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Predator-induced bottom-up effects in oligotrophic systems

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Abstract

Five treatments (replication n=2) were applied to mesocosms in an oligotrophic lake (TP=6–10 $\mu g\ l^{-1}$) to assess the effects of fish on planktonic communities. The treatments were: (1) high fish (30 kg ha^{-1} *Lepomis auritus*, Linnaeus), (2) low fish (10 kg ha^{-1}), (3) high removal of zooplankton, (4) low removal of zooplankton and (5) control. Total phosphorus, chlorophyll *a*, zooplankton biomass, and species richness decreased from high fish > low fish > control > low removal > high removal treatments. The fish treatments were dominated by crustacean zooplankton, while rotifers outnumbered the other zooplankters in the removal treatments. Calculations of zooplankton grazing rates suggested that clearance rates seldom exceeded 2% of the enclosure volume d^{-1} and were unlikely to have had much influence on phytoplankton biomass. Calculations from a phosphorus bioenergetics model revealed that when fish were present, their excretion rates were higher than the rates ascribed to zooplankton. Diet analysis showed that the fish derived most of their energy from the benthos and periphyton, and that fish excretion and egestion made significant contributions to the very oligotrophic pelagic phosphorus pool. In the absence of fish, zooplankton excretion was highest in the control treatments and lowest in the zooplankton removal treatments. Our results suggest that in oligotrophic systems, planktivorous fish can be significant sources of phosphorus and that fish and zooplankton induced nutrient cycling have significant impacts on planktonic community structure.

Introduction

Numerous studies have focused on the effects that planktivorous fish have on zooplankton population structure and algal production (e.g. Zaret, 1980; Kerfoot & Sih, 1987; Carpenter, 1988) and in recent years, lake and enclosure biomanipulations have contributed to our understanding of these problems (Shapiro & Wright, 1984; Carpenter *et al.*, 1985, 1987; Carpenter & Kitchell, 1993). These studies have shown that zooplankton and phytoplankton size and species compositions are altered by changes in both predation pressure and nutrient availability (Brooks & Dodson, 1965; Lynch & Shapiro, 1981; reviewed by Carpenter, 1988; McQueen *et al.*, 1992). Protozoans and bacteria are also involved as nutrient recyclers accounting for more than half the organic carbon generated in aquatic ecosystems (Scavia *et al.*, 1986; Scavia & Laird, 1987; Pace *et al.*, 1990; Pace & Funke, 1991).

The results of biomanipulation studies have also fueled controversy. Persson *et al.* (1988) pointed out the importance of the trophic status of the system in explaining the way direct and indirect interactions in the food web occur. McQueen *et al.* (1986) suggested that in oligotrophic systems, top-down control affected all trophic levels including herbivores and primary producers, whereas in eutrophic systems, top-down control was strongest at the fish levels (piscivore and planktivore) and bottom-up forces predominated in the lower food web levels.

At the root of the controversy, are disagreements about the magnitude of the relative effects of fish (McQueen *et al.*, 1992) and zooplankton (Taylor & Lean, 1991) on aquatic food webs. Nakashima &

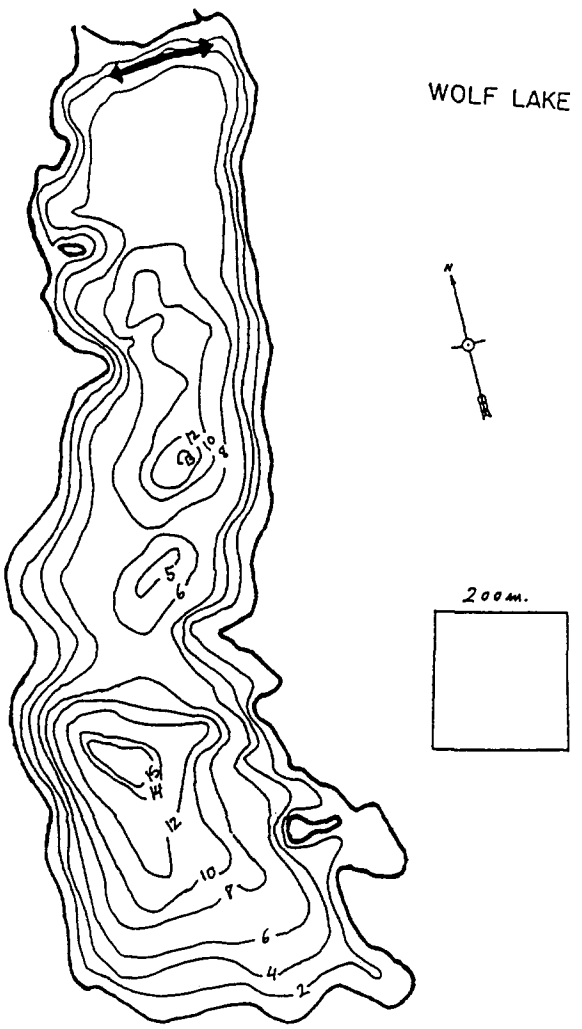

Fig. 1. Bathymetric map of Wolf lake. The arrow indicates the alignment of the mesocosms.

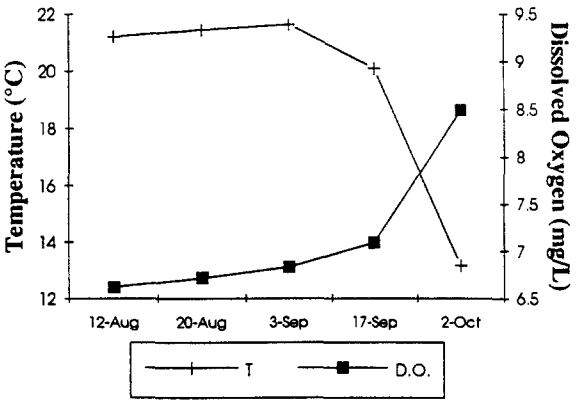

Fig. 2. Temperature and dissolved oxygen measurements for five dates from the beginning to the end of the experiment.

Leggett (1980) believed that the contribution of phosphorus (P) from fish excretion is insignificant in natural aquatic ecosystems. Alternatively, Vanni & Findlay (1990) and Kraft (1992) defended the role of fish excretion and egestion in the food web nutrient cycling in their mesocosms. Likewise, the importance of zooplankton excretion to phytoplankton communities is a subject of debate. Lehman (1980) found that excretion by grazers and phytoplankton production were highly coupled processes, whereas McCauley & Kalff (1987) found P regeneration by crustacean zooplankton to be of little importance for algae.

In this study, we evaluate the relative importance of (1) fish predation and nutrient excretion, and (2) zooplankton grazing and nutrient turnover. Fish were assumed to have a dual role in the system: to remove zooplankton and to increase nutrient levels. Fish effects on the phosphorus pool are explored, as well as zooplankton composition, size and species richness, and phytoplankton biomass. The goals of the study are to identify the food web components and mechanisms that regulate the planktonic community.

Methods

Study site

Wolf Lake is a small oligotrophic lake located in the Huntington Wildlife Forest, Newcomb, New York with an elevation of 557 m, a surface area of 62.3 ha and a maximum depth of 15 m (Heady, 1942) (Fig. 1). The lake is surrounded by undeveloped forest.

The lake bottom is mostly rock and gravel, with sand predominating on the north shore. The mesocosms used for the study were installed *in situ* aligned between the 3 m and 4.5 m isopleths along the North shore of the lake (Fig. 1) in an area of flat sandy bottom.

The most common crustacean zooplankton species in the lake during the study period were *Leptodiaptomus minutus* (Lillj.), *Epischura lacustris* (Forbes), *Mesocyclops edax* (Forbes), *Cyclops spp.*, *Diaphanosoma brachyurum* (Liéven) and *Bosmina longirostris* (O.F.M.).

Ten mesocosms were constructed of Falcolene™, a black (UV protected) nylon-woven polyethylene material. The mesocosms were cylindrical (3.8 m diameter, 4.5 m depth) with bottoms open to the sediment

interface. To hold the mesocosms vertically, the bottoms were weighted with chains and the tops were floated on collars of floatation material. The mesocosms were attached to wood frames anchored to the bottom by six 40 kg concrete blocks. SCUBA divers pushed the bottom chains of the mesocosms into the sediment and secured them with 0.5 m PVC poles at four points. A pump was used to add lake water to the mesocosms which were then left to stabilize before starting the treatments. The depth of each mesocosm averaged from 3 to 3.5 m, depending upon the lake bottom. Volumes ranged from 23 to 27 m^3. In order to prevent fish intrusions and to discourage piscivorous birds, the top of each mesocosm was surrounded by a 30 cm fence made of netting.

Experimental design

Five replicated treatments were applied to the mesocosms. The ten enclosures were divided into two groups of five and the experimental treatments were randomly assigned to each group. The treatments were: Control (C), where the mesocosms contained no fish and no manipulation was done; fish treatments at two levels, high (HF) and low (LF); and zooplankton removal at two levels high (HR) and low (LR). The HF treatment consisted of the addition to the mesocosms of 18 redbreast sunfish (*Lepomis auritus*, Linnaeus), age 1^+ (mean total length = 48.56 mm, mean weight = 1.87 g). The LF treatment consisted of the addition of 6 fish. Zooplankton removal treatments were designed to match the feeding rate of the fish in HF and LF, but without the nutrient input from fish excretion and egestion. Therefore, zooplankton were removed with a 200 μm mesh size plankton net at two levels, high removal (HR) and low removal (LR). Redbreast sunfish (*Lepomis auritus*) were chosen for the fish treatments because they occurred naturally in Wolf Lake and because stomach content analysis of age 1^+ redbreast sunfish revealed that zooplankton were an abundant item in their diet.

The redbreast sunfish were collected on August 8 and 9 in Wolf Lake using a beach seine and minnow traps, and added to the HF and LF mesocosms on the same dates. Thirty additional age 1^+ redbreast sunfish were kept in an aquarium in the laboratory as a backup. One fish died during the experiment in one LF mesocosm and was replaced with a fish from the laboratory. There was no other fish mortality.

In order to determine zooplankton removal rates based on the feeding rates of fish, we analyzed stomach contents from yearling redbreast sunfish taken from the lake. The zooplankton present in the stomachs were attributed to the feeding effort of the previous three hours (Seaburg & Moyle, 1964; Elliot & Persson, 1978) and fish were assumed to feed twelve hours every day. To determine ambient abundance, zooplankton samples from four random mesocosms were collected using a 25 l Schindler trap. The crustacean zooplankton were counted and the mean density calculated and used as the standard density of zooplankton in the mesocosms. The plankton net used for the removal treatments had a diameter of 0.5 m, and the average depth of the mesocosms was about 3.3 m. Zooplankton were removed on a weekly basis one day before sampling.

Water and zooplankton samples were collected from August 15 to October 2, 1991. Total phosphorus (TP), chlorophyll (chl) *a* and zooplankton were sampled weekly. Nitrate, dissolved oxygen (D.O.) and temperature were determined bi-weekly. The samples were collected from the center of each mesocosm. Dissolved oxygen and temperature were measured at 0, 1.5, and 3 m using a YSI™ Model 57 D.O. meter. A 1.5-cm-diameter 4-m-long vinyl tube was used to collect water samples for determination of TP, nitrate and chl *a* from the whole water column. Six water samples were collected per mesocosm on each sampling date. The water from the six samples was poured into a lake-rinsed bucket and then homogenized by stirring. One litre of water was then collected from the bucket in an amber Nalgene™ bottle for chl *a* and nitrate determinations and 0.5 l was collected in a white Nalgene™ bottle for TP determinations. The samples were kept in a cooler with ice packs during sampling and were filtered and/or preserved in the laboratory the same day.

A 25 l Schindler sampler with a 63 μm net attached was used to sample zooplankton. Samples were collected at three depths (just below surface, 1.5 m and 3 m) and combined in the field. When the sampler was retrieved from the mesocosm, the net was carefully rinsed to concentrate all of the organisms. The net was then tightly tied just above the bucket to avoid the loss of organisms and the sampler was again lowered to sample the next depth. This procedure was repeated until the bucket contained the three samples from the mesocosm. The contents of the bucket was then poured into a Whirl-Pack™ bag and preserved in a 5% formaldehyde-sucrose solution. In this way, a combined sample of three depths representing 75 l filtered water was obtained for each mesocosm.

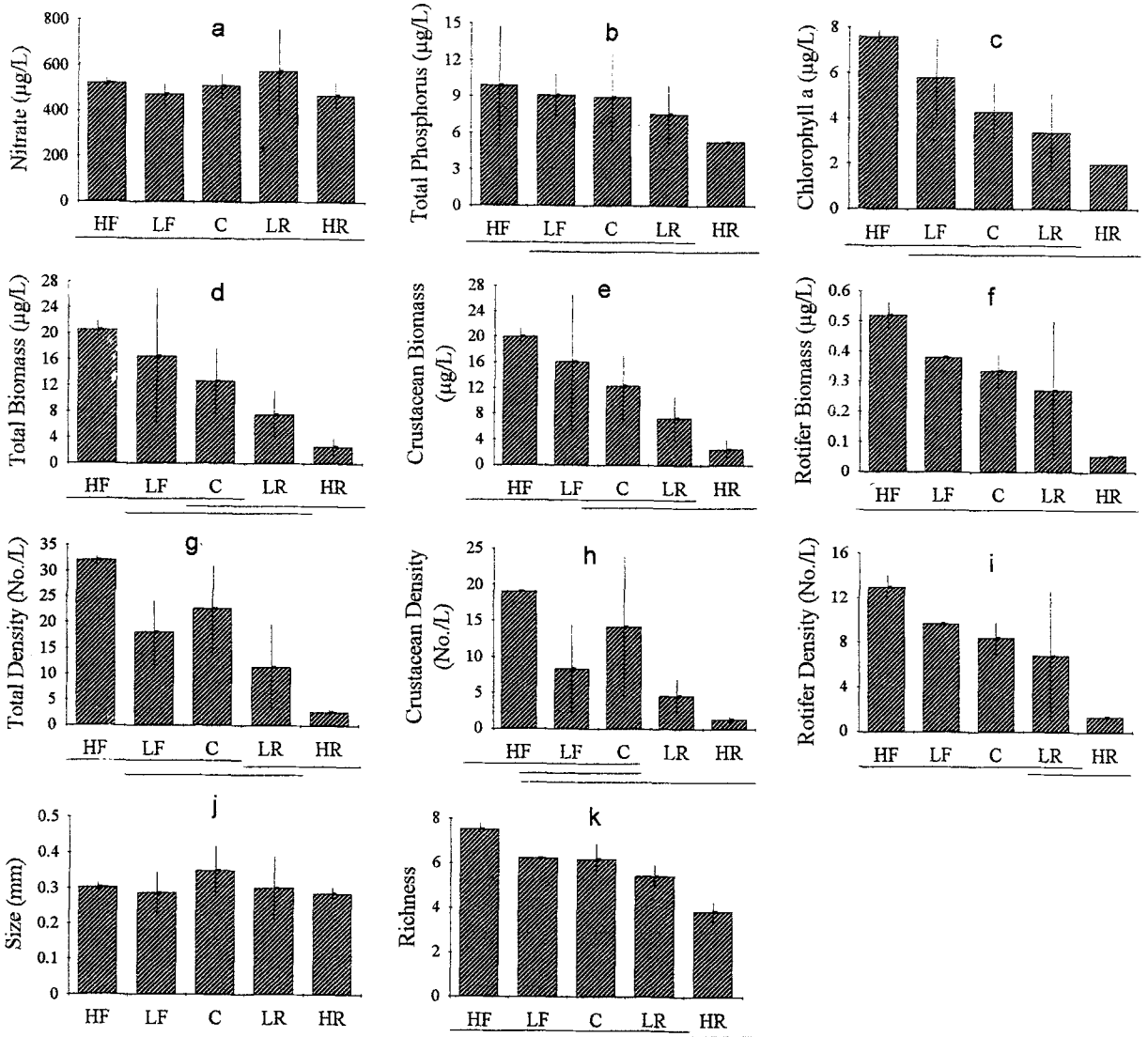

Fig. 3. Treatment means for all sampling dates for nitrate ($n = 3$), total phosphorus and chlorophyll *a* ($n = 8$), zooplankton biomass and density ($n = 4$), zooplankton size and species richness ($n = 4$). Vertical lines are standard deviations. Treatment codes are C = control, LF = low fish, HF = high fish, LR = low removal and HR = high removal. The lines below the graphs are the results of Waller-Duncan tests ($\alpha = 0.05$). Means of treatments underlined by the same line are not significantly different. Note: (h) LF is statistically different from HF and C, and C is statistically different from LF, LR and HR.

Laboratory analysis

The total phosphorus content of unfiltered water from the mesocosms was analyzed using the isobutanol extraction method (Wetzel & Likens, 1991). Absorbance was measured with a Spectronic™ 21 DV spectrophotometer. The water samples were preserved in a chest freezer at − 20 °C in the laboratory at the Huntington Wildlife Forest, and the analysis were performed within 2 days of collection. Nitrate analyses were made by reducing the nitrate to nitrite with a Cadmiun-reduction column (APHA 1985; Wetzel & Likens, 1991). The water samples were filtered through 0.45 µm fiberglass Whatman™ filters and frozen for 1 or 2 days at −20 °C before the NO_3-N and NO_2-N spectrophotometric determinations were made. One

litre of water was filtered through a 0.45 μm fiberglass Whatman™ filter for chl *a* determination. The filters were folded and wrapped in absorbent paper, stored in a darkened desiccator and frozen. Extraction with acetone and spectrophotometric determination of chl *a* followed Wetzel & Likens (1991); the calculations were made according to Lorenzen's Monochromatic Method (1967).

Zooplankton were identified (Edmondson, 1959; Balcer *et al.*, 1984; Pennak, 1989), counted and measured using the computer program WSAM (Mills & Confer, 1986) on a MacIntosh computer at the Cornell University Biological Field Station, Bridgeport, New York. Samples were counted for every other week of sampling from August 15, 1991 to September 24, 1991.

Statistical analysis

Repeated Measures Analysis (RM) using individual mesocosms as experimental units (EU) was used to investigate the effects of treatments over time. Response curves describing these effects were generated from orthogonal polynomials using the method of Meredith & Stehman (1991). The response curves were compared for significant differences across time and if a response curve was not found to be significantly different, a second test was used to determine whether the overall trend was different from zero when averaged over all treatments.

Repeated Measures (RM) Analysis (SAS, PROC GLM, Sas Institute 1990) was applied to chl *a*, TP and nitrate data for the whole study period, and to zooplankton biomass and density data for all but the first date and was also applied to zooplankton size and species richness data for all dates. The rarefaction method (Simberloff, 1972) was used to estimate species richness. In addition, the last date of zooplankton biomass was analyzed using ANOVA to test for cumulative differences among treatments. A Waller-Duncan test was used to discriminate among treatment means for the overall main effects in the RM analysis and in the ANOVA. Finally, a multivariate cluster analysis (SAS, PROC CLUSTER) for the biomass of the main eight zooplankton groups was used to describe the response of zooplankton to treatment effects. One cluster involving data from August 27, September 11 and September 24, 1991, was used to explore the way in which treatments affected zooplankton biomass over time. A second cluster involving average zooplankton species biomass per treatment was used to investigate the separation of treatments in the overall experiment.

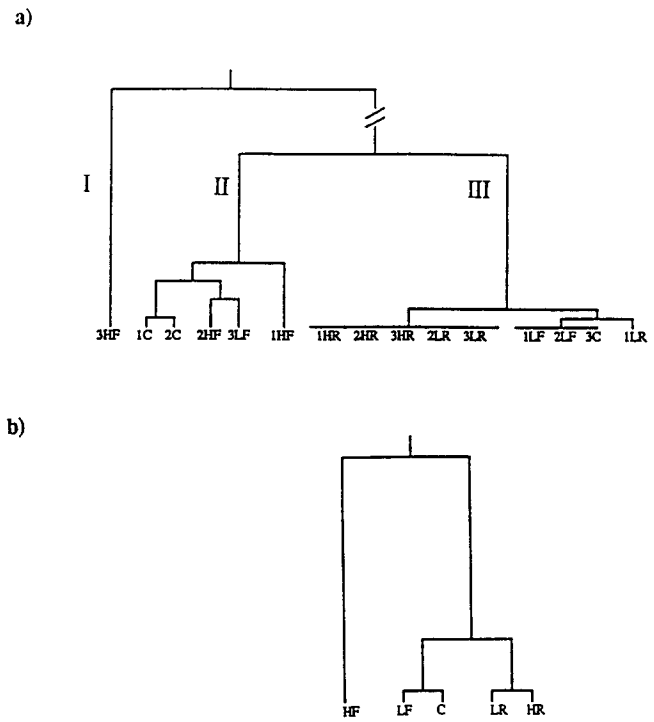

Fig. 4. (a) Cluster analysis of zooplankton biomass over time for three dates. The number in front of the treatment indicates date 1 = August 27, date 2 = September 11 and date 3 = September 24. (b) Cluster analysis on the zooplankton biomass average of the three dates above. The clusters separate the biomasses of the six main zooplankton groups plus nauplii and rotifers. The capital letters indicate treatments: C = control, HF = high fish, LF = low fish, HR = high removal and LR = low removal.

Phosphorus bioenergetic model

Models were used to estimate phosphorus content and excretion rates for zooplankton and fish. Zooplankton phosphorus content and excretion rates were calculated using the taxon-specific P content and release values reported by Taylor & Lean (1991). Zooplankton community P release estimates were obtained by multiplying species population densities by individual content and release values and adding the products to calculate mean values per treatment per litre per day.

To calculate fish excretion rates, a model was implemented using the software of Hewett & Johnson (1992). This model incorporated the feeding parameters that were appropriate for mesocosm fish growing from 1.87 g to 3.28 g (field data) over a 42-day peri-

od. Stomach contents from fish recovered from the mesocosms at the end of the experiment revealed that 25% of the diet was zooplankton and that 75% were organisms from the benthos or periphyton growing on the enclosure walls. The model was adjusted for the water temperature in the mesocosms during the 42-day period and for the caloric values of the prey. The data from the redbreast sunfish was incorporated into the standard configuration file for bluegill physiology (Kitchell *et al.*, 1974) in Hewett & Johnson's software and P consumption, growth, and egestion were calculated. The Hewett & Johnson Bioenergetics Model yields results as calories g^{-1} of predator d^{-1}. To transform the energy units into P units, the calories were transformed into weight units. The P content of fish was calculated by converting wet weight to dry weight and was estimated 2% of dry weight (McQueen *et al.*, 1992; Kraft, 1992). P excretion (μg P l^{-1} d^{-1}) was calculated as:

$$P_{\text{excretion}} = P_{\text{consumption}} - P_{\text{growth}} - P_{\text{egestion}}$$

The P excretion value obtained from this equation was multiplied by average fish wet weight and population size to give the total daily excretion of the fish population.

Zooplankton grazing rates

We estimated zooplankton clearance rates using published equations developed from *in situ* studies of zooplankton herbivory. Models developed from laboratory studies (e.g Peters & Downing, 1984) tend to underestimate zooplankton grazing (Knoechel & Holtby, 1986). Zooplankton grazing rate is positively related to body size and negatively related to food level. We did not have estimates of edible phytoplankton biomass and rotifer body size and species to include in clearance rate calculations. Therefore, we 'bounded' our calculations by estimating a low and a high clearance rate. The low clearance rate calculations included the effects of food level and assumed that all rotifers were small *Keratella*. For the high clearance rate calculations we ignored food level and assumed that all rotifers were large *Keratella*.

Except for rotifers, all equations to estimate grazing rate were of the form:

$$\log_{10}(\text{CR}) = a \log_{10}(\text{BL}) + b \log_{10}(\text{ED}) + c,$$

where: CR = clearance rate (ml d^{-1}), BL = body length (mm), ED = edible algal biovolume (μg l^{-1}), a, b, and c = coefficients and intercept of the least-squares regression between $\log_{10}$ (body length), $\log_{10}$ (algal biovolume) and $\log_{10}$ (clearance rate).

For *Leptodiaptomus* spp. we could not find a function for clearance rate that included food level, therefore, we used values for just a and c from Chow-Fraser (1986). To calculate a low estimate of clearance rate for *Bosmina* and *Diaphanosoma*, we used a general cladoceran grazing rate function (Chow-Fraser & Knoechel, 1985) that included a term for edible algal biovolume (ED). We estimated edible algal biovolume from chl a using the equation, ED = 250 × chl a, that was based on the following conversion factors (Reynolds, 1984): chl a = 0.02 × dry mass, carbon = 0.5 × dry mass, wet mass = 0.1 × dry mass. To calculate a high estimate of clearance rate for *Bosmina* and *Diaphanosoma*, we used species-specific values for a and c provided by Chow-Fraser & Knoechel (1985) and P. Chow-Fraser (McMaster University, Hamilton, Ont., unpublished data).

For rotifers our data provided only numbers per litre for all species combined. For a low estimate of clearance rate we multiplied rotifer density by Bogdan *et al.* (1980) average measurements for small *Keratella* feeding on *Chlamydomonas*. For a high estimate of feeding rate we used Bogdan *et al.* (1980) average values for large *Keratella*. The carnivorous zooplankters, *Epischura*, *Cyclops*, and *Mesocyclops* were assumed to have a clearance rate of zero. Community clearance rate was calculated by summing the clearance rates for each species (ml l^{-1} d^{-1}) and dividing by 1000 (ml) to give the proportion of the enclosures cleared per day.

Results

Chemical and biological trends through time

Time trends in dissolved oxygen and temperature trends were similar in all enclosures and in the lake (ANOVA, $P > 0.05$) (Fig. 2). The temperature remained mostly stable at 21 °C from the beginning of the experiment until September 17, 1992. Thereafter, the temperature decreased to 13 °C by October 2, 1991. Dissolved oxygen levels at the start of the experiment were 6.5–7.0 mg l^{-1} (80% oxygen saturation) and gradually increased to 8.5–9.0 mg l^{-1} (90% oxygen saturation).

The Repeated Measures analysis showed significant differences over time in the linear response curves

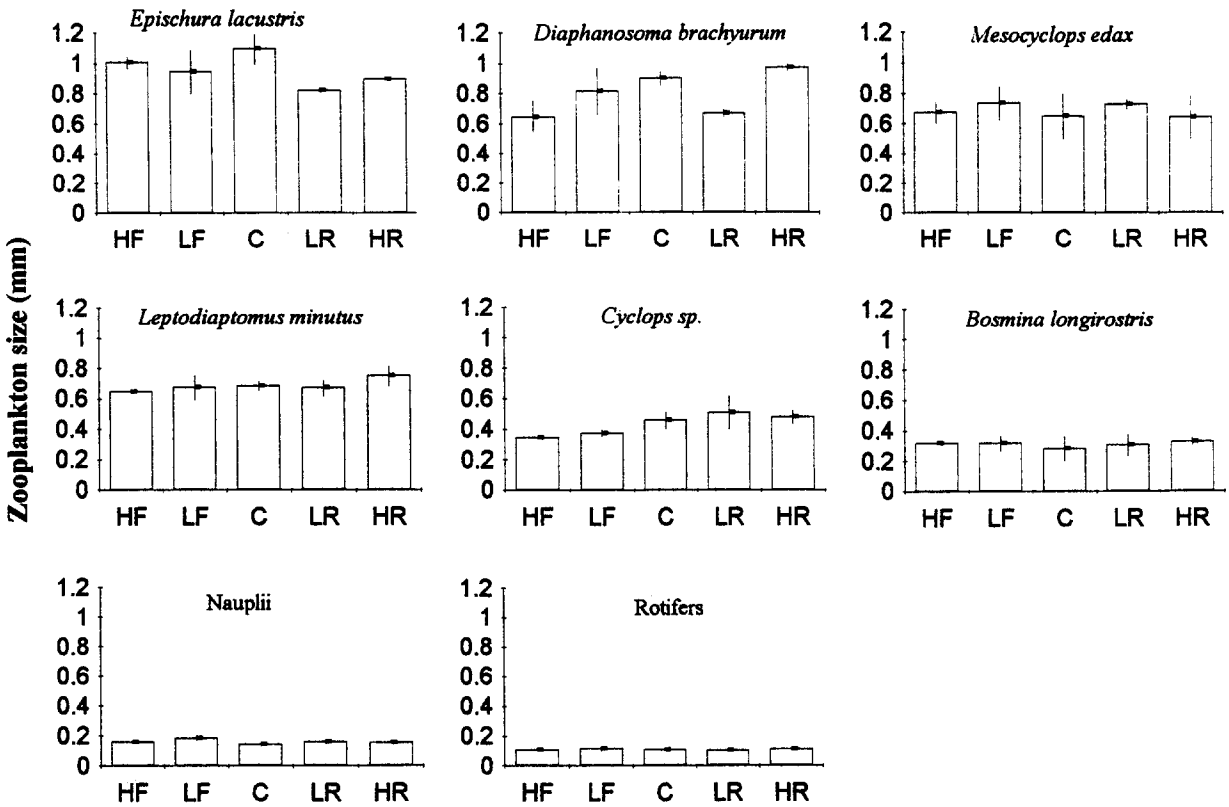

Fig. 5. Mean size per treatment ($n=2$) for the main zooplankton groups. Treatment codes are C = control, LF = low fish, HF = high fish, LR = low removal and HR = high removal.

Table 1. Repeated Measures Analysis results. The model indicates the polynomial that best fits the data ($p<0.05$). The trend indicates the data tendency to fit a certain polynomial ($p<0.05$). The main effects average the treatments over time ($p<0.05$).

	Model	Trend	Main effects
Total P	linear	–	present
Nitrogen	–	linear quadratic	present
Chlorophyll *a*	linear	–	present
Zooplankton			
Total Biomass	linear	–	present
Crustacean Biomass	linear	–	present
Non-crustacean Biomass	–	quadratic	present
Total Density	–	quadratic	present
Crustacean Density	linear	–	present
Non-crustacean Density	–	quadratic	present
Size	cubic	–	present
Richness	linear	–	present

of the treatments ($p<0.1$) (Table 1) for TP ($p=0.056$), chl *a* ($p=0.04$), total zooplankton biomass ($p=0.01$), crustacean biomass ($p=0.01$) and density ($p=0.01$) and zooplankton richness ($p=0.067$). Therefore, significant interactions between treatments and time were present, i.e., time was an important factor in treatment evolution. Zooplankton size had significantly different cubic response curves over time for the different treatments ($p=0.06$). Nitrogen, rotifer biomass, rotifer density and total zooplankton density failed to fit any treatment × model time interaction ($p>0.1$), but showed overall curve trends that were significantly different from zero ($p<0.05$). The treatments effect averaged over time (Table 1), or main effects independent of the time factor, were statistically significant ($p<0.01$) for all of the variables investigated.

In most cases, the Waller-Duncan test discriminated the means of the two more extreme treatments, HF and HR (Fig. 3b–e, g–i, k). For nitrate and non-crustacean biomass (Fig. 3a, f) the test failed to discriminate among treatment means. The Waller-Duncan

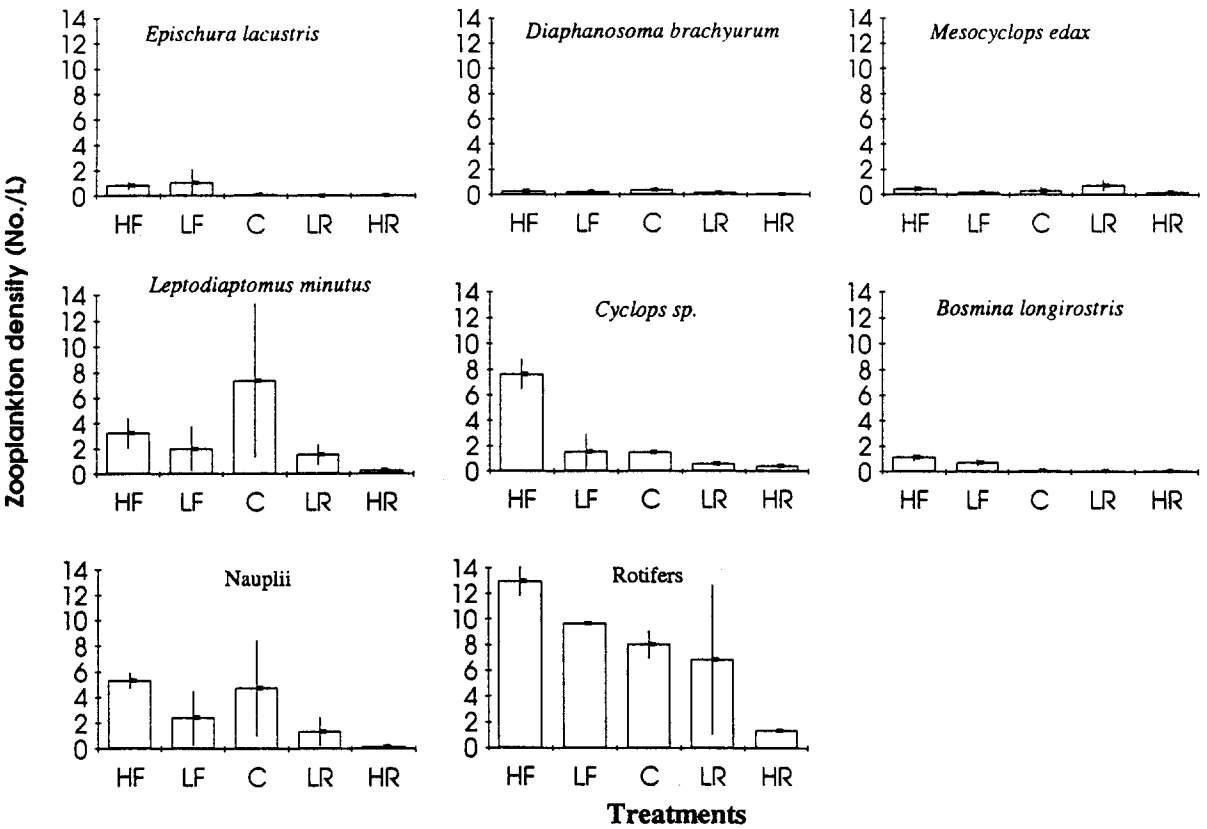

Fig. 6. Mean density per treatment ($n = 2$) for the main zooplankton groups. Treatment codes are C = control, LF = low fish, HF = high fish, LR = low removal and HR = high removal.

test was not applied to the zooplankton size treatment means (Fig. 3j) because the F values were too small.

Treatment means

The treatment means followed a gradient for most of the variables studied from the highest mean values in the HF treatment, followed by LF, Control, LR, and HR (Fig. 3b–f, i, k). The exceptions were nitrate and zooplankton size, which showed little variability, and total density and crustacean density which had higher mean values for the Control than for LF.

An ANOVA using the August 24, 1991 data for zooplankton biomass (Table 2) showed that the highest means were found in the fish treatments, which had almost equal biomass and were statistically similar (Waller-Duncan test).

Cluster Analysis of zooplankton biomass for three dates (Augustus 27: date 1; September 11: date 2; September 24: date 3) separated three major groups (I, II, III) (Fig. 4a). The first group comprised only the 3-HF treatment which was separated from the rest due to increased biomasses of *Epischura lacustris*. The second group linked two of the early controls and three of the fish treatments because the treatments on those dates had similar species biomass. 1-HF appeared as a subgroup because the presence of *Mesocyclops edax* increased the biomasses. The third group joined the treatments (HR and LR) and the dates (1-LF, 2-LF and

Table 2. Mean, SD and Waller-Duncan test for Sept. 24, 1991 zooplankton biomass ($\mu g\ l^{-1}$)

Treatments	Mean*	SD
HF	25.26a	2.17
LF	25.06a	18.98
C	3.67b	4.87
LR	1.29b	1.13
HR	0.45b	0.44

* Means with the same letter are not significantly different at $\alpha = 0.05$

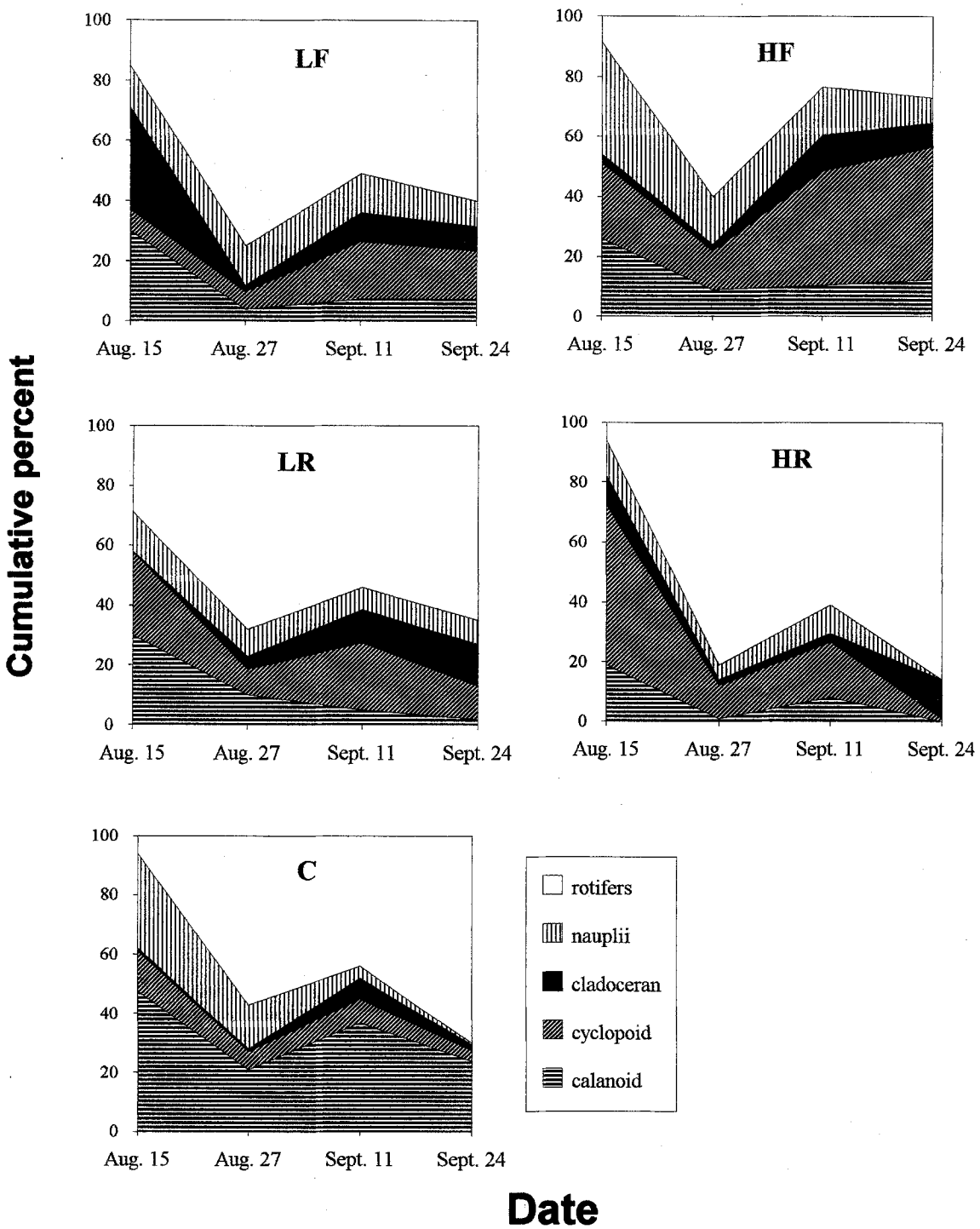

Fig. 7. Treatment mean ($n = 2$) percentage of zooplankton density for each zooplankton group present in the treatments.

Table 3. P released by the zooplankton populations (pM l^{-1} h^{-1}) averaged for the replicate mesocosms ($n = 2$), over time ($n = 4$). The values are dependent on zooplankton density. Estimates are based on P release rates for zooplankton groups reported by Taylor and Lean (1991).

Group	P release Control	HF	LF	LR	HR
Epischura	0.42	3.40	4.24	0.11	0.05
Mesocyclops	0.40	0.52	0.23	0.88	0.23
Diaptomus	30.22	13.28	8.20	9.45	1.10
Cyclops	1.73	8.86	1.80	0.69	0.49
Diaphanosoma	14.91	11.87	9.61	5.53	1.26
Bosmina	0.35	4.03	2.56	0.28	0.13
Other Cladocerans	0.87	3.47	4.00	1.73	2.30
Nauplii	2.92	3.28	1.48	0.83	0.10
Rotifers	1.61	2.59	1.93	1.37	0.27

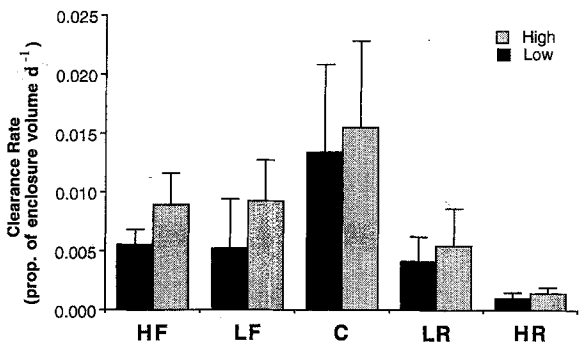

Fig. 8. Zooplankton grazing rates. Estimates are 'bounded' by calculations of low and high clearance rates. The low clearance rate calculations included the effects of food level and assumed that all rotifers were small *Keratella*. For the high clearance rate calculations we ignored food level and assumed that all rotifers were large *Keratella*.

3-C) with the lowest biomass per species. 1-LR was separated from the other removal treatments because, *Cyclops spp.*, *Mesocyclops edax* and *Diaphanosoma brachyurum* were more abundant than in the other removal treatments. 1-LF and 2-LF had lower species biomass than 3-LF, and 3-C was the last date of the decline in biomass of the Control, therefore, they were grouped together.

A second cluster analysis based on the average biomass of the eight species of zooplankton (Fig. 4b) separated the HF treatments from the rest, grouped the Control and LF, and both removal treatments.

Zooplankton species size and density

In general, mean sizes of the zooplankton species (Fig. 5) were slightly different among treatments. Large calanoids (like *E. lacustris*) attained their largest size in the Controls. *D. brachyurum* was largest in Controls and HR treatments. The largest Cyclops spp. were found in the no-fish treatments. *M. edax*, *L. minutus*, *B. longirostris*, nauplii and rotifers showed no treatment effects.

Altogether, there was an abundance of small taxa and a higher abundance of copepods than of cladocerans for all treatments (Fig. 6). *Epischura lacustris* was most dense in the fish treatments. *Diaphanosoma brachyurum* was always found at low densities. *Mesocyclops edax* was most abundant in the LR mesocosms. *Leptodiaptomus minutus* was most abundant in the Controls followed by the HF treatments and was rare in the HR treatment. *Cyclops spp.* was most abundant in HF enclosures and was rare in the LR and HR treatments. *Bosmina longirostris* was most abundant in the fish treatments and was almost non-existent in the other treatment samples. Copepod nauplii were most abundant in the HF and Control treatments, and were rare in the HR treatments. Rotifers had the highest overall densities and followed the treatment pattern described for TP and chl *a* (Fig. 3).

Zooplankton community organization

The zooplankton community composition (Fig. 7) changed in response to the two major disturbances: fish additions and zooplankton removals. The Control treatment showed an increase in rotifers and a relatively large population of *Leptodiaptomus minutus*. The LF and LR treatments also showed increased rotifers, but the calanoid copepods decreased as cyclopoid copepods increased. Most cyclopoids were small and could pass through the removal net or avoid predation. The HF and HR treatments were more extreme cases of the pattern observed for the moderate treatments. The HF treatment had a crustacean dominance that increased over time, with cyclopoids dominating over calanoids and cladocerans increasing in numbers. The HR treatment shifted towards a dominance by rotifers, with a continuous decrease of the copepod population and a final increase in small cladocerans.

Table 4. Zooplankton phosphorus content and excretion rates, fish phosphorus excretion, and the total phosphorus excretion of fish and zooplankton per treatment ($\mu g\ P\ l^{-1}\ d^{-1}$). Zooplankton P content and release rates are based on Taylor and Lean (1991). Fish P excretion rates are based on calculations using Hewett and Johnson's model (1992).

Treatment	Zooplankton		Fish	Total
	P content	P excretion	P excretion	P excretion
Control	60.38×10^{-2}	3.98×10^{-2}		3.98×10^{-2}
HF	65.22×10^{-2}	3.82×10^{-2}	10.69×10^{-2}	14.50×10^{-2}
LF	40.50×10^{-2}	2.53×10^{-2}	3.56×10^{-2}	6.10×10^{-2}
LR	32.91×10^{-2}	1.55×10^{-2}		1.55×10^{-2}
HR	6.47×10^{-2}	0.44×10^{-2}		0.44×10^{-2}

Zooplankton grazing rates

Zooplankton grazing rates were calculated by estimating a low and a high clearance rate. The low clearance rate calculations included the effects of food level and assumed that all rotifers were small *Keratella*. For the high clearance rate calculations we ignored food level and assumed that all rotifers were large *Keratella*. Both sets of calculations yielded clearance rates that were never higher than 2% of the enclosure volume d^{-1} (Fig. 8). This low clearance rate was due to the dominance of *Leptodiaptomus minutus*, whose clearance rate is very low, and to the low densities of better grazers (i.e., cladocerans).

Predicted phosphorus concentrations and release rates

Estimated phosphorus release by zooplankton in each treatment was influenced by the density of the animals and by their size (Table 3). Important P contributions were made by the less numerous but larger cladocerans. Zooplankton P content (Table 4) decreased for each treatment as the zooplankton density decreased. The HF treatment had the highest zooplankton density and the highest P content, followed by the Control, LF, LR, and HR treatments. Zooplankton estimated P release was similar for the Control and the HF treatments and lower for the other treatments. The calculations for estimated fish P excretion were within the ranges reported by Kraft (1992) on a per fish basis. The 18 fish from the HF treatment added more than two and a half times as much P as the zooplankton in the Control (Table 4), and the HF treatment had the highest P excretion rates, followed by LF, C, LR, and HR treatments (Fig. 9a, b).

Discussion

Our experiment was designed to assess the relative impacts on algal biomass of: (1) nutrient inputs from fish excretion, and (2) grazer removal from planktivory. Our expectation was that both the fish addition treatments and the grazer removal treatments would stimulate algal growth. For the fish addition treatments we expected that algal production would be increased by the confounded impacts of increased nutrient additions due to fish excretion and reduced grazer abundance due to fish consumption. For the zooplankton removal treatments we expected that algal stimulation would result from grazer removal.

The general treatment means (Fig. 3) showed strong, statistically significant trends (HF > LF > C > LR > HR) for: total phosphorus, chlorophyll *a*, total zooplankton biomass, crustacean zooplankton biomass, and non-crustacean zooplankton biomass. As expected, the control treatments yielded intermediate results and featured taxa with the largest body sizes (Fig. 5) and the largest densities of moderately large sized (i.e., *Leptodiaptomus minutus*) species (Fig. 6).

Surprisingly, both treatments (LF and HF) involving the addition of fish showed increased concentrations of total phosphorus (Mazumder *et al.*, 1988; Vanni & Findlay, 1990) and decreased densities of large bodied zooplankton (Lynch & Shapiro, 1981; Vanni, 1987). These results are not in agreement with those of Nakashima & Legget (1980), who found fish excretion

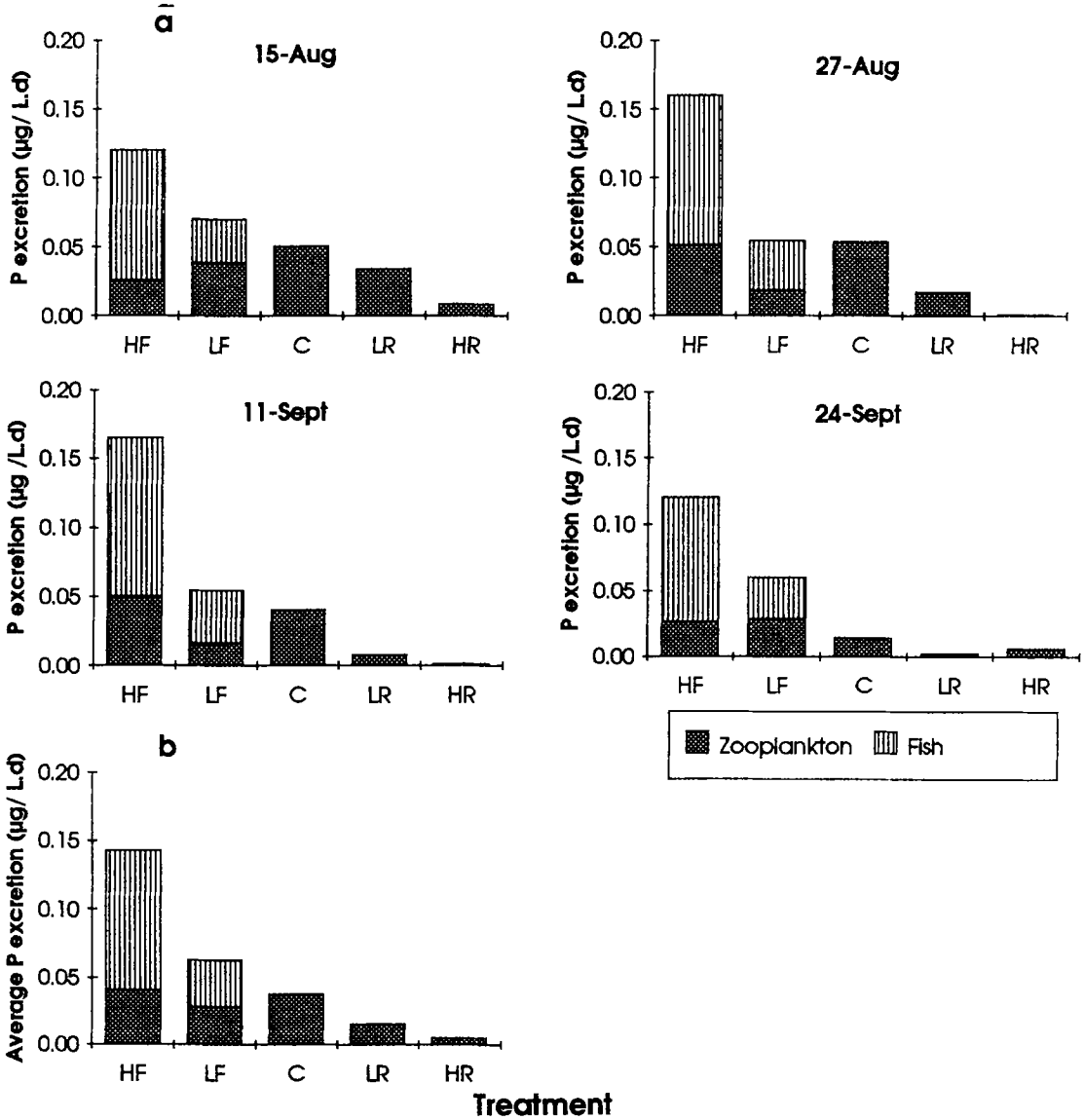

Fig. 9. (a) Phosphorus excretion by fish and zooplankton (μg P l^{-1} d^{-1}) for August 15, 1991, August 27, September 11, and September 24. (b) Mean combined P excretion by fish and zooplankton (μg P l^{-1} d^{-1}) per treatment over time. The standard deviations are based on dates as replicates.

to be negligible as a source of P for primary producers. In our experiment, the addition of fish also greatly enhanced the total community rate of phosphorus excretion. The implications are that both bottom-up and top-down factors were associated with increased concentrations of chlorophyll *a* and increased densities of small bodied cyclopoid copepods. Our data also suggest that chlorophyll *a* increased because the fish imported nutrients by feeding on the sidewalls and sediment of the mesocosms and excreting in the water column. This nutrient import enhanced the phosphorus availability for algal growth. Also, small bodied zooplankton proliferated because increased nutrient availability stimulated the algal community, and because fish predation removed large bodied zooplankton and reduced zooplankton competition.

Because increased TP levels in the fish treatments were not noted in the other mesocosms, it seems likely that abiotic factors were not implicated. It could be argued, however, that fish behavior involving sedi-

ment bioturbation, may have enhanced P availability to algae. Although this possibility can not be discarded, other studies support the view that fish excretion can be a major cause of increased P availability to algae (Vanni & Findlay, 1990). In addition, fish bioturbation is usually related to sediment suspension and, because the substrate in the mesocosms was sand, solids suspension was probably very low (Meijer *et al.*, 1990).

Surprisingly, all of the treatments (LR and HR) that involved the removal of zooplankton, resulted in significant decreases in: total phosphorus, chlorophyll *a*, and zooplankton biomass. All of these responses appeared to be driven by the bottom-up effects that resulted from the loss of nutrients associated with the removal of zooplankton biomass from each LR and HR mesocosm (i.e., zooplankton P content and P excretion). Because fish were unavailable, nutrient transport from outside the water column was greatly diminished and continued zooplankton removal resulted in very small populations of intermediate sized cyclopoids, mesocyclopoids and diaptomids which were incapable of contributing much to the rates of total phosphorus turnover. The result was grazing rates that were very low and algal populations that failed to develop because nutrients were unavailable (McCauley & Briand, 1979). These results are in conflict with those published by other authors (Hamilton & Taylor, 1987; McCauley & Kalff, 1987), who found that turnover rates did not decrease with removal of zooplankton, and who speculated that protozoan P cycling was more important than that of metazoans. Our data suggest that in very oligotrophic systems, nutrient 'availability' is of paramount importance.

Overall our experiments suggest that in oligotrophic systems (TP 6–10 $\mu g\ l^{-1}$), fish populations ranging from 10 to 30 kg ha^{-1} can have strong bottom-up impacts on algal communities. Part of the effect is due to increased nutrient turnover from fish excretion, but a more important portion is due to fish induced nutrient import from littoral regions through feeding and excretion patterns. Zooplankton grazing rates certainly had some impact on phytoplankton but, because daily clearance rates were <2% of the enclosure volume, fish and zooplankton induced nutrient increases appear to be more important for algal communities.

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