i) water transparency was high; (ii) temperature was high; and (iii) concentrations of DIN and SRP were low. In fact, over 85% of the variation in chlorophyll *a* response can be explained by Secchi transparency alone. This result does not simply reflect differences in irradiance in the incubation tanks, because that variable explains only 32% of the chlorophyll *a* response.

Discussion

The major conclusion that can be drawn from this study is that macrozooplankton do not play a major role in regulating phytoplankton biomass in Lake Okeechobee. In terms of phytoplankton-limiting factors, the relative importance (based on the chlorophyll *a* response) was: nutrients (fifteen out of twenty experiments) some unmeasured factor, perhaps light (three out of fifteen experiments) zooplankton grazing (two out of twenty experiments). In three of the nutrient-limited cases, the magnitude of chlorophyll *a* increase was a function of macrozooplankton density, with lesser increases in chlorophyll *a* occurring where macrozooplankton were reduced.

Nutrient effects

The factors affecting the response of chlorophyll *a* to nutrient addition are quite clear in this case; lake water transparency plays the key role. At locations where high turbidity resulted in poor light penetration into the water column, chlorophyll *a* concentrations were low, and there were surplus levels of SRP and DIN in the water column. Experiments at these locations resulted in only small (or no) increases in chlorophyll *a* relative to untreated controls. This situation was most common during autumn–winter, and at the central lake site. In contrast, during mid-summer (July), and at sites located most distant from the central

Table 3 Results of two-way ANOVAs for the response variables chlorophyll *a* and net primary productivity measured at the end of the twenty mesocosm experiments. The *P* values are given for each treatment effect tested in the ANOVA (Z = zooplankton effect, N = nutrient effect, and NZ = interaction effect). *P* values of 0.05 or less are considered statistically significant. On two occasions (November at the south site and January at the central site) there was an unbalanced experimental design and one-way ANOVAs were performed in order to compare replicated treatments

	South	Central	North	West
Chlorophyll *a*				
Nov.	Z 0.78	Z 0.82	Z 0.31	Z 0.23
	N 0.01	N 0.94	N 0.01	N 0.01
	NZ –	NZ 0.51	NZ 0.37	NZ 0.52
Jan	Z 0.25	Z 0.03	Z 0.17	Z 0.01
	N 0.01	N 0.11	N 0.26	N 0.02
	NZ 0.44	NZ –	NZ 0.04	NZ 0.47
May	Z 0.67	Z 0.29	Z 0.35	Z 0.12
	N 0.01	N 0.54	N 0.01	N 0.01
	NZ 0.89	NZ 0.39	NZ 0.16	NZ 0.19
July	Z 0.68	Z 0.94	Z 0.31	Z 0.02
	N 0.02	N 0.01	N 0.01	N 0.01
	NZ 0.90	NZ 0.94	NZ 0.03	NZ 0.07
Sept.	Z 0.33	Z 0.27	Z 0.56	Z 0.21
	N 0.01	N 0.10	N 0.01	N 0.01
	NZ 0.71	NZ 0.61	NZ 0.27	NZ 0.31
Primary productivity				
Nov.	not measured	not measured	not measured	not measured
Jan.	Z 0.25	Z 0.15	Z 0.70	Z 0.50
	N 0.01	N 0.70	N 0.20	N 0.60
	NZ 0.11	NZ –	NZ 0.74	NZ 0.40
May	Z 0.25	Z 0.09	Z 0.17	Z 0.04
	N 0.01	N 0.64	N 0.01	N 0.01
	NZ 0.17	NZ 0.01	NZ 0.42	NZ 0.22
July	Z 0.75	Z 0.05	Z 0.98	Z 0.58
	N 0.01	N 0.01	N 0.01	N 0.01
	NZ 0.51	NZ 0.05	NZ 0.88	NZ 0.49
Sept.	Z 0.65	Z 0.43	Z 0.30	Z 0.81
	N 0.01	N 0.01	N 0.01	N 0.01
	NZ 0.49	NZ 0.84	NZ 0.40	NZ 0.83

lake region (the south and west sites), there always were significant chlorophyll *a* responses to nutrient additions. These responses, and corresponding changes in NPP, are consistent with the results of laboratory bioassays performed monthly during 1990–92 (Aldridge *et al*., 1995). Those authors found that in the north lake region, nutrients and light were limiting to phytoplankton growth during 53 and 47% of the bioassays, respectively. In the central lake region, there was 65% light and 35% nutrient limitation, while in the south near-littoral region, there was only 18% light, but 82% nutrient limitation. Results at two west sites were similar to those found in the south, except that there was a slightly higher incidence of light limitation. In those studies, where enhanced (120 $\mu E\ m^{-2}\ s^{-1}$) rather than natural light levels were used, light limitation was inferred in cases where there was a significant algal growth response (measured as an increase of *in vivo* fluorescence) in untreated controls. These laboratory experiments did not consider zooplankton grazing effects.

The seasonal and spatial patterns of light *v* nutrient limitation can be explained by sediment composition (Olila & Reddy, 1993), water depth and seasonal variation in wind velocity (Maceina & Soballe, 1990). The central lake site is deep and overlies a region of unconsolidated mud. Sediment resuspension by wind occurs frequently and, due to the high turbidity, mixed depth can greatly exceed the critical depth for algal photosynthesis (Phlips *et al*., 1995). This situation is most common during late autumn to early spring, when average wind velocities are nearly double those

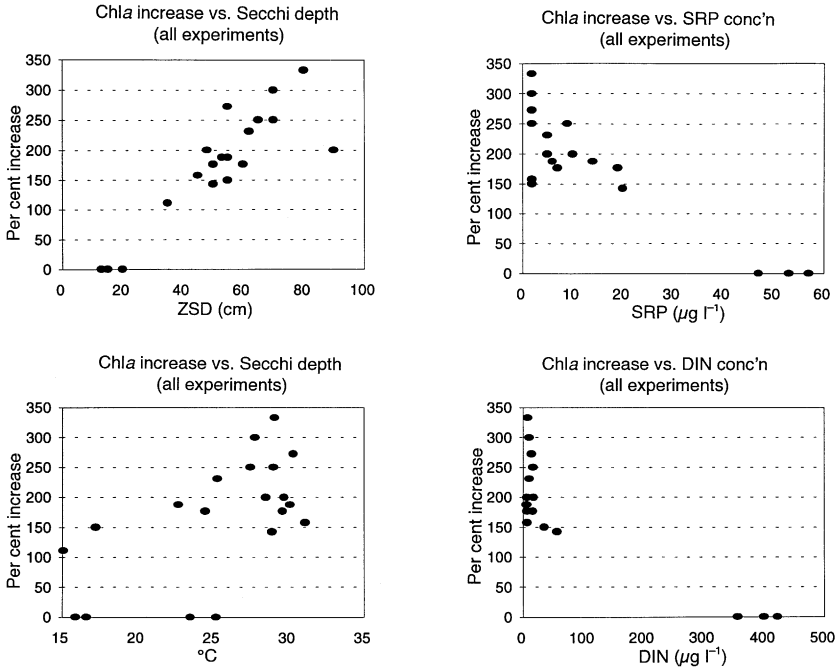

Fig. 9 Relationships between chlorophyll *a* response to nutrient additions (the relative increase in the NP treatment compared with the control) and selected limnological variables measured at the lake sites: Secchi disk transparency (ZSD) water temperature, SRP and DIN.

in summer. The north site also overlies mud but, since water column depth is less than in the central region, the ratio of euphotic depth to mixed depth is more constrained, and the phytoplankton less often experience light-limiting conditions. The situation is markedly different at sites located near the littoral fringe (the south site in this study). Here the bottom sediment is peat, and is less prone to resuspension by wind, and the water column is shallow (less than 2 m). Hence there is no light limitation, and a predominance of nutrient-limited conditions are found here.

Stimulatory effects of zooplankton on phytoplankton

On three occasions chlorophyll *a*, or its response to nutrient additions, was suppressed by zooplankton removal, indicating net positive impacts of the macrozooplankton on phytoplankton growth. One interpretation of these results is that some nutrient element (e.g. DIN or SRP) was limiting to phytoplankton growth, and that regeneration of that nutrient by macrozooplankton sustained a net positive growth of phytoplankton. However, the supporting data are equivocal. On the first occasion when the positive zooplankton effect was observed (January at the central site), there were high concentrations of DIN and SRP in the water column. On the second occasion (January at the north site), we have no data on soluble nutrients to consider (samples were lost in transport to the analytical lab). Only on the third occasion (July at the north site) were the low concentrations of SRP consistent with the hypothesis of a nutrient regeneration effect. On two other occasions (May at the west site and July at the central site), NPP or its response to nutrient additions was suppressed by zooplankton removal. In both cases there were very low ambient concentrations of DIN in the lake water, and a significant stimulation of productivity where nutrients were added. At the west site, there was also a very high density (compared with other dates) of a medium-sized cladoceran, *Diaphanosoma brachyurum*. Cladocerans in this size range (0.5–1 mm) have been shown to have significant impacts on phytoplankton, through nutrient regeneration (Vanni, 1987).

Grazing impacts of zooplankton on phytoplankton

We conclude that zooplankton grazing is not an important overall regulator of phytoplankton biomass or productivity in Lake Okeechobee. Grazing effects were found in only two out of twenty experiments. There was, however, a conspicuous feature of the macrozooplankton assemblage on those two dates. In January at the west site, chlorophyll *a* increased by 2 μg l^{-1} (about 10%) when macrozooplankton density was reduced, and we observed the only case where a

daphnid (*Daphnia ambigua*) was among the dominant macrozooplankton taxa. It has previously been shown that zooplankton assemblages dominated by large *Daphnia* can dramatically suppress the abundance of phytoplankton (Lampert *et al.*, 1986; Gulati, 1990; Theiss, Zielinski & Lang, 1990). However, small cladocerans appear to have a considerably lesser impact than large ones (Dawidowicz, 1990). This may explain why there was only a small increase in chlorophyll *a* in our experiment; *Daphnia ambigua* is the smallest of the North American daphnid taxa. In July at the west station, there again was a significant increase in chlorophyll *a* when macrozooplankton were removed. In this case, the chlorophyll *a* response was more pronounced and there was a $25\ \mu g\ l^{-1}$ difference between the N and NZ treatments, where presumably any dependence on zooplankton regeneration of DIN or SRP was overcome by the high levels of added nutrients. The fact that the zooplankton grazing effect was much less in the low-nutrient treatments (differing by $< 5\ \mu g\ l^{-1}$ between the C and Z treatments) indicates that there were indeed some beneficial effects of macrozooplankton. On this date, when the most pronounced zooplankton effects were found, a small cladoceran, *Eubosmina tubicen*, was dominant and its density was 10-fold higher than the total density of cladocerans recorded on other sampling dates.

Grazing impacts in other tropical lakes

The results of this study indicate only minimal impacts of macrozooplankton on the natural phytoplankton assemblages of Lake Okeechobee. This is consistent with results from other studies on tropical and subtropical lakes, and supports the hypothesis of Crisman *et al.* (1995), that 'zooplankton are unlikely to be significant grazers of phytoplankton biomass in Lake Okeechobee'. Their hypothesis was based on: (i) the rarity of cladocerans in the plankton of Lake Okeechobee; (ii) the small average size of zooplankton whereas phytoplankton are large (Cichra *et al.*, 1995); and (iii) the results of fish exclusion experiments performed in the late 1970s (Crisman & Beaver, 1990), in which both zooplankton and phytoplankton increased in lake enclosures that were devoid of the natural planktivorous fish (that included the pump filter-feeder *Dorosoma*). Crisman & Beaver (1990) obtained similar results in experiments performed in the shallow lakes Apopka and Wauberg, located in northern and central Florida, respectively. They generalized their findings, and concluded that in subtropical and tropical lakes, grazing by zooplankton is of little importance to controlling phytoplankton community structure and biomass. This view now is borne out by the results of our controlled experimental studies, performed under a variety of limnological conditions. The results are also consistent with findings from other tropical lowland lakes (Moriarty *et al.*, 1973; Lewis, 1978; Saunders & Lewis, 1988; Fernando, 1994; Magadza, 1994). All of these studies reached the conclusion that the zooplankton are unable to utilize colonial algal species that develop in such nutrient-rich tropical environments.

Factors affecting zooplankton–phytoplankton interactions in Lake Okeechobee

In Lake Okeechobee, as in the other lowland tropical lakes mentioned above, it appears that the considerable overlap in size between large cyanobacteria-dominated phytoplankton and the small zooplankton herbivores is responsible for the lack of top-down control. The dominance of cyanobacteria, in particular nitrogen-fixing species, may be a result of nitrogen-limiting conditions (Aldridge *et al.*, 1995; Phlips *et al.*, 1996) that occur in Lake Okeechobee and in other tropical and subtropical lakes (Lewis, 1978; Henry *et al.*, 1985; Dierberg, Williams & Schneider, 1988). Cyanobacteria in general are favoured under conditions of nitrogen deficiency, because they can sequester DIN from the water when concentrations are too low for utilization by other phytoplankton (Tilman, 1982; Smith, 1983). Nitrogen-fixing cyanobacteria become dominant at extremely low concentrations of DIN, because they can obtain N from the potentially limitless atmospheric pool (Reynolds, 1993). It has also been demonstrated that cyanobacteria are superior competitors for nutrients at water temperatures $> 20°C$ (Tilman, 1986). At high temperatures, cyanobacteria appear to dominate over a wider range of N : P and Si : P ratios than they do at lower temperatures where diatoms are favoured.

The dominance of small crustacean zooplankton taxa has several possible explanations. Crisman & Beaver (1990) noted that 'the size range of most macrozooplankton in Florida lakes regardless of trophic state is comparable with the small-bodied assemblages dominating temperate zooplankton com-

munities experiencing intense visual zooplanktivory.' They suggested that the very high densities of planktivorous fish in Lake Okeechobee and other lowland tropical lakes provide intense top-down control over zooplankton, eliminating all but the smallest taxa. As in temperate lakes (Schoenberg & Carlson, 1984; Elser & MacKay, 1989), the small zooplankton cannot effectively control phytoplankton biomass when it is dominated by cyanobacteria.

Another factor is water temperature, which might limit the abundance of the most effective herbivores during summer, a peak phytoplankton growth period. Beaver & Havens (1996) noted that cladoceran zooplankton display their lowest densities during midsummer, and attributed this to a deleterious effect of high water temperature on daphnid populations. Crisman *et al*. (1995) noted that the Lake Okeechobee *Daphnia* populations form ephippia during May to early June, and then essentially disappear from the community until autumn. Between April and October, the average water temperatures in Lake Okeechobee (and in many other lowland tropical lakes where large daphnids are rare) are between 25 and 30 °C. Mallin & Partin (1989) demonstrated that the fecundity of *Daphnia ambigua* peaks at 25 °C, and then declines. It has also been demonstrated (Lampert, 1977; Vidal, 1980) that high water temperature increases the threshold food concentration for cladocerans and copepods, and that this effect is most pronounced for larger animals.

Potential impacts of microzooplankton

Two potentially important components of the zooplankton, the rotifers and protozoa, were not considered in this study. This was because it is not physically possible to size-fractionate phytoplankton from the entire zooplankton assemblage, except in rare cases where only very small phytoplankton occur (e.g. Havens, 1991, 1993). Hence, most experimental studies have considered macrozooplankton effects, and generally in lakes where large taxa (e.g. *Daphnia pulex*) dominate. The few studies dealing specifically with microzooplankton indicate net positive impacts on the phytoplankton, probably due to nutrient regeneration (Hamilton & Taylor, 1987; Caron, Goldman & Dennett, 1988; Bloem *et al*., 1989; Havens, 1993).

We currently are investigating microzooplankton grazing using ^{14}C tracer studies of C transfer from pico-, nano- and microphytoplankton to microzooplankton (and macrozooplankton). Results to date indicate that microzooplankton contributions to total zooplankton C uptake range from 15 to 90%. However, the combined rate of C uptake generally accounts for $< 10\%$ of phytoplankton C uptake (K.E. Havens, unpublished). It is unlikely that grazing by the complete zooplankton assemblage exerts control over the cyanobacteria-dominated phytoplankton community.

Finally, a new member of the Lake Okeechobee macrozooplankton, the exotic cladoceran *Daphnia lumholtzii*, was discovered in July 1993 (K.E. Havens, unpublished). This daphnid can reach lengths of over 2 mm, is native to East African lakes (Green, 1967) and has now invaded lakes in the south-eastern U.S.A. (Havel & Hebert, 1993). It differs from native daphnids in that it can tolerate water temperatures over 25 °C (Chapman & Lewis, 1976; Venkataraman, 1981). Given its large size, it is expected to have high filtering rates (Knoechel & Holtby, 1986) and the ability to consume large particles (Burns, 1968), perhaps including cyanobacterial colonies. It remains to be seen whether *D. lumholtzii* will become abundant in Lake Okeechobee. If so, there is a potential for dramatic changes at the phytoplankton–zooplankton interface of this ecosystem.

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