Phosphorus limited community dynamics of stream benthic algae and insects

by
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B.Sc., The University of British Columbia, 1988

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

Department of Zoology

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
March 1994

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Date March 30/94

DE-6 (2/88)

ABSTRACT

The relationship between external soluble phosphorus (P) concentration and the abundance and taxonomic composition of stream insects was determined in streamside artificial troughs. The response of peak algal biomass (PB) to target P concentrations of 0, 0.5, 2.5, 5, 10, 50 $\mu g\ P \cdot l^{-1}$ was also monitored. A log-linear function of P concentration was used to approximate PB and insect abundance. PB measured as chlorophyll *a* increased with P concentration linearly to 7.4 $mg \cdot m^{-2}$ at 2.5 $\mu g\ P \cdot l^{-1}$ and reached an asymptote at 9.2 $mg \cdot m^{-2}$ (2.7X the controls). Adult baetid mayflies showed a significant increase in number after 23 days of P addition; this effect was maintained over 9 weeks of treatment. Numbers of benthic baetids, nemourid and perlodid stoneflies and hydroptilid tricopterans sampled at the end of the experiment significantly increased with P concentration. Adult and benthic insects of these taxa exhibited similar rapid increases in abundance from 0 - 2.5 $\mu g\ P \cdot l^{-1}$ and all showed signs of saturation at approximately 1.5 - 3 times the controls at concentrations greater than 2.5 $\mu g\ P \cdot l^{-1}$. Increased abundances of insects resulted from greater food availability. There was no detectable difference in the numbers of large Baetid nymphs drifting from the troughs with increasing P concentration. Increased survival of Baetidae nymphs with increasing P level was thought to account for higher numbers of adult and benthic baetids observed with increasing P concentration. Graphical comparisons between the control and treated troughs showed that they were similar in taxonomic composition of insects. Insect taxonomic richness did not change with increasing P concentration. These findings are important to fisheries researchers who are assessing the potential of stream fertilization as a technique to enhance salmonid populations in nutrient deficient streams.

TABLE OF CONTENTS

2.0 LIST OF TABLES

3.0 LIST OF FIGURES

4.0 ACKNOWLEDGEMENTS

I would like to thank my advisory committee which included Dr. M.L. Bothwell, Dr. T.G. Northcote, Dr. J.D. McPhail, Dr. G.G.E. Scudder, Mr. P.A. Slaney and Dr. C.J. Walters for advice and constructive comments on my thesis. I, also, appreciate the helpful reviews provided by Dr. N.T. Johnston and Dr. H.A. Quamme. The following people were important in the support of the project; Mr. K.I. Ashley, Mr. A.D. Martin, Mr. C.J. Perrin, Mr. B.O. Rublee, Mr. B.R. Ward and Mr. K.W. Wilcox. Also, Dr. J.H. Mundie and Dr. J.R. Post provided valuable suggestions on experimental design and techniques. This work was supported by an NSERC Operating Grant to Dr. T.G. Northcote and funding from the British Columbia Ministry of Environment, Fisheries Branch and the Nechako Fisheries Conservation Program. Valuable technical assistance was provided by Mark Beere, Jeff Burrows, Ray Carriere, Vera Bredow, Chris Giroux, Franzika Gross, Lindy Looy, Heather Quamme, Stephan Schug, Ryan Slaney, Katharine Staiger-Williams, Lynnel Steinke, Michelle Venne and the staff of the North Vancouver Island Salmonid Enhancement Society. Thanks to T.W. Chamberlin and the staff of the B.C. Ministry of Environment, Fish and Wildlife Branch, Skeena Region Headquarters for work space and support provided in Smithers, British Columbia.

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5.0 INTRODUCTION

The relative importance of predators and resources in controlling the abundance or biomass of aquatic organisms has been long studied in lakes and ponds (e.g. Hrbacek et al. 1961, Arruda 1979, Shapiro 1979, Shapiro and Wright 1984, Carpenter et al. 1985, 1987, Ranta et al. 1987, Perrson et al. 1988). About half of the explained variation in productivity among lakes is thought to result from nutrient supply, turnover time of the water and vertical mixing (Schindler 1978, Schindler et al. 1978, Carpenter and Kitchell 1987, 1988). The remainder results from the effects of predation "cascading" through to lower trophic levels (Carpenter *et al.* 1985, Carpenter and Kitchell 1988).

In contrast, experimental assessments of bottom-up (resource limitation) and top-down (predation) trophic interactions in riverine and stream ecosystems are relatively few (Deegan and Peterson 1992, Power 1984b, Peterson *et al.* 1993a, Peterson *et al.* 1985, Feminella et al. 1989, Johnston et al. 1990). The extent to which bottom-up nutrient control in streams propagates throughout the food web has been poorly studied.

Recently, studies have shown that the biomass of insects (Hart and Robinson 1990, Mundie *et al.* 1991) and insectivorous fish (Slaney and Ward 1993, Peterson *et al.* 1990)

may be enhanced by addition of inorganic phosphorus and nitrogen through increases in autotrophic production.

Some periphytic algae are thought to be high quality food for many aquatic insect grazers (Lamberti and Moore 1984). Nitrogen and phosphorus augmentation can enhance areal biomass of benthic algae (Stockner and Shortreed 1978, Elwood *et al.* 1981, Grimm and Fisher 1986, Perrin et al. 1987, Bothwell 1989, Lohman *et al.* 1991) and microbial growth in streams (Peterson *et al.* 1985, Hullar and Vestal 1989). The effect of external phosphorus concentration on algal biomass (periphytic diatoms) has been well described by Bothwell (1989).

The abundance or biomass of insect algal grazers in streams may be set by the availability of periphytic algae. It is though that the stream invertebrates are food limited (Richardson 1993). Evidence to support this hypothesis comes from correlative studies between macroinvertebrate densities and their food supply (Egglishaw 1964, McKay and Kalf 1969, Hawkins and Sedell 1981, Drake 1984, Flecker 1984, Murphy *et al.* 1986, Richardson and McKay 1991), invertebrate density manipulations (Lamberti *et al.* 1987, McAuliffe 1984a, b, Hart 1985, 87, Richardson 1993) and food supply manipulations.

The extent to which nutrient levels affect different elements of the periphytic community and translate into population effects for aquatic insects has rarely been determined. Information concerning insect response to nutrient enhancement in terms of abundance, composition, and timing of response is limited (Mundie *et al.* 1991). The relationship

between ambient nutrient concentration and the insect abundance, biomass and composition has never been quantified experimentally in streams over a broad range of nutrient levels.

Previous fertilization experiments have usually involved a single treatment at a high level of nutrients in either artificial stream troughs or whole rivers. Mundie *et al.* (1991) assessed the insect community response to nutrient enrichment for one level of phosphorus (10 ug $P \cdot l^{-1}$) in fish-excluded flow-through troughs and found increases in total insect numbers mainly due to higher numbers of Chironomidae. Hart and Robinson (1990) followed the effect of phosphorus addition at one high level (60 ug $P \cdot l^{-1}$) on two species of grazing caddisflies, *Leucotrichia pictipes* and *Psychomyia flavida*, in wooden flumes where fish, crayfish and predatory insects were present. They found that the larvae of both insect species had higher individual mass, developmental rates, and population densities in phosphorus treated flumes.

Three whole river fertilization studies (Elwood *et al.* 1981, Johnston *et al.* 1990, Peterson *et al.* 1993a) have resulted in greater abundance or biomass at higher trophic levels including invertebrates and/or fish. Increased densities of the snail, *Goniobasis clavaeformis*, were found in an experimentally enriched reach of Walker Branch, a Tennessee woodland stream (Elwood *et al.* 1981). Johnston *et al.* (1990) and Deegan and Peterson (1992) found that fertilization resulted in greater fish growth. Increases in sizes of fish have been attributed to increased algal productivity and higher insect abundances, a major component of fish diet.

On the Keogh River, in British Columbia, mean weights of juvenile steelhead trout and

coho salmon increased with fertilization (Johnston *et al.* 1990). A preliminary study, by the same researchers, suggested that the upper Keogh River produced 3-5 times the total insect biomass in fertilized sections than untreated sections; however, the effects of nutrient additions could not be separated from location effects. The authors suggested that increases in fish biomass may have resulted from greater insect abundance with nutrient treatment. Their proposition was supported by previous studies in which lotic salmonid abundance (Slaney and Northcote 1974, Mason 1976, Wilzbach et al. 1986) and size (Mason 1976, Wilzbach et al. 1986) had been shown to increase with food availability. Salmonid standing stocks (Murphy *et al.* 1981, Bowlby and Roff 1986) and growth rates (Warren et al. 1964, Wilzbach *et al.* 1986) are often correlated with biomass of benthic prey. Researchers have also found that fish growth (Gibson and Haedrich 1988) or standing crop (Hoyer and Canfield 1991) is correlated with nutrient levels measured in stream surveys.

Whole river fertilization increased the size of both young of the year and adults of Arctic grayling on the Kupuruk River in Alaska (Peterson *et al.* 1993a). Neutral lipid storage in adult grayling was increased in treated areas compared to controls (Deegan and Peterson 1992). The abundance of the total number of insects was not strongly affected by phosphorus additions but the relative importance of different species shifted over time. There were increases in numbers of *Baetis lapponicus* and *Brachycentrus americanus* while *Prosimulium martini* declined in abundance (Peterson *et al.* 1993a). The growth rates of the four dominant large insect species increased in response to treatment. By examining the nitrogen and carbon stable isotope ratios of Kuparuk River food web components, Peterson *et al.* (1993a) traced algal production stimulated by fertilization through to tissues of insect

ivorus grayling.

It has been suggested that fertilization may be used as a technique to enhance stream rearing salmonid populations that are food limited (Johnston *et al.* 1990). Whole river fertilization has been shown to increase smolt size and may improve marine survival of stream reared coho and steelhead (Johnston et al. 1990 and Slaney and Ward 1993). Increased adult returns have been reported for coho salmon (Hager and Nobel 1976) and steelhead trout (Ward and Slaney 1988) with greater smolt size.

Despite the body of knowledge described above, few studies of streams have examined the effect of nutrient concentration on the abundance or biomass of higher trophic levels under a uniform set of environmental conditions. The objectives of this study were to quantatively establish the relationships between: (1) phosphorus concentration and the areal biomass of periphytic algae, and (2) phosphorus concentration and the abundance and composition of stream insects. Uniform physical conditions were established by carrying out experiments in a stream mesocosm, 17 artificial stream troughs located on the Keogh River. This river near Port Hardy, British Columbia, was selected as a study site because it is a nutrient limited coastal stream. Previous research involving a whole river fertilization experiment conducted on the Keogh River between 1983 and 1986 (Johnston *et al.* 1990), provided background experimental data. Experiments were simplified by excluding insectivorous fish from the mesocosm.

Previous work has shown that phosphorus is very low ($< 1\ \mu g\ P \cdot l^{-1}$) in the Keogh River and suggested that phosphorus may be the primary limiting nutrient to productivity (Perrin *et*

al. 1987). Target nutrient concentrations for this study (0.5 - 50 g $P \cdot l^{-1}$) were selected to enhance growth rates of cells within the algal mat that might be phosphorus limited due to slow diffusion of phosphorus to the underlying cells (Bothwell 1989). Nitrogen was added at a constant ratio to ensure that it did not become limiting.

The establishment of the above relationships is important to fisheries researchers who are assessing the potential for fertilization of nutrient deficient coastal streams as a technique to enhance salmonid populations in British Columbia (Johnston *et al.* 1990, Slaney and Ward 1993). This study will also provide information for aquatic resource managers concerned with riverine eutrophication.

6.0 DESCRIPTION OF STUDY SITE

The experiment was carried out on the Keogh River (127°25' W by 50°35'N), a third order coastal stream on northeastern Vancouver Island, near the town of Port Hardy in southwestern British Columbia. The experimental mesocosm was located 31 km upstream of the river mouth, approximately 1 km downstream from Keogh Lake outlet (see Figure 1).

The river is 32 km long with a 130 km^2 watershed in the Coastal Western Hemlock forest. Western hemlock (*Tsuga heterophylla*), red cedar (*Thuja plicata*), and spruce (*Picea sitchensis*) dominate mature forests. Approximately 45% of the watershed has been logged during the last 30 years. The headwaters of the Keogh River were logged to the streambank about 20-25 years ago including the area where the experiment was located. In logged areas the major riparian species are red alder (*Alnus rubra*), salal (*Gaultheria shallon*), willow (*Salix spp.*), and sedges and grasses (Johnson *et al.* 1990) and to a lesser extent coniferous species. Detailed descriptions of the Keogh River are given in Ward and Slaney (1979), Slaney *et al.* (1986), Perrin et *al.* (1987), and Johnston *et al.* (1990).

The wetted mean width of the river at mean summer flow is 8.1 m (range 5-15 m). Mean annual discharge is 5.3 $m^3 \cdot s^{-1}$ with a minimum in mid-summer of 0.1 $m^3 \cdot s^{-1}$ and an estimated winter maximum flow of 254 $m^3 \cdot s^{-1}$. Mean summer flows in the upper-river (28 km from the mouth) and near the mouth (3 km) are about 0.5 $m^3 \cdot s^{-1}$ and 1.6 $m^3 \cdot s^{-1}$, respectively (values from Johnston *et al.* 1990). In 1991, at this experimental site, the wetted width ranged from 6.0 - 7.0 m and the flows ranged from 0.14 - 0.39 $m^3 \cdot s^{-1}$ between May 10 and

July 8.

Ambient nutrient concentrations of the Keogh River in spring to summer are very low. Johnston *et al.* (1990) determined soluble reactive phosphorus (SRP) levels to be $< 1\ \mu g \cdot l^{-1}$; total dissolved phosphorus, $5\ \mu g \cdot l^{-1}$; nitrate nitrogen, $< 15\ \mu g \cdot l^{-1}$; and total ammonia, $< 5\ \mu g \cdot l^{-1}$. Nutrient concentrations have been found to elevate with declining flows through the summer in the upper river (Perrin *et al.* 1987); inorganic dissolved phosphorus increased slightly while nitrate nitrogen increased up to 4-fold. Mean pH is 6.9, total alkalinity is 7.0 mg $\cdot l^{-1}$ and total dissolved solids are 30 mg $\cdot l^{-1}$ (Johnston *et al.* 1990). Mean pH at the study site was 6.9; mean true colour, 19; mean turbidity, 1.3; and mean total alkalinity, 9.0 mg $\cdot l^{-1}$ at the mesocosm head tank, based on five collection dates (1991; May 29, June 4, 10, 18, 25) at a mean flow of 0.24 $m^3 \cdot s^{-1}$. The extremes of water temperatures at the study site were 12.5 - 21 °C over the course of the experiment.

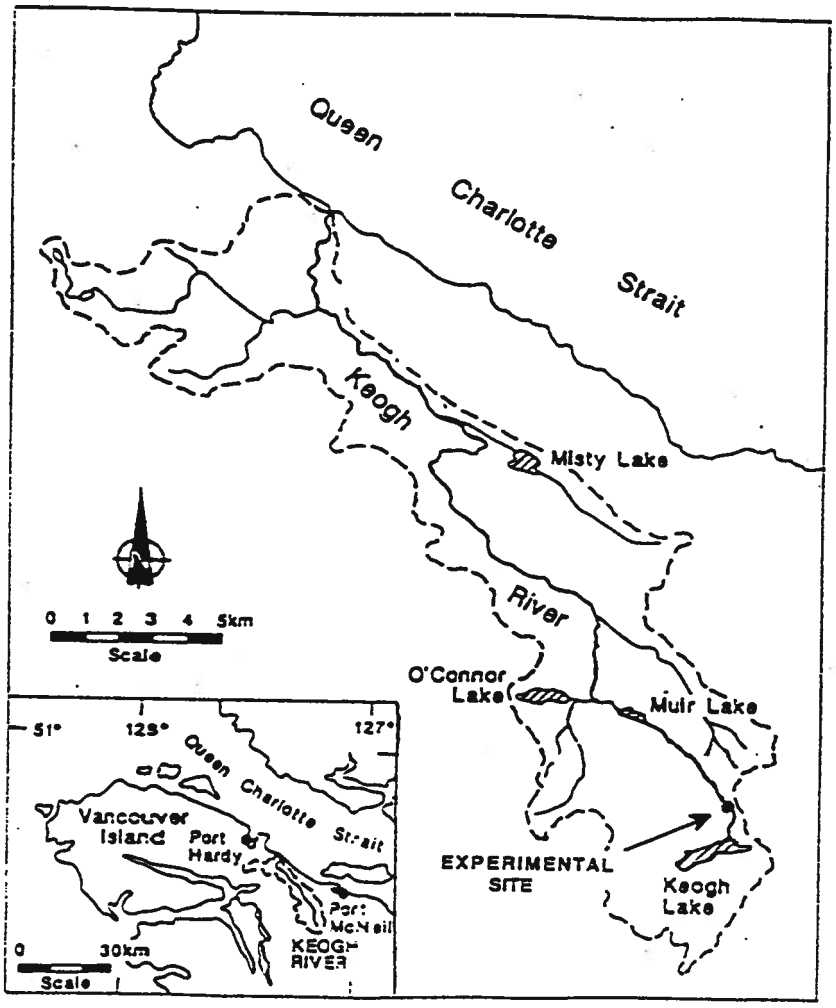

Figure 1. **Keogh River watershed with the location of the artificial stream troughs.**

7.0 METHODS

7.1 Description of mesocosm apparatus

The mesocosm consisted of seventeen flow-through troughs (each 1.52 m x 0.20 m x 0.20 m) assembled at the stream side. The troughs were fabricated from clear plexiglass. Water and biota from Keogh River were delivered to the mesocosm by gravity through a 300 m long (15 cm diameter) plastic pipeline fitted to a head tank. Water flow from the head tank to each of the troughs was adjusted to approximately 1 $l \cdot s^{-1}$ by the use of rotating polyvinyl chloride (PVC) standpipes and flexible nylon tubing similar to Mundie *et al.* (1991). High rates of hydraulic flushing within the troughs (approximately 9 seconds residence time) ensured that trough water was similar in quality to river water and that added nutrients remained constant over the trough length. Water flows in the troughs were checked and adjusted at least 3 times per week. Excess water, maintained in order to adjust water flow to the troughs, overflowed from slots at the back of the head tank and a valve off the main pipeline.

Each trough was filled with gravel to a depth of 7 cm over an area of 0.30 m^2. Numbers of lotic insect larvae have been found to be highest in the upper 10 cm of stream substrates (William and Hynes 1979). The design of the artificial streams in this experiment did not allow for vertical and horizontal migration of crawling insects to and from the troughs. Seventeen percent of trough sand and gravel passed through a seive size of size 7.9 mm; forty-three percent was 7.9 - 19.1 mm, and forty percent was 19.1 - 50.8 mm (by mass). Four baskets (100 cm^2 each) filled with gravel were placed at the downstream end of the

gravel for purposes of subsampling benthic insects. Water in the troughs covered the gravel to a depth of 3.0 cm (standard error (SE) = 0.3, n = 17). Surface velocities of the troughs averaged 21.3 $cm \cdot s^{-1}$ (SE = 0.5, n = 17). Results of simple linear regression analyses demonstrated that there was no systematic variation in surface velocity across the mesocosm ($p = 0.34$, $r^2 = 0.00$, $t_{.05(2)16} = -0.98$). The trough environment was designed to simulate the characteristics of a stream riffle including a fast current, coarse substrates, some sand content and a low accumulation of organic matter. Water depths in the troughs were similar to only the shallowest areas of the natural stream riffles where water depths ranged 5 - 14 cm and water velocities averaged 27.3 $cm \cdot s^{-1}$ (for six sites located near the mesocosm).

The bottom of the trough, downstream of the gravel, was fitted with a sheet (320 cm^2) of open cell Styrofoam DB (Snowfoam Products Ltd., El Monte, California) that provided a substrate for periphytic algae that could be easily monitored throughout the study. Artificial substrates such as styrofoam are commonly used to reduce periphyton variability. In a recent study by Morrin and Cattaneo (1992), chlorophyll estimates were found to be significantly less variable on artificial than on natural substrates. However, other estimates of biomass in this study (including ash-free dry mass, dry mass, density and biovolume) did not confirm this finding. I used chlorophyll *a* per area as a means to estimate algal biomass on the styrofoam substrates. Styrofoam substrates selectively promote the colonization of periphytic diatom communities (for example Bothwell 1989). The mesocosm site was partially shaded by a vascular plant canopy. All troughs received full shade, partial shade and full sunlight during the course of a day as shadows moved across the mesocosm.

A funnel trap for emerging adult insects covered the length and completely sealed the top of each trough (Mundie *et al.* 1991). Openings on the side walls of the traps were fitted with 355 μm mesh Nitex netting to allow air movement but, prevent the escape of captured insects. All adult insects were funneled into a drop trap containing 50% ethanol plus several drops of liquid soap to act as a surfactant to reduce surface tension in order to trap insects more easily.

Nitex drift nets (100 μm mesh) were used to monitor insect immigration to and emigration and from the troughs by filtering the inflowing or outflowing stream water. The inflow nets prevented insect immigration and colonization of the troughs one day a week during the experimental period (described in Methods).

Figure 2. **The mesocosm apparatus. The experimental treatments of the troughs from left to right were 0.5, 0 + no insect immigration, 0, 0, 2.5, 5, 10, 2.5, 5, 10, 0.5, 2.5, 5, 0, 0.5, 10, 50 μg $P \cdot l^{-1}$.**

7.2 Nutrient treatments and physical measurements

This experiment involved six target levels of total phosphorus; 0, 0.5, 2.5, 5, 10, and 50 $\mu g\ P \cdot l^{-1}$. Each treatment was replicated 3 times except for the 50 $\mu g \cdot l^{-1}$ treatment which was unreplicated. Treatments were assigned to the troughs at random so as not to correspond with possible effects resulting from horizontal gradients across the troughs.

Nitrogen was added to troughs at a constant ratio of 2:1, N:P (atomic weight) or 0.9:1 (wt/wt). Blooms of inedible blue-green algae can occur at low N:P ratios in lakes (Schindler 1975, Tilman 1977). Previous whole river fertilization of the Keogh River at an N:P ratio of 1:1 (wt./wt.) in 1984 did not result in a bloom of blue-green algae (monitored using styrofoam substrates). A similar N:P ratio was chosen for the present experiment. Background levels of dissolved inorganic nitrogen ($< 20\ \mu g\ N \cdot l^{-1}$) on the Keogh River were thought to be high enough to permit maximum algae cellular growth rates under natural conditions. A bioassay conducted on the Nechako River (Perrin 1989) examined the biomass levels of periphytic algae as a function of nitrogen addition ($0 - 100\ \mu g\ N \cdot l^{-1}$) at surplus phosphorus concentrations. In Perrins's experiment sixty to seventy percent of the maximum biomass response measured was achieved at a N concentration of $10\ \mu g \cdot l^{-1}$.

The source of nutrients (supplied by Coast - Agri, Abbotsford, British Columbia) used in the present study was a liquid agricultural fertilizer blend of 32-0-0 (50% urea, 25% ammonium and 25% nitrate by mass) and 10-34-0 (10% ammonium and 34% total phosphorus as P_2O_5). Total phosphorus was 100% water soluble and available as 25-35% ortho-phosphate and 65-75% 4-12 chain polyphosphates. The ammonium polyphosphate

fertilizer (10-34-0) was also comprised of micronutrients. These included Boron (0.01% B by mass), Calcium (0.07% CaO), Copper (0.0005% CuO), Iron (0.56% Fe_2O_3), Magnesium (0.5% MgO), Manganese (0.015 MgO), Potassium (0.12% K_20), Sulfate (1.8% SO_4) and Zinc (0.10% ZnO). This fertilizer blend was used because it has been shown to be cost efficient and easily applied to whole rivers in large scale studies (Slaney and Ward 1993).

Beginning April 27, 1991 water from the stream was run through the troughs for 21 days to allow colonization by stream biota. Nutrient additions began May 18 and ran until July 8, 1991. A second experiment was carried out from July 8 - August 22. It was thought that polyphosphates in the agricultural fertilizer might not have been biologically available over the length of the troughs. Nutrient levels in the second experiment were the same as the first experiment but fertilizer types were switched from the agricultural fertilizer to readily available reagent grade nutrients in an attempt to achieve a more dramatic increase in algal biomass with increasing phosphorus concentration. In the second experiment, Total dissolved phosphorus was available as Soluble orthophosphate. The second experiment was, however, confounded by the first because gravel and insects from the first experiment were not replaced. Styrofoam substrates for algal biomass accrual were replaced. Results of the second experiment are not reported in detail here.

Fertilizer was dripped into the head of the artificial stream troughs via microbore tubing using a Technicon auto-analyzer pump. Rate of nutrient delivery was adjusted by altering microbore tubing size and stock concentration. Phosphate concentrations in troughs were calculated from known dilutions of standard phosphorus and nitrogen solutions. A plexiglass baffle at the head of each trough created water turbulence and ensured mixing of stream

water and nutrient additions.

Samples for water chemistry were taken at weekly intervals from all troughs in order to check computed nutrient additions. Because of limited sensitivity of analytical methods for phosphorus, only higher levels of phosphorus additions (2 - 50 $\mu g\ P \cdot l^{-1}$) could be accurately verified. Water samples were collected and analysed within 24 hours. Nitrogen and phosphorus analyses were carried out by Zenon laboratories, Burnaby, British Columbia on a Technicon AA2 auto-analyzer. Analyses of $N0_3 + NO_2$ -N, NO_2-N, Total P, Soluble Total P and Soluble ortho-P were performed according to modified procedures of Taras et al. (1971) described in McQuaker (1976). Analyses of NH_4-N were performed according to modified procedures of Greenberg (1980) described in McQuaker (1989). The limit of detection was 3 $\mu g\ P \cdot l^{-1}$ for Total P, Soluble Total P and Soluble ortho-P; the limit for low level Soluble ortho-P was 1 $\mu g\ P \cdot l^{-1}$. The detection limit for NH_4-N and NO_2-N was 5 $\mu g\ N \cdot l^{-1}$; low level NO_2-N was 1 $\mu g\ N \cdot l^{-1}$ and $N0_3 + NO_2$ -N and NO_3-N was 20 $\mu g\ N \cdot l^{-1}$.

Water temperature was measured with a continuously recording Ryan model J-90 submersible thermograph, placed in the mesocosm head tank. The instrument was calibrated weekly. No difference was found between stream temperature and water running through the mesocosm.

7.3 Algal community

Algal biomass was sampled by removing two periphyton cores (6.2 cm^2), weekly, from styrofoam sheets in each trough. The time-course of algal biomass accrual as measured by chlorophyll *a* was monitored on styrofoam plates from April 2 - May 31. These plates were replaced when algae the sloughed from styrofoam, and new plates were monitored from May 31 - July 8.

Chlorophyll *a* analyses followed the procedure of Parsons *et al.* (1984). The styrofoam cores were frozen at -20 °C until later (3-5 months) chlorophyll *a* flourometric determination. Algal cells were disrupted in 10-15 mL of 90% acetone (at 0°C) using a Potter-Elvehjem tissue grinder (3 minutes) and a sonication bath (5 minutes). The homogenate was incubated in a dark refrigerator (3 °C) for approximately 20 hours and then centrifuged for 5 minutes at setting 5 in a Damon IEC clinical centrifuge to remove solids. Chlorophyll *a* from each core was measured separately using a Turner Designs model 10 flourometer. A correction was made for phaeophytin (Parsons *et al.* 1984). Duplicate cores from each trough were averaged for each date. Bothwell (1983) found that chlorophyll *a* levels extracted from individual cores (5.0 cm^2) of algae (n = 5) adhering to styrofoam had a coefficient of variation of 10.9%. In my study, duplicate cores from each trough had coefficients of variation that ranged from 2 - 55% (mean = 14%) across the seventeen troughs (determined before treatment initiation, May 17).

The peak algal biomass (PB) found on the styrofoam substrate over time was used to

describe the relationship between P concentration and areal algal biomass (Bothwell 1989). PB was estimated by averaging chlorophyll *a* values observed on the second set of styrofoam sheets (May 31 - July 8) for the final two collection dates (July 3 and 8). Peak chlorophyll *a* levels on the first set of styrofoam sheets occurred after only eight days of treatment application and were thus not used to estimate PB.

Extraction and quantification techniques of chlorophyll *a* used in this study were compared to those used previously (Johnston *et al.* 1990 and Perrin *et al.* 1987). Four cores of periphyton were sampled per sheet of styrofoam with various levels of accrued periphyton biomass from the Slocan River near Nelson, B.C. Eighteen styrofoam sheets were sampled in total. Chlorophyll *a* on two of the cores of each sheet was measured using techniques of this study described above and two were analyzed using previous techniques and were carried out by Zenon laboratories.

Periphyton adhering to gravel was sampled on July 8 and fixed in Lugol's solution for taxonomic identification and cell counts. Two stones per trough were dropped directly in Lugol's solution of a standard volume of 500 ml; later, algae was scraped from both stones and pooled. Quantitative cell counts were made at 500X magnification in Utermöhl chambers from subsample volumes of 25 ml. A minimum of 100 individuals of the predominant species and at least 500 cells in total were counted. The areas of the rocks were calculated with a planimeter after obtaining an impression of the surface with aluminium foil.

7.4 Insect community

Adult insects were collected weekly from emergence traps and preserved in 90% ethanol. Drift nets that collected emigrating insects from the outflow of the troughs were emptied twice a week (3 day collection periods). Once a week, drift nets were placed on the inflow of the troughs for 24 hours to assess the immigration of insects to each trough. One pipe from the head tank was monitored for immigrating insects three times a week (two 3 day and one 24 hour collection period). As a result drift nets excluded insects from one trough following the 21 day colonization period described above.

Benthic insects from two of the baskets in each trough (200 cm^2) were sampled at the end of the experiment, July 8 . Drift nets (100 μm mesh) were simultaneously placed on inflow and outflow of each trough while baskets full of gravel were removed from the trough. Insects were released from the gravel by gently brushing and rinsing the stones. Released insects were captured in the outflow net. Drifting and benthic insects were preserved in 5% formalin.

Benthic insects were also sampled directly from the stream using a Hess sampler of 0.05 m^2 with a 100 μm mesh net. The substratum was sampled to a depth of approximately 10 cm during base flow conditions, in water depths of 7 - 15 cm. Three samples were taken from three different riffles.

Samples were hand-picked at 10X magnification. Sorting efficiencies were >90% for benthic and drifting insects determined by repeated picking. All adult insects were identified

and enumerated. Drifting and benthic insects were sieved through nested screens. Benthic insects greater than 650 μm were identified and enumerated. Generally, drifting insects greater than 1000 μm were enumerated and identified. All sizes of drifting insects sampled near the beginning of the experiment (May 31 and June 3) were examined.

Insect taxonomy follows Merritt and Cummins (1984). Invertebrates were identified at least to the family level and occasionally to genus. Generally, insect taxa were not sub-sampled. However, a gridded petri dish was used to sub-sample drifting Baetidae. Variance to mean ratio tests (χ^2 tests) for agreement with a Poisson series were performed according to Elliott (1977).

Results (below) show that Ephemeroptera (mayflies) was the only order collected to contain adult taxa that increased in number with increasing phosphorus treatment. Thus the effect of treatment on Ephemeroptera adult body length and total biomass was assessed for insects collected near the end of the experiment (June 27). Body length measurements were made using a dissecting scope at 10X magnification and a Summasketch Model MMIII digitizer calibrated with a stage micrometer. To make biomass measurements, insects were removed from ethanol, oven dried for approximately 20 hours at 60°C, and weighed on a Cahn/Ventron 21 automatic electrobalance.

7.5 Statistics

All linear regression analyses were completed using Microsoft Excel version 4.0 by least squares fitting methods. In all tests, the critical level of significance was $\alpha = 0.05$. When the relationship between the variables was visibly non-linear, I did a log transformation of the x axis that linearized the data prior to the analyses (Zar 1984). A log transformation of the y axis was made occasionally in order to stabilize the variance. Assumptions of the regression were validated before and after transformation by graphical examination of residuals.

All regressions were initially completed on replicated treatments only (0 - 10 μg $P \cdot l^{-1}$) to test for significance. These results are presented in tables and text. If the above regressions were significant I carried out regression analyses of the same data, but also included the high unreplicated treatment 50 μg $P \cdot l^{-1}$ and displayed the results graphically.

8.0 RESULTS

8.1 Nutrient treatments and Algal Community Response

Increases in phosphorus addition to troughs led to measured increases in Total P (Table 1). Measured Total phosphorus above background levels was approximately three times lower than target levels of phosphorus for treatments of 2.5-10 $\mu g\ P \cdot l^{-1}$. Measured nutrients were elevated up to 8.3 and 2.6-3.75 times the controls for Total P and Dissolved Inorganic Nitrogen, respectively (Table 1 and 2). Measured N:Total P ratios ranged from 1.5 - 5 in experimental and control troughs.

There was no significant difference among troughs in chlorophyll *a* levels before treatments began (measured from cores collected on May 17, 45 days after initial placement of the first set of styrofoam plates in the troughs, $p = 0.66$, $r^2 = -0.06$, $t_{.05(2)14} = -0.44$, for treatment troughs 0-10 $\mu g\ P \cdot l^{-1}$). There was no systematic effect of trough location on chlorophyll *a* levels across the mesocosm for the same date ($p = 0.40$, $r^2 = -0.02$, $t_{.05(2)14} = -0.86$). A significant increase in chlorophyll *a* with increasing phosphorus concentration was observed after only 6 days (May 24) of treatment ($p = .001$, $r^2 = 0.54$, $t_{.05(2)14} = 4.05$) (Figure 3.1). However, I was not able to follow the effects of phosphorus treatment on the accrual of algal biomass on these styrofoam plates over time because algae began sloughing off the plates.

Table 1. **Mean inorganic phosphorus concentrations ($\mu g\ P \cdot l^{-1}$) measured for each target treatment.**

Target Total P Addition	Measured Total P[1] mean(SE)	Soluble Total P[2] (range)	Soluble ortho-P[2] (range)
0	4.6(0.6)	<3-3	<1[3]
0.5	4.6(0.4)	<3-3	<1[3]
2.5	5.1(0.1)	<3	<3
5.0	6.3(0.2)	4-6	<3
10.0	9.4(0.4)	5-6	<3-4
50.0	38.3	32	32

[1]Mean of three replicate troughs. Each replicate is an average value of total P measured on June 18,25 and July 2,91. Standard errors are given in brackets.

[2]Ranges of three replicate troughs measured on July 2,91. Values are typical of those measured weekly from May 22 to July 2.

[3]Values from low level nutrient analyses.

Table 2. **Mean inorganic nitrogen concentrations ($\mu g\ N \cdot l^{-1}$) measured for each target treatment**

Target Dissolved Inorganic Nitrogen Addition	Measured Dissolved Inorganic Nitrogen[1]
0	16-23[2]
0.5	14-23[2]
2.3	<25-25
4.5	<25-26
9.0	<25-29
45.1	60

[1]Measured total N (range) is based on adding the ranges of soluble NH_4-N and NO_3 + NO_2-N. Ranges are based on water samples from three replicate troughs measured on July 2, 91. Values are typical of those measured weekly from May 22 to July 2.

[2]Values from low level nutrient analyses.

Twenty-one to twenty-eight days (June 21 - 28) after placing a second set of styrofoam sheets in the troughs, there was an exponential increase in chlorophyll *a* for all nutrient treatments (Figure 3.2). One trough from which insects were excluded did not follow this pattern (Figure 3.3). Algal biomass built up quickly on the styrofoam sheets in this trough and remained high but fluctuated widely with time. Sloughing of the algae from the styrofoam was noted and may have accounted for some of the variability that was observed. Measurements of chlorophyll *a* from the insect exclusion trough were greater than control troughs over time for four of five sampling dates.

A significant relationship was observed between algal biomass and the log of phosphorus concentration (Figure 4). Peak algal biomass increased rapidly with phosphorus concentrations of 0 - 2.5 $\mu g\ P \cdot l^{-1}$ but showed diminishing returns at 2.5 - 10 $\mu g\ P \cdot l^{-1}$.

Chlorophyll *a* levels determined from styrofoam cores of this experiment were lower than previous studies of phosphorus concentration on periphytic areal biomass (Bothwell 1989, Perrin *et al.* 1987, Mundie *et al.* 1991). A check on the extraction and quantification techniques for chlorophyll *a* used here showed that this study had on average higher measurements than Zenon laboratories (mean from this study = 33.4 $mg \cdot m^{-2}$, mean from Zenon = 19.7 $mg \cdot m^{-2}$, paired-sample Student's t test, $t_{.05(2)(17)} = 6.74$, $p < 0.05$). Both laboratories showed similar relative trends in chlorophyll *a* levels. Thus, low chlorophyll *a* levels observed in this study did not result from a methodological artifact.

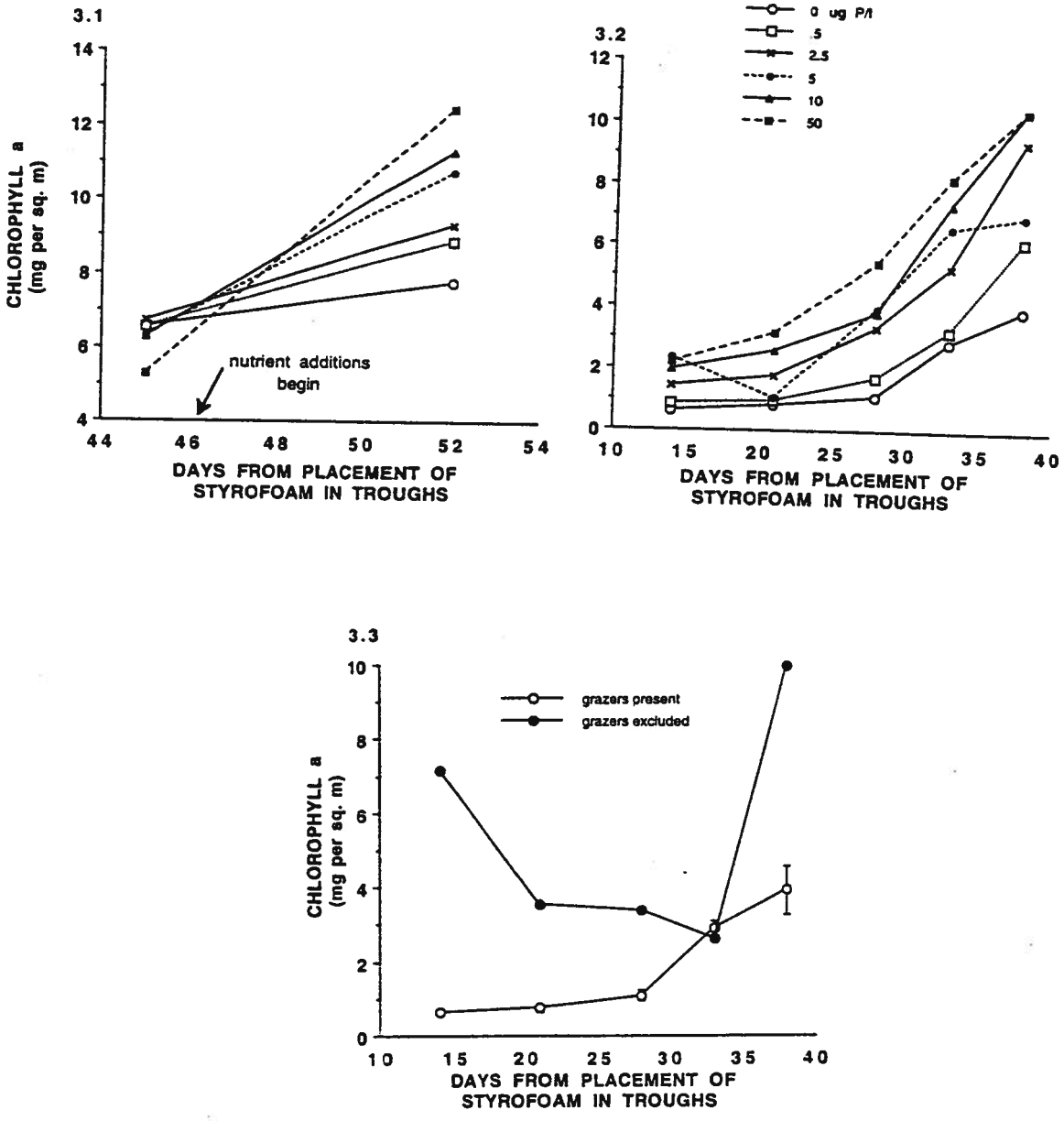

Figure 3. **Mean algal biomass accumulation measured as chlorophyll *a* from styrofoam plates. Sample size (n) = 3 except at 50 ug $P \cdot l^{-1}$ where n = 1. Nutrient treatments started May 18.**
(3.1) First set of styrofoam plates, placed in troughs from April - May 31.
(3.2) Second set of styrofoam plates, placed in troughs from May 31 - July 8.
(3.3) Algal biomass accumulation (chlorophyll *a*) on the second set of styrofoam plates. The grazer excluded trough with no phosphorus addition (n = 1) compared to the means of the control troughs (n = 3).

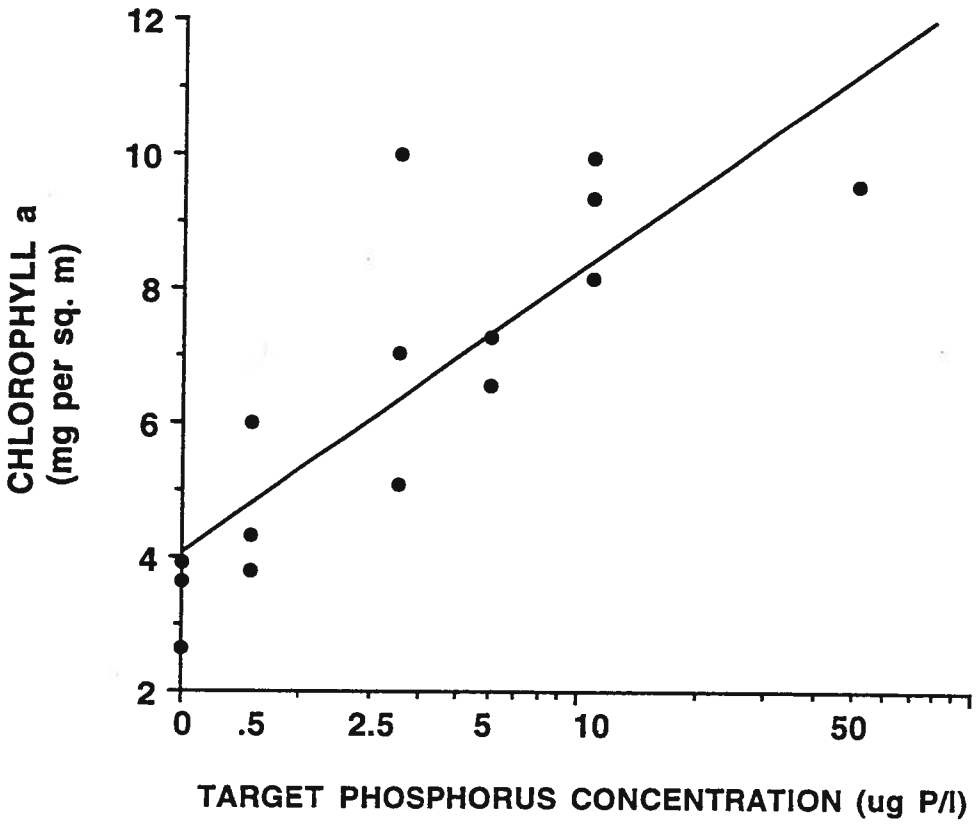

Figure 4. Peak biomass on styrofoam plates measured as chlorophyll *a* ($mg \cdot m^{-2}$) against target phosphorus concentration. Linear regression of the data fitted by least squares. Regression line above (all data) is $y = 4.05 + 4.19 \log(P)$. $r^2 = 0.67$. $p < 0.001$. Regression line (not shown) for treatments 0 - 10 ug $P \cdot l^{-1}$ only is $y = 5.09 * \log(P) + 3.70$. $r^2 = 0.69$ $p < 0.001$

The density of total cells, *Ocillatoria* sp., *Achnanthes minutissima* significantly declined with increasing phosphorus concentration (Figure 5). Regression analyses of *Synedra ulna*, and *Eunotia* sp. showed no significant changes in number with increasing phosphorus concentration ($p = 0.57$, $r^2 = -0.05$, $t_{.05(2)14} = -0.57$ and $p = 0.72$, $r^2 = -0.07$, $t_{.05(2)14} = -0.37$, respectively for treatments 0-10 $\mu g \cdot P \cdot l^{-1}$). Low numbers of other algal taxa did not permit similar analyses.

Algal cell composition sampled from the trough gravel substrate showed that cyanophytes, especially *Oscillatoria* sp., predominated at lower phosphorus treatments, while at higher concentrations *Achnanthes mimutissima* comprised a greater percentage of the total cell number (Table 4). There was no difference in the number of algal taxa with increasing nutrient additions ($p = 0.26$, $r^2 = 0.03$, $t_{.05(2)13} = -1.17$, for treatments 0-10 $\mu g \cdot P \cdot l^{-1}$).

The density of total algal cells (9726 cells $\cdot$ mm^{-2}), *Achnanthes mimutissima* (884 cells $\cdot$ mm^{-2}), and *Oscillatoria* sp. (5581 cells $\cdot$ mm^{-2}) in the insect excluded trough were 4.5, 2.4 and 4.2 times greater than the controls, respectively. In the controls, mean total cell density was 2178 cells $\cdot$ mm^{-2} (SE = 728), mean density of *Achnanthes mimutissima* was 365 (SE = 88) and mean density of *Oscillatoria* sp was 1314 cells $\cdot$ mm^{-2} (SE = 429). Visual observations of algae biomass suggested that removal of insects from the trough had a dramatic effect of increasing the algal standing crop. The composition of algal cells in the insect excluded trough was generally similar to control troughs (Table 4), except that there was an increase in the percent composition of one chlorophyte genus,

Oedogonium sp., 24% of total cells, in the insect excluded trough, compared to 0.1 - 1.4% of total cells in control and treatment troughs.

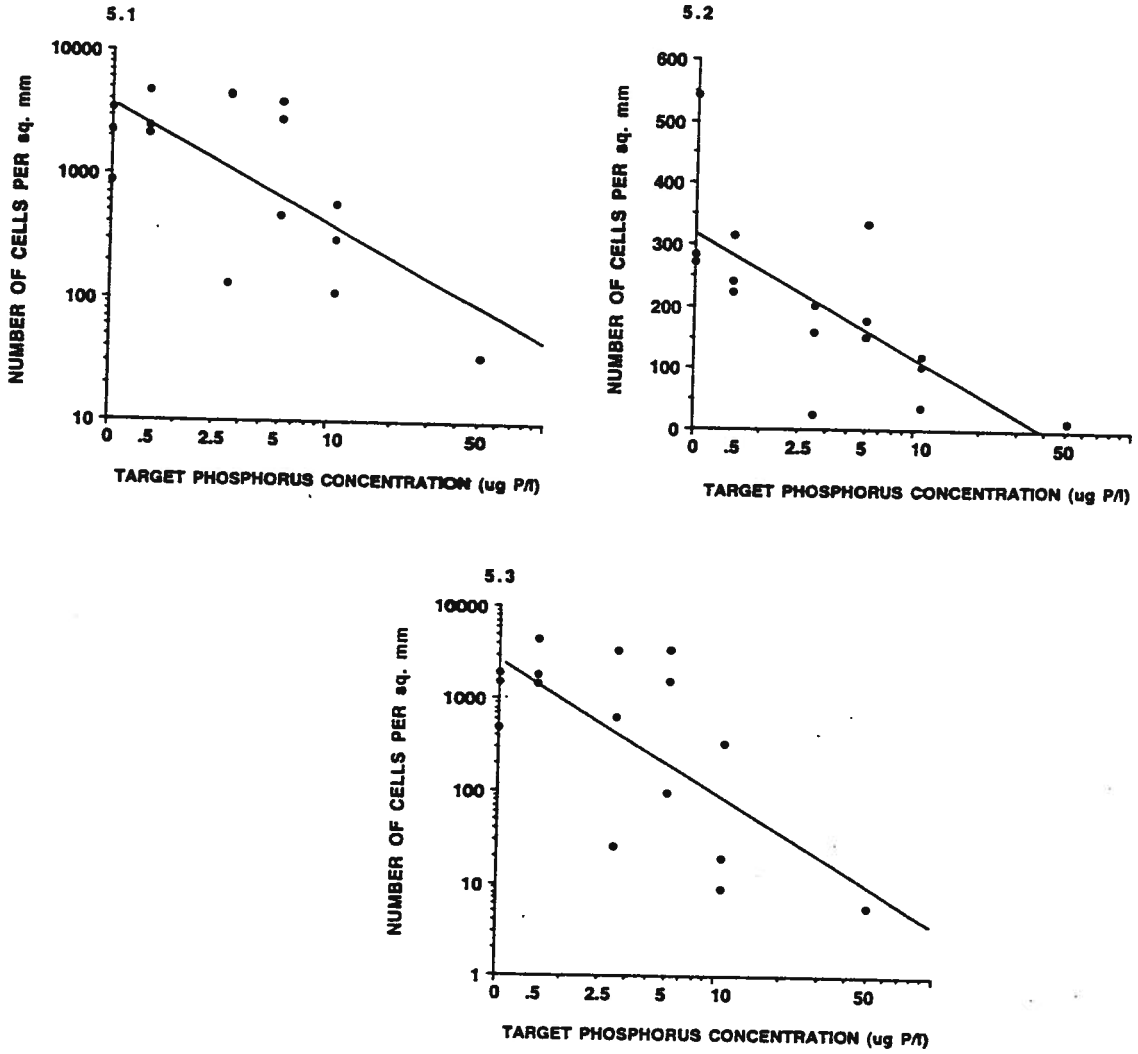

Figure 5. Density (cells·mm^{-2}) of algal cells collected from the trough gravel at the end of the experiment (July 8) against target phosphorus concentration. Linear regressions of the data were fitted by least squares.
(5.1) Total cell numbers. Regression line above (for all data) is $\log(y) = 3.56 + -0.95 * \log(P)$. $r^2 = 0.44$. $p = .003$. Regression line for treatments 0 - 10 ug P·l^{-1} only is $\log(y) = -0.73 * \log(P) + 3.48$. $r^2 = 0.21$. $p = 0.05$.
(5.2) *Achnanthes mimutissima*. Regression line above (for all data) is $y = 316.41 + -200.19 * \log(P)$. $r^2 = 0.48$. $p = .001$. Regression line for treatments 0 - 10 ug P·l^{-1} only is $y = -221.96 * \log(P) + 324.83$. $r^2 = 0.41$. $p = 0.005$.
(5.3) *Oscillatoria* sp. Regression line above (for all data) is $\log(y) = 3.36 + -1.39 * \log(P)$. $r^2 = 0.45$. $p = .002$. Regression line for treatments 0 - 10 ug P·l^{-1} only is $\log(y) = -1.29 * \log(P) + 3.32$. $r^2 = 0.29$. $p = 0.02$.

Table 4. **Percent composition of the algal cell number by taxa of the artificial stream troughs for each target phosphorus concentration (ug $P \cdot l^{-1}$). Percentages are based on algae collected from trough gravel at the end of the experiment (July 8).**

Taxon	0[a] + no insect immigration	0[b]	0.5[b]	2.5[b]	5.0[b]	10[b]	50[a]
Cyanophyta							
Oscillatoria sp.	57.4	60.3	83.3	71.5	74.1	38.1	16.4
Lyngbya sp.	5.7	2.0	3.5	7.6	5.5	6.9	0.0
Other	0.0	4.9	0.0	0.0	2.0	11.4	0.0
Chrysophyta-Bacillariophyceae							
Achnanthes mimutissima	9.1	16.8	8.4	7.7	9.3	26.2	42.7
Eunotia sp.	0.3	0.6	0.3	1.1	0.7	3.1	7.3
Synedra ulna	0.2	1.2	0.4	1.5	1.8	1.3	8.2
Tabellaria fenestra	1.4	2.2	0.0	4.3	1.5	2.6	5.5
Other	1.8	2.8	1.3	3.5	1.1	5.5	3.5
Chlorophyta							
Oedogonium sp.	24.0	0.1	1.4	1.3	0.8	1.1	0.0
Other	0.1	9.2	1.2	1.4	3.1	3.8	16.4

[a]percent composition from one unreplicated trough
[b]percent composition based on pooled counts from 3 replicate troughs

8.2 Insect Community Response

8.2.1 Adult insects

The timing pattern of total adult insect emergence was not affected by phosphorus concentration (Figure 6.2). Five to six weeks after the treatment initiation, the total adult insects reached peak numbers for all phosphorus concentrations. High numbers of emerging adults coincided with high stream temperatures (Figure 6). Total adult insect abundance collected at the end of the experiment (July 4) in emergence traps increased with phosphorus concentration; the relationship was nearly significant ($y = 85.68*\log(P) + 184.4$, $p = 0.08$, $r^2 = 0.15$, $t_{.05(2)13} = 1.89$, power $(1-\beta) = 0.71$, for 0-10 $\mu g\ P \cdot l^{-1}$). At 50 $\mu g\ P \cdot l^{-1}$ (unreplicated), total insect abundance appeared to increase after 17 days of fertilization and reached approximately three times the level of the controls after 47 days (Figure 6.2). Adult insects were also collected in drift nets placed on the outflow of the troughs. The total abundance of adults collected in drift nets near the experiment end (June 24) increased with increasing phosphorus concentration. The relationship was nearly significant ($y = 67.66*\log(P) + 113.8$, $p = 0.07$, $r^2 = 0.20$, $t_{.05(2)13} = 2.00$, for treatments 0-10 $\mu g\ P \cdot l^{-1}$). The regression statistics for the total number of adult insects collected in emergence traps over the entire experiment are given in Table 4.

The adult insect taxa (emergent insects traps) were comprised largely of Baetidae, Chironomidae, Simuliidae, and Trichoptera (see Figure 7). Adult Baetidae caught in emergence traps showed a significant increase in number to nutrient treatment ($y = 14.4*\log(P) + 10.79$, $p = 0.01$, $r^2 = 0.34$, $t_{.05(2)14} = 2.93$, for treatments 0-50 $\mu g\ P \cdot l^{-1}$)

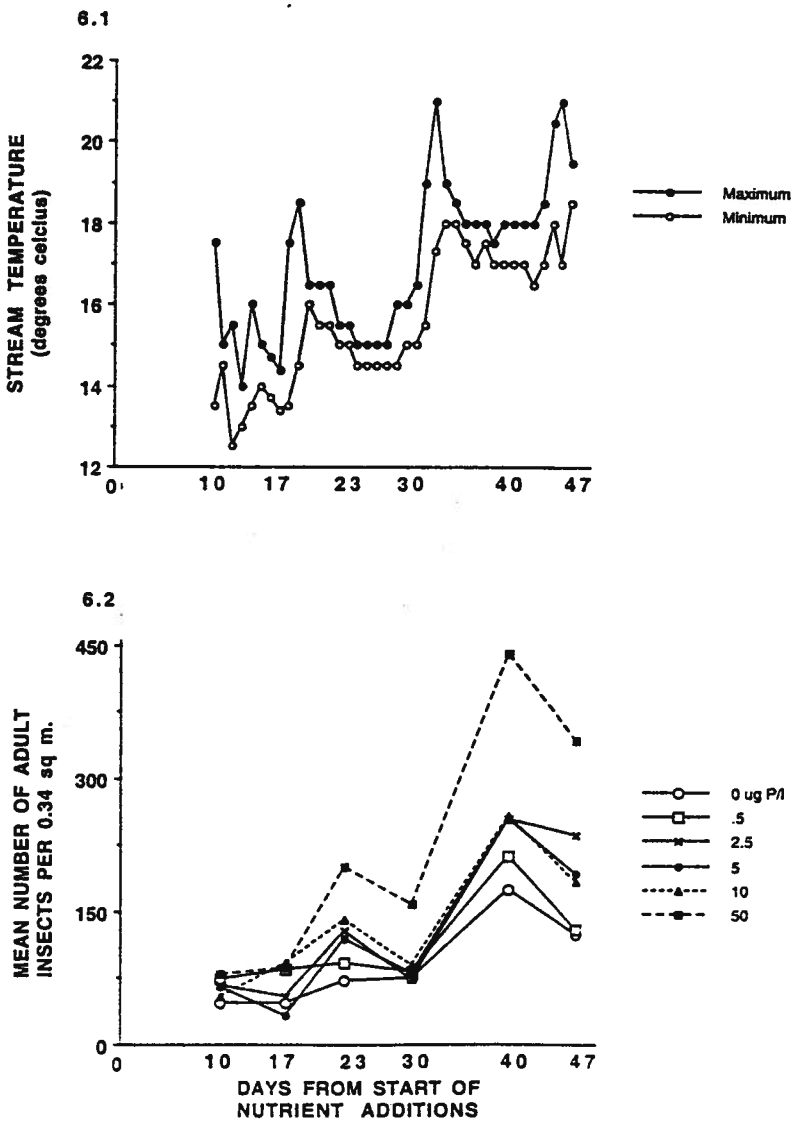

Figure 6. **(6.1) Daily minimum and maximum stream temperatures measured at the mesocosm head tank as a function of time.**
(6.2) Numbers of adult insects caught in emergence traps between May 19 and July 4 by target phosphorus concentration ($ugP \cdot l^{-1}$). In each case, the mean number of adult insects is plotted per date. Sample size (n) = 3 except at 50 ug Pl^{-1} where n = 1.

Table 4. **Linear regression analyses relating total numbers (y) of various insect taxa collected as adults from the emergence traps to target phosphorus concentration. Sample size (n) = 15 in all cases. Ordered with respect to decreasing p value.**

Insect Family (Order)	Regression[1] Equation	p	$t_{\alpha.05(2),13}$	r^2
Baetidae (Ephemeroptera)	y = 18.95 * log(P) + 15.13	0.004[2]	3.39	0.42
Total insects	y = 40.0 * log(P) + 101.09	0.08	1.86	0.15
(Miscellaneous Tricoptera)	y = 2.21 * log(P) + 2.31	0.10	2.92	0.13
Chironomidae (Diptera)	y = 19.07 * log(P) + 62.08	0.22	1.28	0.04
(Miscellaneous Plecoptera)	y = 0.08 * P + 1.92	0.29	1.11	0.02
Simuliidae (Diptera)	y = -0.28 * P + 11.90	0.34	-0.99	0.00
(Miscellaneous Diptera)	y = 0.40 * log(P) + 2.87	0.62	0.51	-0.06
Leptophlebiidae (Ephemeroptera)	y = 0.03 * log(P) + 2.00	0.69	0.40	-0.06
Heptageneiidae (Ephemeroptera)	y = -0.02 * log(P) + 1.93	0.73	-0.35	-0.07
(Miscellaneous Coleoptera)	y = log(P) + 0.63	0.96	-0.05	-0.08

[1] Regression analyses are based total taxon counts collected in emergence traps over time divided by the number of weeks for phosphorus treatments of 0-10 $\mu g\ P \cdot l^{-1}$ only.

[2] Regression analysis was determined to be significant at the "table-wide" α level using the sequential Bonferroni technique (Rice 1988). Taxa without this subscript next to the p value were nonsignificant at the "table-wide" α level.

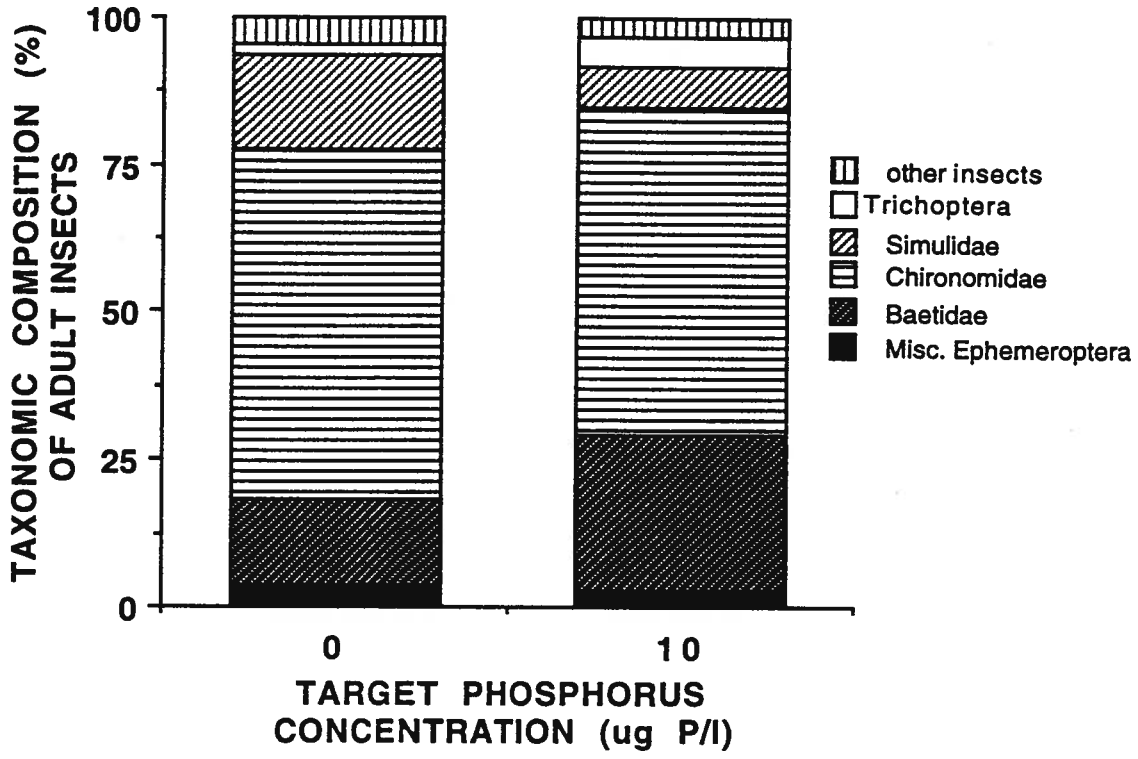

Figure 7. Percent composition of the predominant adult insect taxa collected from emergence traps of the artificial stream troughs at two phosphorus concentrations. Percentages are based on total insects collected from May 19 to July 4 and result from the mean of three replicate troughs.

after 23 days (June 10) (Figure 8). The magnitude of this response increased from May 28 - June 27, over the first 40 days of the experiment. The mean number of adult Baetidae immigrating to troughs in the drift was very low and averaged (for example) 1.3 per day (see Table 5). Adult Baetidae were captured both in emergence traps and drift nets. Numbers of adult Baetidae caught in both emergence traps and drift nets at the end of the experiment showed similar positive responses to increasing nutrient concentration (Figure 9). Numbers of baetid adults increased rapidly with increasing phosphorus concentrations of 0 - 2.5 μg P $\cdot$ l^{-1} but showed diminishing returns at 2.5 - 10 μg P $\cdot$ l^{-1}. The regression statistics for the total number of baetid adults collected in emergence traps per week over the course of the experiment are given in Table 4.

Numerically, adult Ephemeroptera comprised 20.3 - 35.1 % of total adult insects collected in emergence traps near at the end of the experiment (June 27). However, biomass measurements of the same samples indicate that Ephemeroptera contributed to a larger percentage (46.7 - 71.7) of the total insect dry mass (Figure 10). The effect of phosphorus concentration on total adult Ephemeroptera biomass was significant (Figure 11), but was nonsignificant for the biomass of other adult insects (taxa pooled) ($p = 0.72$, $r^2 = -0.07$, $t_{.05(2)13} = 0.35$, for treatments 0 - 10 μg P$\cdot l^{-1}$). The biomass of total ephemeropteran adults increased rapidly with increasing phosphorus concentrations of 0 - 2.5 μg P $\cdot$ l^{-1} but showed saturation at 2.5 - 10 μg P $\cdot$ l^{-1}. Treatment responses of ephemeropteran numbers and biomass, largely, resulted from positive increases of the genus *Baetis* (Family Baetidae) (Figure 12). Average mass per individual for adult Ephemeroptera did not change significantly with increasing phosphorus concentration ($p = 0.44$, $r^2 = -0.03$,

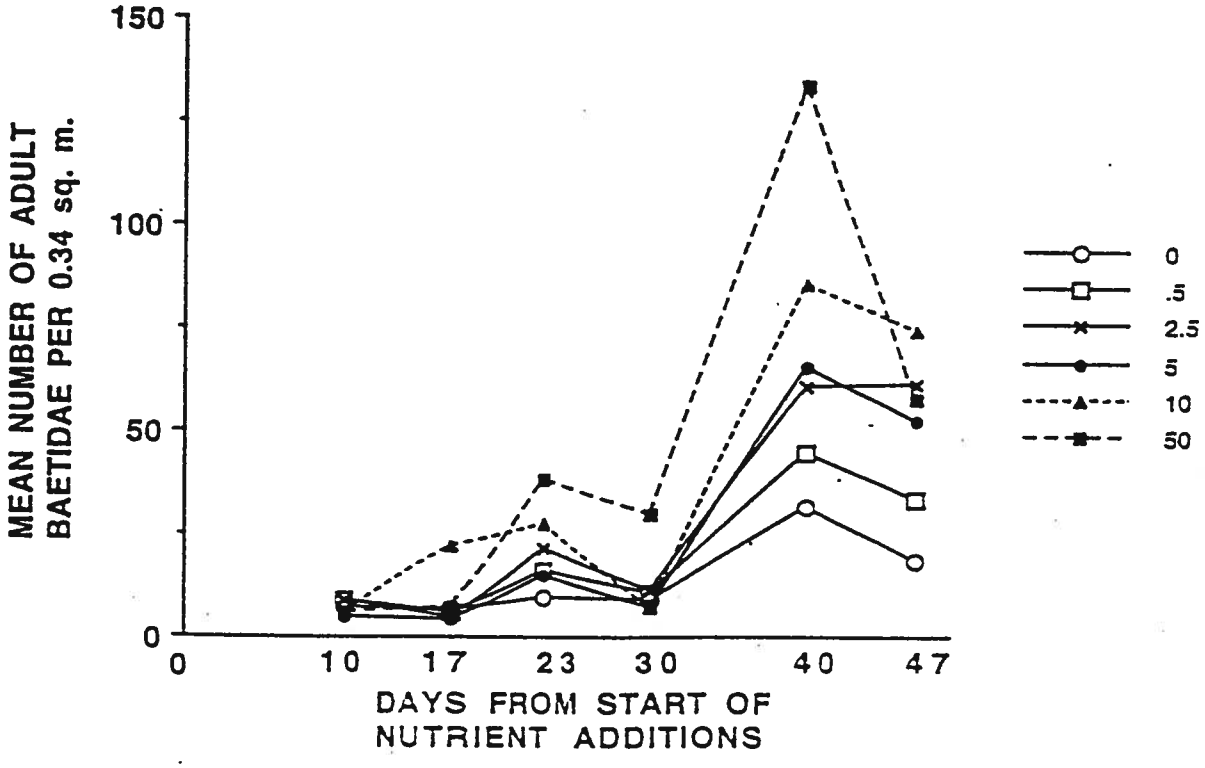

Figure 8. Number of adult Baetidae caught in emergence traps between May 19 and July 4 by target phosphorus concentrations (ug $P \cdot l^{-1}$). In each case, the mean number of adult insects is plotted per date. Sample size (n) = 3 except at 50 ug $P \cdot l^{-1}$ where n = 1.

Table 5. **Mean number of adult insects immigrating and emigrating per trough·day^{-1} by taxon. Sample size (n) = 3. Standard error is given in parentheses.**

Taxon	Mean number of adults drifting[1] to troughs·day^{-1} (Standard error)	Mean number of adults emigrating[2] from control troughs·day^{-1} (SE)	Mean number of adults emigrating[2] from 10 ug P·l^{-1} troughs·day^{-1} (SE)
Baetidae	1.3 (0.3)	14.4 (0.6)	33(3.0)
Chironomidae	57.0 (11.9)	37.9 (5.2)	39.6 (8.7)
Trichoptera	0.33 (0.33)	1.6 (0.6)	2.1 (0.8)
Simuliidae	24 (3.5)	4.6 (1.4)	3.0 (1.0)

[1]Immigration rates are based on 24 hour drift samples collected at inflow of troughs on July 3.

[2]Emigration rates are based on total numbers of adults trapped per day in emergence traps (10 day sample collected June 27) and drift nets (3 day sample collected June 24) for each trough.

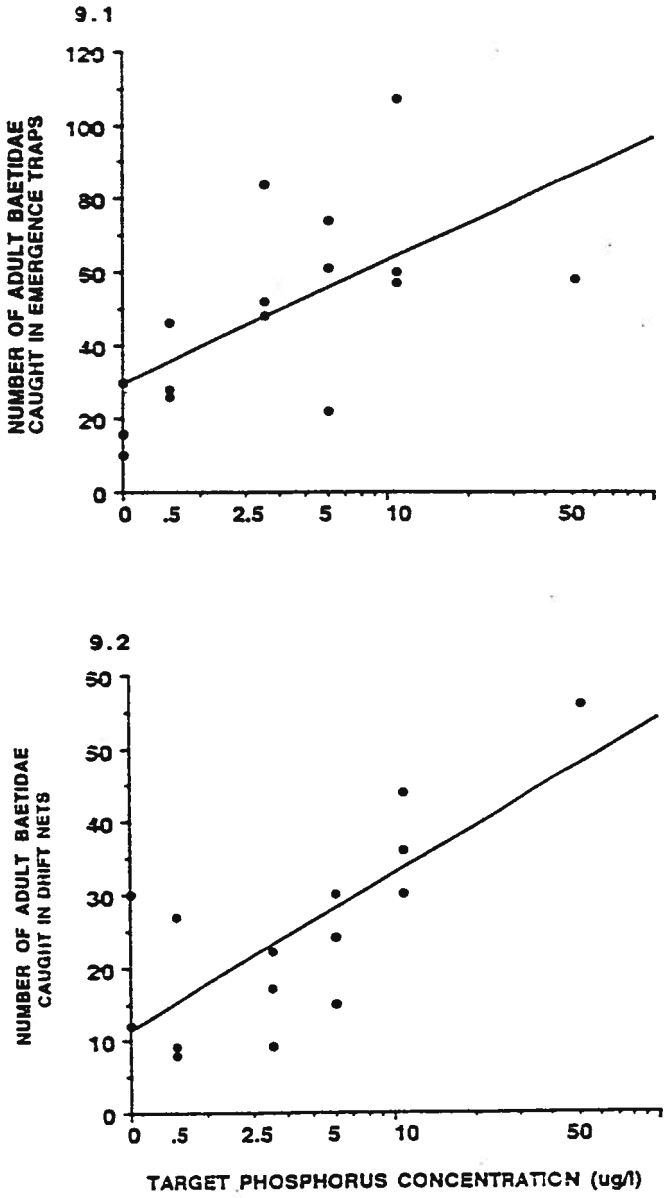

Figure 9. Number of adult Baetidae captured at the end of the experiment as a function of target phosphorus concentration (ug $P \cdot l^{-1}$). Linear regression lines of the data were fitted by least squares.
(9.1) Numbers caught in emergence traps on July 4. Regression line above (all data) is $y = 29.19 + 33.46 * \log(P)$. $r^2 = 0.34$. $p = 0.011$. Regression line (not shown) for treatments 0 - 10 ug $P l^{-1}$ only is $y = 23.16 * \log(P) + 49.03$. $r^2 = 0.51$ $p = 0.002$
(9.2) Numbers caught in drift nets on July 1.
Regression line above (for all data) is $y = 11.32 + 21.43 * \log(P)$. $r^2 = 0.69$. $p < .001$. Regression line for treatments 0 - 10 ug $P l^{-1}$ only is $y = 20.47 * \log(P) + 10.27$. $r^2 = 0.51$ $p = 0.001$

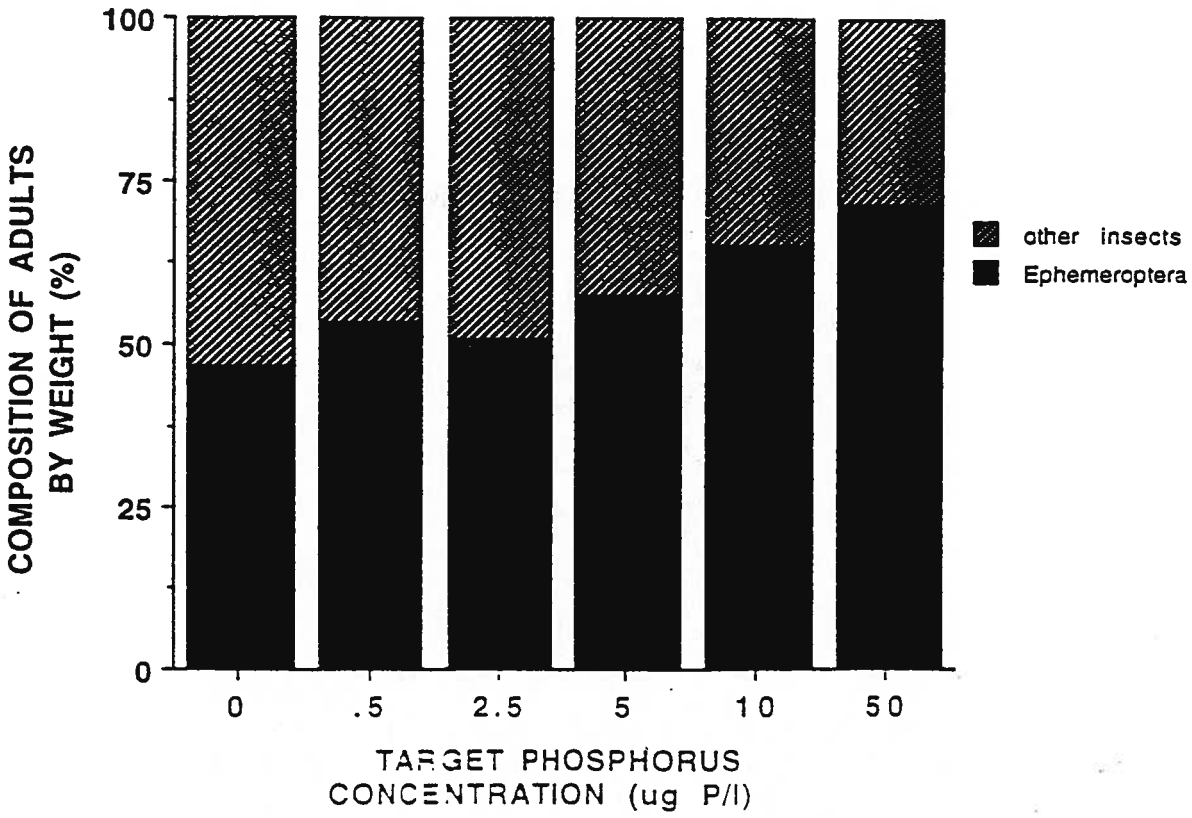

Figure 10. Contribution of Ephemeroptera to total biomass of adults collected in emergence traps on June 27 by target phosphorus concentration (ug $P \cdot l^{-1}$).

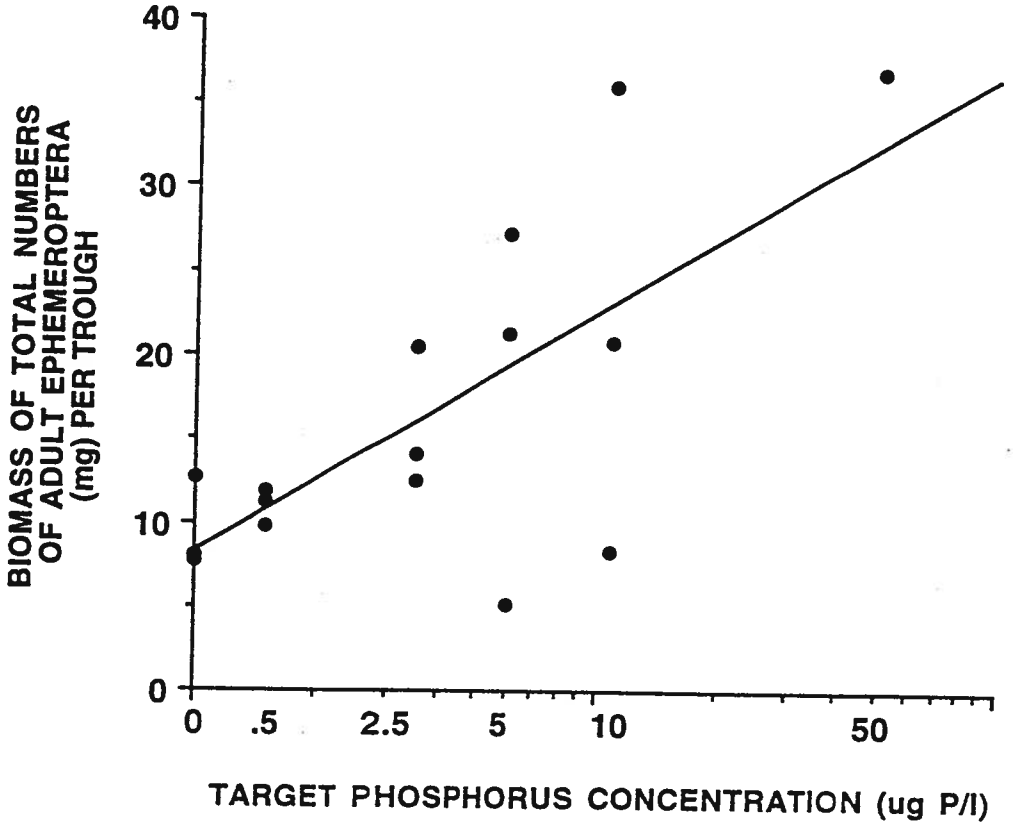

Figure 11. Adult Ephemeroptera biomass (total dry weight of all individuals) collected on June 27 as a function of target phosphorus concentration (ug $P \cdot l^{-1}$). Linear regression line of the data fitted by least squares. Variances were not stabilized by transformation. Regression line above (all data) is $y = 8.193 + 14.241 * \log(P)$. $r^2 = 0.48$. $p = 0.002$.
Regression line (not shown) for treatments 0 - 10 ug $P \cdot l^{-1}$ only is $y = 11.76 * \log(P) + 9.15$. $r^2 = 0.25$ $p = 0.03$.

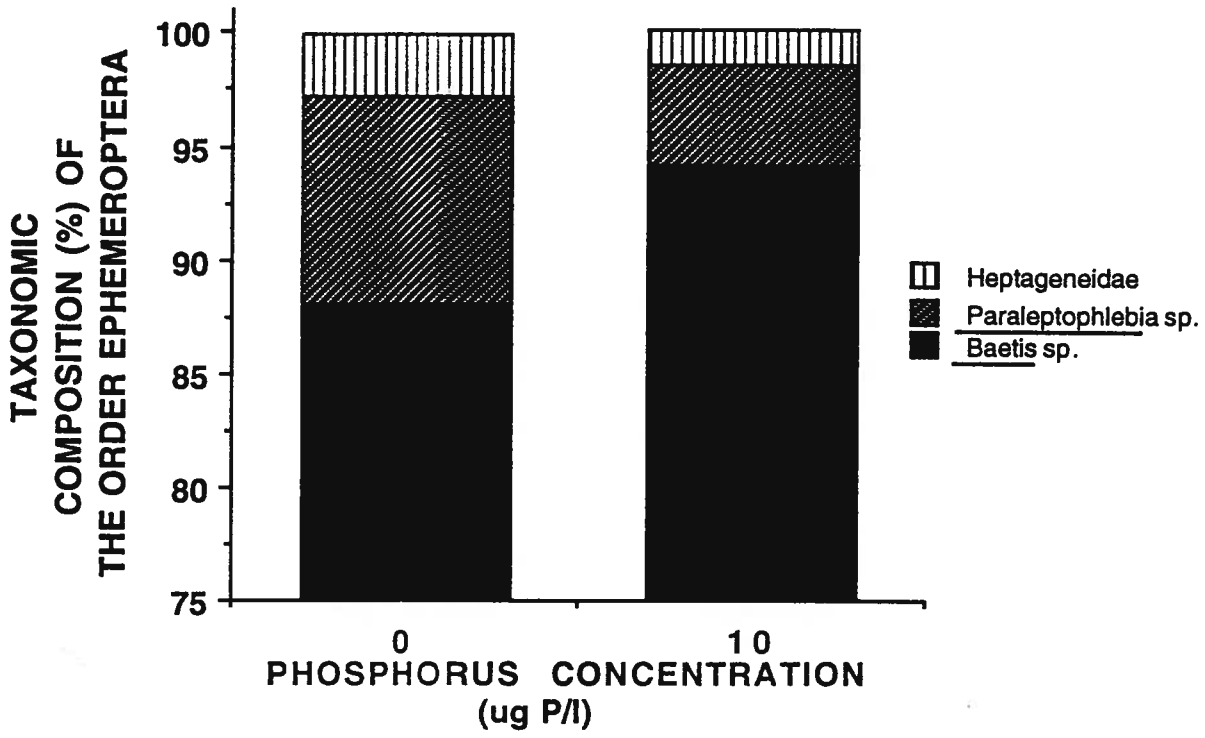

Figure 12. Percent composition of Ephemeroptera collected as adults at the end of the experiment on June 27 by target phosphorus concentration (ug $P \cdot l^{-1}$).

$t_{.05(2)13}$ = -0.80, for treatments 0 - 10 μg P.l-1). Adult mayflies (collected near experiment end on July 4) exhibited no difference in mean body length per trough as a result of treatment ($p = 0.49$, $r^2 = -0.04$, $t_{.05.(2)13} = 0.71$, for treatments 0 - 10 $\mu g\ P{\cdot}l^{-1}$). Adult body lengths ranged from 2.04 to 6.85 mm.

In two taxa, Chironomidae and Tricoptera, adults captured in emergence traps increased in number only at the highest nutrient concentration of 50 $\mu g\ P{\cdot}l^{-1}$ (unreplicated trough). Increasing phosphorus concentration increased adult Chironomidae and Trichoptera numbers but the effect was nonsignificant from 0-10 $\mu g\ P{\cdot}l^{-1}$ (see Table 4 for regression statistics). However, at 50 $\mu g\ P{\cdot}l^{-1}$ the numbers of adult Chironomidae collected at the end of the experiment (July 4) were three times the controls (Figure 13). The number of adult Trichoptera captured from the 50 $\mu g\ P{\cdot}l^{-1}$ trough was eight times that of the control troughs at peak emergence (June 27) (Figure 13). The numbers of adult Chironomidae collected in drift nets on trough outflows near the experiment end (June 24) showed no significant response to increasing phosphorus concentration ($p = 0.92$, $r^2 = -0.08$, $t_{.05(2)13} = -0.10$, for treatments 0-10 $\mu g\ P{\cdot}l^{-1}$).

The mean number of adult Plecoptera emerging per week declined over the course of the experiment to less than one per week by July 4 for all treatments (Figure 13). No significant treatment effects were observed on the total number of Plecoptera captured from May 19 to July 4 (see Table 4). Other major insect taxa collected in the emergence traps (Simuliidae, miscellaneous Diptera; Leptophlebiidae; Heptageniidae; and Coleoptera) showed no significant response to fertilization (Table 4). The relationship of increasing phosphorus concentration on the numbers of adults of taxa other than Baetidae and Chironomidae

collected in the drift near the end of the experiment (June 24) could not be assessed because of low numbers.

A descriptive comparison was made between number of adults drifting into the troughs per day and those emigrating from the troughs per day for 0 and 10 μg $P \cdot l^{-1}$ treatments. The total number of adults immigrating per day to the troughs was based on a 24 hour drift sample. The total number of adults emigrating from the troughs per day was estimated by adding the daily catch of adults of the emergence trap (sampled over 10 days) to those in the drift nets (sampled over 3 days). Greater than 91% and 79% of the baetid and trichopteran adults trapped per day, respectively, originated from trough gravel for these treatments (Table 5). None of the simuliid nor chironomid adults trapped per day originated from trough gravel (Table 5). Comparisons for other taxa were not made because of low numbers.

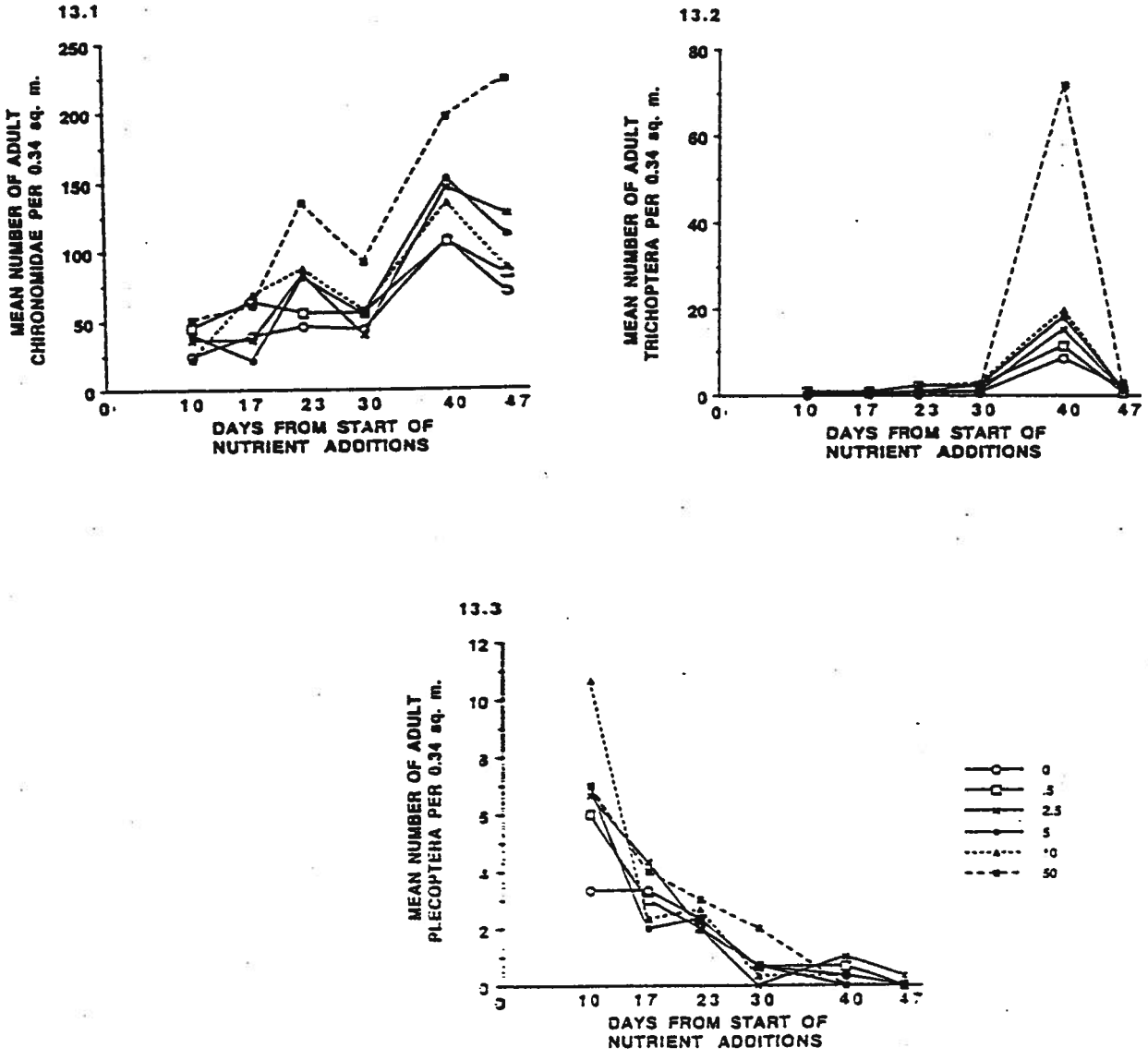

Figure 13. Numbers of adult insects by target phosphorus concentration collected in emergence traps. All insects were captured between May 19 and July 4. In each case, the mean number of adult insects numbers is plotted per date. Sample size (n) = 3 except at 50 ug $P \cdot l^{-1}$ where n = 1.
(13.1) Chironomidae. (13.2) Trichoptera. (13.3) Plecoptera.

8.2.2 Benthic insects

Increasing phosphorus concentration resulted in an increase in total benthic insects counts sampled at the end of the experiment. The relationship was nearly significant ($y = 349.85*\log(P) + 1000.55$, $p = 0.06$, $r^2 = 0.20$, $t_{.05(2)11} = 2.05$, power $(1 - \beta) = 0.67$, for treatments 0 - 10 ug $P \cdot l^{-1}$).

Numbers of benthic Baetidae, Hydroptilidae, Nemouridae, and Perlodidae showed a significant increase with increasing nutrient levels (Figure 14 and Table 6). Numbers of all four of these insect taxa showed rapid increases at low phosphorus concentrations of 0 - 2.5 $\mu g\ P \cdot l^{-1}$ and showed signs of saturation at 2.5 - 10 $\mu g\ P \cdot l^{-1}$. Other major insect taxa collected from the benthos showed no significant response to fertilization (Table 6).

The number of taxa per sample (richness) of the trough benthos was not influenced by treatment ($p = 0.80$, $r^2 = -0.08$, $t_{.05(2)12} = 0.25$). A comparison of the number of taxa per sample in the control troughs to the natural stream showed no significant difference ($p > 0.10$, $t_{.05(2)4} = 1.52$).

The control trough benthos was comprised of four main families including Chironomidae, Philopotamidae, Baetidae, and Nemouridae which made up 82.6 - 99.1 percent of the total insects. While the benthos of shallow natural riffles near the mesocosm were comprised of Baetidae, Chironomidae, Chloroperlidae, Elmidae and Leptophlebidae which made up 89.2 percent of the total insects (Figure 15). Although the percent composition of the control troughs and stream benthos appears different, the same taxa were at least present in both

trough and stream benthos.

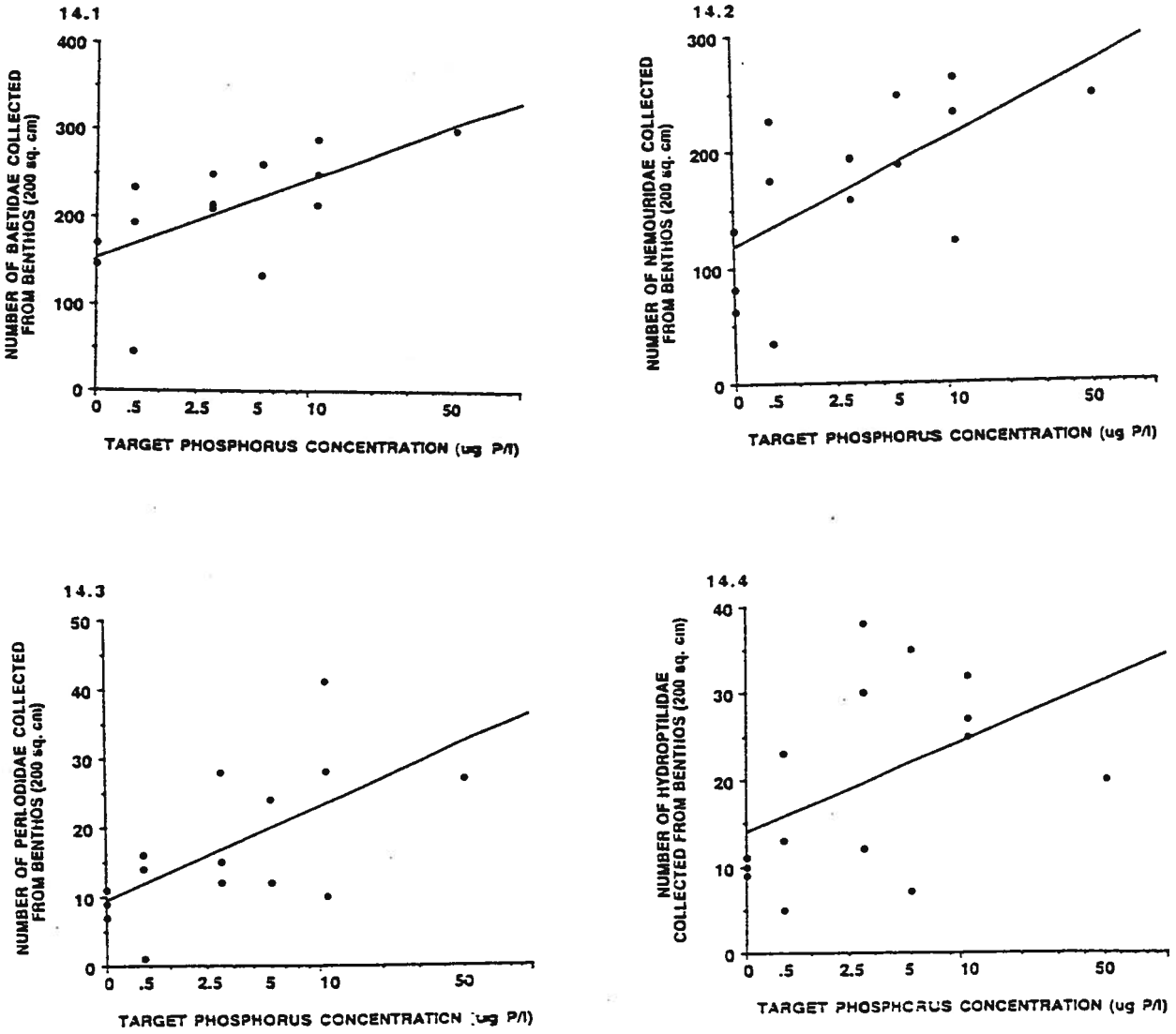

Figure 14. Number of insects collected from the benthos at the end of the experiment on July 8 as a function of target phosphorus concentration (ug $P \cdot l^{-1}$). Linear regression lines of the data were fitted by least squares. See Table 7 for the results of regression analyses carried out on 0 - 10 ug $P \cdot l^{-1}$ treatments for the same data.
(14.1) Baetidae. $y = 152.06 + 89.96 * \log(P)$. $r^2=0.443$. $p=.006$.
(14.2) Nemouridae. $y=117.92 + 93.02 * \log(P)$. $r^2=0.421$. $p=0.008$
(14.3) Perlodidae. $y=9.41 + 13.31 * \log(P)$. $r^2=0.402$. $p=0.01$
(14.4) Hydroptilidae. $y=13.95 + 10.26 * \log(P)$. $r^2=0.16$. $p=0.08$

Table 6. **Linear regression analyses relating the numbers (y) of various insect taxa collected from the trough benthos collected at the end of the experiment to target phosphorus concentration. Sample size (n) = 14 in all cases. Ordered with respect to increasing p value.**

Insect Family (Order)	Regression Equation[1]	p[2]	$t_{0.05(2),12}$	r^2	Trophic Relationship
Perlodidae (Plecoptera)	y = 16.29 * log(P) + 16.29	0.02	2.77	0.34	predators
Nemouridae (Plecoptera)	y = 108.54 * log(P) + 112.25	0.02	2.72	0.33	shredders, collectors
Hydroptilidae (Tricoptera)	y = 16.91 * log(P) + 14.01	0.02	2.58	0.30	scrapers, piercers, collectors
Baetidae (Ephemeroptera)	y = 93.25 * log(P) + 150.86	0.03	2.49	0.29	scrapers, collectors
Polycentropodidae (Tricoptera)	y = 3.56 *log(P) + 5.40	0.07	1.96	0.18	collectors, some predators
Philopotamidae (Tricoptera)	y = 70.45 * log(P) + 206.72	0.09	1.84	0.15	collectors
Miscellaneous Ephemeroptera	y = 0.21 * P + 4.68	0.15	1.54	0.09	scrapers, collectors
Elmidae (Coleoptera)	y = 0.25 * P + 5.35	0.26	1.18	0.03	collectors
Chloroperlidae (Plecoptera)	y = -0.26 * P + 4.82	0.31	-1.06	0.01	predators
Hydropsychidae (Tricoptera)	y = -0.47 * P + 14.01	0.39	-0.88	-0.02	collectors, some predators
Chironomidae (Diptera)	y = 4.17 * P + 453.82	0.56	0.60	-0.05	various
Miscellaneous Diptera	y = 0.32 * P + 24.03	0.79	0.27	-0.08	various

[1] Regression analyses included phosphorus treatments of 0-10 $\mu g\ P \cdot l^{-1}$ only.
[2] None of the regression analyses tested were significant at a "table-wide"α level according to the sequential Bonferroni technique (Rice 1988).

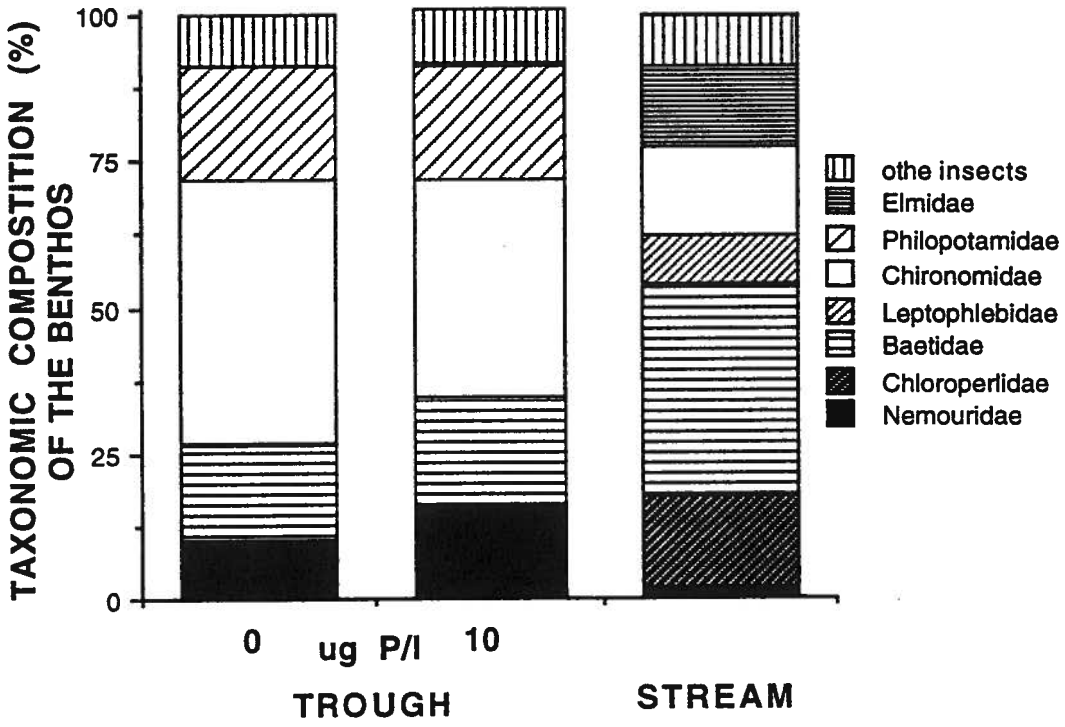

Figure 15. **Dominant insect families collected from the benthos of the artificial stream troughs on July 8 as a function of phosphorus concentration. Percentages are based on the mean of three replicate troughs.**

8.2.4 Drifting immatures

The total number of insect immatures captured in drift nets at the trough inflows was not highly variable (mean = 108.7, standard error = 1.29, n = 3) on June 21. The composition of immigrating immatures on this date was largely made up of Baetidae (42.3%), Chironomidae (15.9%), Simuliidae (10%), Trichoptera (10%), and Leptophlebiidae (5%). Perlodidae and Nemouridae had very low immigration rates and comprised only .02 and .01 percent, respectively, of the total insects collected on June 21.

The effect of phosphorus concentration on emigration rates of drifting large Baetidae nymphs (those retained on a 1 mm sieve) was, generally, not significant (for dates June 3, 6, 13, and July 1, 1991). The total number of emigrants pooled over time showed a nonsignificant relationship with increasing phosphorus concentration ($y = 21.30 * P + 723$, $p = 0.13$, $r^2 = 0.11$, $t_{.05(2)12} = 1.59$, $(1 - \beta) = 0.77$, for treatments of 0 - 10 $\mu g\ P \cdot l^{-1}$). However, on June 24, emigration rates showed a significant positive response to increasing phosphorus concentration ($y = 109.27 * \log(P) + 160.56$, $p = 0.01$, $r^2 = 0.32$, $t_{.05(2)13} = 2.74$). Daily immigration rates and daily emigration rates of Baetidae nymphs over time are depicted in Figure 16.

Immigrating nymphs less than 1 mm in size comprised 50% of total drifting Baetidae (mean per day = 32.3, standard error = 11.0, n = 3) enumerated on May 31, 1991. Emigrating Baetidae nymphs less than 1 mm in size showed no significant response to nutrient treatment as of June 3 ($p = 0.76$, $r^2 = -0.07$, $t_{05(2)13} = -0.31$, for treatments of 0 - 10 $\mu g\ P \cdot l^{-1}$).

Immigration and emigration rates of Hydroptilidae, Nemouridae and Perlodidae were not assessed because of very low numbers in the drift.

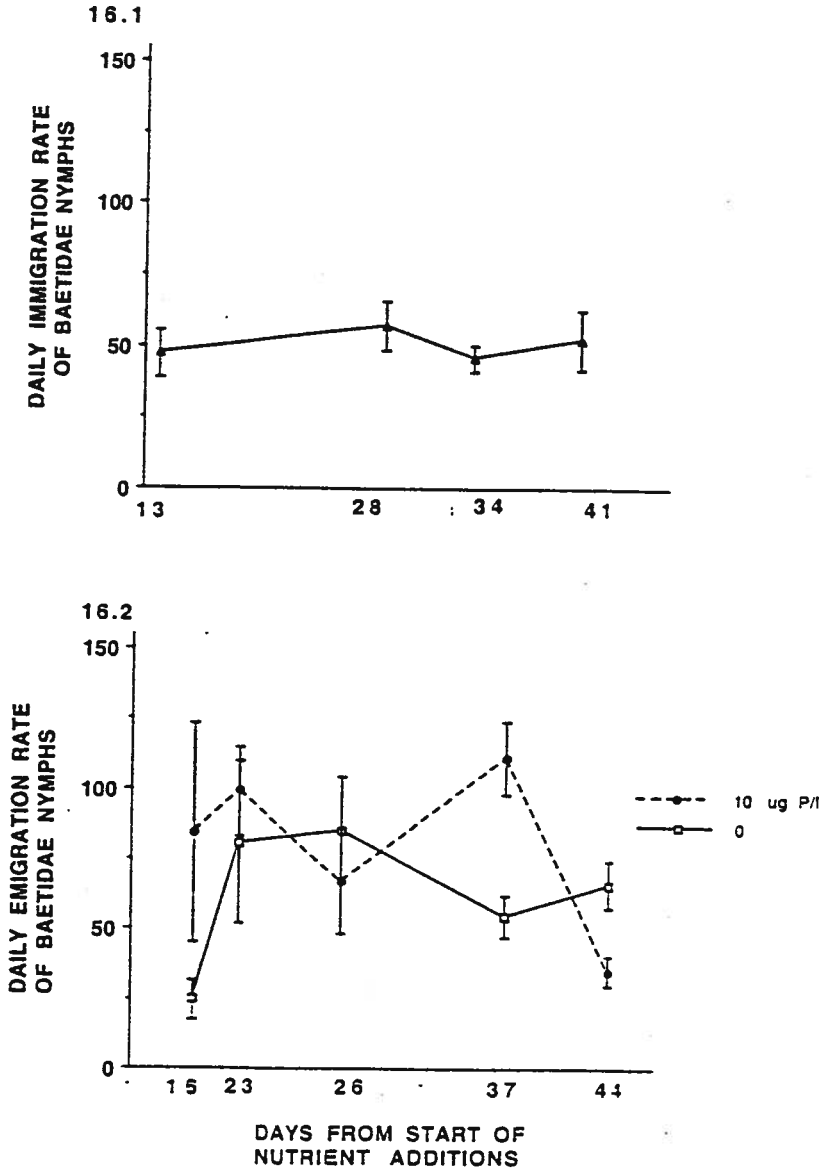

Figure 16. (16.1) Daily immigration rates of large Baetidae nymphs to the artificial stream troughs over time. Immigration rates are based on 24 hour drift samples taken at the trough inflow.
(16.2) Daily emigration rates of mature Baetidae nymphs from the artificial stream troughs over time by target phosphorus concentration (ug $P \cdot l^{-1}$). Emigration rates are based on 3 day drift samples collected from the trough outflow. In each case, the mean number of Baetidae nymphs is plotted per date with the associated error bars. Sample size (n) = 3, for all points.

9.0 DISCUSSION

This is the first study to describe the relationship between insect abundance and composition and nutrient concentration in a freshwater stream. Results showed a significant increase in peak algal biomass with increasing phosphorus concentration measured from Styrofoam substrates. PB increased with phosphorus concentration linearly up to 2.5 $\mu g\ P \cdot l^{-1}$ after which a diminishing response was observed. In contrast, a significant decline in total algal cell density with higher phosphorus concentrations was observed on trough gravel. The family Baetidae was the only taxon collected as adults to show a significant increase with phosphorus addition. Adult baetids comprised 47 - 72 % of total insect biomass at the end of the experiment. Numbers of benthic baetids, nemourid and perlodid stoneflies and hydroptilid tricopterans sampled at the end of the experiment significantly increased with phosphorus concentration. Adult and benthic insects of these taxa exhibited similar rapid increases in abundance from 0 - 2.5 $\mu g\ P \cdot l^{-1}$ and showed signs of saturation at 1.5 - 3 times the controls at concentrations greater than 2.5 $\mu g\ P \cdot l^{-1}$. Removal of immigrating insects from one trough resulted in increased in algal biomass on styrofoam plates and higher cell numbers on trough gravel compared to controls. There was no detectable difference in the numbers of large baetid nymphs emigrating from the troughs with increasing phosphorus concentration. Graphical comparisons between the control and treated troughs showed that they were similar in taxonomic composition of insects. Insect taxonomic richness did not change with increasing phosphorus concentration.

9.1 Effect of Phosphorus Additions on Periphyton

Peak algal biomass collected from Styrofoam substrates and plotted as a function of target phosphorus concentrations showed saturation kinetics similar to that found by Bothwell (1989). About 70% of the maximum chlorophyll *a* value was achieved at low P additions (between 0.5 and 2.5 $\mu g\ P \cdot l^{-1}$) similar to Bothwell's results (Figure 17). Peak biomass increased with phosphorus concentration linearly to 7.4 $mg \cdot m^{-2}$ at 2.5 $\mu g\ P \cdot l^{-1}$ and reached an asymptote at 9.2 $mg \cdot m^{-2}$ (2.7X the controls). Areal biomass may have increased from 2.5 - 10 ug $P \cdot l^{-1}$ but at a lower rate; this trend is unclear, however, because of the low response seen in the 5.0 ug $P \cdot l^{-1}$ replicates.

The levels of chlorophyll *a* from the styrofoam substrates were more than 40 times lower than those reported by Bothwell (1989) and 3 - 6 times lower than those described by (Mundie *et al.* 1991). Grazing, in my study, had considerable impact on the algal biomass levels measured from the styrofoam plates. The removal of insects from one trough resulted in up to a 7 fold increase in chlorophyll *a* levels on the styrofoam plates compared to the controls. It is possible that high grazing rates may have accounted for the low chlorophyll *a* levels observed compared to previously reported values (Bothwell 1989, Mundie *et al.* 1991, Stockner and Shortreed 1978). The mean density of insects in the control (47,350 $insects \cdot m^{-2}$) and the 10 $\mu g\ P \cdot l^{-1}$ treated (66,950 $insects \cdot m^{-2}$) trough gravel of this study were 2.1 and 1.7 fold higher, respectively, than the mean density of invertebrates at the same treatments in a similar artificial trough study by Mundie *et al.* (1991). In my study, mean insect densities were based on numbers of animals retained on a 630 μm mesh sieve while in Mundie *et al.* (1991) insects were sampled with a much smaller 50 μm net. As a result the

relative difference in mean insect density between the two studies is underestimated. Numbers of insects grazing directly on artificial substrates used to collect algal biomass were not quantified in the present experiment nor in previous work.

Many researchers have shown that grazers can significantly reduce algal biomass in streams (Lamberti and Resh 1983, McAuliffe 1984, Jacoby 1987, Hart and Robinson 1990, Scrigeour *et al.* 1991). High macroinvertebrate abundances have been associated with lower than expected algal biomass levels in two studies of point source nutrient enrichment in a British Columbian River (Bothwell *et al.* 1992) and New Zealand streams (Welch *et al.* 1992). Recently, Bothwell (pers. comm. Dr. M.L. Bothwell, 1993) observed lower chlorophyll *a* levels in experimental stream troughs in the Thompson River, British Columbia compared to past observations (Bothwell 1989) and has hypothesized that lower levels are due to increased grazing pressure.

The discrepancy between low values of algal biomass reported in my study and higher values in past work may have also resulted from differing physical conditions such as current velocity, flow stability, light levels, sediment scouring, within the troughs (Bothwell 1993). Mean water velocity in the troughs of the present study (21.3 $cm \cdot s^{-1}$) was lower than in troughs of Stockener and Shortreed (1978) (40 $cm \cdot s^{-1}$)and Bothwell (1989) (50 $cm \cdot s^{-1}$) but much higher than Mundie *et al.* (1991) (5.3 $cm \cdot s^{-1}$). Increased turbulence and water velocity generally has a positive effect on the metabolism and nutrient uptake of attached algae; it can result in higher biomass accrual (Bothwell 1993). Variations in mean water velocity between

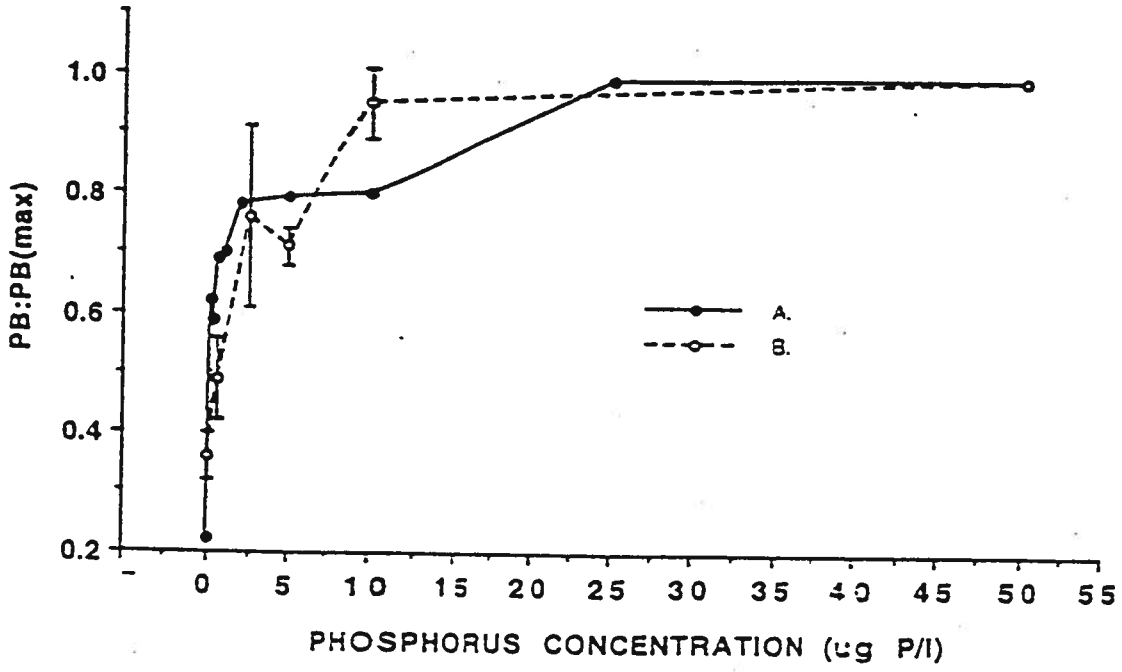

Figure 17. Relative peak algal biomass (PB: PB(max)), chlorophyll *a*, as a function of phosphorus treatment (ug $P \cdot l^{-1}$). PB(max) is PB at 50 ug $P \cdot l^{-1}$. A. modified from Bothwell (1989). B. Present study. Sample size (n) = 3 at each treatment level except at 50 ug $P \cdot l^{-1}$ where n = 1.

the studies did not consistently explain differences in algae biomass. Comparisons of flow stability, light level, and sediment scouring could not be made among the above studies because these variables were not consistently monitored.

Finally, low chlorophyll *a* levels might be expected if long chain polyphosphates (comprising 65 - 75% of total dissolved phosphorus added) were not biologically available over the length of the mesocosm (pers. comm. Dr. M.L. Bothwell). However, in a second experiment (see Methods) where I switched to a readily available form of phosphorus (orthophosphate) but maintained the same treatment levels, low levels of algal biomass were still observed. Low levels of algal standing crop observed in my study may have resulted from the interaction of several of physical or chemical factors as well as invertebrate grazing.

Background dissolved nitrogen levels of the Keogh river were thought to be high enough to saturate cellular growth rates. However, underlying cells of the periphyton mat may have been nitrogen limited if nitrogen diffusion within the mat was slow (similar to phosphorus limited growth kinetics described by Bothwell 1989). Perrin (1989) showed periphytic biomass increased logarithmically from 0 - 10 ug $N \cdot l^{-1}$, but continued to increase linearly from 10 - 100 ug $N \cdot l^{-1}$ at surplus phosphorus. However, thick algal mats did not develop within my troughs instead there was a thin film that was approximately 3 mm thick with some longer filaments. Hydraulic retention times of the troughs were short; this assured that nutrient levels remained constant in the bulk water. Thus, the nitrogen requirements of cells within the algal mat were thought to have been satisfied (Bothwell 1993).

The total number of algal cells sampled from gravel within the troughs significantly

declined with increasing phosphorus concentration. This decline may have resulted from increased grazing pressure (increased numbers of Baetidae) which was positively correlated with phosphorus concentration in the troughs. There was a 4.5 fold increase in total cell numbers collected from the grazer excluded trough compared to the controls. This also suggests that the stimulatory effect of phosphorus on total cell number was offset by increases in grazing pressure indicating that in fact fertilization can result in successful propagation of increased production up the food chain. Styrofoam substrates provide habitat for only small instars of chironomid and simuliid insects (pers. comm. Dr. M.L. Bothwell, 1993). Higher grazing pressure on gravel versus Styrofoam likely accounts for differences in algal accumulation response observed on the two substrates. Algal standing crop and herbivore grazing rates on Styrofoam substrates may not correspond to standing crop and grazing rates on gravel (Aloi 1990). I did not assess the effect of phosphorus concentration on the biomass of algae attached to trough gravels.

Diatoms and cyanophytes made up over 89.6% of the total cell numbers collected from the trough gravel. Diatoms are high quality food for grazing insects (Lamberti and Moore 1984). Cyanophytes and filamentous algae are generally thought to be less readily digested by insect grazers (Lamberti and Moore 1984). However, Mundie *et al.* (1991) found that filamentous algae made up 88% of insect gut contents and suggested that cyanophytes may also be an important food item for some insect grazers. They showed that an increase in total insect number occurred with increased phosphorus concentration despite an increase in the percentage of cyanophytes making up the algae in their artificial stream troughs.

9.2 The effect of phosphorus additions on the abundance of the insect community

The families of insects that showed the greatest increases in density with nutrient enrichment were Baetidae, Nemouridae, Perlodidae and Hydroptilidae. Densities of all of these taxa showed signs of saturation at high phosphorus levels. Densities initially increased rapidly at phosphorus concentrations of 0 - 2.5 ug $P \cdot l^{-1}$ and reached asymptotes at concentrations of 2.5 - 10 ug $P \cdot l^{-1}$.

Positive responses of Baetidae density to increasing phosphorus concentration were observed for adults in the emergence traps and drift nets (Figure 9) and for nymphs collected from the benthos (Figure 14). Numbers of Baetidae immigrating into troughs were similar (Figure 16.1). Thus, either emigration or mortality rates must have been lower in fertilized troughs to account for increased numbers. Lower emigration rates of Baetidae nymphs from the troughs were not found over the course of the experiment. As a result, aggregation of Baetidae nymphs in the enriched troughs was not predominately responsible for the increased number of individuals found with treatment. However, I cannot separate whether aggregation and increased survival or increased survival alone account for the higher numbers of Baetidae found in treated troughs because I was not able to estimate what proportion of the outflowing drift originated from the trough benthos. Increased survival of Baetidae nymphs must partly account for the higher numbers of adults and benthic nymphs. Higher survivals can be attributed to increased quality and/or amounts of available food. The periphytic community, including attached algae, is high quality food for *Baetis* nymphs (Chapman and Demory 1963, Kohler 1985). Bacteria, a good source of protein for stream insects (Lamberti and Moore 1984), may have also contributed to higher grazer survival.

Bacterial productivity may have been enhanced by phosphorus additions in my experiment (Elwood *et al.* 1981, Hersey *et al.* 1988, Peterson *et al.* 1993) but was not monitored.

Emigration rates for small baetids (those passing through a 1 mm seive) were assessed only for one date, early in the experiment. Thus, I may have missed an aggregative response of immature baetids by undersampling. However, in order for aggregating baetids of less than one mm to account for a significant adult response 24 days (June 10) after treatments began (Figure 8), high aggregations rates might be expected very early in the experiment. Small baetids would require time to develop into adults. For example, *Baetis* nymphs that hatched in July in an Ontario river took three and a half months to develop into adults (Corkum and Pointing 1979). Thus, even if the number of sampling days is low, one might expect to find depressed emigration rates of small baetids early in the experiment if these individuals were to account for the significant increase in adults later in the experiment.

Drift is thought to be a means by which algal feeding stream invertebrates move between patches of high and low quality food . Drift rates of invertebrates have been shown to decrease with increasing density of periphyton in artificial stream troughs (Hildebrande 1974). Mature *Baetis tricaudatus* will actively drift when food abundance is low (Kohler 1985) in laboratory streams. Substrates with high periphyton densities have been shown to be more rapidly colonized by grazers compared to substrates with low periphyton densities (McAuliffe 1983). In contrast to these studies, my data agree with Mundie *et al.* (1991) who found no evidence of depressed insect drift with increased phosphorus enrichment and higher algal biomass in artificial stream troughs. The stream side experimental mesocosm

approach that was used by myself and Mundie *et al.* (1991) incorporated greater complexity compared to previous experiments. Our experiments were conducted over a longer time frame that allowed for natural colonization, instar growth, development and variable survival rates. Aggregation of insects in patches of high quality food have generally been observed in studies where insect survival rates were constant and growth and development were not permitted (Hildebrande 1974, McAuliffe 1983, Kohler 1985).

Numbers of baetid mayflies emerging from the troughs peaked at the end of the experiment. The synchrony of phosphorus enrichment, algal response and nymphal development probably resulted in strong positive responses of Baetidae to treatment observed in emergence traps, drift nets and benthos. A number of short term food enrichment studies conducted in artificial streams have found that insects with short generation times may be able to exploit increased food abundance (Mundie *et al.* 1991, Richardson 1991). The midge, *Brilla retifinis*, increased more than ten times in density in detritus enriched troughs compared to control troughs (Richardson 1991). Mundie *et al.* (1991) found that phosphorus enrichment favored small chironomids (1.76-2.25 mm) such as *Corynonera*, *Thienemanniella*, *Synorthocladius*, and *Cladotanytarsus*. Baetid mayflies have a "fast seasonal life history type". For example, species of *Baetis* typically have two generations per year. Generation time in general is highly variable and temperature dependent (Edmunds *et al.* 1976).

The benthic nymphs of two plecopteran families, Perlodidae and Nemouridae, also showed a positive response to enrichment. Plecopteran emergence for all nutrient levels was highest

when treatments were initiated and declined to very low levels by the end of the experiment. Plecopteran emergence patterns were not synchronized with nutrient treatments. It is not surprising, then, that a positive response of adult plecopteran numbers was not observed with phosphorus treatment. Also, there may be a lag in stonefly response time to nutrient treatment if their numbers depend on interactions mediated through prey (Begon *et al.* 1990) and/or other indirect effects of fertilization.

Nemourids depend on organic matter as a food resource. The family Nemouridae is made up of species that are either collector-gathers feeding on fine particulate organic matter (FPOM) or shredder-detrivores that feed on coarse particulate organic matter (CPOM) (Merritt and Cummins 1984). It may be that phosphorus treatment directly enhanced nemourid food abundance by increasing the abundance of dead and decaying algae available to these nymphs. Alternatively, increases in the numbers of grazers correlated with increasing phosphorus may have facilitated an increase in abundance of FPOM. It is commonly thought that insects make finer particles of detritus available to collectors through their feeding and defecation activities (Merritt *et al.* 1984). Increased fecal material from grazers as a food resource indirectly may have benefitted nemourids in treated troughs. Finally, nemourids may have benefitted from increases in algal or bacterial productivity with phosphorus enrichment if they fed directly on the periphytic community. Collector-gatherers can often be opportunistic in their choice of food (Lamberti and Moore 1984).

In this study, I observed a "bottom-up response" of perlodid predators to increasing nutrient concentration. Increased biomass at the consumer trophic level may have resulted in increased available prey for perlodid stoneflies. Only recently has nutrient augmentation in

rivers been shown to increase biomass at higher trophic levels such as insectivorous fish (Johnston *et al.* 1991, Peterson *et al.* 1993). Previous to this study, predatory insect responses to experimental nutrient enhancement have rarely been demonstrated. Johnston *et al.* (1990) described increases in stonefly populations with whole river fertilization. Predatory stoneflies have been shown to depress baetid mayfly populations by displacing them to refuge areas (Cooper *et al.* 1993). However, the importance of "top-down" control by insect predators on consumers was not assessed in this experiment; such control would likely involve longer time scales than were practical to to study with this mesocosm.

Benthic nymphs of one family of Trichoptera, Hydroptilidae, increased in abundance with increasing phosphorus concentration. Hydroptilids are piercer-herbivores, scrapers or collector gatherers (Merritt and Cummins 1984). Their numbers may have been enhanced by increased food abundance through direct fertilization effects on periphyton biomass or indirect effects on the availability of FPOM. The mechanism by which plecopteran or tricopteran numbers increased was not examined. They may have aggregated in treated troughs where food resources were more abundant, and/or the survival rates of nymphs may have been higher in treated troughs.

Adult Chironomidae and Trichoptera showed increased densities only at 50 ug $P \cdot l^{-1}$. This suggests (based on one unreplicated treatment) that that abundances of certain insect taxa may increase only at higher phosphorus levels.

The ability to detect a positive effect of fertilization on numbers of adult insects produced in the troughs depended on the magnitude of the effect relative to the number and variability

of adults drifting into the troughs. Data from Table 5 suggest that possible small effects of fertilization on Chironomidae and Simuliidae adults may be undetectable because the numbers of adults drifting into troughs was high relative to numbers emigrating (in outflow drift and emergence traps) from troughs. Numbers of adult Baetidae, Chironomidae, Trichoptera and Simuliidae drifting into the troughs per day were estimated from one 24 hour sample while numbers emigrating from troughs per day were estimated from three day (drift nets) and weekly catches (emergence traps). A twenty-four immigration rate may not be a good estimate of a three day or weekly emigration rate if drift is variable through time. However, the trends described in Table 6 were maintained on other dates in the second experiment that I conducted in July and August (see Methods).

An alternative hypothesis to food limitation for why insect numbers increased with increasing phosphorus concentration is that increasing algal mat thickness may have improved insect survival. An increased algal mat may have provided improved habitat, reduced competitive interference among nymphs, or reduced predation rates (Richardson 1989). This is unlikely, however, since I did not see any consistent increase in the size of the algal mat with increasing phosphorus concentrations. Total algal cell numbers per area scraped from gravel showed no increase with greater phosphorus concentration. Also, algal biomass was higher in the trough where insects were excluded indicating that grazers were feeding on periphytic algae.

The percent composition of benthic insect taxa was different between the troughs and the stream. This may have resulted from differences in physical characteristics between the the artificial stream troughs and natural riffles or if colonization rates of the artificial substrates

by insect groups was not proportional to their abundance in the river. There was no difference between the troughs and the stream in the kinds of insect taxa present and richness.

Increases in the densities of insects (baetid adults and nymphs, nemourid and perlodid nymphs) with higher phosphorus treatment observed in this experiment were maintained in a second experiment that I carried out in the same troughs in July and August (Appendix 1, Figures 18 and 19).

9.3 Effect of nutrient enrichment on ephemeropteran size, biomass and timing of emergence

The quantity and quality of food resources may significantly alter aquatic insect life history characteristics (Sweeney 1984). Insect growth (ie. Colbo and Porter 1979, Collins 1980, Richardson 1991) has been shown to increase with greater food availability. Measurements that I made of adult ephemeropteran lengths and mass per individual showed no detectable increase with phosphorus concentration. However, I did not examine the sizes and masses by species nor by sex. Also, individual mass loss is probable because adults were preserved and stored in 90% ethanol but shrinkage in total length is unlikely to have occurred (Giberson and Galloway 1985). In contrast to my findings, *Baetis* showed a growth response in all four years of a whole river fertilization study on the Kupuruk River, Alaska (Peterson *et al.* 1993a). Development time may also be affected by food quantity. Delayed emergence has been observed for aquatic insects on suboptimal diets (Anderson and Cummins 1979, reviewed in Sweeney 1984) or under severe food reduction (Danks 1978, Colbo and Porter 1979). No change in emergence timing was observed with phosphorus

concentration in this study for any taxa of insect. Brittain (1976) found that providing unlimited quantities of food compared to field conditions did not change insect emergence timing. Increasing food supported denser, but not faster growing ephemeropteran populations, in my experiment and in others by Hawkins (1986) and Mundie *et al.* (1991). If food per capita was similar amongst treatments, it may account for denser ephemeropteran populations with higher phosphorus treatment but no detectable change in length and mass or timing of emergence.

9.4 Extrapolation of Mesocosm Results to Whole River Fertilization

The mesocosm approach used in this study is powerful because it allowed for experimental comparisons with replication and appropriate controls. Whole stream manipulations are difficult, and whole stream replication is not always possible.

The stream-side mesocosm in which I conducted these experiments was an open flow-through system. Exchange of nutrients and organic material, immigration and emigration of stream organisms, and physical conditions such as temperature appeared to mimic natural conditions. Some of the disadvantages to using these types of artificial stream troughs are that there is reduced physical and biological heterogeneity, variation in natural discharge variation is usually damped, and the immigration and emigration of organisms that crawl along the benthos is eliminated. In my experiment, fish predators that may have impacted insect populations were excluded from the troughs. In addition, most studies conducted in mesocosms are short term in nature. Short term studies of community responses, such as the present one, may not be adequate to predict long term ecosystem responses. Peterson *et al.* (1993a) were not able to predict an Alaskan river's community response to a four year

fertilization treatments from short term studies (days to weeks). Unanticipated long term interactions included: 1. a switch from bottom up nutrient control of algal biomass in the first two years to top down grazer control in the last two years; 2. a decline in blackfly abundance with fertilization in years two and three.

To manage a river for enhanced sports or commercial fish production through fertilization, it will be important to understand long term, interacting responses. For instance, it may be important to know if a baetid mayfly response such as that observed in my experiments could be maintained and translated into improved adult salmon returns in a long term whole river fertilization study. Baetid mayflies were a very important component of both steelhead and coho salmon fry diet on the Keogh River in 1984-85 (Johnston *et al.* 1990).

We may not be able to predict long term complex types of interactions from a short term mesocosm study. However, experiments such as this one can be powerful tools if they are integrated with closely related field research and mathematical modelling (McIntire 1993). My study provides important information on the potential of at least three different trophic groups to respond to increases in nutrient concentrations. It also suggests that particular insect groups may increase numerically even at relatively low levels of nutrient additions. It is the first study to describe the relationship between insect abundance and composition in relation to nutrient concentration in a freshwater stream.

In the future, food web tracers (Hall 1993, Peterson *et al.* 1993a, Peterson *et al.* 1993b, Shepard and Waddill 1976) could be used with studies of streamside artificial troughs that incorporate natural invertebrate colonization to determine whether abundance changes (of

adults or benthos) with treatment result from differences in aggregation or survival rates. It may be possible to identify whether individual emigrating nymphs were actually feeding within the troughs or just drifting through.

This study best describes the relationship between phosphorus concentration and insect abundance from 0 - 10 ug $P \cdot l^{-1}$. However, the relationship should be better quantified at concentrations greater than 10 ug $P \cdot l^{-1}$. Also, the generality of the relationship and the effects of long term biotic and abiotic interactions on it should be assessed in whole rivers.

10. REFERENCES

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11. APPENDIX 1

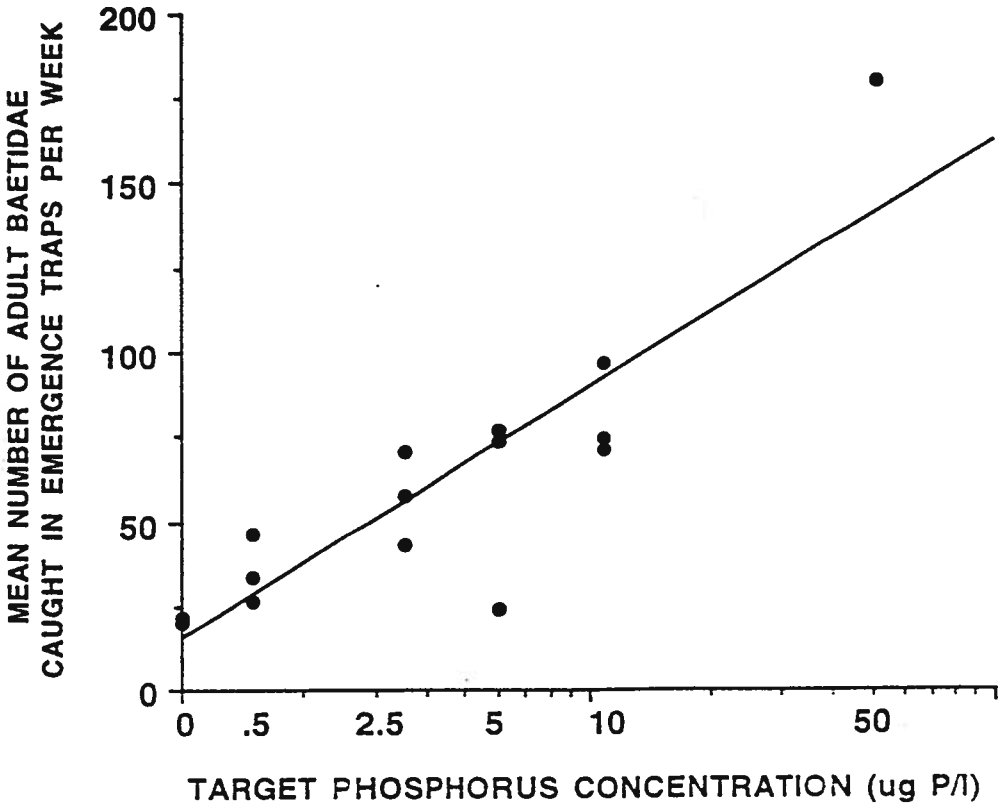

Figure 18. Number of adult Baetidae captured in emergence traps per week from July 8 - August 22 as a function of target phosphorus concentration (ug $P \cdot l^{-1}$). Linear regression lines of the data were fitted by least squares. Regression line above (all data) is $\log(y) = 1.41 + 0.49 * \log(P)$. $r^2 = 0.74$. $p < 0.001$. Regression line (not shown) for treatments 0 - 10 ug $P \cdot l^{-1}$ only is $\log(y) = 1.41 + 0.48 * \log(P)$. $r^2 = 0.62$ $p = 0.002$

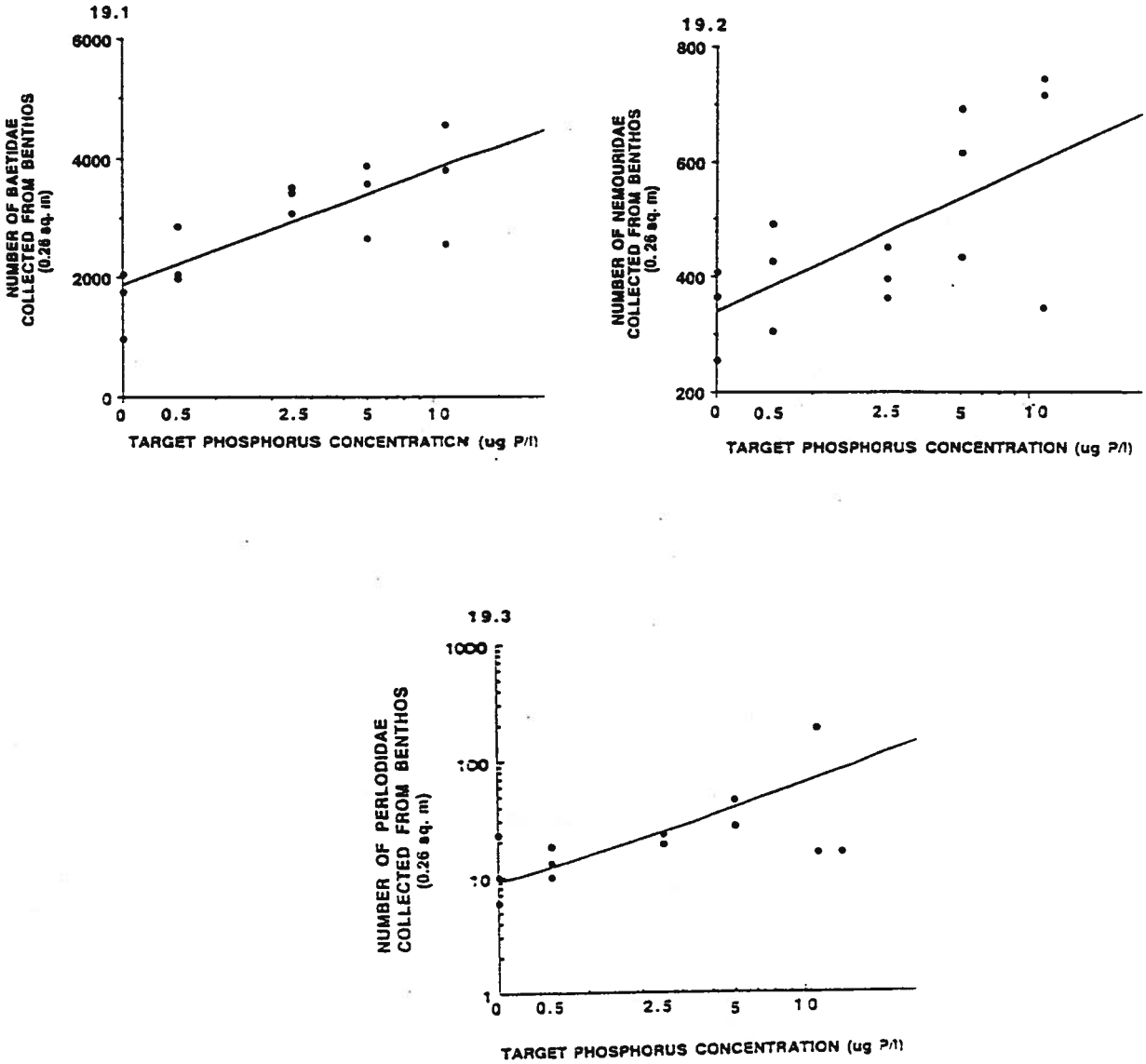

Figure 19. Number of insects collected from the benthos at the end of the second experiment on August 22 as a function of target phosphorus concentration (ug $P \cdot l^{-1}$). Linear regression lines of the data were fitted by least squares.
(19.1) Baetidae. $y = 2088.56 + 1701.56 * \log(P)$. $r^2=0.45$. $p=.003$.
(19.2) Nemouridae. $y = 339.45 + 252.29 * \log(P)$. $r^2=0.37$. $p=.008$
(19.3) Perlodidae. $\log(y) = 1.07 + 0.52 * \log(P)$. $r^2 = 0.29$. $p=.02$