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Predation, enrichment, and phytoplankton community structure[1]

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Abstract

The significance of grazing and enrichment to the Pleasant Pond phytoplankton community was examined through a series of enclosure experiments. The addition of planktivorous fish led to the removal of large herbivores and to an order-of-magnitude increase in total phytoplankton biomass. This was a result of the appearance of several new algal species as well as the increase of most initial resident species. *Aphanizomenon flos-aquae* was an exception to this pattern. This filamentous blue-green attains its maximum density in the presence of large *Daphnia* by forming large, ungrazeable colonies; *Daphnia* may provide a service to *Aphanizomenon* by removing most potential algal competitors. The addition of phosphorus and nitrogen had no quantitative effect on total phytoplankton biomass either in the presence or absence of fish; changes in species composition did occur, several algae disappearing with enrichment. We summarize the varied responses of lakes to enrichment and suggest that the community-level effects of enrichment can only be understood in the context of a framework that considers initial nutrient status and the structure of planktivorous fish populations.

Our knowledge of factors affecting zooplankton populations has developed to the point where generalized models for the structure of zooplankton communities have begun to emerge (Dodson 1974; Lynch 1979). Given a description of the predators found in a body of water, these models predict which zooplankton species will be excluded from the community. Since planktonic herbivores may have a significant impact on the composition of phytoplankton communities (Porter 1977), it logically follows that predators, through their effects on the herbivore community, may be important determinants of phytoplankton community structure (Hrbáček 1962; Losos and Heteša 1973).

The significance of nutrients in aquatic environments has also long been appreciated, and several hypotheses have been proposed to explain the dominance of certain phylogenetic lines of algae under particular nutrient regimes (Schelske and Stoermer 1971; Shapiro 1973; Schindler 1977). The chemical characteristics of a body of water may influence the structure of phytoplankton communities by direct mediation of competitive interactions or by several indirect routes determined by the connections among the members of the community (Lane and Levins 1977). Consequently, while the response of a phytoplankton community to enrichment is often dramatic and predictable, the mechanisms promoting the response are rarely known.

We examine here the phytoplankton community structure of Pleasant Pond, Minnesota. Since the factors responsible for the distribution of zooplankton species in this pond are known (Lynch 1978, 1979), any changes in the phytoplankton community associated with herbivore activity can ultimately be related to mechanisms regulating the zooplankton community. Here we report on the structure of the Pleasant Pond phytoplankton community in relation to predator-mediated changes in zooplankton community composition, the immediate effects of herbivory as indicated by the short term removal of zooplankton, and the results of longer term enclosure experiments to determine the relative effects of enrichment and predation on the phytoplankton community.

A complete description of the pond, its predators, and zooplankton community

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was given elsewhere (Lynch 1979). Vertebrate predators were absent in 1975, but in midsummer a dense population of the predacious midge, *Chaoborus americanus*, developed; by August all herbivorous zooplankton were removed except for rotifers and small numbers of *Daphnia pulex*. In April 1976 the pond was partitioned in half with a curtain. The south half (PP S) developed a dense population of fathead minnows (*Pimephales promelas*) which removed nearly all herbivorous cladocerans and copepods by July. The north half (PP N) contained few planktivorous fish and maintained dense populations of *D. pulex* and *Ceriodaphnia reticulata*.

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Methods

Surface phytoplankton was sampled weekly in the pond and all enclosures, fixed with Lugol's solution, and stored in amber bottles. Counts were made at 500× magnification (1,000× for bacteria) with a Wild inverted microscope; at least two diameter strips (2.2%) of a settled 5-ml subsample were counted. Although direct counts may greatly underestimate actual bacterial cell densities (compared to fluorescence techniques), we assume that they adequately portray relative differences between samples. Mean cell volumes were estimated for all species from measurements of 10–50 individuals approximated to common geometric shapes and used to convert counts to units of $\mu m^3 \cdot ml^{-1}$.

Phytoplankton productivity was measured periodically in PP N and PP S by the ^{14}C method. Standard 300-ml light bottles were inoculated at 0800 with 3 μCi $NaH^{14}CO_3$ and incubated at a depth of 0.5 m, always, fortuitously, on cloudless days. After 24 h the samples were fixed with Lugol's solution and stored in the dark at 4°C. Community primary production was immediately measured with a Picker proportional flow detector; subsamples were first concentrated on 0.45-μm Millipore filters, rinsed with distilled water, and air-dried under a heat lamp. In addition to the general problems associated with estimating productivity with bottled samples (Venrick et al. 1977), this analysis rests on other assumptions. First, we have assumed that 24-h incubations measure something close to net incorporation of carbon (growth); this is supported by several recent investigations (Eppley and Sharp 1975; Hobson et al. 1976; Paerl and Mackenzie 1977). Second, since samples were incubated at only one depth, we must assume that the carbon fixation measurements are proportional to integral production in the euphotic zone.

Several measurements were also made weekly throughout the study. Dissolved oxygen concentration and water temperature were determined with a YSI meter (model 54). pH was determined in the laboratory with a Beckman meter. Total phosphorus, soluble reactive phosphorus, NO_3-N + NO_2-N, and alkalinity were measured (Am. Public Health Assoc. 1971) as was ammonia (Chaney and Marbach 1962). Dissolved inorganic carbon was estimated from total alkalinity measures with the tables in Saunders et al. (1962).

The immediate effect of grazing activity on the phytoplankton community was determined with several short term zooplankton removal experiments run simultaneously on both sides of the pond in 1976. Zooplankton was removed by passing surface water through 64-μm Nitex netting; this procedure removes all cladocerans and adult copepods, but is not 100% efficient for nauplii and rotifers. An additional problem which arose in the early experiments was the removal of most of the filamentous *Aphanizomenon* by the straining procedure. Strained and unstrained samples were suspended in duplicate at a depth of 0.3 m in 3.5-liter Plexiglas cylinders, the ends of which were covered with 0.42-μm Duralon Millipore filters. The experiments lasted for 4 days (7 days in one case), following which samples were collected.

Two large-scale experiments were done in 1-m-diameter polyethylene bags suspended from the surface of the pond

Table 1. Bluegill sunfish added and recovered from enclosures in experiment 1. Enclosures 1 and 7 were controls. Since its one fish only lived for 5 days, enclosure 2 is treated as a control.

	Added—18 Jun		Recovered—2 Aug	
Enclosure	No.	Σ wet wt. (g)	No.	Σ wet wt. (g)
2	1	7.8		
8	1	7.8	1	21.7
9	2	15.8	2	32.4
3	2	25.0	2	41.1
11	4	50.0	4	45.7
6	5	83.0	5	87.0

to examine the longer term (4–8 week) response of the zooplankton and phytoplankton communities to predators and enrichment. In experiment 1 (15 June 1975) we examined the effects of varying densities of bluegill sunfish (*Lepomis macrochirus*) in enclosures; the experiment ran for 6 weeks. Fish densitites are recorded in Table 1; the response of the zooplankton community to these predators was detailed elsewhere (Lynch 1979).

Experiment 2, established in PP S on 29 May 1976 (before the appearance of fathead minnows), was designed to determine the influence of enrichment on plankton community composition in the presence and absence of fish. Six 1.8-m-deep bags received two small (60–75 mm) *L. macrochirus*, six were left without fish. Three levels of enrichment were used so that for bags with and without fish, two were left as controls, two received 10 $\mu g \cdot liter^{-1}$ of phosphorus and 110 of nitrogen per week, and two received 30 $\mu g \cdot liter^{-1}$ of phosphorus and 330 of nitrogen per week. Nutrients were added as concentrated solutions of KH_2PO_4 and NH_4NO_3, stirred into the bags after weekly samples had been taken. A P:N ratio of 1:11 was chosen because this was the ratio of available forms of these nutrients in the pond at the outset of the experiment. Two enclosures were disturbed by turtles during the experiment and are not considered here. Upon termination on 15 July only one fish was recovered from bags 2, 4, and 12; both fish were recovered from the other fish enclosures.

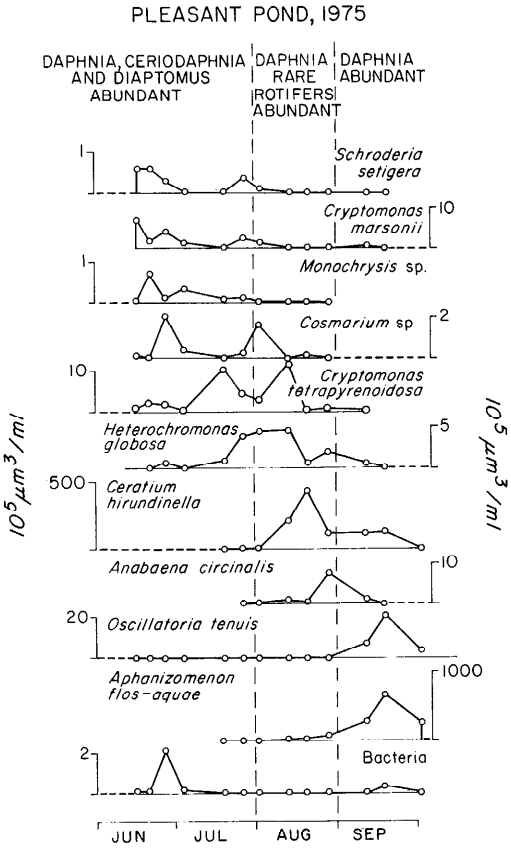

Fig. 1. Seasonal pattern in Pleasant Pond phytoplankton community, 1975, during periods characterized by different zooplankton species.

Phytoplankton community structure

1975—Pleasant Pond did not stratify thermally or chemically and remained well oxygenated throughout 1975. Levels of soluble reactive phosphorus (mean = 101 $\mu g \cdot liter^{-1}$, range = 48–174), NO_3-N + NO_2-N (mean = 37 $\mu g \cdot liter^{-1}$, range = 11–118), NH_3-N (mean = 165 $\mu g \cdot liter^{-1}$, range = 7–705), and dissolved inorganic carbon (mean = 22.3 $mg \cdot liter^{-1}$, range = 20.2–25.5) remained very high at least until mid-August (when chemical analyses were terminated). Such high concentrations strongly suggest that the pond phytoplankton was not limited by these

nutrients in 1975, and that seasonal alterations to the structure of the community resulted from factors other than competition for nitrogen, phosphorus, or carbon.

The seasonal pattern for the 1975 phytoplankton community is divided into three periods in Fig. 1 according to the relative abundances of different herbivores (*see* fig. 1: Lynch 1979). During June and July the zooplankton community consisted of large numbers of herbivorous *D. pulex*, *C. reticulata*, and *Diaptomus siciloides*, and all algal species were very rare. Those present were either small, delicate, and presumably easily digested (the green alga *Schroderia setigera* and several flagellates) or large with hard outer coverings (*Cosmarium* spp.).

All of these algae declined in August and were replaced by a dense bloom of *Ceratium hirundinella*. During this period, the herbivorous crustaceans (including *D. pulex*) were held to very low densities by *Chaoborus* predation (Lynch 1979), but rotifers were abundant.

As *Chaoborus* predation relaxed in September, the *D. pulex* population expanded, and a dense bloom of the filamentous blue-green *Aphanizomenon flos-aquae* developed. This bloom consisted of large colonies (up to 3 × 30 mm) which look very much like small grass blades and are not ingested (Lynch 1980). As the *Daphnia* population increased, the bloom developed to very high densities, while all other algae (except *Oscillatoria tenuis*) declined below detectable levels, until by mid-September the water was very clear except for the numerous *Aphanizomenon* colonies.

Pleasant Pond North, 1976—The pond stratified thermally in 1976. The bottom waters of PP N became anoxic in mid-July, and by August oxygen levels were very low at a depth of 1 m. As dense stands of macrophytes (*Callitriche* sp.) developed throughout the summer, the pH increased above 1975 levels (when it never exceeded 8.9), approaching 10.0 in late summer. Levels of nutrients in PP N were much lower than in 1975: mean soluble reactive phosphorus = 10 $\mu g \cdot liter^{-1}$ (range = 4–21), mean NO_3-N + NO_2-N = 9 $\mu g \cdot liter^{-1}$ (range = 4–14), mean NH_3-N = 27 $\mu g \cdot liter^{-1}$ (range = 0–52), and mean dissolved inorganic carbon = 19.4 $mg \cdot liter^{-1}$ (range = 16.3–24.6). In late summer total phosphorus declined to a very low level (12 $\mu g \cdot liter^{-1}$), but the high proportion of soluble reactive phosphorus (83%) reflects the small standing crop of phytoplankton at that time.

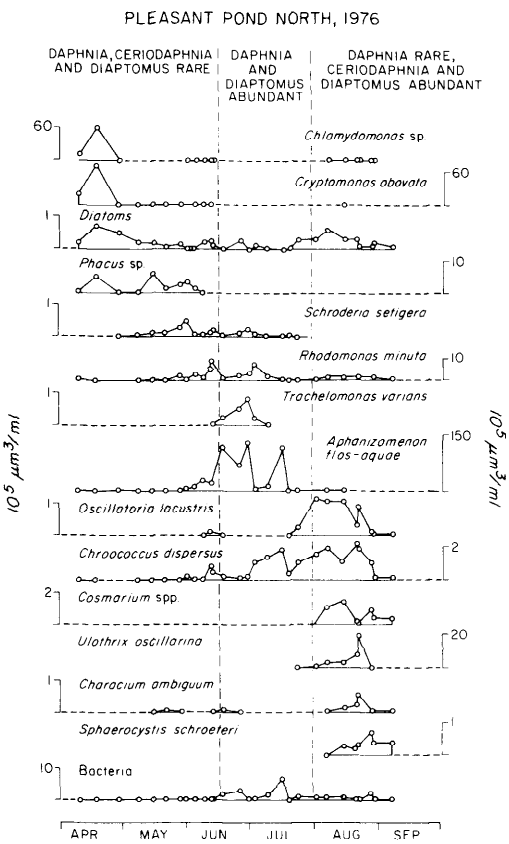

Fig. 2. Seasonal pattern in PP N phytoplankton community, 1976, during periods characterized by different zooplankton species.

Dense populations of flagellates (*Chlamydomonas* spp., *Cryptomonas obovata*, and *Phacus* sp.) which dominated the community in late spring were quickly reduced when *D. pulex* and *Diaptomus clavipes* increased (Fig. 2). In contrast to 1975 these flagellates, and the *Cosmarium* species, remained un-

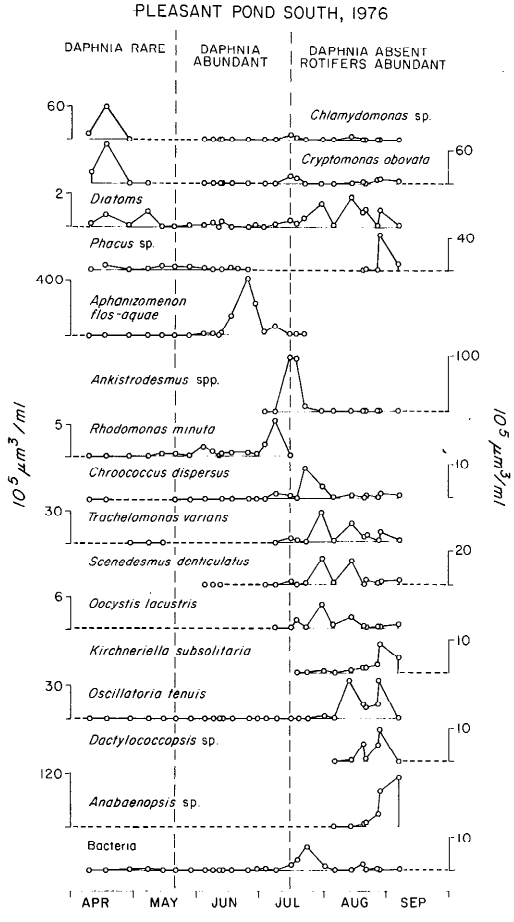

Fig. 3. Seasonal pattern in PP S phytoplankton community, 1976, during periods characterized by different zooplankton species.

detectable while the large herbivores were abundant in early summer. In addition to "grass-blade" *Aphanizomenon*, two other well protected species were most successful during this period: *Trachelomonas varians* (a hard-walled flagellate which is ingested but not digested: Lynch 1978) and *Chroococcus dispersus* (a gelatinous blue-green alga which is poorly digested: Lynch 1978).

As in 1975, the *Aphanizomenon* bloom increased and maintained a high density even while *Daphnia* was abundant. However, when the *Daphnia* population temporarily declined in late June (fig. 2: Lynch 1979), the bloom crashed, while *Rhodomonas minuta*, *T. varians* and bacteria increased. As the *Daphnia* population increased again in early July, these small algae declined and *Aphanizomenon* attained previous levels. The bloom finally crashed in mid-July while the sediments were anoxic, perhaps preventing the recruitment of new colonies from akinetes (Lynch 1980).

In August *Daphnia* was replaced by a smaller species, *C. reticulata*, and a variety of algal species increased—several delicate flagellates, diatoms, *Cosmarium* spp., the gelatinous green alga *Sphaerocystis schroeteri*, and the filamentous forms *Oscillatoria lacustris* and *Ulothrix oscillarina* (and its epiphyte *Characium ambiguum*). However, despite the appearance of many new species, total algal biomass in PP N remained very low for the remainder of the summer (for the month of August, mean phytoplankton biomass = 1.19×10^6 $\mu m^3 \cdot ml^{-1}$; range = $0.34–2.55 \times 10^6$).

Pleasant Pond South, 1976—The chemical environment of PP S diverged from that of PP N as summer progressed. The bottom waters of PP S went anoxic in mid-June, a month earlier than in PP N. Beginning in late June levels of dissolved nutrients were slightly higher in PP S than in PP N. At the end of the summer dissolved nutrients declined as they did in PP N; however, the total phosphorus concentration was three times that in PP N.

The pattern of development of the phytoplankton community in early summer was very similar to that in PP N (Fig. 3), and the *Aphanizomenon* bloom initially crashed at the same time on both sides of the curtain. However, while a secondary bloom had developed in PP N by 15 July, *Aphanizomenon* did not reappear in PP S. Instead, in the absence of *D. pulex* which had been eradicated by fathead minnows (Lynch 1979), a dense population of the edible green algae, *Ankistrodesmus* spp., developed. As virtually all herbivores, except rotifers and nauplii, were removed by fish, several other small phytoplankton species (the green algae *Scenedesmus denticulatus* and *Oocystis lacustris*, the blue-green *C. dispersus*

and the flagellate *T. varians*) and bacteria increased and replaced *Ankistrodesmus*. These were then succeeded by three delicate blue-greens, *O. tenuis, Dactylococcopsis* sp., and *Anabaenopsis* sp., and a green *Kirchneriella subsolitaria*. None of these species reached comparable levels in PP N, and *Dactylococcopsis* was never detected there.

By the end of summer total phytoplankton biomass in PP S (for August, mean phytoplankton biomass = 7.79×10^6 $\mu m^3 \cdot ml^{-1}$; range = $0.27–24.49 \times 10^6$) was nearly an order of magnitude greater than that in PP N, and the two halves of the pond contained completely different species assemblages. This increase in phytoplankton biomass in PP S was reflected by an increase in the community production rate. By 20 August the carbon fixation rate of the PP S community was more than an order of magnitude greater than that in PP N (Table 2).

Three facts suggest that the changes observed in PP S following the arrival of fish were not so much a result of an enhancement of nutrient conditions supported by fish excretion as of decreases in algal loss rates to grazers, i.e. that the PP N algae were at least as well nourished as those in PP S. In late summer (except for 20 August), the phytoplankton in PP N were incorporating carbon at higher specific rates [pg C fixed·(μm^3 phytoplankton)$^{-1}$·d^{-1}] than in PP S (Table 2). Also with the exception of 20 August, the ratio of phytoplankton biomass to total phosphorus in PP N was only about a third of that in PP S (Table 2). Finally, there were no systematic differences between species in growth rates estimated with track autoradiographic techniques in PP N and PP S (Lynch unpubl.).

Table 2. Phytoplankton community production (mg C fixed·liter^{-1}·d^{-1}), specific carbon fixation rates (10^{-4} pg C fixed·μm^3 phytoplankton^{-1}·d^{-1}), and ratios of phytoplankton biomass to total phosphorus (10^7 μm^3 phytoplankton·$\mu g \Sigma P^{-1}$) in Pleasant Pond North and South, 1976.

	Production		Fixation		Biomass : ΣP	
	PP N	PP S	PP N	PP S	PP N	PP S
14 May	0.05	0.06	0.7	1.0	2.5	2.1
27 May	0.06	0.10	1.2	2.2	1.2	1.0
12 Jun	1.40	0.86	4.8	3.9	2.4	3.1
25 Jun	1.15	0.87	1.5	0.2	6.4	21.4
9 Jul	0.74	0.93	3.5	1.4	1.9	5.8
23 Jul	0.23	0.92	3.7	2.7	0.6	2.2
20 Aug	0.11	1.66	0.4	5.0	21.2	8.5

Zooplankton removal experiments

The effect of herbivory is best interpreted as an alteration of the phytoplankton community rather than as a simple depression of algal species. In short term zooplankton removal experiments certain phytoplankton species often decrease in the absence of herbivores—results which can be interpreted either as a response to reduced competition when other algal species are depressed by grazing or as a direct response to nutrient regeneration and digestive activity by herbivores (Porter 1976).

Because the zooplankton removal experiments were run only in duplicate and sampled only once, our ability to resolve statistically significant differences between treatments is limited. At least four replicates should probably be run with experiments of this type to permit an analysis by standard parametric procedures, and running many more replicates once or twice would be worthwhile to provide some baseline information on the normality of data and homogeneity of variances for such data. For lack of recourse to any other statistical test for such a small sample size we have used the *t*-test based on range (p. 120: Snedecor and Cochran 1973). Although the adherence of our data to the assumptions of this model is not known, an examination of the limited data provides no strong indication that the variances of different treatments are unequal.

The results of these experiments are too voluminous to be included here. We restrict the following discussion to the general patterns and to those differences between treatments which were significant at the $P < 0.05$ level, keeping in mind that many additional biologically important differences between treatments have probably been overlooked;

detailed results of the PP N experiments are given by Lynch (1978). Almost all significant differences between treatments are $>0.5 \times 10^5$ $\mu m^3 \cdot ml^{-1}$.

In several experiments many algal species increased in the controls relative to the pond. Since the initial water for these experiments was taken from directly below the surface, we probably did not obtain a full complement of the large herbivores; when these were present, they were generally most abundant at a depth of about 1 m.

Two differences between treatments were consistent in most experiments. In all cases, a unicellular, gelatinous bluegreen (either *C. dispersus* or *Chroococcus minutus*) attained its highest density in chambers with zooplankton. Bacteria were lowest in chambers with zooplankton in all experiments in PP N and in two of four in PP S.

Pleasant Pond North—The density of zooplankton (primarily *D. pulex*) was very low in PP N during experiments 1 (8–12 June) and 2 (29 June–3 July). Even so, in experiment 1 three small flagellates (*Euglena* sp., *Heterochromonas globosa*, and *Ochromonas vallesiaca*) increased when grazers were removed. Except for *Heterochromonas*, these species were rare in the pond, and none was found in the controls. In the second experiment zooplankton had little effect on these flagellates. In both experiments, *S. setigera* maintained much higher densities in the presence of grazers ($P < 0.05$).

The *Daphnia* population was at a maximum during experiment 3 (18–22 July), and most phytoplankton species increased upon the removal of zooplankton; most significant was the appearance and dramatic increase of a tiny species of *Selenastrum* ($P < 0.01$).

During experiment 4 (19–26 August) *Daphnia* was scarce while *Ceriodaphnia* was at its maximum. With the exception of the gelatinous forms, all species of phytoplankton increased when herbivores were removed.

Pleasant Pond South—Daphnia was abundant during experiment 1 (8–12 June) in PP S, and several species (*Gomphonema* sp., *H. globosa*, *R. minuta*) increased upon the removal of grazers, although because of the wide ranges none of these differences was statistically significant. By the second experiment (29 June–3 July) *Daphnia* had declined because of fish predation, and there were no significant differences between treatments, except for the usual greater abundance of *C. minutus* and bacteria in the presence of herbivores.

Experiments 3 (18–22 July) and 4 (19–26 August) were done after all herbivorous crustaceans had been reduced to low numbers by fathead minnows. There was a very dense population ($\approx 6 \times 10^6$ individuals $\cdot m^{-1}$) of the rotifer *Conochiloides* sp. during experiment 3. Although most algal species were abundant at the outset of this experiment, with the exception of *C. minutus*, all of them increased in the absence of rotifers. Most significant was the increase in flagellates (*Chlamydomonas* spp., *H. globosa*, and *O. vallesiaca*) (all $P < 0.01$). Even rotifers were rare by treatment 4, and then there were no significant differences between treatments.

These results provide direct evidence that the grazing activity of *D. pulex* and *C. reticulata* frequently regulates the abundance of algal species in Pleasant Pond. When they are abundant, even rotifers may have a depressive effect on some algae (especially flagellates).

Enclosure experiments

The nature of the enclosure experiments is significantly different from that of the zooplankton removal experiments. Although treatments in the removal experiments reduced the abundance of all zooplankton species, the enclosure experiments reflect a more natural situation—while some zooplankton species were removed by predators, other less vulnerable species were able to increase.

Experiment 1: Effects of varying levels of fish predation—During this experiment both the pond and three enclosures containing no fish were dominated by the large herbivores, *D. pulex*, *D. siciloides*, and *C. reticulata* (fig. 3: Lynch 1979).

Table 3. Total phytoplankton biomass in 10^5 $\mu m^3 \cdot ml^{-1}$ (mean for last three sampling dates ± 1 SD) and proportion of total biomass of five most abundant species in enclosure experiment 1. Fish enclosures listed in order of increasing fish density.

No fish	
Pond	15.91±3.59
Cryptomonas tetrapyrenoidosa	0.50
Ceratium hirundinella	0.18
Heterochromonas globosa	0.14
Cryptomonas marsonii	0.07
Botrydiopsis arhiza	0.05
Enclosure 1	6.01±3.57
C. hirundinella	0.46
C. tetrapyrenoidosa	0.21
H. globosa	0.10
Closterium moniliferum	0.06
Cosmarium sexnotatum	0.04
Enclosure 7	4.97±2.00
C. tetrapyrenoidosa	0.43
C. moniliferum	0.31
C. hirundinella	0.11
C. sexnotatum	0.05
Aphanizomenon flos-aquae	0.02
Enclosure 2	8.77±1.23
Penium sp.	0.27
C. tetrapyrenoidosa	0.26
C. moniliferum	0.22
C. hirundinella	0.16
Cosmarium reniforme	0.02
Fish enclosures	
Enclosure 8	114.73±4.21
Oocystis lacustris	0.52
Scenedesmus armatus	0.20
Sphaerocystis schroeteri	0.08
Ankistrodesmus falcatus var. *mirabilis*	0.03
Schizochlamys planctonica	0.03
Enclosure 9	106.60±37.85
Anabaena circinalis	0.47
C. tetrapyrenoidosa	0.37
C. sexnotatum	0.04
Pediastrum boryanum	0.03
S. planctonica	0.02
Enclosure 3	83.41±36.18
O. lacustris	0.46
A. circinalis	0.09
C. sexnotatum	0.08
H. globosa	0.07
S. schroeteri	0.07
Enclosure 11	88.78±26.37
A. circinalis	0.64
C. tetrapyrenoidosa	0.30
A. flos-aquae	0.02
Treubaria crassispina	0.01
S. schroeteri	0.01
Enclosure 6	308.05±248.80
A. flos-aquae	0.72
H. globosa	0.08
A. circinalis	0.07
S. schroeteri	0.04
C. tetrapyrenoidosa	0.02

These species declined with increasing levels of fish predation and were replaced by smaller *Bosmina longirostris* and rotifers, resulting in dramatic alterations to the phytoplankton community. The mean total density of phytoplankton and the percentage composition of the dominant species for the last 3 weeks of the experiment are outlined for increasing densities of fish in Table 3. Table 4 compares the average densities of different phytoplankton species in all enclosures.

Both the fish-free enclosures and the pond were characterized by a sparse phytoplankton community dominated by delicate flagellates (*Cryptomonas marsonii*, *Cryptomonas tetrapyrenoidosa*, and *H. globosa*) and large, heavily armored species (the desmids *Cosmarium* spp., *Closterium moniliferum*, and *Penium* sp., and the dinoflagellate *C. hirundinella*). Except for *Closterium* and *Penium* all of these species increased in the presence of fish. However, their importance in fish enclosures was masked by an even greater increase of other species.

At even the lowest level of fish predation (enclosure 8), all *D. pulex* were removed, and total algal biomass increased over the control densities by more than an order of magnitude. This community was dominated by several species of green algae (*Ankistrodesmus falcatus* var. *mirabilis*, *Oocystis lacustris*, *Scenedesmus armatus*, *Schizochlamys planctonica*, and *S. schroeteri*), all barely detectable in the absence of fish.

Except for the highest level of fish predation (enclosure 6), further increases in the abundance of fish did not lead to any additional accumulation of algae. However, while the algal species dominating

Table 4. Biomass in 10^5 $\mu m^3 \cdot ml^{-1}$ (mean for last three sampling dates ± 1 SD) for major algal species in enclosure experiment 1. Fish enclosures listed in order of increasing fish density.

			Fish enclosures				
	Pond	Controls	8	9	3	11	6
			Chlorophycophyta				
Ankistrodesmus falcatus var. *mirabilis*			3.64±4.76	0.16±0.25	3.61±3.27		
Closteriopsis longissima			0.02±0.02		5.39±4.56		0.02±0.04
Closterium moniliferum		1.30±1.26					
Coelastrum microporum	0.01±0.01	0.01±0.01	3.48±2.28	1.50±1.77	1.18±1.28	0.10±0.01	1.84±2.27
Cosmarium sexnotatum	0.19±0.27	0.19±0.17	2.08±1.98	3.93±2.26	6.95±1.17	0.58±0.14	4.19±4.88
Oocystis lacustris		0.01±0.01	59.89±10.02	0.11±0.04	0.04±0.04	0.16±0.17	0.62±0.52
Pediastrum boryanum		0.07±0.08	0.14±0.15	2.75±3.39	0.20±0.25	0.23±0.27	4.17±3.46
Planktosphaeria gelatinosa			3.10±4.37	0.04±0.04			
Scenedesmus armatus	0.01±0.01		22.61±5.69	0.35±0.37	0.06±0.06	0.02±0.01	1.45±1.00
Schizochlamys planctonica			3.25±4.15	2.39±4.14		0.30±0.42	
Sphaerocystis schroeteri	0.02±0.03	0.01±0.02	8.61±9.21		5.50±5.72	0.66±0.79	11.03±12.68
Treubaria crassispina				0.04±0.05		0.90±1.14	0.74±0.58
			Chrysophycophyta				
Cryptomonas marsonii	1.18±1.63	0.04±0.03		0.10±0.14		0.08±0.11	
Cryptomonas tetrapyrenoidosa	7.89±3.56	1.88±1.50	1.15±1.64	39.65±34.68	0.15±0.26	26.83±18.95	7.26±5.79
Heterochromonas globosa	2.21±2.05	0.24±0.28	2.78±2.40	0.54±0.76	5.91±6.22	0.05±0.07	23.97±35.78
			Cyanochloronta				
Anabaena circinalis		0.01±0.02	0.05±0.07	50.03±8.63	7.42±7.83	56.55±11.02	21.14±20.76
Aphanizomenon flos-aquae	0.10±0.15	0.05±0.08	0.03±0.04	1.64±2.32		1.69±2.38	222.39±277.59
			Pyrrhophycophyta				
Ceratium hirundinella	2.89±4.09	1.56±2.09	0.41±0.58		3.58±6.20		

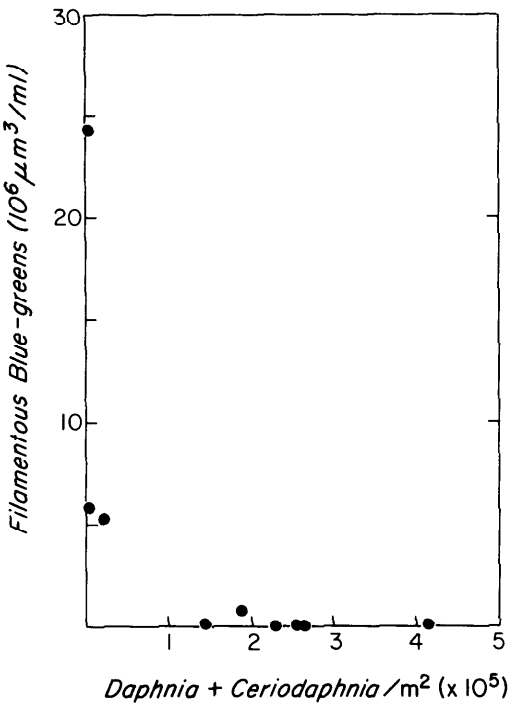

Fig. 4. Mean density of filamentous blue-greens vs. mean density of *Daphnia* and *Ceriodaphnia* for last three sampling dates in enclosures of experiment 1.

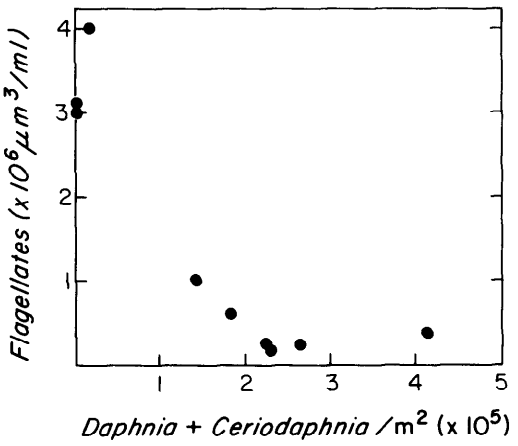

Fig. 5. Mean density of flagellates vs. mean density of *Daphnia* and *Ceriodaphnia* for last three sampling dates in enclosures of experiment 1.

the less heavily preyed upon enclosures (controls and number 8) remained fairly abundant at the higher levels of fish predation (enclosures 9, 3, 11, and 6), the community became increasingly dominated by filamentous blue-greens. *Anabaena circinalis* increased dramatically in all of these enclosures, and at the highest level of fish predation a dense bloom of *Aphanizomenon* developed. This bloom was very different from the "grass-blade" blooms noted in the pond; the colonies consisted of single filaments and many coexisting species were present.

The density of *Anabaena* and *Aphanizomenon* was inversely related to the abundance of *Daphnia* and *Ceriodaphnia* in the enclosures in such a way that there seemed to be a threshold density of these herbivores ($\approx 5 \times 10^4 \cdot m^{-2}$) above which the filamentous blue-greens could not withstand grazing (Fig. 4). The results are significantly different from those for the pond, where the densest blooms of "grass-blade" *Aphanizomenon* occurred in the presence of large *Daphnia*. The absence of "grass-blade" forms from all of these enclosures provides further evidence that the sediments may be the source of developing "grass-blade" colonies.

The abundance of delicate flagellates also appears to be inversely related to the density of *Daphnia* and *Ceriodaphnia* (Fig. 5). However, unlike the filamentous blue-greens, the flagellates did not disappear at high levels of these grazers but maintained a relatively constant density when *Daphnia* and *Ceriodaphnia* exceeded $\approx 2 \times 10^5 \cdot m^{-2}$.

There is little evidence that the changes in phytoplankton community composition in this experiment were related to changes in the nutrient regime. Total phosphorus concentrations did not vary markedly between enclosures, nor were there any noticeable trends in NH_3-N or NO_3-N + NO_2-N concentrations between treatments (Table 5). Soluble reactive phosphorus concentrations did drop significantly in fish enclosures, but it is possible that its turnover rate was greater there as a result of regeneration by both fish and the large numbers of small herbivores. Since the algal

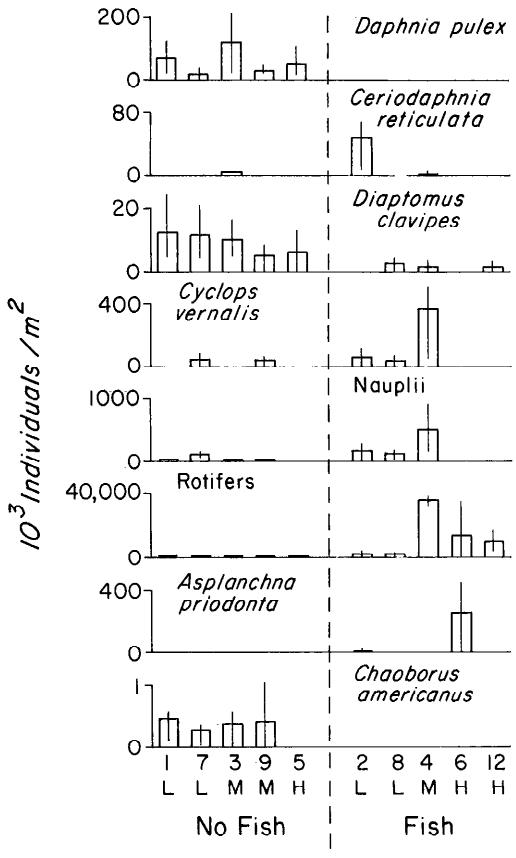

Fig. 6. Mean and range for abundance of zooplankton species for last three sampling dates in enclosure experiment 2. Different nutrient levels: L—low (controls); M—medium; H—high.

species dominating the control enclosures often increased in the presence of fish, this reduction in the concentration of available phosphorus does not seem to have been an important determinant of the outcome of this experiment.

Experiment 2: Enrichment, fish predation, and phytoplankton community composition—The significance of the results of this factorial experiment was estimated by an analysis of variance (p. 344: Snedecor and Cochran 1973) by treating the last three sampling dates as replicates and then approximating missing data points by least-squares analysis. Although the normality of the data cannot be verified statistically, large departures from normality were not apparent; Bartlett's test (p. 296: Snedecor and Cochran 1973) identified no large departures from homoscedasticity. Nonetheless, we do suggest that future experimentation of this type should be performed at least in triplicate to enhance the resolution of statistical procedures and to minimize the possibility of obtaining results without replication.

If the herbivores were food-limited in the fish-free controls in this experiment, enrichment did not alter their resource base in such a way as to allow them to increase. In the absence of fish, enrichment had no significant effect on the composition of enclosed zooplankton communities (Fig. 6). All enclosures without fish were dominated by *D. pulex*, with lesser numbers of *C. reticulata*, *D. clavipes*, *Cyclops vernalis*, nauplii, and rotifers.

These results strongly suggest that those algae that *Daphnia* was most dependent on as food were not limited by nitrogen or phosphorus in the absence of fish. Table 6 shows that neither community primary production nor specific production rates increased with enrichment of these enclosures. The fact that the ratio

Table 5. Chemical data for enclosure experiment 1 (mean for last three sampling dates). Fish enclosures listed in order of increasing fish density.

		Controls			Fish enclosures				
	Pond	1	7	2	8	9	3	11	6
Σ P ($\mu g \cdot liter^{-1}$)	160	100	119	134	100	121	106	92	128
PO_4-P ($\mu g \cdot liter^{-1}$)	84	23	38	43	4	3	4	2	9
NH_3-N ($\mu g \cdot liter^{-1}$)	26	26	31	38	2	7	20	48	0
NO_2-N + NO_3-N ($\mu g \cdot liter^{-1}$)	14	13	13	19	30	37	12	26	30
pH	8.02	8.00	8.10	8.00	8.18	9.00	8.26	8.41	8.28

of phytoplankton biomass to particulate phosphorus did not decrease with enrichment (Table 6) provides further evidence that the nutritional status of the algae with respect to phosphorous did not improve with the addition of nutrients.

As a consequence of the constant grazing pressure exerted by the large herbivores in all fish-free enclosures, total phytoplankton biomass remained relatively low at all levels of enrichment (except for enclosure 3: Table 7). However, several of the species which dominated at low nutrient levels (*C. moniliferum, Staurastrum paradoxum, R. minuta,* and *U. oscillarina*) did appear to decline at higher levels of enrichment, while *C. dispersus* and *Cosmarium* spp. increased (Tables 7 and 8).

The addition of fish resulted in the disappearance of *D. pulex* and a uniform reduction of *D. clavipes* at all levels of enrichment (Fig. 6), but the rest of the zooplankton community was sensitive to the addition of nutrients when fish were present. Rotifers, *C. vernalis,* and nauplii increased in fish enclosures above the densities attained without fish; but while rotifers increased dramatically with enrichment, *Cyclops* and nauplii disappeared at the highest nutrient level. Gut analyses indicated that *Lepomis* consumes both *Cyclops* and nauplii, but it does not seem likely that its effectiveness in removing them would increase with the level of enrichment. An alternate possibility is that the combination of high pH and ammonia concentrations in these enclosures (Table 6) was toxic to these zooplankton.

In the absence of *Daphnia,* total phytoplankton biomass increased about fivefold over that in fish-free enclosures, independent of the level of enrichment (Table 7). Several species increased significantly in the presence of fish, including species which dominated the fish-free enclosures (*Cosmarium* spp. and *S. paradoxum*), as well as *Cyclotella* sp. and *C. hirundinella* which were rare in the absence of fish. On the other hand, *C. dispersus* declined significantly in the presence of fish.

Table 6. Chemical data (mean for last two sampling dates) and carbon fixation rates for enclosure experiment 2; levels of significance indicated where $P < 0.25$.

	No fish					Fish							
	1 LN	7 LN	3 MN	9 MN	5 HN	2 LN	8 LN	4 MN	6 HN	12 HN	Predators	Nutrients	Interaction
Σ P ($\mu g \cdot liter^{-1}$)	34	24	60	44	58	29	44	61	108	108	0.025	0.01	0.05
PO_4-P ($\mu g \cdot liter^{-1}$)	2	4	5	3	5	2	3	18	14	10	0.01	0.01	0.025
NH_3-N ($\mu g \cdot liter^{-1}$)	40	23	56	58	76	16	59	96	111	70	0.25	0.10	
NO_2-N + NO_3-N ($\mu g \cdot liter^{-1}$)	6	22	76	34	196	6	8	36	186	134	0.25	0.01	
pH	9.5	9.0	9.4	9.7	9.9	9.2	9.1	9.7	9.8	10.0		0.05	
mg C fixed $\cdot liter^{-1} \cdot d^{-1}$	0.07	0.09	1.11	0.07	0.06	0.36	0.15	2.02	6.56	2.35	0.10		
10^{-4} pg C fixed $\cdot \mu m^3$ phytoplankton$^{-1} \cdot d^{-1}$	0.8	0.8	1.6	0.3	0.4	0.7	0.3	4.40	13.48	1.95	0.25		
10^7 μm^3 phytoplankton $\cdot$ μg part $\cdot P^{-1}$	2.5	4.9	11.5	5.1	2.4	17.6	11.7	7.5	4.5	11.5	0.10		0.25

Table 7. Mean biomass of major phytoplankton species (10^5 $\mu m^3 \cdot ml^{-1}$) for final two sampling dates in enclosure experiment 2; levels of significance indicated where $P < 0.25$.

	Controls—*no fish*					Fish enclosures					ANOVA		
	1 LN	7 LN	3 MN	9 MN	5 HN	2 LN	8 LN	4 MN	6 MN	12 HN	Predators	Nutrients	Interaction
Chlorophycophyta													
Chlamydomonas sp. 1		0.21	1.09		0.03		0.10	0.10					
Closterium moniliferum	5.27						10.54						
Cosmarium angulosum	0.06	0.25	0.19	0.03	0.03	0.19	0.50	0.62	0.16	0.38	0.05		
Cosmarium nitidulum					0.17	0.34	1.02	0.17		0.17	0.25		0.25
Cosmarium sexnotatum		0.43	6.95		5.22	2.61	4.35	4.78	16.08	2.61			
Gloeocystis vesiculosa		0.47	0.03			0.54	1.28					0.10	
Pediastrum boryanum		0.45	0.68						0.62				
Scenedesmus denticulatus	0.01	0.04			0.03	0.09	0.18		0.05	91.43			
Sphaerocystis schroeteri		0.15	1.22			0.06				0.19			
Staurastrum paradoxum	1.07	3.57	0.36	1.07	0.71	28.94	3.22	35.37	29.66	20.00	0.025		
Ulothrix oscillarina	0.89			0.22	0.20	0.07	0.77			0.79			
Chrysophycophyta													
Cyclotella sp.		0.12				1.39	5.26				0.25	0.25	
Heterochromonas globosa	0.11		0.46	0.15		0.34		0.04					
Rhodomonas minuta	0.05	4.11	0.23	0.08	0.08	0.29	0.74						
Cyanochloronta													
Aphanizomenon flos-aquae	0.05		3.41				0.17						
Chroococcus dispersus	0.89	1.40	41.32	20.64	6.86	0.36	0.24	0.87	1.61	0.54	0.05	0.10	0.10
Oscillatoria tenuis	0.11	0.21	0.94	0.09	0.42	0.03	0.06	0.16		1.67			
Pyrrhophycophyta													
Ceratium hirundinella						14.86	22.29	3.72			0.01	0.025	0.025
Bacteria													
	0.17	0.30	0.19	0.45	0.33	0.94	0.55	1.46	0.27	0.24	0.01	0.025	0.025
Total phytoplankton	8.55	11.71	69.06	22.38	13.88	51.05	51.55	45.89	48.67	120.38	0.10		

Table 8. Total phytoplankton biomass in 10^5 $\mu m^3 \cdot ml^{-1}$ (mean for last two sampling dates) and proportion of total biomass of five most abundant species in enclosures of experiment 2.

No fish	
Enclosure 1—LN	8.55
Closterium moniliferum	0.62
Staurastrum paradoxum	0.13
Ulothrix oscillarina	0.10
Chroococcus dispersus	0.10
Heterochromonas globosa	0.01
Enclosure 7—LN	11.71
Rhodomonas minuta	0.35
S. paradoxum	0.31
C. dispersus	0.12
Pediastrum boryanum	0.04
Gloeocystis vesiculosa	0.04
Enclosure 3—MN	69.06
C. dispersus	0.60
Cosmarium reniforme	0.17
Cosmarium sexnotatum	0.10
Aphanizomenon flos-aquae	0.05
Sphaerocystis schroeteri	0.02
Enclosure 9—MN	22.38
C. dispersus	0.92
S. paradoxum	0.05
U. oscillarina	0.01
H. globosa	0.01
Oscillatoria tenuis	<0.01
Enclosure 5—HN	13.88
C. dispersus	0.49
C. sexnotatum	0.38
S. paradoxum	0.05
O. tenuis	0.03
U. oscillarina	0.01
Fish enclosures	
Enclosure 2—LN	31.05
S. paradoxum	0.57
Ceratium hirundinella	0.29
C. sexnotatum	0.05
Cyclotella sp.	0.03
G. vesiculosa	0.01
Enclosure 8—LN	51.55
C. hirundinella	0.43
C. moniliferum	0.20
Cyclotella sp.	0.10
C. sexnotatum	0.08
S. paradoxum	0.06
Enclosure 4—MN	45.88
S. paradoxum	0.77
C. sexnotatum	0.10
C. hirundinella	0.08
C. dispersus	0.02
Chlamydomonas sp. 1	0.01
Enclosure 6—HN	48.67
S. paradoxum	0.61
C. sexnotatum	0.33
C. dispersus	0.03
P. boryanum	0.01
Trachelomonas sp. 1	0.01
Enclosure 12—HN	120.38
Scenedesmus denticulatus	0.76
S. paradoxum	0.17
Scenedesmus quadricauda	0.02
C. sexnotatum	0.02
O. tenuis	0.01

As in the fish-free enclosures, while enrichment did not affect the total standing crop of phytoplankton in fish enclosures, it did have a qualitative effect on the community. Desmids, *C. hirundinella*, and *Cyclotella* sp. dominated the community at low nutrient levels (Table 8), but at higher levels of enrichment *Ceratium* and *Cyclotella* disappeared, as did *Gloeocystis* and bacteria. Clear patterns do not exist for the remaining species, although a very dense bloom of *S. denticulatus* developed in one of the high-nutrient enclosures. The mechanisms responsible for these changes are not known; the disappearance of some species from enriched enclosures may be related to the enhanced uptake of critical secondary nutrients by other species when nitrogen and phosphorus availability is increased.

Discussion

As several earlier studies have shown (Hrbáček 1962; Hurlburt et al. 1972; Losos and Heteša 1973), the removal of large herbivores by fish often results in a significant increase in phytoplankton standing crop. In Pleasant Pond the large herbivores (*D. pulex, D. clavipes*, and *C. reticulata*) were capable of suppressing all algal species (except *Chroococcus* spp.), and total phytoplankton biomass generally increased by an order of magnitude in the presence of fish. This observation cannot be generalized, since the *Aphanizomenon* blooms that devel-

oped in the presence of *D. pulex* comprised some of the densest aggregations of phytoplankton ever noted in the pond. However, apparently not even *Aphanizomenon* is completely immune to grazing by *Daphnia*. The fact that "grass-blade" blooms developed only when the bottom waters were well oxygenated suggests that the sediments provide a refuge which allows new *Aphanizomenon* colonies to grow to an ungrazeable size before they enter the water column. "Grass-blade" blooms never appeared in the presence of *D. pulex* when the bottom waters were anoxic or when the water column was artificially isolated from the sediments.

Three other algal groups which tended to persist in the presence of *D. pulex* seem to cope with herbivory in different ways. The gelatinous *Chroococcus* species were the only algae not suppressed by large grazers; their consistent decrease in the absence of herbivores suggests that they may derive a nutritional advantage from passing through herbivore guts, as some gelatinous greens do (Porter 1976). The delicate flagellates are highly vulnerable to grazers, but comprise a significant proportion of the phytoplankton community when grazing is most intense. Their persistence in the face of heavy losses may result from their high reproductive rates when nutrient availability is high, as it is in the presence of dense *Daphnia* populations. We do not have the data to verify this for Pleasant Pond, but Fott (1975) has found it to be true in similar European ponds. The desmids have very low reproductive rates (Lynch unpubl.) and are ingested by herbivores (Lynch 1978); their ability to persist in low numbers in the presence of *Daphnia* must mean either that they are ingested less than other species or that they can survive passage through herbivore guts.

The increase of most algal species in the absence of large herbivores in both short and long term experiments suggests that the Pleasant Pond phytoplankton community is not tightly regulated by competitive interactions. This does not imply that nutrients are of no significance, but rather that while the chemical and physical regime of the pond ultimately determines which species may live there, over the experimental time scales (<2 months) the densities of individual species are primarily influenced by losses to large herbivores. Although dense populations of small herbivores often developed in fish enclosures, they were not capable of lowering the abundance of any algal species to the extent that the large herbivores were. Many of the large phytoplankton (desmids, colonial green algae, filamentous blue-greens) are probably not vulnerable to the small herbivores (Gliwicz 1977).

If these conclusions are correct, then the number of phytoplankton species in the pond should increase in the absence of the large herbivores. We have tested this hypothesis by counting the number of species in a standard volume of all of our phytoplankton samples. The prediction held in all but one of the eight zooplankton removal experiments ($\chi^2 = 6.12$, $P < 0.05$). For the 1975 enclosure experiment the average numbers of phytoplankton species (±0.95 C.L.) for the last three sampling dates were 26.8 ± 10.5 for control enclosures and 34.0 ± 4.2 for fish enclosures. Although this difference is not significant, it is consistent with our hypothesis. The results for the 1976 enclosure experiment were not so clear; while the mean number of algal species increased with the removal of large herbivores at the lowest level of nutrients (from 20 to 28), it remained constant and much lower (13–15) in all enriched enclosures.

An increase in species richness when grazing pressure is relaxed is not to be expected in all phytoplankton communities, particularly when the algae are tightly constrained by nutrients. For instance, McCauley and Briand (1979) noted a tendency for phytoplankton species richness to decline with reduced grazing in a low-nutrient Canadian lake. In such environments, the growth of most algae is likely to be nutrient-limited even under intense grazing, and the removal of this pressure

may allow a few competitively superior species to increase to the extent that species with lower affinities or utilization efficiencies for critical nutrients are excluded.

Our enrichment experiment established the potential significance of altering the nutrient regime for the Pleasant Pond community. Although additions of phosphorus and nitrogen did not result in significant changes in total phytoplankton biomass, many species disappeared from the enriched enclosures. Since herbivores did not increase with enrichment, it is unlikely that they were responsible for these changes. A more likely explanation is that the imposed enrichment of N and P altered the species composition of the phytoplankton community in a way that led to the depression of other micronutrients below levels necessary for some species. If that were the case, then we would not expect removing the large herbivores from the enriched enclosures to enhance the number of phytoplankton species, and it did not.

As pointed out by Lanc and Levins (1977), enrichment of a complex system can lead to various and unexpected results, depending on the connections among the community's members. Although in the most celebrated cases enrichment has resulted in dramatic qualitative as well as quantitative changes in the phytoplankton community (Edmondson 1972; Schindler and Fee 1974), lakes may not always respond to nutrient additions in this way. Enrichment may change species composition without changing total algal biomass (Komárková 1974; this study). Increases in primary productivity in response to enrichment may not be accompanied by changes in phytoplankton abundance or species composition (e.g. Losos and Heteša 1973; Ostrofsky and Duthie 1975). Examples presented by Parsons et al. (1972) and O'Brien and deNoyelles (1974) show that this occurs when enhanced algal production is passed onto increased zooplankton populations. These apparent exceptions to the rule deserve close scrutiny.

The response of a lake to enrichment will depend on the structure and density of its planktivorous fish populations as well as on its initial nutrient status. For instance, the phytoplankton communities in planktivore-free lakes will be less sensitive to enrichment than those in lakes with planktivores if, in the former, the large herbivores can keep the algae below levels at which nutrient availability becomes critical. The response of a phytoplankton community to the removal or culling of planktivorous fish populations will similarly depend on the level of enrichment. In the most highly enriched lakes, when nutrients are not at critical levels, the phytoplankton community will be much more sensitive to changes in predators than to changes in nutrient levels.

We propose the following as a series of hypotheses to be tested with future work on the community-level effects of enrichment. Consider serial additions of one nutrient—

1. Beyond a certain high level of enrichment, further addition of the nutrient will not alter phytoplankton species composition or abundance.

2. A second (lower) threshold of nutrients will exist above which further enrichment results in changes in phytoplankton species composition but in negligible increases in total algal abundance; i.e. another factor limits total phytoplankton biomass at this point.

3. Both of these thresholds will be lower in the presence of large herbivores (in the absence of fish).

4. In very dilute lakes, enrichment may alter the phytoplankton community both quantitatively and qualitatively, but changes of a quantitative nature will be more significant because many species may be excluded by scarcity of secondary nutrients.

5. The major response of the phytoplankton community of fish-free lakes to all levels of enrichment will be qualitative rather than quantitative. However, there is a possible exception to this when large ungrazeable algae, such as *Aphanizomenon*, are present.

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