EFFECTS OF NUTRIENTS AND GRAZERS ON PERIPHYTON PHOSPHORUS IN LAKE ENCLOSURES

A. Mazumder[1], W.D. Taylor[1],
D.J. McQueen[2] and D.R.S. Lean[3]

NWRI Technical Contribution No. 89-40

[1] Department of Biology, University of Waterloo, Waterloo, Ontario, Canada N2L 3G1
[2] Department of Biology, York Univeristy, North York, Ontario, Canada M3J 1P3
[3] Lakes Research Branch, National Water Research Institute, Canada Centre for Inland Waters, Burlington, Ontario, Canada L7R 4A6

December 1989

EXECUTIVE SUMMARY

Enclosure experiments and indeed whole lake investigations are complicated by the contribution of the community growing on the edge of the enclosure or in the littoral zone of lakes. It consists of algae, bacteria, and invertebrates (zooplankton, amphipods, chironomids and snails).

In the following investigation, the relative importance of top-down (fish) vs bottom-up (nutrients) on the biomass and composition of the littoral community on large lake enclosures was determined. The influence of wall growth on the phosphorus cycling in the enclosure was shown to be no more important than the influence of the littoral zone on small temperate lakes.

RÉSUMÉ

Les études réalisées dans des enclos ou même dans un lac sont compliquées par la présence de la communauté vivant sur les bords de l'enclos ou dans la zone littorale du lac. La communauté comprend des algues, des bactéries et des invertébrés (zooplancton, amphipodes, chironomidés et escargots).

La présente étude vise à déterminer l'importance relative de l'effet descendant (poisson) et de l'effet ascendant (éléments nutritifs) sur la biomasse et la composition de la communauté littorale dans de gros enclos ménagés dans des lacs. On a montré que l'influence des organismes colonisant les parois de l'enclos sur le cycle du phosphore à cet endroit n'était pas plus importante que l'effet de la zone littorale sur les petits lacs tempérés.

Summary 1. Periphyton, measured as particulate phosphorus (PP) and expressed as periphyton PP, growing on vertically oriented substrata (polyvinyl impregnated nylon) under different nutrient loadings, light intensities (exposures), and grazer communities was examined in eight large enclosures (750 m^3) where nutrients (N and P) and planktivorous fish (1+ yellow perch) were added in a 2x2 factorial design.

2. During the first three weeks (25 June-15 July), there was a significantly higher accumulation of phosphorus into periphyton (periphyton PP) with fertilization, but fish addition had no effect. During the fourth to seventh weeks (16 July-12 August), addition of fish was associated with lower abundance of amphipods and chironomids and higher concentration of periphyton PP. In the enclosures without fish, these invertebrates were over 25 times more abundant, and periphyton PP decreased substantially compared to the June-July period. Fertilization increased periphyton PP only at high exposures in the enclosures with fish.

3. Exposure had a significant effects on periphyton PP. In the enclosures with fish, high abundance of nanoplankton reduced water transparency, and periphyton PP was lower in the deeper waters which may have been due to limitation by low light. Lower periphyton PP was also observed at the surface on sunny sides of enclosures without fish, and therefore with high water transparency, may have been due to inhibitory effects of high light intensity.

4. Periphyton communities in the enclosures with fish had higher uptake rates for planktonic phosphorus, and lower rates of phosphorus release, suggesting that periphyton with high phosphorus demand may have high internal cycling of assimilated phosphorus.

Résumé. 1. Les auteurs ont examiné, dans huit gros enclos (750 m^3) auxquels ils ont ajouté des éléments nutritifs (N et P) et des poissons planctonophages (perchaude 1+) selon un plan factoriel 2x2, le périphyton, mesuré sous forme d'équivalent en phosphate particulaire, ou PP du périphyton, colonisant un substrat vertical (nylon imprégné de polyvinyle) en fonction de divers apports en éléments nutritifs, intensités lumineuses (exposition) et communautés de brouteurs.

2. Au cours des trois premières semaines (25 juin - 15 juillet), une accumulation de phosphore dans le périphyton (PP du périphyton) significativement plus élevée a été observée dans le cas de l'addition d'éléments nutritifs, mais pas de celle de poissons. Entre la quatrième semaine et la septième (6 juillet au 12 août), l'addition de poissons a conduit à une plus faible abondance d'amphipodes et de chironomidés et à une concentration plus élevée de PP du périphyton. Dans les enclos sans poisson, ces invertébrés étaient environ 25 fois plus abondants et le PP du périphyton a diminué de façon importante par rapport à sa valeur en juin et juillet. Dans les enclos avec poissons, l'apport d'éléments nutritifs n'a eu l'effet d'accroître le PP du périphyton qu'à de fortes doses.

3. L'exposition a eu des effets importants sur le PP du périphyton. En effet, dans les enclos avec poissons, la transparence de l'eau est réduite par la grande abondance de nanoplancton; le PP du périphyton était plus faible dans les eaux plus profondes, peut-être parce qu'alors la faible intensité lumineuse devient un facteur limitant. Le PP du périphyton était également plus faible à la surface du côté ensoleillé des enclos sans poisson, donc là où la transparence de l'eau est élevée; cela pourrait toutefois être dû aux effets inhibants d'une grande intensité lumineuse.

4. Dans les enclos avec poissons, les communautés de périphyton présentaient des taux d'absorption de phosphore

planctonique plus élevés, et des taux d'élimination de phosphore plus faibles; le périphyton dont la demande en phosphore est élevée pourrait donc comporter un cycle particulièrement actif d'assimilation du phosphore.

Introduction

Aufwuchs or periphyton communities in streams and lakes are complex assemblages of organisms: algae, bacteria, fungi, protozoans and micrometazoans. Their aggregate biomass is sensitive to changes in nutrient concentrations (Cattaneo & Kalff, 1980; Goldman, 1981; Sand-Jensen & Søndargaard, 1981; Cattaneo, 1987), and phosphorus is the limiting nutrient for both phytoplankton (Schindler et al., 1971; Dillon & Rigler, 1974) and periphyton in most freshwater systems (Riber et al., 1983; Riber & Wetzel, 1987; Bothwell, 1985, 1988; Hansson, 1988). Periphyton must compete with the plankton for phosphorus in lentic systems, and Hansson (1988) demonstrated that phytoplankton are competitively superior to periphyton in utilizing the phosphate in the water. Nutrient concentration and light are of major importance in controlling the development of the periphyton communities (Loeb et al., 1983; Martin et al., 1983; Müller, 1983; Wetzel, 1983) and the effects of nutrients can further be complicated by nutrient-light interactions (Hansson, 1988; Cattaneo, 1987), which are still poorly understood.

Grazing by invertebrates, such as amphipods, chironomids and snails, has been reported to reduce periphyton biomass. Cattaneo and Kalff (1980) suggested that the summer minimum in periphyton biomass is brought about by grazing, and Sand-Jensen (1983) speculated that periphyton is effected by the grazers only during the late phases of growth. Similar observations have been reported by others (Mason and Bryant, 1975; Doremus and Harman, 1977). Most of these grazing studies have examined the effect of one type of grazer in the laboratory or in the field; very little has been done on the effects of natural grazers on natural periphyton assemblages (Moss, 1976).

We have conducted experiments in large enclosures for two summers to investigate the effects of fertilization and addition of planktivorous fish on community structure and dynamics in aquatic systems. We were interested in investigating the effects of these

manipulations on community structure and dynamics of phosphorus because phosphorus is an important factor regulating the community structure and biomass of plankton (Vollenweider, 1968; Schindler et al., 1971; Dillon and Rigler, 1974) as well as periphyton (Cattaneo & Kalff, 1980; Riber et al., 1983; Bothwell, 1985, 1988; Cattaneo, 1987; Hansson, 1988) in most temperate lakes, and also because consumers can modify the impacts of fertilization on aquatic organisms (Shapiro, 1980; McQueen et al., 1986; Mazumder et al., 1988). Despite the fact that there may a variable amount of phosphorus per unit biomass among different algae, our results from enclosure experiments indicated that the size-distribution of particulate phosphorus can be used as a convenient indicator of community structure and biomass of plankton in phosphorus limited systems (Mazumder et al., 1988). Other commonly used indices of plankton or periphyton biomass, for example, chlorophyll content and protein content, may also be influenced by similar variable relationships. Morin and Peters (1988) found that although chlorophyll content per unit dry weight of seston varied an order of magnitude, chlorophyll concentration was the best indicator of grazer (black fly) abundance. As chlorophyll concentration is strongly correlated with phosphorus concentration (Sakamoto, 1966; Dillon and Rigler, 1974; Chapra and Tarapchek, 1976) in lakes, we assumed that although the concentration of particulate phosphorus in periphyton may not represent actual biomass, it may still indicate the effects of treatments on periphyton which may be due to changes in periphyton biomass.

A problem associated with experiments in enclosures is the development of periphyton on enclosure walls (Uehlinger et al., 1984; reviewed in Goldsborough et al., 1986). Periphyton may also act as a sink for nutrients from the epilimnion, and due to the relatively greater area to plankton volume in enclosures, create effects not due to direct effect on plankton. Therefore we were interested to estimate the amount of phosphorus lost into periphyton growing on enclosure walls. Goldsborough et al. (1986) suggested that

people using enclosures should consider the ratio of wall surface to the enclosed volume (A/V). Attempts to alleviate the 'wall effects' or intense periphyton growth have involved the use of large diameter enclosures with low A/V (Lack and Lund, 1974). The enclosures we used were large (8 m diameter and 15 m deep), and we hoped that the interference caused by wall growth of periphyton would be insignificant.

However, as pointed out by Goldsborough et al. (1986), manipulations conducted in enclosures may also contribute to our knowledge of processes influencing the biomass and growth of periphyton. Changes that occurred in the size-distribution of plankton, nutrient limitation, and water clarity following manipulation in the first year (1986) of our study motivated us to explore effects of these changes on periphyton in our manipulated enclosures. Our gut content analysis of fish from the experimental enclosures indicated that these fish were preying on invertebrates such as amphipods and chironomids that live on periphyton (unpublished data). Therefore we assumed that addition of fish may have some effects on these invertebrates which are known to graze on periphyton, and thus may effect the overall periphyton biomass.

The purpose of this paper is to examine how the periphyton, expressed as periphyton PP, growing on the enclosure walls are affected by the addition of nutrients and planktivorous fish. Specifically, we examine how the nutrient loading and changes in abundance of grazers colonizing on periphyton affect accrual of phosphorus in periphyton, and how planktonic PP and periphyton PP interact in terms of availability of light and nutrients. As our treatments produced significant changes in water clarity (Mazumder et al., 1988) and the opaque enclosures walls produced additional shading on the north side of all enclosures, we were interested to examine the effects of shading caused by plankton and enclosure walls on vertical distribution of periphyton expressed as periphyton PP. We also used ^{32}P as a tracer to look at phosphorus exchange between periphyton communities and plankton.

Materials and methods

Measurements of periphyton PP and its accrual rate were made in eight large enclosures (8 m in diameter, 15 m deep and open to the sediment interface) in Lake St. George, Oak Ridges, Ontario, during June through August of 1987. Nutrients (N and P) and planktivorous fish (1+ yellow perch, 2.98 g mean wet weight, 9000 ha^{-1}) were added in a 2x2 factorial design with two replicate enclosures per treatment. Treatments were control (without nutrients and fish), +F (with fish), +N (with nutrients), and +NF (with nutrients and fish). See Mazumder et al. (1988) for details.

Four substrata (4 m long, and 2.5 cm wide), were placed 30 cm away from the wall on both the sunny (high light exposures) and shady (low light exposures) sides of each enclosures on 25 June, 1987. The sub-surface water on one side (shady side) of each enclosure received less light during a major portion of the day-light period because of shading produced by the opaque enclosure walls. We describe the sunny and shady sides as low and high exposure, respectively. The vertically oriented substrata were tied 10 cm apart to plexiglass bars which were suspended immediately above the water surface. Materials that were used to make the substrata were of same age and kind (14 yr. old, 0.25 mm polyvinyl impregnated nylon) as the enclosure walls.

On 15 July, 1987 (after 20 days), subsamples (2.5 x 2.5 cm each) were collected from two substrata at each of 0.5, 1.5, 2.5, 3.5 m depths on both sides of the eight enclosures. Care was taken to minimize detachment of material. Each subsample (substratum containing periphyton community) was placed into a clean screw-capped test tube containing 35 ml of deionized distilled water. In the laboratory, the amount of P (mg P m^{-2}) in each subsample was determined after oxidation with potassium persulfate under pressure (Menzel and Corwin, 1965) with the ascorbic acid modification of the molybdenum blue method (Strickland and Parsons, 1972). Measured concentrations were

corrected for the initial amount of P in the substrata. On 12 August, 1987 (after 48 days), in addition to the determination of P, the remaining substrata from each enclosure were preserved in 4% buffered formalin. The material from each preserved substratum was scraped into a 100 μm mesh sieve and the animals that were associated with the periphyton were collected from the sieve. Invertebrates (amphipods, chironomids, copepods, cladocerans, planarians, hydroids, and gastropods) were counted and were expressed as individuals per m^2. Qualitative estimates (rare, common, or abundant) were obtained for bryozoan colonies.

Light intensity was measured for every meter depth from the surface to 4 m on both sides of the enclosures using a Li Cor (Model LI 185B) light meter. Concentrations of dissolved and particulate phosphorus in the water, and PO_4^{3-} turnover time were measured from 0 - 4 m integrated tube samples collected on the same dates. Details for estimating PO_4 turnover time are described in Mazumder et al. (1988).

On 12 August, 1987, experiments were conducted at the lakeside laboratory to determine the exchange of phosphorus between the periphyton and the planktonic communities in each enclosure. Plankton samples were collected from 1.5 m depth of each enclosure using a 4 L van Dorn sampler. Two 2.5 x 2.5 cm subsamples of substrata were collected from 1.5 m on the sunny side of each enclosures and placed in polyethylene beakers containing water from the same enclosure. Two 100 ml subsamples from each plankton sample were placed in 150 ml polyethylene beakers and spiked with carrier free $^{32}PO_4^{3-}$ (2.5 MBq). After one and a half hours of incubation at 20 - 22°C, one substratum subsample containing the periphyton community was placed vertically into the spiked plankton from its respective enclosure. As soon as the substratum was added, four 1 ml aliquots were collected from each beaker. Two of the four aliquots were filtered through 0.2 μm Nuclepore™ membrane filters. The filters were collected in scintillation vials and the assimilated radioactivity was measured (Mazumder et al., 1988). The other

two aliquots were collected in scintillation vials and were measured for total radioactivity in the water. The same collections and measurements were made from 1 ml aliquots at 15, 30, 60, and 120 min after the addition of the substrata. Uptake rate of ^{32}P per unit surface area of substratum containing periphyton (% of water cm^{-2} h^{-1}) was calculated from the linear portion of the plot of % disappearance of isotope from water against time. Losses of ^{32}P from the water were assumed to represent assimilation by the periphyton communities, and were expressed as volume of water cleared of P per unit surface area of substratum containing periphyton per unit time (mL cm^{-2} hr^{-1}). At 120 min, the two replicate substrata for each enclosure were removed from the beakers, dipped gently into filtered enclosure water several times and were transferred to two beakers containing 100 ml of unspiked plankton from their respective enclosures. After nine hours, three 5 ml aliquots of water from each beaker were collected into individual scintillation vials and were measured for radioactivity released from the periphyton into the water.

Results

Periphyton PP on 15 July 1987- Concentration of phosphorus in periphyton (mg P m^{-2}) was different for individual depth among treatments and among depth within each treatment (Figure 1). For all depths on both light exposures taken together, there was no effect of either the addition of nutrients or fish on periphyton PP, but there was heteroscedasticity of variance ($P = 0.007$) among different depths and light exposures. Therefore we analyzed (ANOVA) periphyton PP for individual depths and exposures separately. Periphyton PP at individual depths was higher (high and low exposures analyzed separately) in the fertilized enclosures with and without fish (+N and +NF; $0.000 < P < 0.055$). There was no effect of fish addition on periphyton PP at any depth ($0.124 < P < 0.641$). In the unfertilized enclosures, addition of fish was associated with lower concentrations of periphyton PP at low exposure, but with higher concentrations of periphyton PP at high exposure, relative to the control enclosures. In the fertilized

enclosures, no such pattern was observed. Addition of nutrients and exposure (PP for both exposures at each depth) had significant interaction ($0.006 < P < 0.028$), except at the surface (0.5 m; $P = 0.242$). On this date, the depth-integrated mean PP at low light exposure was as high as or higher than at high light exposure for the enclosures without fish (Control and +N; Figure 2), whereas they were usually lower at low exposure than at high exposure in the enclosures with fish (+F and +NF).

Periphyton PP on 12 August 1987 - After 7 weeks (12 August), enclosures with fish (+F and +NF) had significantly higher periphyton PP at high exposures for individual depth and also for all depths combined ($0.001 < P < 0.006$; Figure 1). At low exposures, periphyton PP was significantly higher with addition of nutrients ($P = 0.003$) only at the surface (0.5 m); deeper water had very similar biomasses among all treatments (Figure 1). As a result, neither the addition of nutrients nor the addition of fish had significant effects on periphyton PP when all depths were analyzed together. Periphyton PP analyzed for each depth, and for all depths together was slightly higher or similar at both exposures in the enclosures without fish, except at the surface where it was significantly higher at low exposure than at high exposure ($0.035 < P < 0.058$). In the enclosures with fish, periphyton PP was significantly lower at low exposure for each individual depth and for all depths combined ($0.001 < P < 0.021$).

The vertical distributions of the periphyton PP were even more variable on 12 August than that observed on 15 July (Figure 1). The depth integrated mean periphyton PP at both low and high exposures decreased substantially in the enclosures without fish (Figure 2; control and +N). In the enclosures with fish (+F and +NF), depth integrated mean periphyton PP increased at high exposure, and decreased at low exposure. The highest biomass increase was at high exposure in the fertilized enclosures with fish. The depth integrated mean biomasses (both exposures combined) were 7.2, 10.4, 8.9, and 20.5 mg P m^{-2} in control, +F, +N, and +NF enclosures, respectively.

Accrual rate of phosphorus in periphyton- During 25 June to 15 July period, the accrual rates of phosphorus in periphyton (all depths and both exposures included) were higher with fertilization (Figure 3). There was no effect of fish addition during this first three weeks. However, addition of fish was associated with lower accrual at low exposure than at high exposure. During this period (25 June-15 July), the accrual rates of phosphorus (for both exposures and all depths combined) in periphyton were 0.56, 0.49, 0.71, and 0.71 mg P m^{-2} d^{-1} in the control, +F, +N, +NF enclosures.

During the 4th to 7th weeks of our experiments (15 July to 12 August), substantial declines were observed in periphyton PP for enclosures without fish, both with and without fertilization. Addition of fish was associated with significant accrual only at high exposure, especially with fertilization. At low exposure, the enclosures with fish had very low (+F) or negative accrual rates (+NF) (Figure 3). The accrual rates of phosphorus in periphyton were -0.15, 0.13, -0.19, and 0.22 mg P m^{-2} d^{-1} in control, +F, +N, and +NF enclosures.

Abundance of colonizing invertebrates - Amphipods (Hyalella azteca) were much more abundant in the enclosures without fish (Student t-test, $P< 0.05$) and this effect was magnified by fertilization ($P < 0.05$; Figure 4). Abundance of chironomids was also higher without fish and with fertilization ($P < 0.05$). Copepods, cladocerans and hydroids were higher with fish in the unfertilized enclosures, while they were lower with fish in the fertilized enclosures. Planarians showed opposite results; abundances were lower and higher with fish in the unfertilized and fertilized enclosures, respectively. Gastropods were more abundant in the enclosures with fish, and with fertilization (Figure 4). Estimates for the bryozoan colonies were only qualitative, but they were abundant only in the enclosures with fish.

Light intensity- Although the light intensity at the surface was same for both sides of all enclosures, the percent of surface light intensity available at any depth was lower with fertilization and addition of fish (Figure 5). At any depth, it was at least an order of magnitude higher at high exposure (sunny sides) than those at low exposure (shady side) of all enclosures.

Exchange of phosphorus - Transfer of $^{32}PO_4^{3-}$ from water and plankton to the substrata containing periphyton was higher in the enclosures with fish ($P = 0.011$), and with fertilization ($P = 0.042$; Figure 6). The highest uptake rate, expressed per unit area, was observed in the fertilized enclosures with fish and the lowest in control enclosures (Table 1). However, this pattern changed when periphyton PP specific uptake rate ($\mu g\ P_{(water)}\ mg\ P_{(periphyton)}^{-1}\ h^{-1}$) is considered, +N periphyton was the most active (Table 1).

When the substrata with assimilated $^{32}PO_4^{3-}$ were transferred to unspiked enclosure waters with plankton, 87 to 96% of the assimilated $^{32}PO_4^{3-}$ was released into the water after 9 h for the enclosures without fish, whereas 40 to 50% was released into the water for the enclosures with fish (Table 1).

Discussion

Concentration of phosphorus in periphyton in our experimental enclosures changed following fertilization and the addition of planktivorous fish. However, the effects of our manipulations on periphyton PP were complicated by light intensity. In the enclosures with fish (+F and +NF), where water transparency was reduced by the abundant nanoplankton (Mazumder et al., 1988), periphyton PP was lower at low light exposures on the shady sides. This suggests that periphyton were light-limited on the shady sides, especially in the fertilized enclosures with fish. The periphyton PP at 0.5 m depth were lower at high

exposures of enclosures without fish (enclosures with high water transparency) during both phases of growth, suggesting that there may be an inhibitory effect of high light at least at the surface.

During the first three weeks, periphyton PP was unaffected by the presence of planktivorous fish in the enclosures, except perhaps indirectly by shading as discussed above. Fertilization increased the accrual of phosphorus in periphyton during this early phase of their growth, as it has been reported for periphyton biomass in previous studies (Moss, 1976; Bothwell and Jasper, 1983; Loeb et al., 1983; Martin et al., 1983; Müller, 1983; Wetzel, 1983; Bothwell, 1985). Growth of periphyton can be estimated during this early phase, as the effect of grazers is of minor importance, and good correlations can be obtained between external parameters and biomass changes (Sand-Jensen, 1983; Bothwell, 1985; Bothwell & Jasper, 1983).

Later during 4th to 7th weeks of our experiment, periphyton PP was reduced by 36% and 37% in the enclosures without fish (control and +N). In the enclosures with fish (+F and +NF), it increased by 6% and 30%, there were much lower abundances of amphipods and chironomids. This suggest that fish can reduce the grazing impact of invertebrates. These animals were also observed in the fish guts (unpublished data). Cooper (1965) reported that yellow perch can effectively reduce the abundance of amphipods by selecting the reproductively mature individuals during the summer months. Moss (1976) reported that addition of planktivorous fish (bluegill sunfish) to fertilized systems caused an increase in biomass of certain macrophytes and epiphytes which was probably due to fish predation on the grazing invertebrates, and Mason and Bryant (1975) found a decline in the standing crop of periphyton that was largely due to the presence of chironomid larvae.

We observed a high abundance of snails in the fertilized enclosures with fish. Snails have been reported to be effective grazers of periphyton. For example, Doremus and Harman (1977) found that the population density of two snails, Physa heterostropha and Prometus exacuous, was inversely correlated with periphyton standing crop under laboratory conditions. But we found that a high abundance of snails was associated with a high concentration of periphyton PP in the +NF enclosures. Although snails are likely to be resistant to predation by small perch, hence favored in the enclosures with fish, we cannot explain why their great abundance is restricted to the +NF treatments.

Our $^{32}PO_4^{3-}$ uptake experiments indicate that there was more rapid translocation of phosphorus from the plankton community to periphyton in the enclosures with addition of nutrients and with fish, which also had higher concentration of periphyton PP. We cannot distinguish the mechanism(s) involved; the greater uptake of ^{32}P from water by the periphyton community may partly be due to feeding on plankton by the periphyton invertebrates. Phosphate was more limiting for plankton in the enclosures with fish, as indicated by faster turnover times and lower concentrations of dissolved phosphorus (Table 2; Mazumder et al., 1988), so the enhanced translocation is not due to greater availability of phosphate. Higher biomass (PP)-specific uptake observed in +F and +N enclosures may be a reflection of higher periphyton invertebrate feeding on plankton. Both of these enclosures had abundant Hydra. Periphyton communities in the enclosures without fish released their assimilated $^{32}PO_4^{3-}$ more rapidly suggesting a more rapid biomass turnover consistent with high grazing. Because most assimilated ^{32}P was released in the fishless enclosures, the release rates are probably underestimated.

The net uptake and release of labelled phosphorus from seston suggest that radioisotopic equilibrium was not achieved during the incubations. Based on uptake rates, turnover times for periphyton PP were 64 - 166 days, which is much longer than would

reasonably be expected. Because particulate phosphorus in the seston would have had a lower specific activity than dissolved phosphorus after short incubation, this indicates that particulate P may have been the important source of P-translocation to periphyton. Conversely, the turnover time for periphyton PP, calculated from the release rate, is 9.4 to 51 hrs, and this is shorter than expected. This indicates that released P had a low specific activity, as would be expected if grazing were responsible for P-release, rather than periphyton directly. Both calculations again suggest an important role for animals in periphyton-plankton nutrient interactions.

Our observations suggest that high light intensity on the sunny sides of enclosures without fish (control and +N) may have inhibited periphyton growth (as indicated by accrual rates of phosphorus), at least at the surface, while low light intensity on the shady sides of the enclosures with fish (+F and +NF) limited the growth of periphyton communities, which was more limiting in deeper waters. Periphyton PP was unchanged or declined at low exposures in the enclosures with fish during last four weeks despite the addition of nutrients, suggesting that light limitation can reduce the effects of fertilization. During this period, maximum accrual of periphyton PP was observed on the sunny side of the enclosures with fish where light intensity may not be limiting and grazing pressure was reduced by the fish, and highest accrual was in +NF enclosures. These observations suggest that nutrient-grazer and nutrient-light interactions were important in regulating phosphorus dynamics in periphyton PP, and therefore growth of periphyton in our experimental enclosures. The large variability of seasonal changes in periphyton PP among 11 lakes in Quebec (Cattaneo, 1987) may be due to these interactions. Meulemans (1988) reported an inhibitory effect of high light intensity on primary production of periphyton. Hansson (1988) demonstrated that periphyton algae decreased following a reduction of light (directly and via shading by algae) in experimental tubes. He also found a weak negative relationship ($r^2 = 0.20$) between total planktonic phosphorus and periphyton algal

biomass. Overall, our results indicated a positive relationship between planktonic PP and periphyton PP. However, this relationship was only marginally significant.

We conclude that fertilization increases accrual of phosphorus into periphyton if light intensity is not a limiting factor, but it is maximized when grazing pressure from invertebrates is also reduced by visual predators. The response of periphyton to nutrient addition is light dependent, as suggested by the lower concentration and accrual of phosphorus into periphyton on the shady sides of the fertilized enclosures with fish. Light limitation was caused by the abundant nanoplankton, which was a result of reduced zooplankton grazing pressure (Mazumder, 1988), and by shading effect caused by the opaque enclosures walls. Maximum light limitation was observed on the shady sides of the enclosures with fish. Inhibitory effects of high light intensity in the clearwater enclosures were less strong than the limiting effects of light. Maximum periphyton PP was observed on the sunny sides of fertilized enclosures with fish and results from a combination of "bottom up" (fertilization) and "top down" (reduced invertebrate grazing associated with fish addition) effects. However, light plays an important role in these effects, especially for "bottom up" effects. Aquatic systems with a high abundance of small fish and high nutrient loading might be expected to support maximum concentration of periphyton for equivalent light regimes.

Acknowledgements

We thank Max Bothwell and Hamish Duthie for their comments on an earlier draft of this manuscript. We thank H. B. N. Hynes for confirming our identification of periphyton invertebrates. This research was supported by NSERC Canada operating grants to W. D. Taylor and D. J. McQueen. We thank Paul Blanchfield and staff at Lake St. George Field Station (Ralph Baehre, Bernie Jamnick, Kevin Nyman) for their assistance.

References

Bothwell M.L. (1985) Phosphorus limitation of lotic periphyton growth rates: An intersite comparison using continuous-flow troughs (Thompson River system, British Columbia). Limnology and Oceanography, **30,** 527-542.

------. (1988) Growth rate responses of lotic periphyton diatoms to experimental phosphorus enrichment: the influence of temperature and light. Canadian Journal of Fisheries and Aquatic Sciences, **45,** 261-270.

------ & Jasper, S. (1983) A light and dark trough methodology for measuring rates of lotic periphyton settlement and net growth: an evaluation through intersite comparison. Periphyton in Freshwater Ecosystems (Ed. R. G. Wetzel), pp 253-265. The Hague, The Netherlands.

Cattaneo A. (1987) Periphyton in lakes of different trophy. Canadian Journal of Fisheries and Aquatic Sciences, **44,** 296-303.

Cattaneo A. & Kalff J. (1980) The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. Limnology and Oceanography, **25,** 280-289.

Chapra S.C. & Tarapchek S.J. (1976) A chlorophyll model and its relationship to phosphorus loading plots for lakes. Water Resource Research, **12,** 1260-1264.

Cooper W.E. (1965) Dynamics and production of a natural population of a freshwater amphipod. Hyalella azteca. Ecology, **35,** 377-394.

Dillon P.J. & Rigler F.H. (1974) The phosphorus-chlorophyll relationship in lakes. Limnology and Oceanography, **19,** 767-773.

Doremus C.M. & Harman W.N. (1977) The effects of grazing by physid and planorbid freshwater snails on periphyton. Nautilus, **91,** 92-96.

Goldman C.R. (1981) Lake Tahoe: two decades of change in a nitrogen deficient oligotrophic lake. Internationale Vereinigung Für Theoretische und Augewandte Limnologie, **21,** 45-70.

Goldsborough, L. G., Robinson, G. G. C. & Gurney, S. E. (1986) An enclosure/substratun system for in situ ecological studies of periphyton. Archiv für Hydrobiologie **106,** 373-393.

Hansson L-H. (1988) Effects of competitive interactions on the biomass development of planktonic and periphyton algae in lakes. Limnology and Oceanography, **33,** 121-128.

Lack, T. J. and Lund, J. W. G. (1974) Observations and experiments on the phytoplankton of Blelham Tarn, English Lake District. I. The experimental tubes. Freshwater Biology, **4,** 399-415.

Loeb S.L., Reuter J.E. & Goldman C.R. (1983) Littoral zone production of oligotrophic lakes. Periphyton in Freshwater Ecosystems (Ed. R. G. Wetzel), pp 161-167. The Hague, The Netherlands.

Mason C.F. & Bryant R.J. (1975) Periphyton production and grazing by chironomids in Alderfer Broad, Norfolk. Freshwater Biology, **5,** 271-277.

Martin T.A., Graham J.M., Graham L.E. & Krauzfelder J.A. (1983) Factors regulating the spatial and temporal distribution of Cladophora and Ulothrix in the Laurentian Great Lakes. Periphyton in Freshwater Ecosystems (Ed. R. G. Wetzel), pp 135-145. The Hague, The Netherlands.

Mazumder A. (1988) Impact of fertilization and planktivorous fish predation on community structure and dynamics in lake enclosures. Ph.D. dissertation, Department of Biology, University of Waterloo, Waterloo, Ontario, Canada N2L 3G1.

------., McQueen D.J., Taylor W.D. & Lean D.R.S. (1988) Effects of fertilization and planktivorous fish (yellow perch) predation on size distribution of particulate phosphorus and assimilated phosphate: Large enclosure experiments. Limnology and Oceanography, **33,** 421-430.

McQueen D.J., Post J.R., & Mills E.L. (1986) Trophic relationships in freshwater pelagic ecosystems. Canadian Journal Fisheries Aquatic Sciences, **43,** 1571-1581.

Menzel D.W. & Corwin N. (1965) The measurement of total P in seawater based on liberation of the organically bound fractions by persulfate oxidation. Limnology and Oceanography, **10,** 280-282.

Meulemans J.T. (1988) Seasonal changes in biomass and production of periphyton upon reed in Lake Maarsseveen I. Archiv Für Hydrobiologie, **112,** 21-42.

Morin A. & Peters R.H. (1988) Effects of microhabitat features, seston quality, and periphyton on abundance of overwintering black fly larvae in southern Quebec. Limnology and Oceanography, **33,** 431-446.

Moss B. (1976) The effects of fertilization and fish on community structure and biomass of aquatic macrophytes and epiphyteic algal populations: An ecosystem experiment. Journal of Ecology, **64,** 313-342.

Müller C. (1983) Uptake and accumulation of some nutrient elements in relation to the biomass of an epilithic community. Periphyton in Freshwater Ecosystems (Ed. R. G. Wetzel), pp 147-151. The Hague, The Netherlands.

Riber H.H. & Wetzel R.G. (1987) Boundary-layer and internal diffusion effects on phosphorus fluxes in lake periphyton. Limnology and Oceanography, **32,** 1181-1194.

Riber H.H., Sørensen J.P. & Kowalczewski A. (1983) Exchange of phosphorus between water, macrophytes and epiphytic periphyton in the littoral zone of Mikolayskie Lake, Poland. Periphyton in Freshwater Ecosystems (Ed. R. G. Wetzel), pp 235-243. The Hague, The Netherlands.

Sakamoto M. (1966) Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. Archiv Für Hydrobiologie, **62,** 1-28.

Sand-Jensen K. (1983) Physical and chemical parameters regulating growth of periphyton communities. Periphyton in Freshwater Ecosystems (Ed. R. G. Wetzel), pp 63-71. The Hague, The Netherlands.

Sand-Jensen K. & Søndargaard M. (1981) Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different trophic status. Internationale Revue der Gesamten Hydrobiologie, **66,** 529-552.

Schindler W.D., Armstrong F.A.J., Holmgren S.K., & Brunskill G.J. (1971) Experimental Lake Area, northern Ontario, by addition of phosphate and nitrate. Journal of Fisheries Research Board of Canada, **28,** 1763-1782.

Shapiro J. (1980) The importance of trophic-level interactions to the abundance and species composition of algae in lakes. Developments in Hydrobiology (Ed. P.L. Brezonik and L.R. Mur), V. 2, pp 105-116, Junk.

Strickland J.D. & Parsons T.R.(1972) A practical handbook of seawater analysis. 2nd ed. Bulletin of Fisheries Research Board of Canada, **167.**

Uehlinger, U., Bloecsh, J., Bürgi, H. R., & Bührer, H. (1984) Ecological experiments in limnocorrals: methodoligical problems and quantification of the epilimnetic phosphorus and carbon cycles. Internationale Vereinigung Für Theoretische und Augewandte Limnologie, **22,** 163-171.

Vollenweider R.A. (1968) Scientific fundamentals of the eutrophication of lakes and flowing waters, with reference to nitrogen and phosphorus as factors in eutrophication. OECD Paris, DAS/CSI/68.27.

Wetzel R.G. (1983) Attached algal-substrate interactions: fact or myth, and when and how. Periphyton in Freshwater Ecosystems (Ed. R. G. Wetzel), pp 207-215. The Hague, The Netherlands.

Table 1. Uptake and release rates of phosphorus by periphyton in different treatments. Uptake rates are expressed as volume of water cleared of $^{32}PO_4^{3-}$ per unit surface area per unit time, P taken up per unit area per unit time (assuming isotopic equilibrium in the seston), and P taken up per unit periphyton PP. Release rates are expressed as the percent of assimilated ^{32}P released into unlabeled water per unit time.

	Control	+F	+N	+NF
	Uptake rates			
mL m^{-2} h^{-1}	244	407	447	517
µg $P_{(water)}$ m^{-2} h^{-1}	3.21	5.73	9.19	10.25
µg P mg P^{-1} h^{-1}	0.25	0.44	0.65	0.27
	Release rates			
% of assimilated $^{32}PO_4^{3-}$ h^{-1}	9.7%	1.9%	10.7%	4.5%

Table 2. Total dissolved phosphorus, total planktic PP, and $^{32}PO_4^{3-}$ turnover times for plankton in June, July, and August. Error estimates are 2 standard errors (n = 4)

	Control	+F	+N	+NF
	Total dissolved phosphorus (μg P liter^{-1})			
22 Jun	9.6 ± 0.63	6.6 ± 0.63	9.9 ± 1.48	7.1 ± 0.2
13 Jul	10.0 ± 1.55	7.9 ± 0.23	9.0 ± 1.5	6.5 ± 0.87
12 Aug	6.8 ± 0.35	5.4 ± 0.72	10.2 ± 2.08	6.8 ± 0.84
	Total particulate phosphorus (μg P liter^{-1})			
22 Jun	6.8 ± 0.43	13.3 ± 1.98	12.3 ± 0.68	14.6 ± 1.4
13 Jul	6.6 ± 0.68	15.1 ± 1.15	13.2 ± 0.95	20.5 ± 2.45
12 Aug	6.4 ± 0.37	8.7 ± 0.73	10.4 ± 0.28	13.0 ± 2.05
	$^{32}PO_4^{3-}$ turnover time (min)			
22 Jun	19.8 ± 4.4	6.4 ± 1.5	58.5 ± 9.8	8.1 ± 1.8
13 Jul	10.1 ± 1.2	3.7 ± 0.5	66.8 ± 14.8	5.0 ± 0.7
12 Aug	13.5 ± 2.7	6.5 ± 1.4	162.8 ± 45.2	7.2 ± 1.6

List of Figures

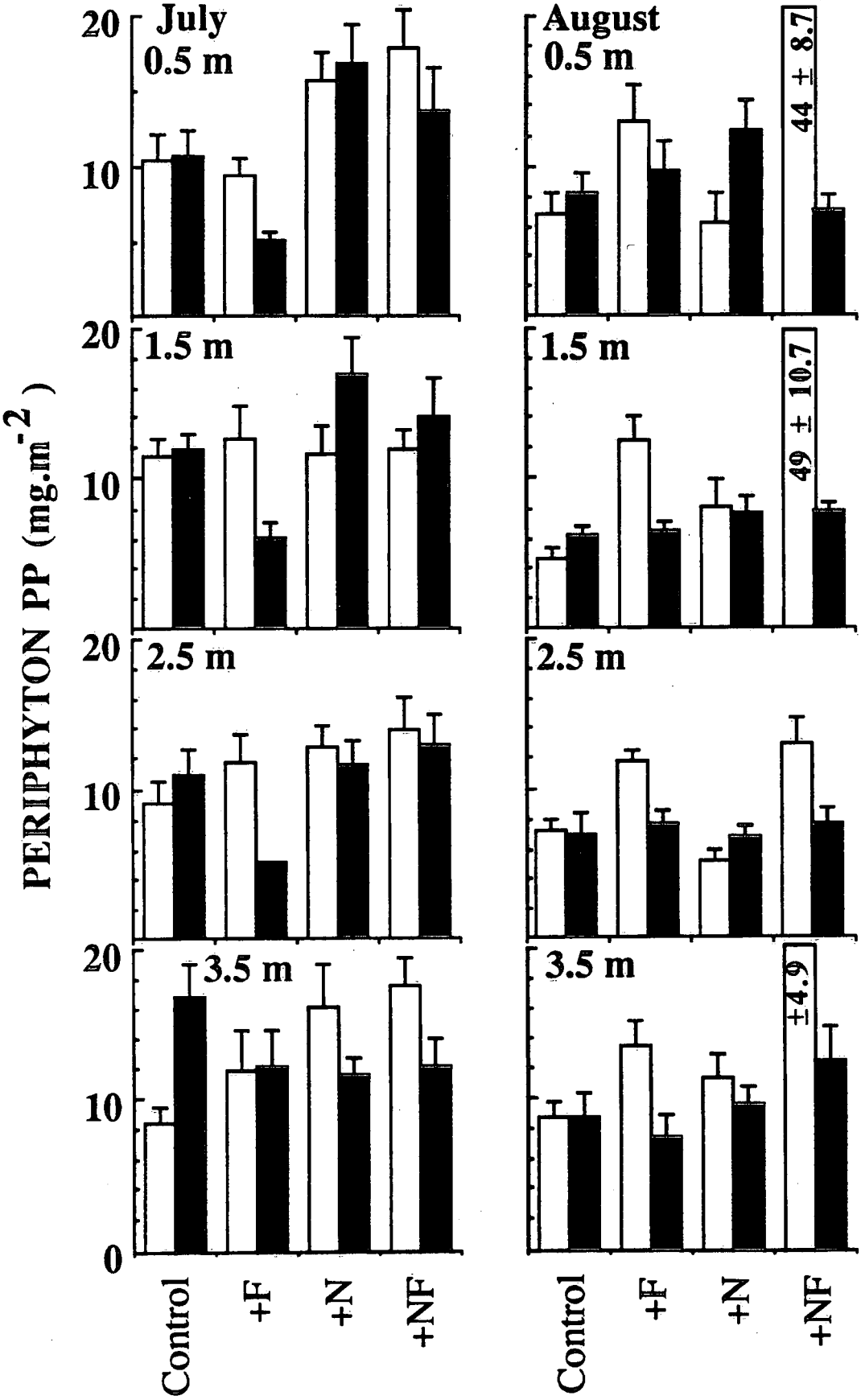
July
0.5 m
August
0.5 m
44 ± 8.7
1.5 m
1.5 m
49 ± 10.7
2.5 m
2.5 m
3.5 m
3.5 m
±4.9
PERIPHYTON PP (mg.m-2)
20
10
0
Control
+F
+N
+NF

FIGURE 1

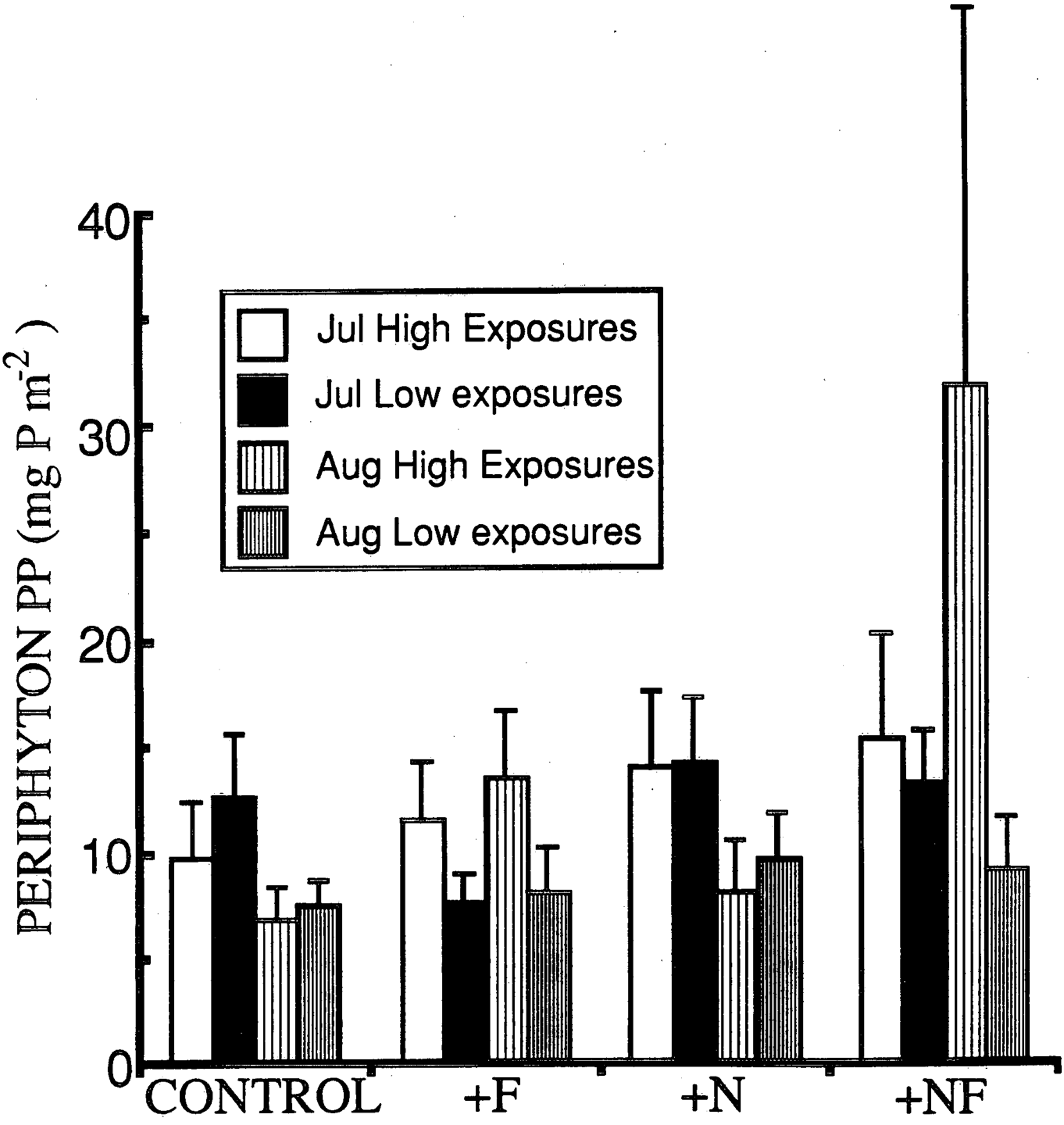
PERIPHYTON PP (mg P m-2)
40
30
20
10
0
Jul High Exposures
Jul Low exposures
Aug High Exposures
Aug Low exposures
CONTROL
+F
+N
+NF

FIGURE 2

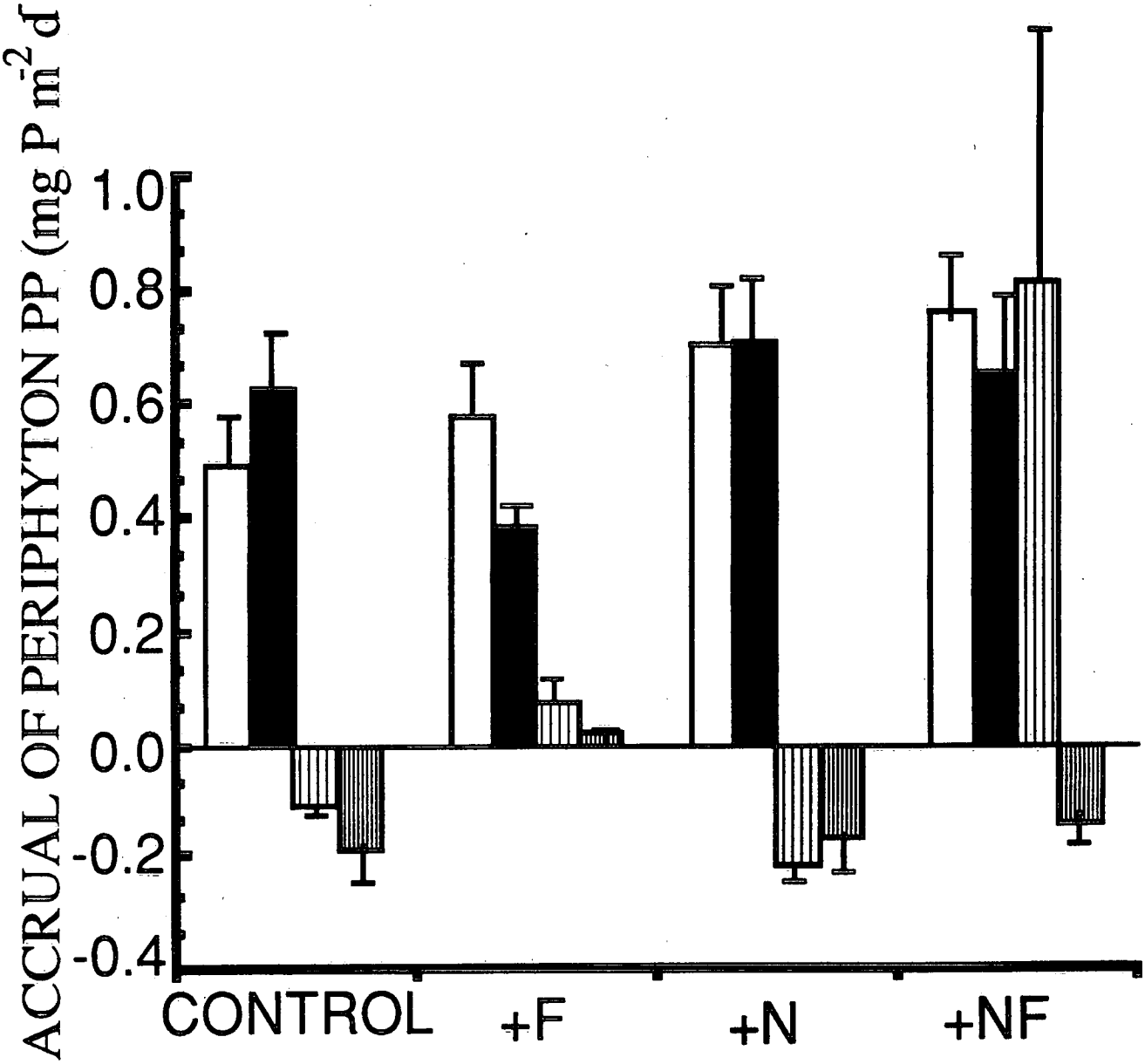
ACCRUAL OF PERIPHYTON PP (mg P m-2 d-1)
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
CONTROL
+F
+N
+NF

FIGURE 3

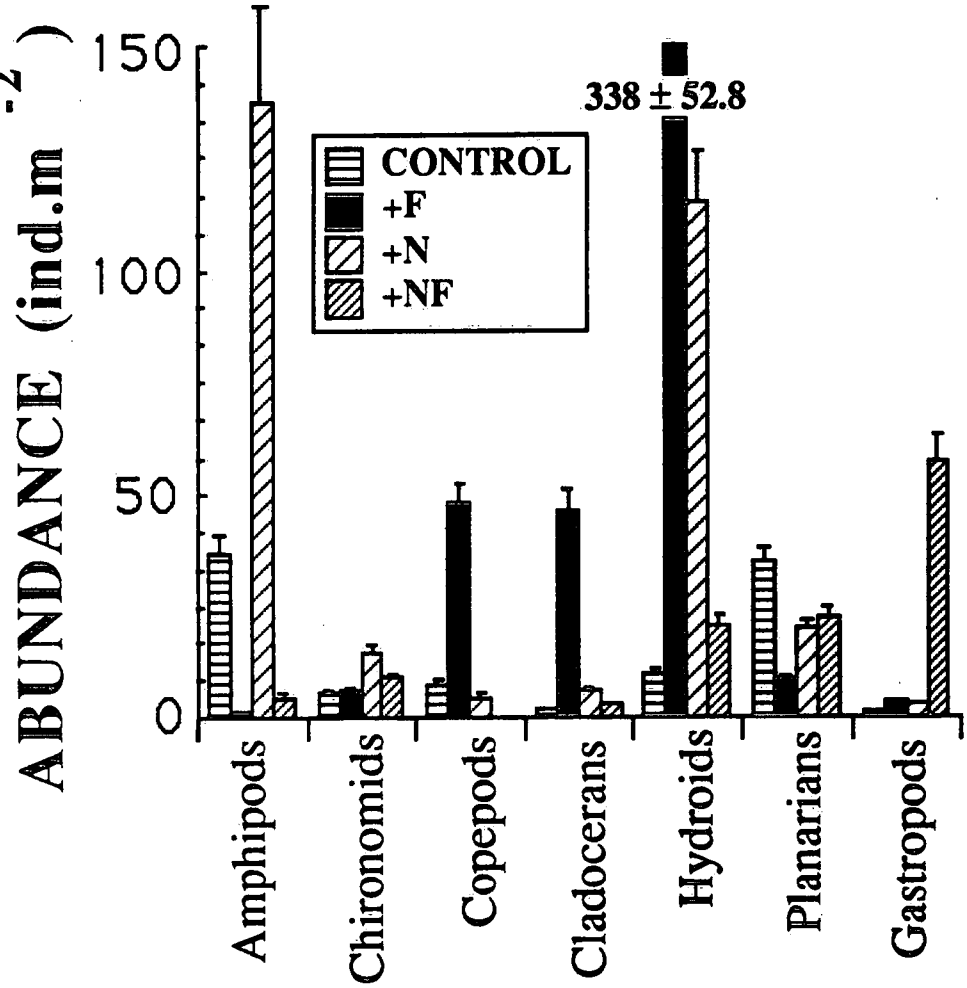
ABUNDANCE (ind.m -2)
150
100
50
0
338 ± 52.8
CONTROL
+F
+N
+NF
Amphipods
Chironomids
Copepods
Cladocerans
Hydroids
Planarians
Gastropods

FIGURE 4

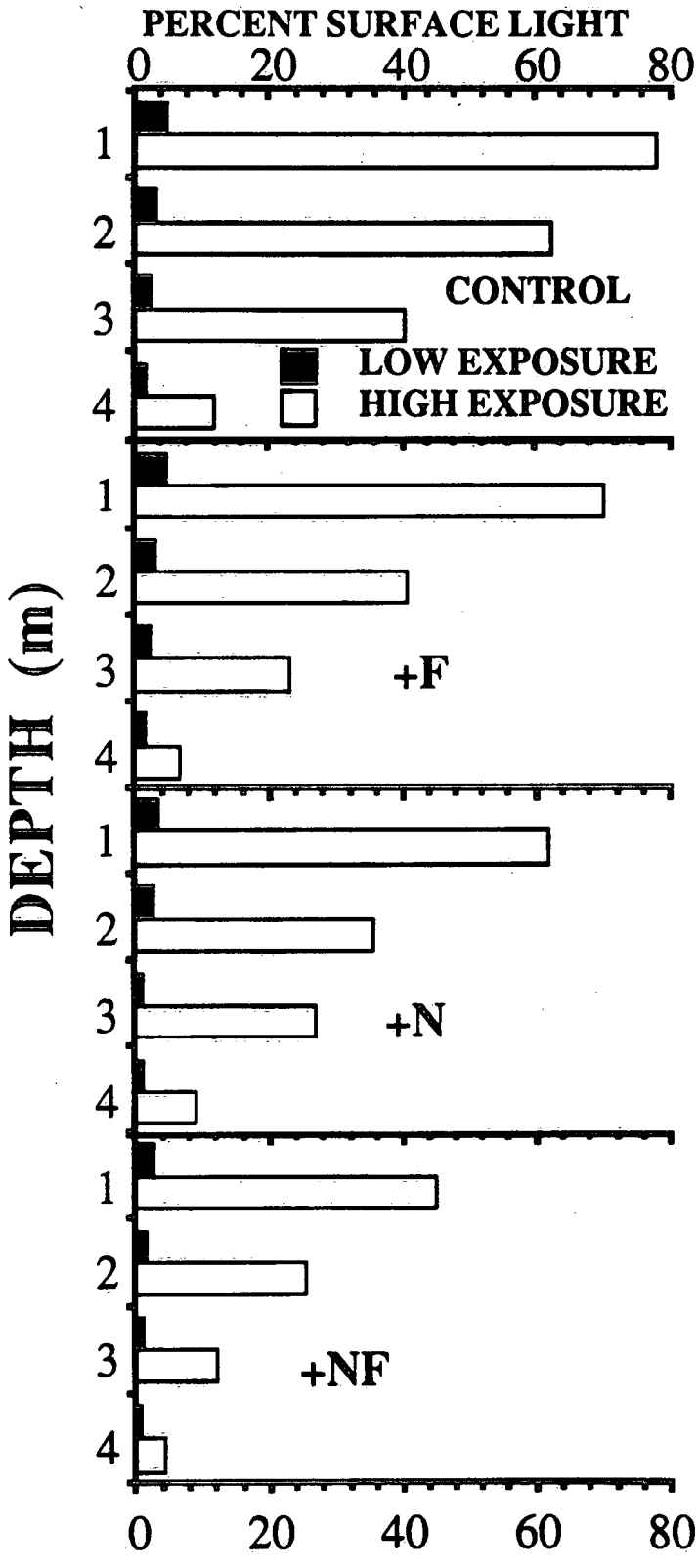
PERCENT SURFACE LIGHT
0
20
40
60
80
DEPTH (m)
1
2
3
4
CONTROL
LOW EXPOSURE
HIGH EXPOSURE
+F
+N
+NF

FIGURE 5

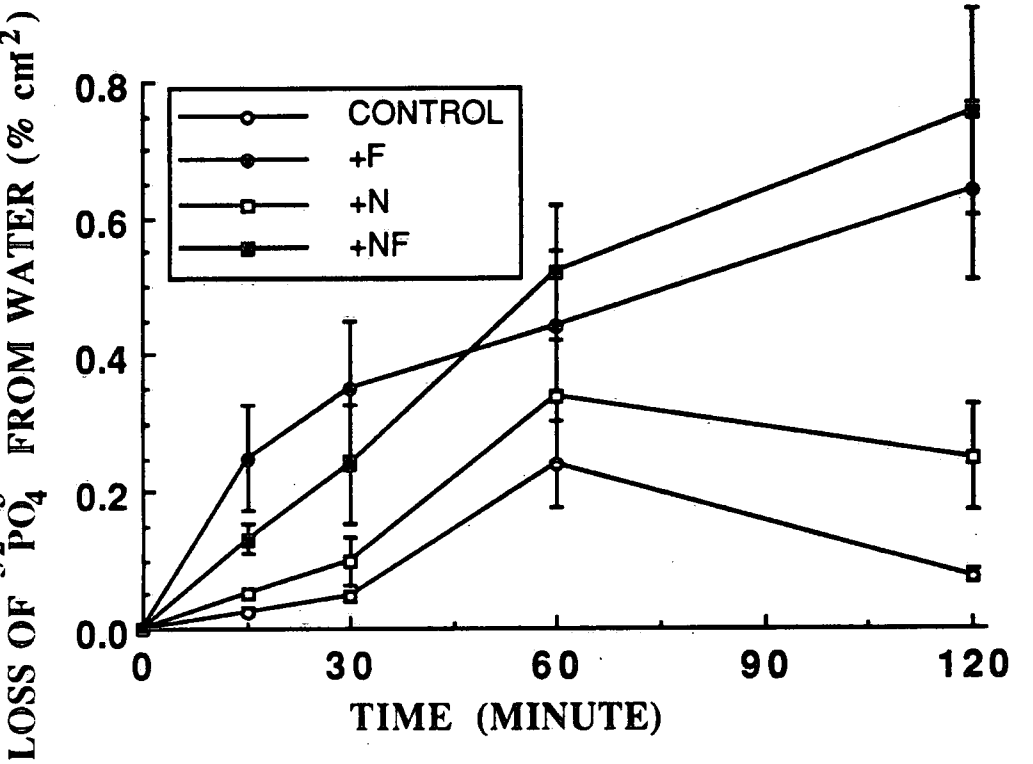
LOSS OF $^{32}PO_4^{3-}$ FROM WATER (% cm^2)
0.8
0.6
0.4
0.2
0.0
CONTROL
+F
+N
+NF
0
30
60
90
120
TIME (MINUTE)

FIGURE 6