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Some Effects of a Grazer, Hyalella azteca on Ecosystem Level Properties in Aquatic Microcosms

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SOME EFFECTS OF A GRAZER, *HYALELLA AZTECA*, ON ECOSYSTEM LEVEL PROPERTIES IN AQUATIC MICROCOSMS

by

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Martin D. Werner

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ABSTRACT

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by

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A study to determine some ecosystem level effects of an aquatic invertebrate grazer, Hyalella azteca, was performed in aquatic microcosms. Impact of the grazer was assessed in three general areas: 1) inorganic nutrient levels of the microcosm water column, 2) productivity and respiration of the biotic community, and 3) plant community composition in the microcosms.

The grazing amphipod caused inorganic phosphorus and nitrogen (except ammonia) levels to be elevated in the microcosms. The increase was due, at least partially, to excretion of nutrients into the water by the amphipod. The presence of H. azteca did not significantly alter levels of gross productivity for the whole system nor for the sediment surface. Productivity to respiration ratios were significantly reduced by the grazing amphipod, indicating the amphipod was inhibiting plant biomass accumulation even though gross productivity was not affected.

Systems exposed to amphipod grazing had a twenty-five percent lower plant biomass than controls at the termination of the experiment. Gross productivity to plant biomass ratios were significantly higher in grazed systems, indicating a more actively growing plant community was being maintained by the grazer's activities. Plant community composition was significantly altered by the amphipod. Chara biomass was higher in grazed systems, while filamentous algae, blue-green algal colonies and periphyton had significantly higher biomasses in the control systems. The phosphorus distribution within the grazed microcosms was significantly different from that found in the controls. More phosphorus was incorporated into filamentous algae, blue-green algal colonies and the overall plant compartment in the control, while Chara and the water column contained more phosphorus in the grazed microcosms. The amphipod also caused the percent content of phosphorus to be higher in certain plant categories.

(96 pages)

INTRODUCTION

Heterotrophic organisms play an important role in the regulation of ecosystem processes (Chew 1974). Grazing organisms in particular have been shown to have important effects on ecosystem processes and structure in both aquatic and terrestrial systems (e.g. Harper 1969; Porter 1977). The most obvious impact of grazing is the direct effect it has on the structure of the plant community (e.g. Harper 1969). Selective removal of certain plants by grazers can significantly alter the original species composition and diversity of the system (Lubchenco 1978). A more subtle but potentially more important effect is that which grazers have on nutrient cycling, particularly the rate at which certain nutrients are cycled. Changes in nutrient cycling patterns due to grazing have been shown to result in changes in the intensity of plant production (McNaughton 1979; Mattson and Addy 1975) and changes in functions of production such as respiration to production and production to plant biomass ratios (Byers 1963).

Extensive literature exists on the nature of grazers' impact on their environment (see reviews by Harper 1969; Porter 1977; McNaughton 1979). However, there has not been a published study which has experimentally investigated aspects of grazer initiated alterations on nutrient cycling rates, productivity, and autotrophic community composition concurrently. The present study is an attempt to analyze these three factors, which are potentially of major importance in understanding the impact grazing organisms have on their ecosystem. The major contribution of the study will be to demonstrate the

relationships of the three factors mentioned in systems which are exposed to grazing.

Hyalella azteca was the grazer used in this research. Hargrave (1970a) investigated the feeding habits of the species and determined that it feeds selectively on epiphytic algae in natural systems. The amphipod would also feed on detritus at the sediment surface but did not prefer that food source. Hargrave calculated an assimilation efficiency for the amphipod of approximately 72-80 percent for epiphytic algae but only 15-23 percent for sediment detritus. Cooper (1965) stated H. azteca populations are often associated with macrophytes such as Chara, Elodea, and Myriophyllum where they feed on epiphytes, filamentous green algae and various types of detritus.

The major objective of the research was to investigate the nature and degree of impact a grazing organism has on its ecosystem. The primary hypothesis tested was that the grazing activities of the amphipod, H. azteca, have no effect on their system. Contributing hypotheses which the research specifically tested were:

1. H. azteca has no effect on the level of measurable inorganic nutrients dissolved in the ecosystem water.
2. The amphipod has no effect on the productivity or respiration of the system as measured by total and benthic community metabolism.
3. H. azteca does not alter the proportion of biomass of the following plant categories: periphyton, filamentous algae, large blue-green algal colonies, and macrophytes.
4. The amphipod does not change the ratio of production to autotrophic biomass in the system.

5. H. azteca has no effect on the distribution of phosphorus within the ecosystem.

The research was performed in aquatic microcosms (38 ℓ aquaria) in a temperature and light controlled room. The use of laboratory microcosms in research of this type is advantageous because of the greater measure of control afforded by this approach. All microcosms used in this study were maintained under similar environmental conditions. Light and temperature intensities are particularly important in this type of research (Byers 1963: Whittaker 1961) and control over these factors would be impossible in the field. Perhaps most important in investigations of this nature is the ability to exclude organisms, which are not desired, from the study and to exclude the "treatment" grazer from controls. These factors allow attention to be drawn only to the factors which are of specific interest, thus lessening the interference of confounding variables. A greater measure of control also lessens variability among treatment units, allowing one to focus on results caused by the treatments.

A major limitation of this approach is the danger of excluding important factors in the composition of the model ecosystem. For this reason it is not realistic to directly extrapolate results from a microcosm study to a more complex "real world" ecosystem. In particular, it is known that factors such as rates and extents of processes derived from microcosm studies cannot always be reliably used for natural systems (King in press).

In short, although the study was conducted under relatively simple and artificial conditions, it provides insights into potential effects

and functions a grazer such as Hyallela azteca may have on an ecosystem.

LITERATURE REVIEW

There are three major ways that grazers may exert regulation on their ecosystem. Grazers may 1) alter plant species composition and/or dominance through selective grazing, 2) affect the rate of nutrient cycling, and 3) affect the productivity and biomass of the autotrophic community. These three areas of potential grazer impact will be discussed in the order presented.

Alterations in Plant Community Composition Due to Grazing

Harper (1969) reviewed several major studies discussing grazer imposed alterations of plant community composition and diversity. He speculated that due to similar environmental and nutritive requirements, little opportunity exists for plants to diversify along resource axes. Animal grazers may therefore be an important factor regulating plant diversity by reducing plant biomass, thereby freeing resources and allowing new plant species to invade the habitat. Many natural grazing studies have demonstrated that grazers can, in fact, reduce plant biomass of certain plant species to the extent that new species invade to utilize freed resources (e.g. Lubchenco 1978; Johnson 1956). The significance of this finding is that not all plants are equally available to a grazer. Certain plants, presumably in response to grazing pressure through evolutionary time, have developed elaborate protective mechanisms against grazers (Cates and Orians 1975). The result is that grazers reduce the standing crop of the palatable

plant species, leaving protected plants to become more dominant, thus changing the plant community structure. For example, Porter (1977) reported filter feeding zooplankton selected particles on the basis of size, shape and texture. Thus zooplankton grazers do not consume algae such as large unicellular desmids, filamentous diatoms and colonial blue-green algae. Conversely, nannoflagellates, crytomnads and other diatoms are selectively removed by the zooplankton. The potential effect on plant community composition due to zooplankton grazing becomes obvious when one considers that zooplankton may filter the entire water volume of some lakes from 1 to 4.7 times per day (Haney 1973; Porter 1977). In fact, Porter noted a shift from more to less edible algae in lake epilimnions subjected to heavy grazing pressure. She attributed the shift to selective feeding and differential digestion by the grazer and changes in nutrient regeneration rates due to grazers' digestive activities.

The effect of grazing on plant species composition can be dramatic. Hazell (1967) documented changes in the plant species composition due to grazing in a short grass prairie in Oklahoma. In ungrazed plots four species of grasses constituted 92.5 percent of the total plant biomass. In plots whose composition was originally similar but were subjected to grazing, the four grass species were essentially nonexistent. Although the situation was experimentally induced there are examples of the same phenomenon occurring in completely natural situations. In fact, Hrbacek et al. (1961) contends that biotic factors, such as grazing, are as important in determining natural phytoplankton associations in lakes as abiotic factors, except when

the abiotic factors are extreme. Lubchenco (1978) rigorously tested several specific hypotheses concerning the impact of grazing by a marine periwinkle snail (Littarina littorea) on algal community composition. This herbivorous snail had a strong preference for small ephemeral algal species which apparently lacked both structural and chemical means for herbivore avoidance. In laboratory food preference tests the snail strongly selected small green algae species such as Enteromorpha intestinalis, which is a dominant algae of high tide pools along the New England coast, where the study took place. Lubchenco (1978) found that by excluding L. littorea from the tide pools an almost pure stand of Enteromorpha developed. Dominance of this algal species resulted from its dispersal abilities and its continuously high reproductive rates. Without snail grazing pressure Enteromorpha became encrusted on other species and out-competed them for light. With a high snail density, however, Enteromorpha was essentially eliminated from the pools, allowing the less preferred long-lived species (specifically Chondrus) to dominate. Thus, although Enteromorpha was the dominant competitor for space, it was susceptible to grazing to the extent that it was eliminated when grazers were at high density. At moderate snail densities Enteromorpha and other emphemeral algal species persisted, but at a reduced density. Thus at moderate grazing pressures competitive exclusion was prevented, and coexistence of both ephemeral and perennial algae resulted. Lubchenco's findings indicate that if grazers prefer the dominant plant species there is a unimodal relationship between plant diversity and grazer density (i.e. highest diversity of plant species at intermediate consumer densities).

If competitively inferior species are preferred there is an inverse correlation between prey diversity and consumer density. Lubchenco identified three factors critical in determining changes in the plant community composition studied. These factors are: 1) food preference of the herbivore, 2) competitive relationships between plant species, and 3) various microenvironmental conditions.

Stimulation of Nutrient Cycling by Grazing

A second major effect grazing animals potentially have on their ecosystems is altering the rate and magnitude at which inorganic nutrients are regenerated. The mechanism of this action might be of two distinct types. First, grazers consume nutrients in organic form (i.e. plant material) and subsequently excrete inorganic nutrients into the ecosystem. Secondly, grazer activity may stimulate the activity of the decomposer organism to more rapidly oxidize organic material.

Rigler (1961) pointed out that although turnover of inorganic phosphorus is often caused primarily by bacteria, it is important to define the role of other organisms in the phosphorus cycle. Rigler found that Dapnia magna loses inorganic phosphorus by both excretion and secretion at an average rate of 8.4 $ng \cdot h^{-1}$ per animal. Several studies have demonstrated that inorganic phosphorus is a very dynamic nutrient in lakes (e.g. Rigler 1956; Hutchinson and Bower 1950). Whittaker (1961) estimates phosphorus turnover rate among phytoplankton to be from 0.10 to 0.34 hours in large aquatic microcosms. Although the phosphorus turnover rate for invertebrate animals was much slower, Whittaker believed phosphorus movement through invertebrates was very

important in his experiment. Hargrave and Geen (1968) calculated the amount of inorganic phosphorus excreted by zooplankton in two Nova Scotian lakes. Their results showed that zooplankton excreted twice the daily phosphorus required to sustain the level of productivity estimated for one of the lakes. In the other lake one-fifth of the phosphorus needed to sustain its level of productivity was excreted by zooplankton.

Johannes (1968) reviewed the importance of aquatic invertebrate animals in nutrient regeneration. He stated that although bacteria may be primarily responsible for nutrient cycling in certain environments, such as soil (MacFadgen 1964), animals are significantly important in aquatic environments. For example, Johannes (1964) demonstrated that a protozoan grazer contributed more to the direct release of phosphorus than did bacteria in a model aquatic ecosystem. Johannes (1968) pointed out that phosphorus regeneration by bacteria occurs only when bacteria respiration rates exceed rates of bacterial synthesis. If this is not the case bacteria actually immobolized phosphorus by incorporating it into their tissue. Since bacteria have a high surface to volume ratio their nutrient uptake kinetics are superior to that of algae (Riger 1956). Barsdate et al. (1974) studied the effect a bacterial grazer had on the nutrient regeneration rate in model ecosystems. They report that the role of direct excretion of phosphorus by the grazer was minor, which contradicts Johannes' (1964) conclusion. However, Barsdate et al. (1974) demonstrated that the grazer did increase the rate of mineralization of detritus, specifically the rate of nutrient release from detritus to the surrounding

environment. The authors attributed the increased nutrient cycling rate to the protozoan cropping of bacterial populations to create a physiologically younger and more active bacteria population. Faster growth rates of microbial populations increased secretion and excretion rates of nutrients, resulting in more rapid nutrient cycling (Barsdate et al. 1974; Harrison and Mann 1975). Due to the dynamic cycling of phosphorus, a result of the grazing activity of protozoan, orthophosphate had a turnover time of approximately two minutes. The two minute cycling within this dynamic nutrient pool proceeded at a rate of more than one hundred times the rate of nutrient release from decomposing plant material in the model ecosystems (Barsdate et al. 1974). Presumably without the grazer, phosphorus cycling would assume a rate determined by the release of nutrients from decomposing organic matter. Other studies indicate that macroinvertebrates have the same effect of stimulating bacterial action. Additionally, larger organisms function to reduce the particle size of organic material, increasing the biologically active surface area of the material, thus the rate of decomposition (Fenchel 1970; Harrison 1977; Lopey et al. 1977).

Mattson and Addy (1975) recently reviewed several ways in which insect grazers impact forest ecosystems, including effects such as: 1) increased light penetration, 2) reduced competition for abiotic factors (e.g. nutrients), 3) increased nutrients leaching from foliage, 4) increased rate of fall of nutrient rich litter, 5) stimulated redistribution of nutrients from nutrient sinks, and 6) stimulated activity of decomposers. Most of these effects directly parallel the effects of bacterial grazers previously reviewed. Autotrophic grazers

may, in fact, have a greater potential to significantly alter the availability and redistribution of abiotic factors than do decomposers or saprophytes. Grazers directly interact with living autotrophs whereas decomposers and saprophytes must rely on dead organic material. Furthermore grazers, which actively seek food not only release nutrients but also redistribute the nutrients formerly incorporated in living material. Additionally, grazers affect the rate of activities of decomposers by making organic material available to the decomposers (Mattson and Addy 1975). My intention is not to suggest that decomposer processes are a less important mechanism of nutrient regeneration but to suggest that autotrophic grazers also have a central function in nutrient regeneration.

Productivity Changes Due to Grazing

Since grazers impact plant community structure and nutrient cycling rates, they may also affect the productivity of autotrophic communities. It is well established (e.g. Dickman 1968; Mason and Bryant 1975; Flint and Goldman 1975) that grazers may significantly reduce the standing crop of the plant community. However, Hargrave (1970b) and Cooper (1973) present evidence that gross primary production of the system may actually be increased in spite of the lowered plant biomass. Alternately, primary production and plant biomass may not be significantly altered, but the species contributing to primary production can change with grazer impact (Hazell 1967; Kehde and Wilhm 1972).

Hargrave (1970b) investigated the effect of the amphipod (H. azteca) on the production of benthic algae at the sediment surface of Marion Lake, British Columbia. Different densities of the amphipod were enclosed in glass cylinders and placed over the sediment surface. After a 48 hour incubation period, Hargrave sealed the cylinders and subsequently measured oxygen production (net production) and consumption (respiration) in the various treatment cylinders. Hargrave found that amphipod grazing increased oxygen production at amphipod densities within the range naturally found in lakes. Primary production rates were significantly lower for amphipod densities above or below the natural density. Hargrave suggested that this evidence supported the hypothesis that a dynamic balance exists between the amphipod and the epibenthic algal community. He determined that the microbial heterotrophic community was also stimulated by amphipod activity at densities from six to ten times those found naturally. Increased microbial activity likely increased the rate of nutrient cycling thus nutrient availability to the autotrophs. This phenomenon may explain the increased autotrophic production at natural amphipod densities. However, at high densities the amphipod reduced the standing crop of the epibenthic algae at a rate for which the autotrophs could not compensate (Hargrave 1970b).

Low level grazing by the crayfish (Pacifastacus leniusculus) in the littoral region of Lake Tahoe, California-Nevada, enhanced primary production (Flint and Goldman 1975). On the other hand a high density of the crayfish inhibited primary production. Flint and Goldman (1975) found that nutrients contributed by the crayfish feces significantly

stimulated epibenthic algal production. The authors concluded that natural primary producers compensated for moderate grazer exploitation by increasing the rate of primary productivity. These results strongly parallel those of Hargrave (1970b).

Brock (1967) measured primary productivity and standing crop of algae along a hot spring thermal gradient in Wyoming. The "natural" experiment included or excluded grazers depending on the water temperature of the particular section of the spring. Brock concluded that the level of primary production is not necessarily correlated with the amount of plant standing crop. In some cases standing crop was significantly reduced by grazers while primary production remained at a high level. By consuming plant material and microbial organisms the grazer released nutrients, allowing the remaining algae to achieve a higher level of production.

METHODS

Research Design

A microcosm approach was used for this research. Sixteen 38 ℓ aquaria contained the experimental units. Sediment for the microcosms was collected from the west shore of Wellsville Reservoir, Wellsville, Utah. The collected sediment was thoroughly mixed then heated in shallow metal containers at 60°C for 6 to 8 hours. This temperature regime and duration of heating assured the destruction of macroinvertebrates and most autotrophs while minimizing the denaturation of proteins and death of microorganisms (F. Post pers. comm.). The partially dried sediment was then rehydrated, thoroughly remixed and divided into 5 kg portions (one for each of the experimental microcosms).

Twenty-six and one-half liters of water from an artesian well at the Logan Fish Hatchery, Logan, Utah were added to each of the aquaria. The artesian well provided a source of water, with a constant chemistry, free of autrotrophs and invertebrates. The artesian well water was available throughout the study for replacement of water sampled. Water which evaporated from the microcosms was replaced with distilled water to maintain a constant water volume (26.5 ℓ) in each microcosm. Since the initial addition of water to the aquaria caused sediment to become suspended, material in the water was allowed to settle for two days before the experiment was begun.

An innoculum was prepared with a limnetic water sample collected from the west shore of the Wellsville Reservoir. A sediment sample

was collected concurrently from the same area of the reservoir. Four hundred milliliters of the limnetic water and 50 g of the sediment were mixed with a magnetic stirrer for 1.5 hours. After the sediment had settled, the water was decanted and filtered through a 500 μm sieve to remove zooplankton and larger autotrophs. Ten milliliters of the innoculum was added to each of the 16 microcosms.

The microcosms were maintained at 21 (± 2)°C in a temperature controlled room. Illumination was provided by 8 cool white florescent tubes (Sylvania #F40CW) and 8 plant light florescent tubes (General Electric #F40PL) arranged alternatively 60 cm above the water surface. Surface illumination was maintained at 88.6 (± 4.3 sd) $\mu E \cdot M^{-2} \cdot S^{-1}$. A 12 hour light-dark cycle was in effect through the duration of the experiment.

A constant air supply was bubbled through each of the microcosms to provide water circulation through the duration of the experiment (except during certain analyses).

The microcosms were allowed a 72 day developmental period after the innoculum was added. During this time period an autotrophic community developed in each of the microcosms. To insure a high degree of homogeneity between microcosms 1 ℓ of water from each microcosm was collected daily, mixed in a common container and 1 ℓ of the mixture was redistributed to each of the microcosms. Care was taken not to disturb the sediment during this process. The cross innoculation process was continued for the first 65 days of the experiment (except on days when metabolism was measured in the microcosms). In previous

studies, cross innoculation proved effective in achieving homogeneity between microcosm units (Byers 1963; Cooper 1973).

Following the 72 day developmental phase, the amphipod, H. azteca, was added to 12 of the microcosms. Four of the microcosms had initial densities of 50 amphipods, 4 had 100, 4 had 200 amphipods and 4 microcosms were left as controls (i.e. without amphipods). Although the food habits of H. azteca were not investigated in the present study, I assumed (based on Hargrave 1970 and Cooper 1965) that the amphipod was primarily a grazer. The treatment phase continued from day 73 to day 160 of the experiment.

Procedures

An outline of chemical water analyses performed, equipment used, sampling frequency, sampling technique and its source appear in Table 1. The water column was sampled using a 22 cm by 3.8 cm diameter glass cylinder. The cylinder was lowered into the water to contain a complete microcosm water profile. It was then corked at the top, raised a few cm and corked at the bottom. Water samples collected in this manner were used for all analyses.

Total phosphorus was determined for several categories of autotrophs (including periphyton, filamentous algae, large blue-green algal colonies and macrophytes) and the sediment surface on day 117 and 160 of the experiment. A small sample of the material to be analyzed was wet weighed, placed in 50 ml of water and hydrolyzed as prescribed for total phosphorus determination (Standard Methods, APHA, 1971). Wet weight to dry weight regressions were determined to convert all

Table 1. Chemical analyses performed on microcosm water, equipment used for analyses, frequency, technique used and their source

Analysis	Equipment	Frequency (roughly)		Technique	Source
		Developmental Phase	Experimental Phase		
Orthophosphate	Beckman (Model B) Spectophotometer	Irregular	Weekly or bimonthly	Ascorbic acid	Strickland & Parsons (1968)
Total phosphorus (water)	Beckman (Model B) Spectophotometer	Irregular	Bimonthly	Ascorbic acid Acid hydrolysis	Strickland & Parsons (1968)
Ammonia	Beckman (Model B) Spectophotometer	Bimonthly	Bimonthly	Indophenol	Solorzano 1969
Nitrite	Bausch & Lomb Spectophotometer 20	Monthly	Monthly	Diazotization	Strickland & Parsons (1968)
Nitrate	Bausch & Lomb Spectophotometer 20	Monthly	Irregular	Cadmium-Reduction	Strickland & Parsons (1968)
Alkalinity	Corning Model 610A pH meter	Monthly	Irregular	Potentiometric	American Public Health Ass. (1971)

Table 1. Cont.

Analysis	Equipment	Frequency (roughly)		Technique	Source
		Developmental Phase	Experimental Phase		
Specific Conductance	Yellow Springs Inst. Co. Model 31 Conductivity Meter	Monthly	Irregular		American Public Health Ass. (1971)
Oxygen		Varied with specific analysis (see Methods)		Winkler with Azide Modification	American Public Health Ass. (1971)

data to grams phosphorus per gram material dry weight. The amount of phosphorus contained in the amphipod population of each microcosm on day 160 was estimated using the same hydrolysis procedure.

Productivity analyses were performed on the total system and on the benthic community (excluding amphipods). Early in the experiment productivity was measured for the water column but was later discontinued because values were low and spurious. Whole system productivity was measured using a light and dark bottle oxygen technique (Vollenweider 1969). The air bubbler was removed from each microcosm and an initial oxygen concentration was determined. The entire microcosm was then covered with clear polyethylene (Glad Wrap) to reduce oxygen diffusion. Following a 12 hour light phase the microcosms were individually partially uncovered, a sample quickly removed and the polyethylene cover replaced. After this procedure was performed the dark phase was initiated. The oxygen concentrations determined at the end of the light phase served as an initial value for the dark phase in each microcosm. Twelve hours were allowed for the dark phase. The sampling procedure was then repeated. In order to conserve water, a sample of 63 ml was used at each sampling session for Winkler oxygen titrations. Fifty milliliters of this sample were titrated with approximately 0.062 N sodium thiosulfate. The dilute titrant was used to increase the accuracy of the titration. Standarization procedures using potassium dichromate as the primary standard were performed to determine precise normality of the titrant (note: YSI Oxygen Meter Model 54 was used to determine oxygen concentrations for total system production on days 59, 62, and 77, but was discontinued later to

increase the accuracy of the analysis). Whole system productivity was measured approximately monthly during the developmental stage, then biomonthly during the early experimental stage and weekly during late experimental stages.

Benthic sediment metabolism was measured using an apparatus consisting of a Whirl-Pak bag stretched over an open end of a section of PVC pipe 4 cm high by 5.5 cm in diameter (see Figure 1). The bag was sealed to the PVC pipe with a silicon sealer. Approximately 2 m of Tygon tubing was passed through a small hole in the PVC pipe and sealed into place. Sixteen of the bag apparatus were constructed so benthic metabolism in each of the microcosms could be measured concurrently. To measure benthic production, 325 ml of water from the Logan Fish Hatchery artesian well with a known oxygen concentration were poured into the bag apparatus. A thick tin cover was then placed over the opening of the apparatus, the apparatus was placed into the microcosm, lowered to the bottom, inverted, and the tin cover removed so the open end of the bag apparatus enclosed a portion of the sediment surface. This procedure was repeated for the 15 remaining microcosms. After a 12 hour light period, a water sample was siphoned from each bag apparatus through the Tygon tubing into an oxygen bottle. An oxygen analysis using the Winkler technique with a 50 ml water sample was performed as described for the whole system productivity analysis. After a 12 hour dark period another water sample was removed from the bag apparatus and analyzed for oxygen concentration. As with the whole system analysis, the oxygen concentration determined at the end of the light phase served as an initial value for the dark phase

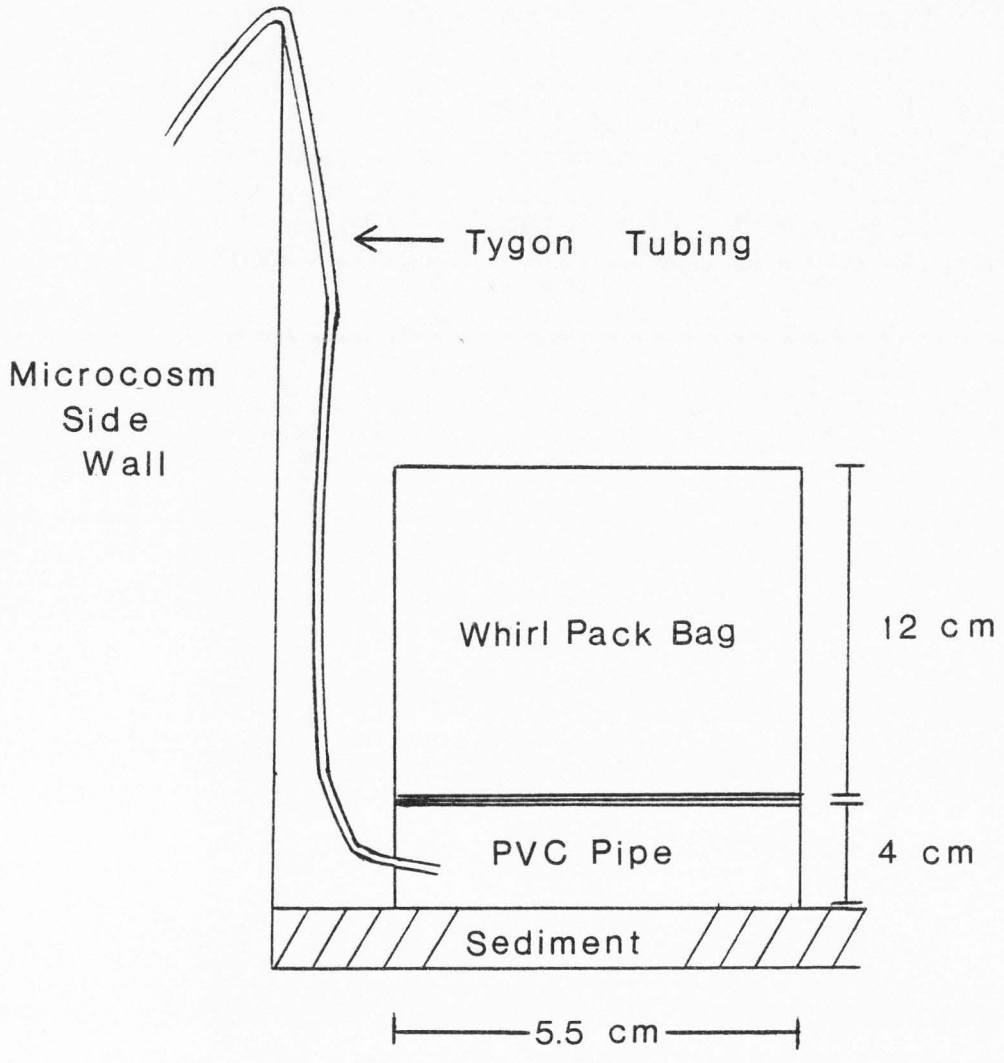

Figure 1. Apparatus for measuring sediment metabolism of the microcosms

in each microcosm. From the oxygen concentration values obtained in this test, oxygen production and consumption could be calculated for a representative area of the sediment surface (note: a correction was made for the reduced volume of water in the bag apparatus during the dark phase of the analysis). Sediment surface productivity was measured monthly throughout the experiment.

Biomass estimates were made for the plant categories of periphyton, filamentous algae, blue-green algal colonies and macrophytes on days 117 and 160. On day 117 a plastic cylinder 9 cm in diameter was lowered into each microcosm. All plants enclosed by the cylinder were removed from the microcosm for analyses. Macrophytes were clipped off at the sediment surface using small scissors to reduce sediment disturbance. After the majority of plant material had been removed by hand, a small dip net (500 μm mesh) was passed through the enclosure to collect what remained. Three of the plant categories (filamentous algae, blue-green algal colonies and macrophytes) were included in this sample. The plant mass collected from each microcosm was carefully separated into the separate categories using forceps. Each separated plant mass from each microcosm was then placed on a preweighed tare (piece of aluminum foil), dried for 24 hours at 105°C in a forced air drying oven (Blue M), cooled in a desiccator and weighed (Mettler Balance, Model H51). Periphyton biomass was sampled from glass microscope slides which had been suspended in each microcosm from strings. The periphyton was scraped from the slides, dispersed evenly in a known volume of water and a known volume of the solution was subsampled using a volumetric pipet. The subsample was filtered

(using a Millipore membrance filtering apparatus) onto an oven-dried and preweighed filter (Whatman, GFA). The filter was oven-dried and weighed, as described for the plant categories, and periphyton biomass was calculated. On day 160 the entire plant community in the categories of filamentous algae, blue-green algal colonies and macrophytes was collected from each microcosm. These plants were separated, dried and weighed in the manner described for day 117. Periphyton was collected on day 160 by scraping a vertical swath 7.6 cm wide through the entire glass surface of each microcosm above the sediment surface and below the air-water interface. Periphyton biomass in the microcosm were estimated using the procedure described for day 117.

All amphipods were collected on day 160 and counted. At least ten percent of the amphipod population from each microcosm was measured to determine a size frequency distribution for each microcosm. From this analysis head length to dry weight, head length to wet weight and head length to whole body phosphorus concentrations equations were determined for the amphipods.

Data Processing and Analysis

In analyzing this data, treatments had to be reduced to grazed and control microcosms. The original density treatments (i.e. 50, 100 and 200 amphipods per aquaria) were abandoned because the amphipods reproduce at fast and uneven rates. In some of the microcosms with low initial densities the amphipod reproduced at a fast rate and appeared to achieve or surpass density levels in treatments which initially had higher densities. However, this trend was complicated by uneven reproduction rates between replicates within density levels. Also,

it was impossible to accurately sample the amphipods due to the complex structure of the microcosms and the amphipods' avoidance behavior. I believe the original density treatments did not critically affect data analysis, particularly during latter parts of the experiment. The reproductive capacity of the amphipods was such that a steady state population appeared to be achieved within a month after treatment initiation, regardless of initial amphipod density.

Mean values were calculated for all parameters measured on all days sampled for grazed (12 replicates) and ungrazed (4 replicates) microcosms. Statistically significant differences between the means were determined using a Student-t-test ($\alpha = 0.10$). In most cases a two-tailed test was utilized, exceptions were where a one-tailed test was justified based on the literature.

RESULTS

Nutrient Levels

Differences between means of each nutrient level for each date sampled were tested using a one-tailed t-test. Alkalinity and conductivity were analyzed using a two-tailed test. Past studies indicate that heterotrophic organisms stimulate the release of nutrients from organic material into the ambient environment (e.g. Johannes 1968; Barsdate et al. 1974). Thus elevated nutrient levels would be expected in grazed relative to ungrazed systems.

Phosphorus

Figure 2 depicts the mean orthophosphate concentrations for the control and treatment microcosms throughout the experiment. Note a sharp initial decline of orthophosphate levels to a measured low on day 52 (this was prior to amphipod addition). Beyond day 52 there was a trend for orthophosphate to steadily increase in both control and treatment microcosms. The treatment microcosms had a significantly higher mean orthophosphate concentration on days 86, 132, 149, and 156.

The fate of total phosphorus in the water column of the microcosms suggests a trend similar to that observed for orthophosphate (Figure 3). The measured low for total phosphorus occurred on day 64. Significantly higher total phosphorus levels for grazed versus control microcosms occurred on days 100, 133, and 155.

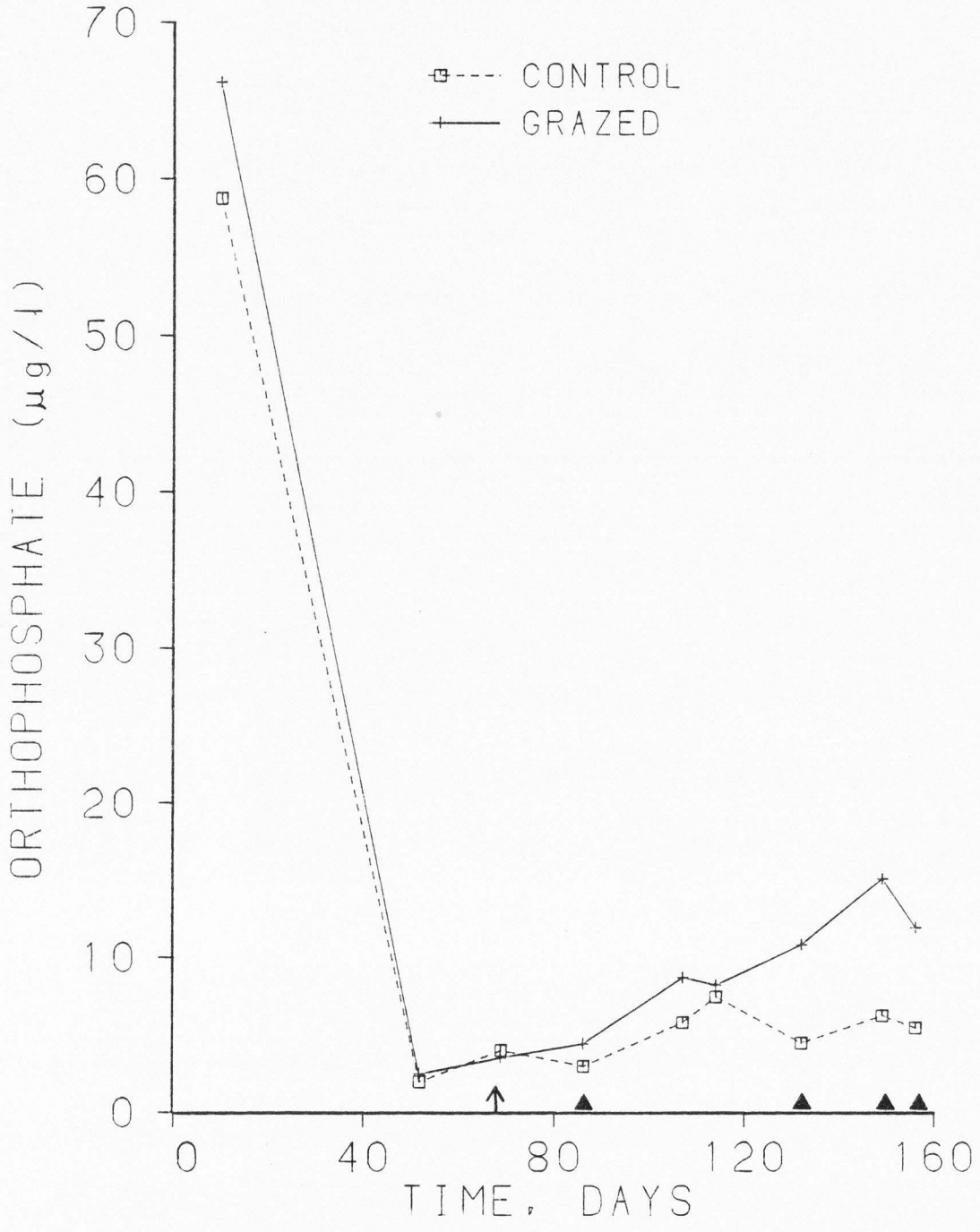

Figure 2. Mean orthophosphate concentrations of control and grazed microcosms plotted against time. A triangle above the time axis signifies a statistically significant difference ($\alpha = 0.10$) between control and grazed microcosms on that date. Treatment initiation was on day 72 (denoted by an arrow on the X-axis).

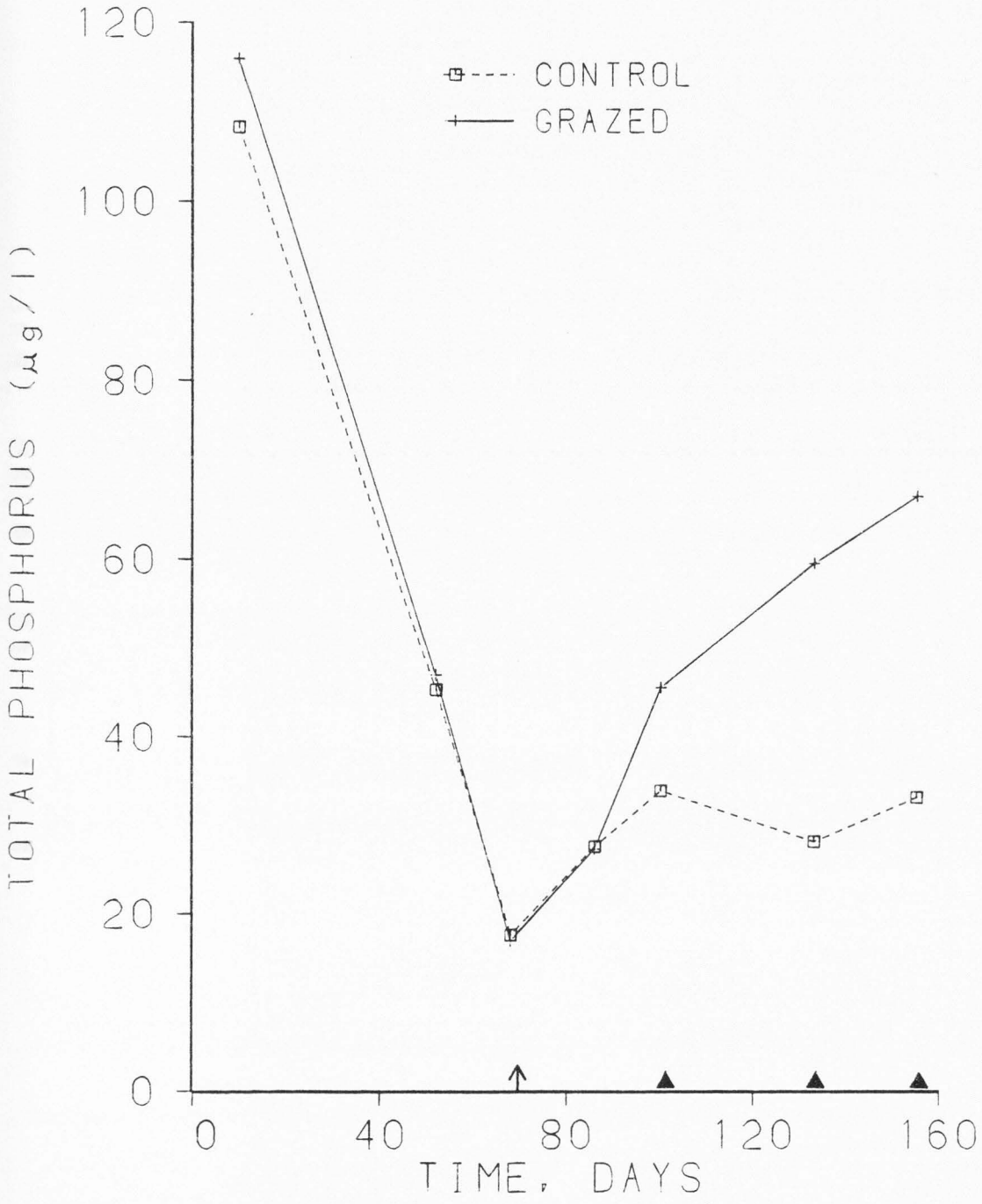

Figure 3. Mean total phosphorus concentrations of control and grazed microcosms plotted against time. A triangle above the time axis signifies a statistically significant difference ($\alpha = 0.10$) between control and grazed microcosms on that date. Treatment initiation was on day 72 (denoted by an arrow on the X-axis).

Nitrogen

Mean ammonia concentrations in both control and treatment microcosms showed a paralleled decrease throughout the experiment (Figure 4). The rate of the decrease lessened as the experiment progressed. There were no significant differences between treatment and control means of ammonia concentrations at any sampling date.

The concentrations of nitrite and nitrate in the microcosms are plotted in Figures 5 and 6 respectively. There was a dramatic initial decrease in both of these nutrients to a relative low on day 50. Subsequently these nutrients increased in concentration with nitrate concentrations being greater than nitrite in both control and treatment microcosms for the remainder of the experiment. In addition, there was a tendency for both of these nitrogen fractions to be higher in grazed microcosms. Significant differences between control and grazed microcosm means occurred for nitrate on day 160 (Figure 6) and nitrite on days 100 and 160 (Figure 5).

Buffering Capacity and Ionic Strength

Mean alkalinity concentrations and conductivity values are plotted against time in Figures 7 and 8, respectively. Both of these parameters initially tended to decrease sharply, then gradually decline in concentration. On sample dates after the treatments were initiated (day 72), mean values for aklalinity and conductivity were consistently higher in the treatment microcosms than in the controls, however, the differences were not statistically significant.

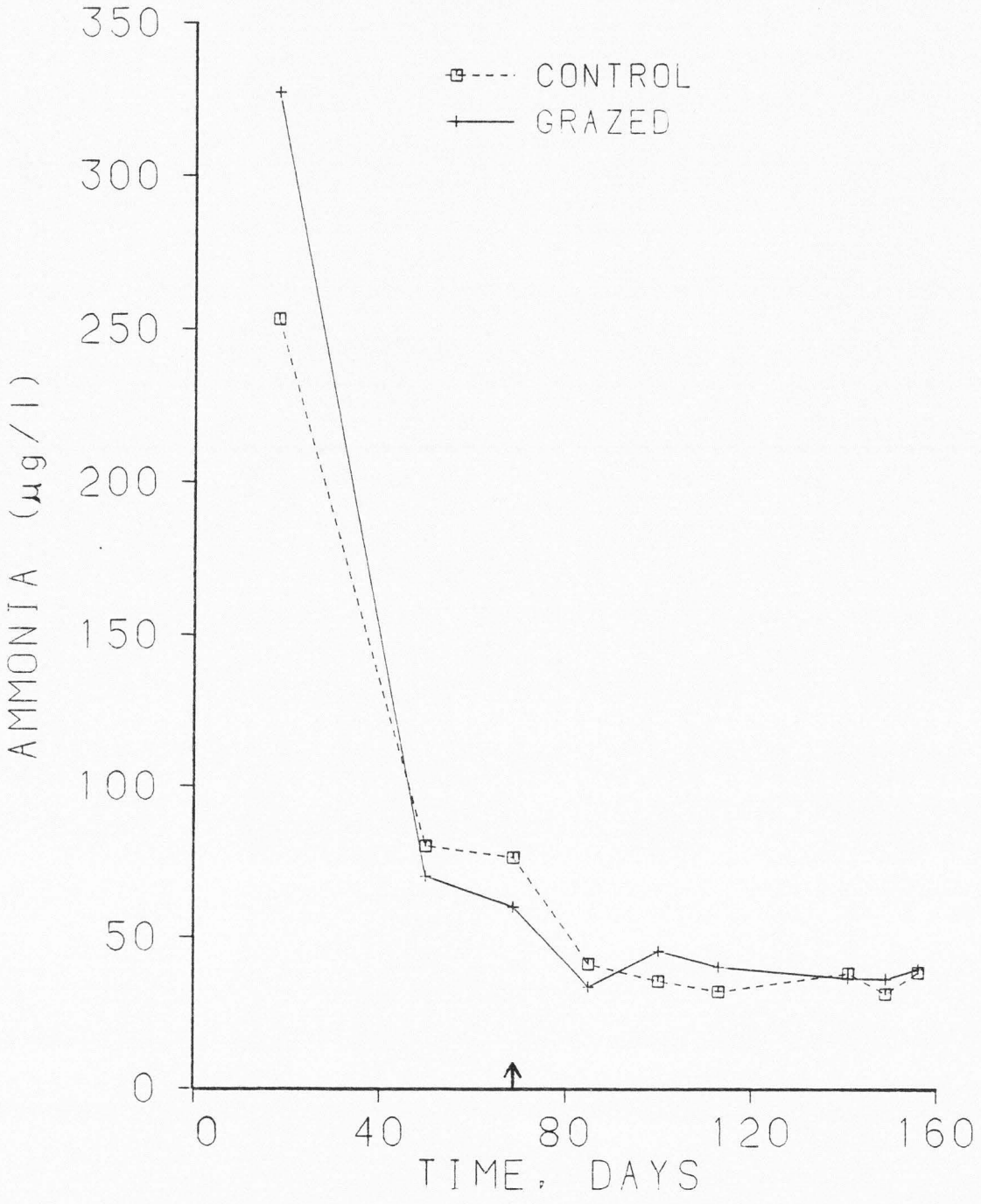

Figure 4. Mean ammonia concentrations of control and grazed microcosms plotted against time. A triangle above the time axis signifies a statistically significant difference ($\alpha = 0.10$) between control and grazed microcosms on that date. Treatment initiation was on day 72 (denoted by an arrow on the X-axis).

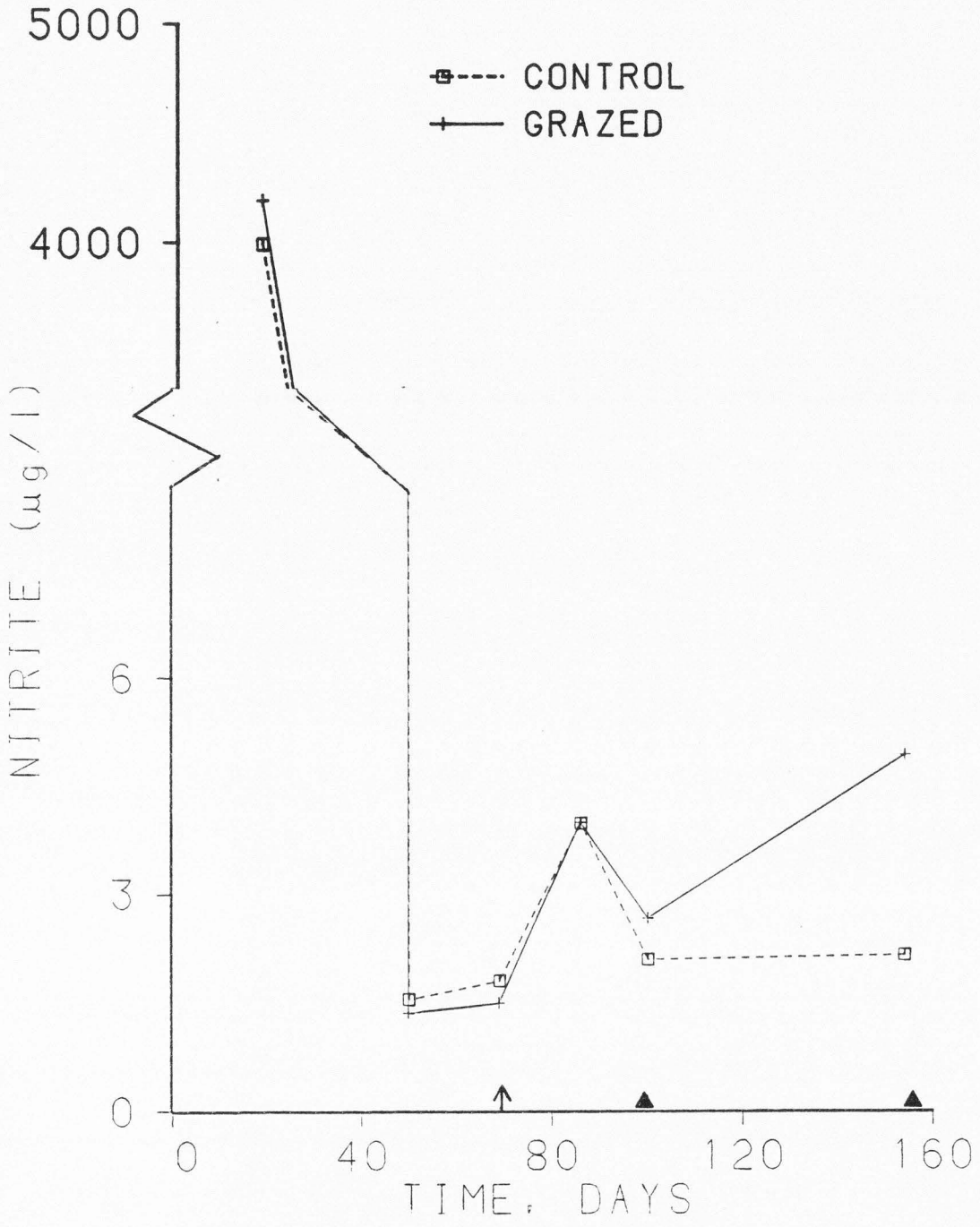

Figure 5. Mean nitrite concentrations of control and grazed microcosms plotted against time. A triangle above the time axis signifies a statistically significant difference ($\alpha = 0.10$) between control and grazed microcosms on that date. Treatment initiation was on day 72 (denoted by an arrow on the X-axis).

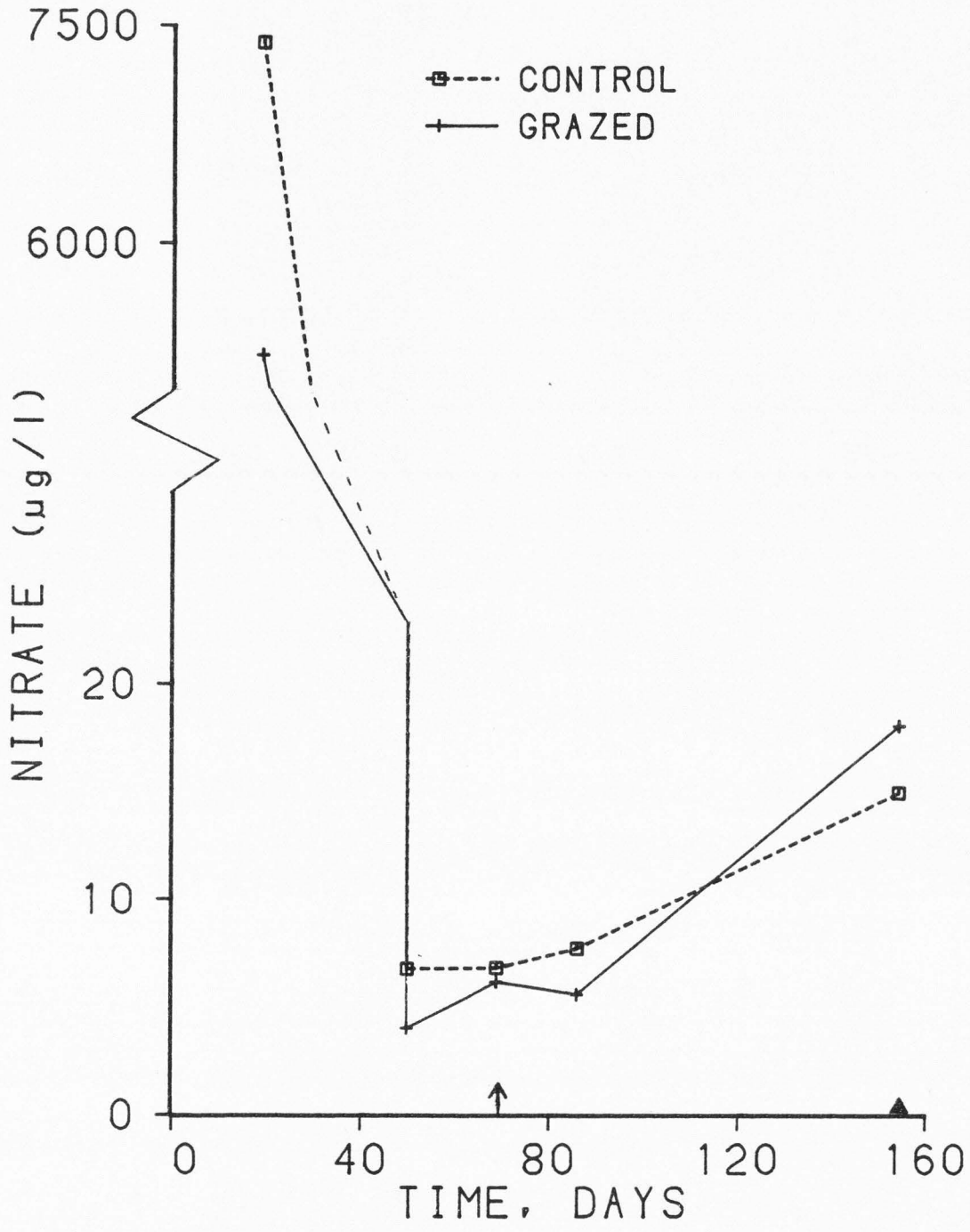

Figure 6. Mean nitrate concentrations of control and grazed microcosms plotted against time. A triangle above the time axis signifies a statistically significant difference ($\alpha = 0.10$) between control and grazed microcosms on that date. Treatment initiation was on day 72 (denoted by an arrow on the X-axis).

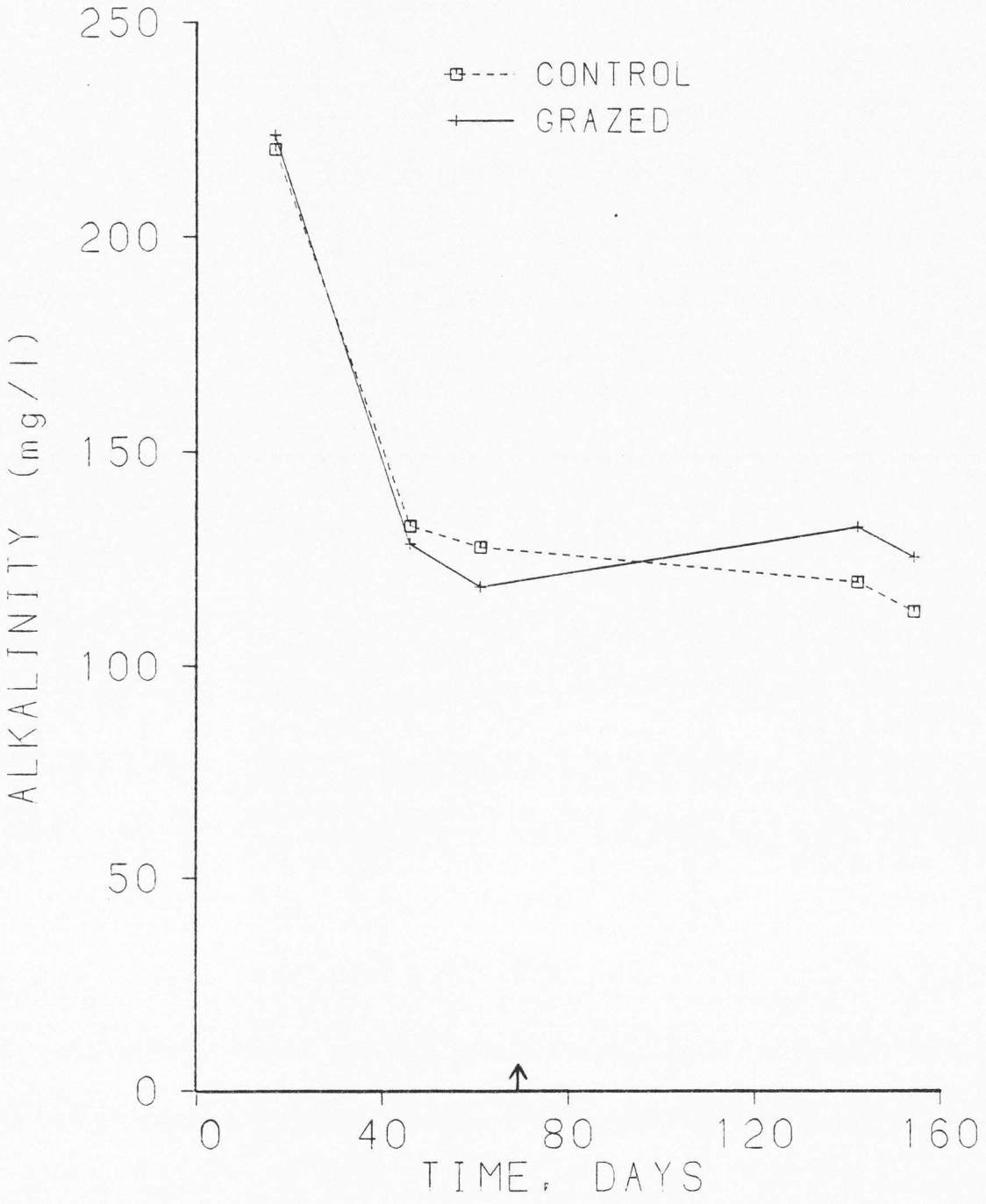

Figure 7. Mean alkalinity of control and grazed microcosms plotted against time. A triangle above the time axis signifies a statistically significant difference ($\alpha = 0.10$) between control and grazed microcosms on that date. Treatment initiation was on day 72 (denoted by an arrow on the X-axis).

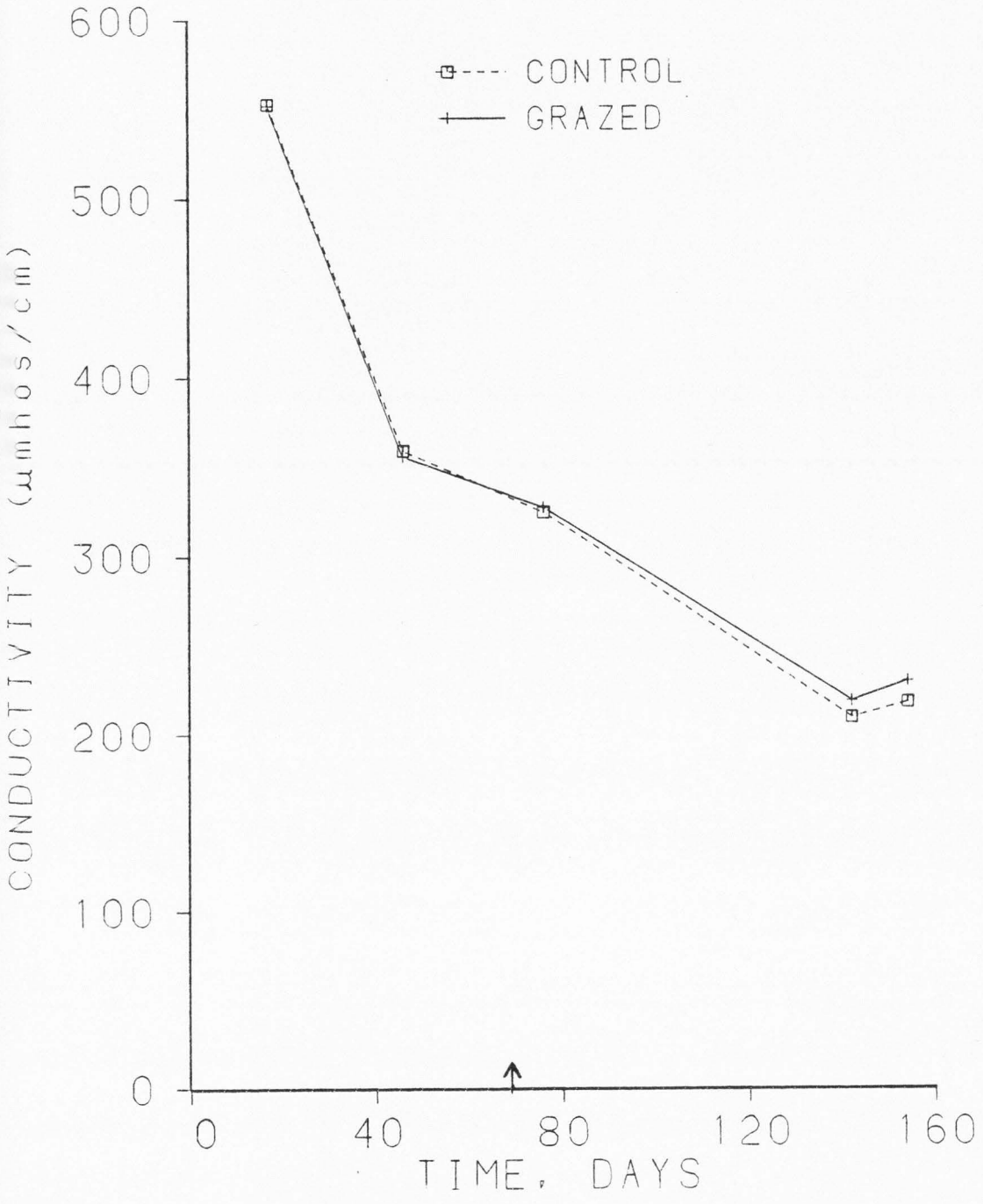

Figure 8. Mean conductivity level of control and grazed microcosms plotted against time. A triangle above the time axis signifies a statistically significant difference ($\alpha = 0.10$) between control and grazed microcosms on that date. Treatment initiation was on day 72 (denoted by an arrow on the X-axis).

Metabolism

The two-tailed Student-t-test was employed to analyze whole system and sediment metabolism data since previous studies indicate grazers may either increase or decrease metabolism parameters, depending on conditions such as grazer density (e.g. Hargrave 1970; Flint and Goldman (1975).

Whole System Metabolism

Mean gross productivity (GP) values of the whole system are plotted against time in Figure 9. Gross productivity tended to increase throughout the course of the experiment. Control and treatment microcosms demonstrated similar patterns, with no significant differences between the magnitude of whole system gross productivity means during the experiment.

Trends in net productivity (NP) and respiration (R) for the whole system are presented in Figure 10 and 11 respectively. As with gross productivity these parameters increase through time with no significant difference between control and treatment means.

Net productivity to respiration ratios (NP:R) were calculated in order to further investigate the impact of grazing on the productivity patterns of the microcosms (Figure 12). NP:R values peaked approximately halfway through the experiment and then declined. Treatment and control microcosms followed a similar pattern, although mean values of the two differed significantly on several days (126, 133, 141, 148, and 155) late in the experiment. In every case in which

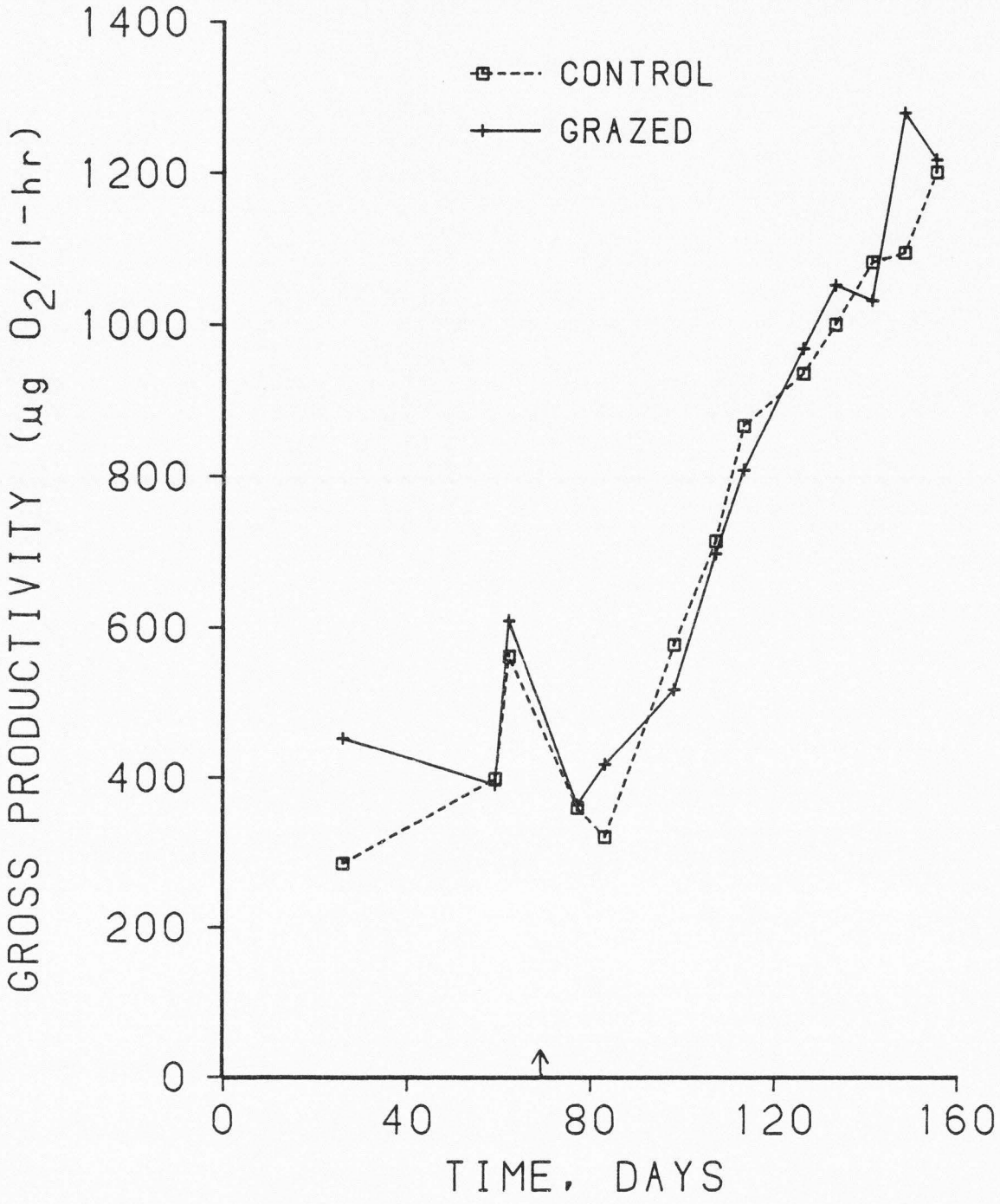

Figure 9. Whole system gross productivity of control and grazed microcosms plotted against time. Treatment initiation was on day 72 (denoted by an arrow on the X-axis).

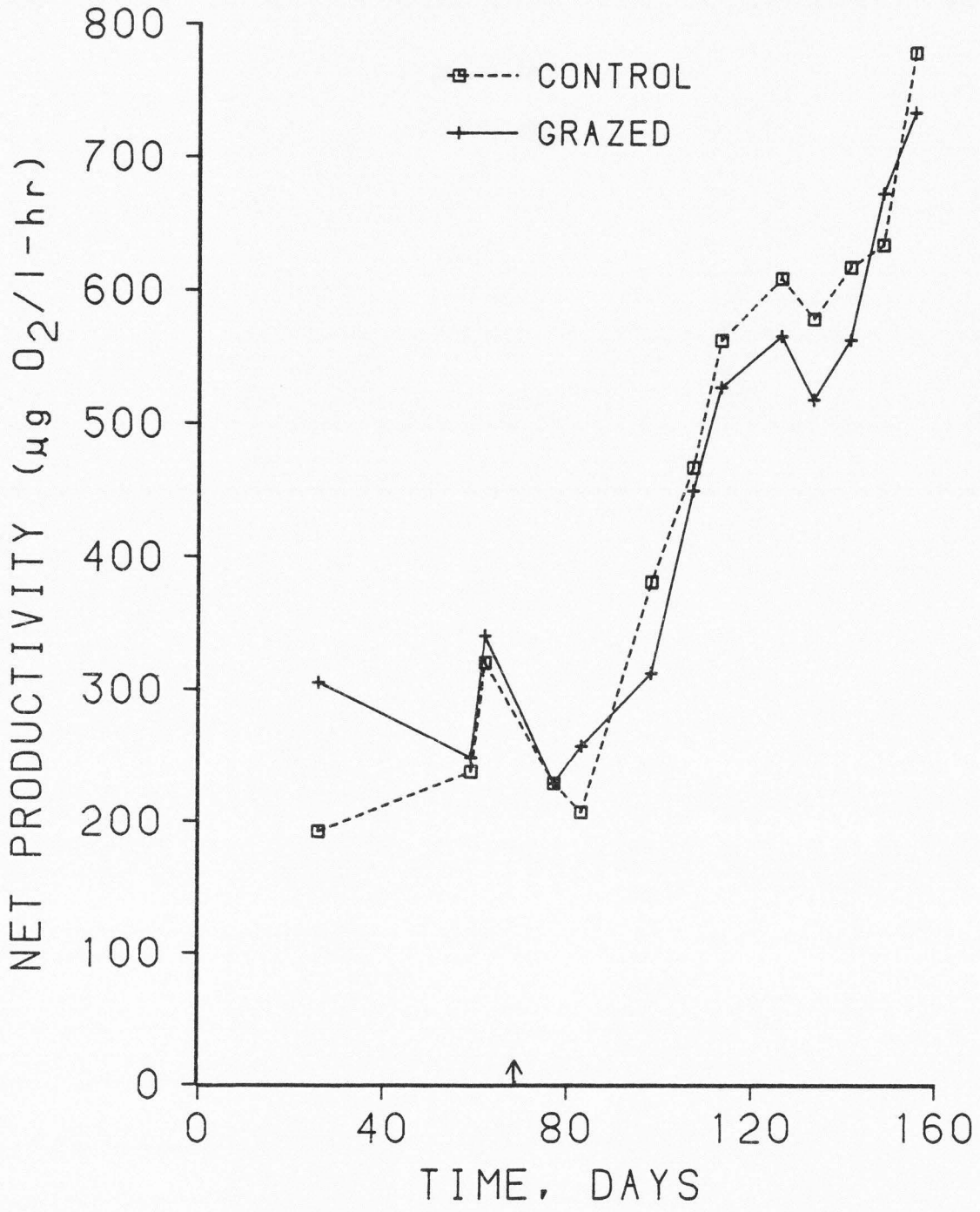

Figure 10. Whole system net productivity of control and grazed microcosms plotted against time. Treatment initiation was on day 72 (denoted by an arrow on X-axis).

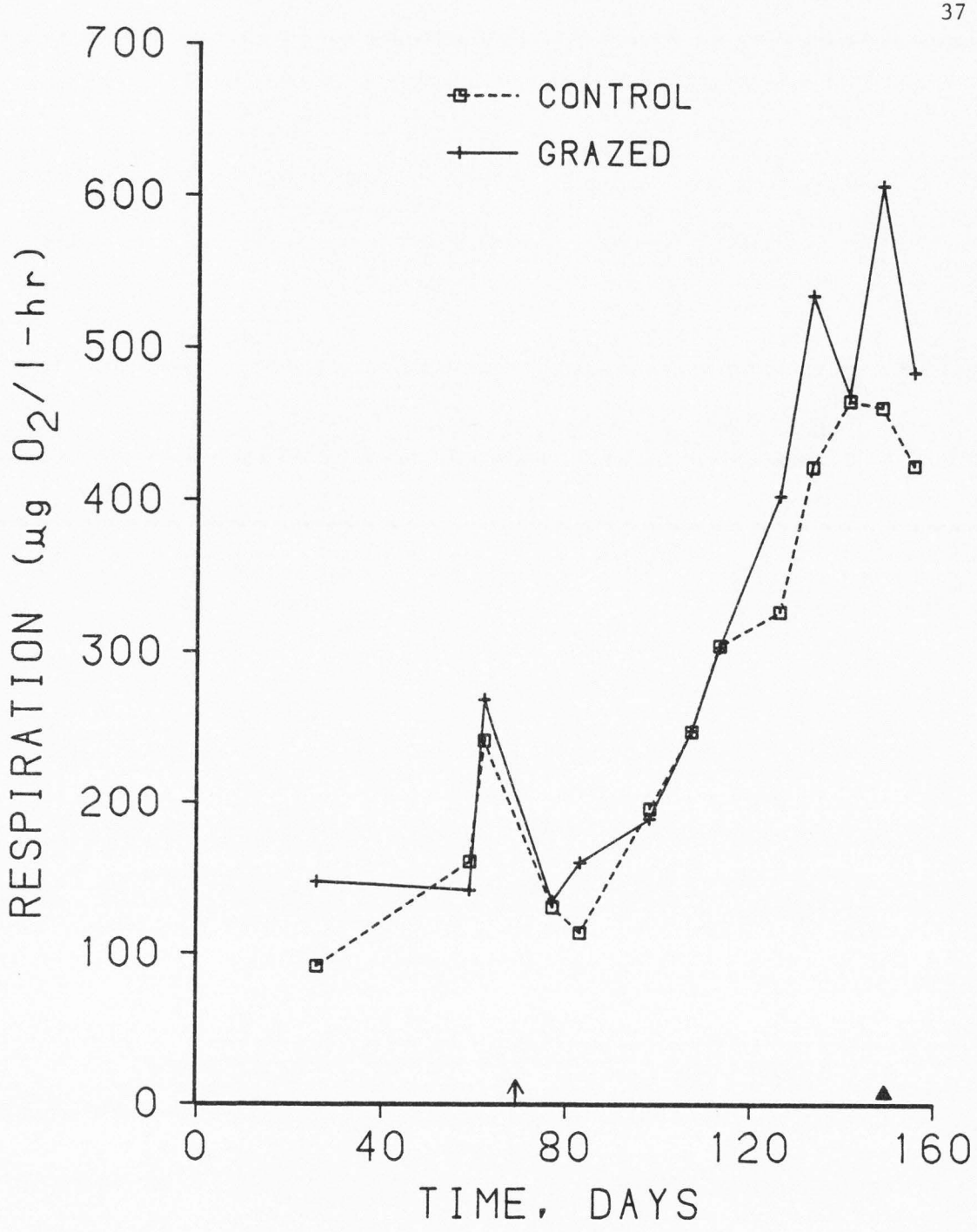

Figure 11. Whole system respiration of control and grazed microcosms plotted against time. A triangle above the time axis specifies a statistically significant difference ($\alpha = 0.10$) between control and grazed microcosms on that date. Treatment initiation was on day 72 (denoted by an arrow on the X-axis).

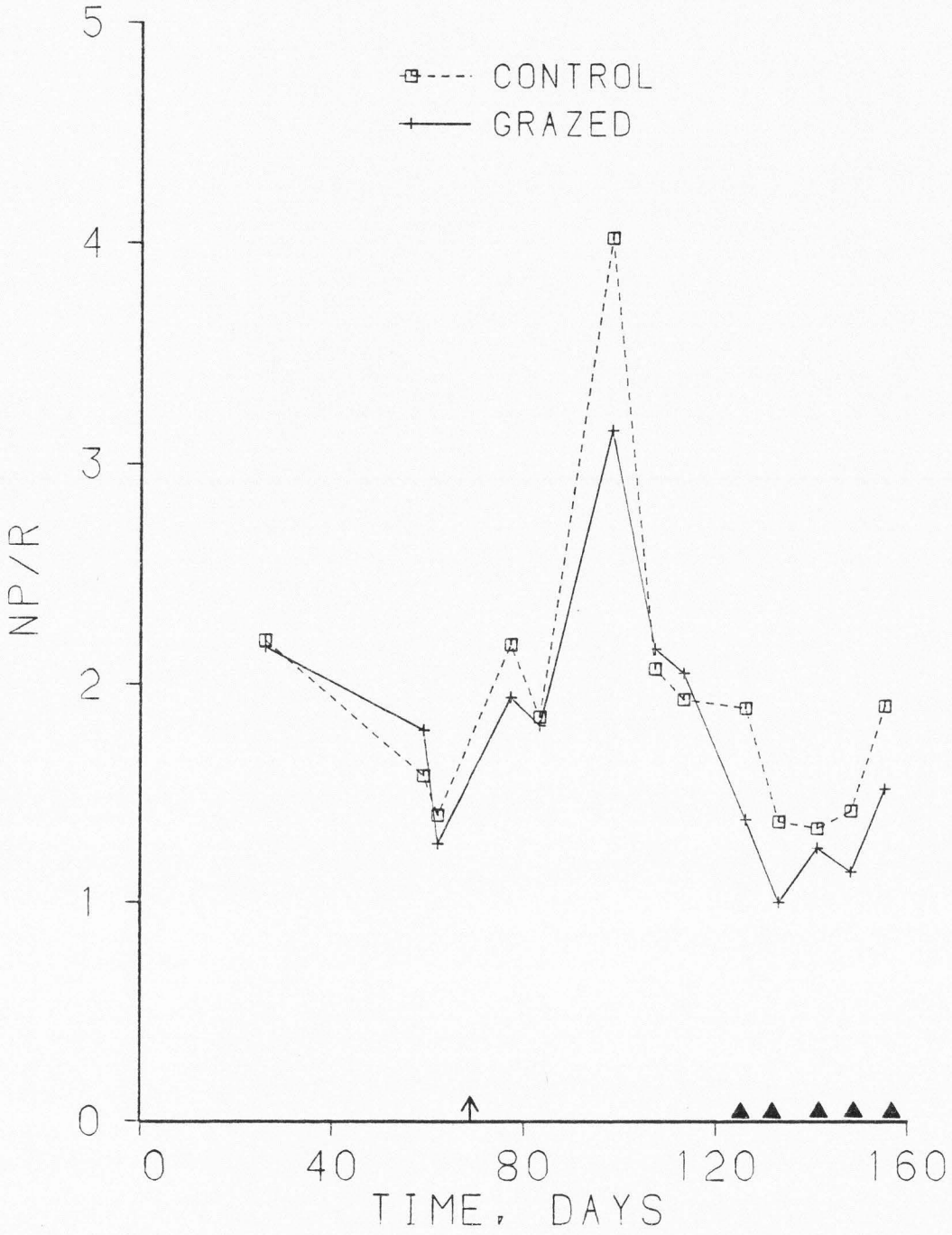

Figure 12. Whole system net productivity to respiration ratio (NP:R) of control and grazed microcosms plotted against time. A triangle above the time axis signifies a statistically significant difference (α = 0.10) between control and grazed microcosms on that date. Treatment initiation was on day 72 (denoted by an arrow on the X-axis).

there was a significant difference, the control had a greater NP:R value.

Sediment Metabolism

The pattern through time of gross productivity, net production and respiration of the sediments are plotted in Figures 13, 14, and 15 respectively. No clear temporal trend is shown by these graphs for gross or net productivity. No significant differences in gross productivity exist between treatment and control means for any date sampled. Only on days 79 and 160 do significant differences in net productivity exist. Respiration at the sediment surface decreased initially to a relative low on day 57, then increased beyond that date. On all sampling dates after amphipod introduction the sediment respiration rate was greater for treatments than for controls, although the differences were statistically different only on day 96.

Ratios of gross productivity to respiration (GP:R) were calculated from sediment metabolism data and are presented in Figure 16. It was convenient to use gross productivity rather than net productivity for this ratio because net productivity was sometimes negative (i.e. respiration sometimes dominated at the sediment surface even during light phases). The difference between the values of the ratios are constant (i.e. GP:R - 1 = NP:R). After amphipod introduction treatments had lower gross productivity to respiration ratios than controls.

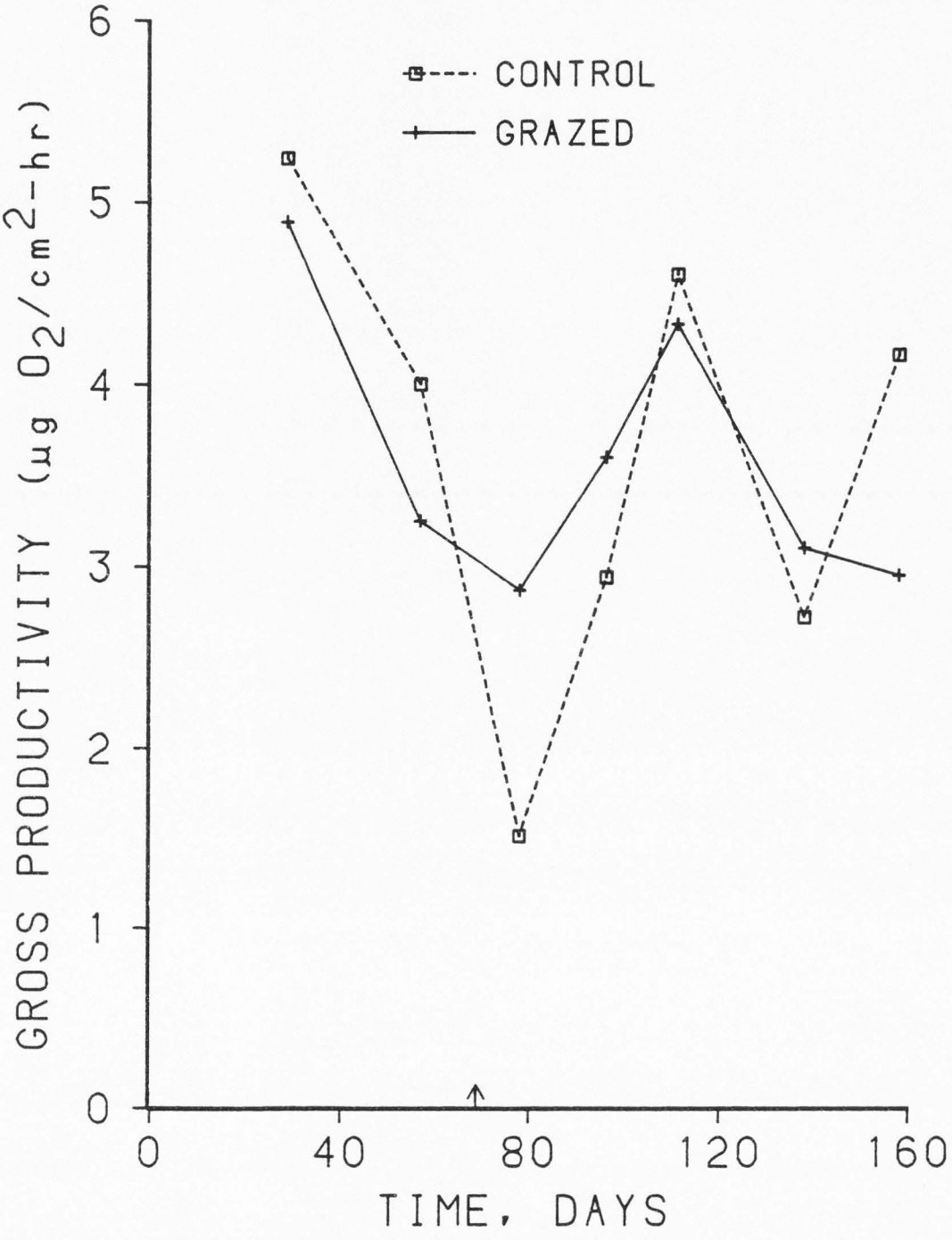

Figure 13. Sediment surface gross productivity of control and grazed microcosms plotted against time. Treatment initiation was on day 72 (denoted by an arrow on the X-axis).

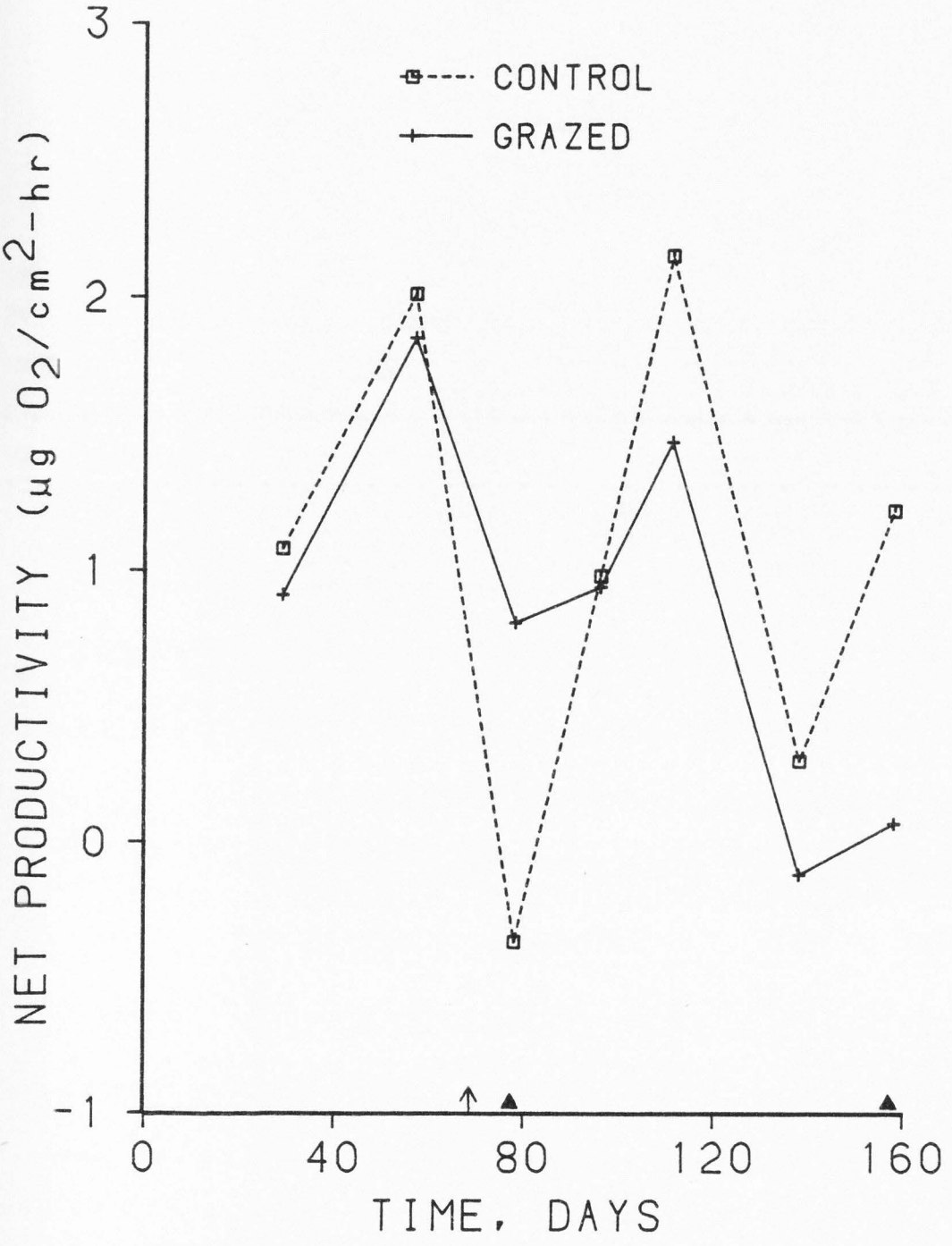

Figure 14. Sediment surface net productivity of control and grazed microcosms plotted against time. A triangle above the time axis signifies a statistically significant difference ($\alpha = 0.10$) between control and grazed microcosms on that date. Treatment initiation was on day 72 (denoted by an arrow on the X-axis).

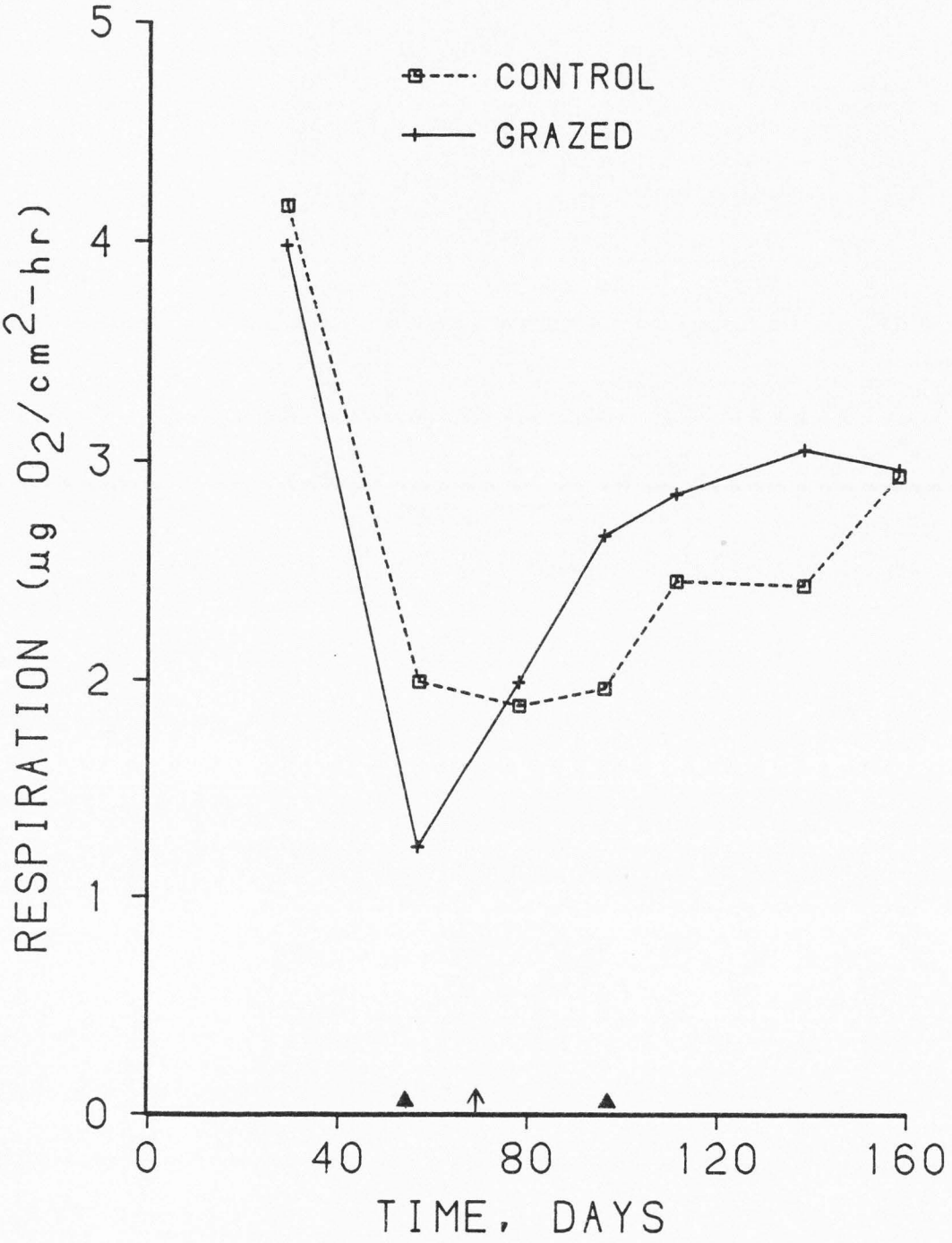

Figure 15. Sediment surface respiration of control and grazed microcosms plotted against time. A triangle above the time axis signifies a statistically significant difference ($\alpha = 0.10$) between control and grazed microcosms on that date. Treatment initiation was on day 72 (denoted by an arrow on the X-axis).

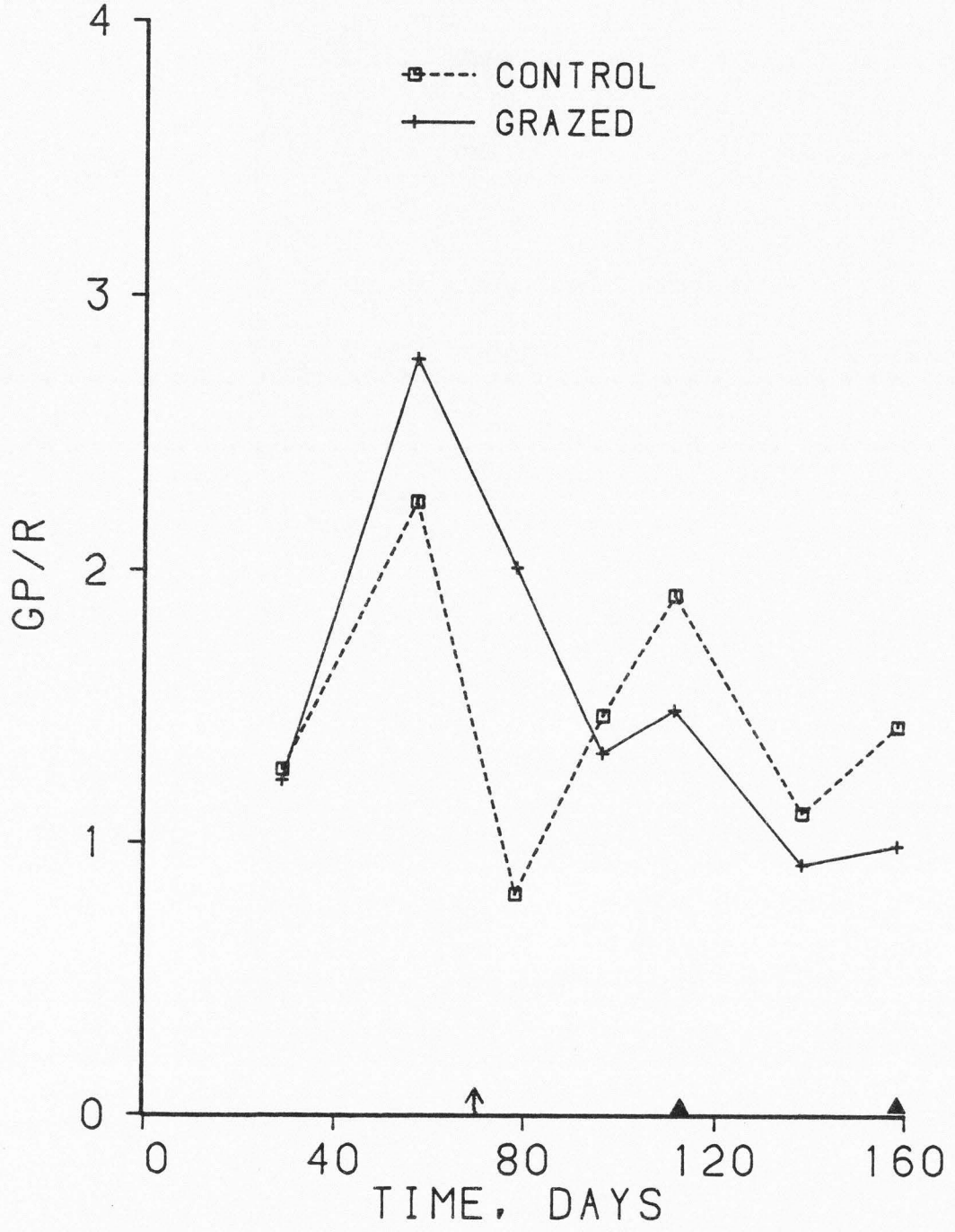

Figure 16. Sediment surface gross productivity to respiration ratio (GP:R) of control and grazed microcosms plotted against time. A triangle above the time axis signifies a statistically significant different (α = 0.10) between control and grazed microcosms on that date. Treatment initiation was on day 72 (denoted by an arrow on the X-axis).

Biomass

The biomass values determined for the major plant categories (macrophytes, filamentous algae, blue-green algal colonies and periphyton) on days 117 and 160 are listed in Table 2. A significantly greater total plant biomass was present in the control microcosms compared to treatment microcosms on both day 117 and 160. However, Chara, (the only macrophyte in the systems) had a significantly greater biomass in the grazed systems on day 160. Filamentous algae was significantly greater in the controls on both days, while periphyton and blue-green algal colonies attain a significantly higher biomass in controls by day 160.

Phosphorus Distribution

The phosphorus distribution on the final day is presented as mean concentrations of phosphorus in several general compartments (all plant categories previously mentioned, sediment surface, water column and amphipods) for control and treatment microcosms (see Table 3). Student's t-test indicates statistically significant differences ($\alpha = 0.10$) for all categores except periphyton, sediment surface, and total community phosphorus. A partial phosphorus distribution is presented for day 117 also in Table 3. The list does not include the amount of phosphorus incorporated in the amphipods, for this reason total community phosphorus could not be calculated. Notice that no large blue-green algal colonies were present in the systems on day 117.

Table 2. Plant biomass (grams, dry weight) in microcosms on day 117 and 160. An asterisk denotes statistically significant differences ($\alpha = 0.10$) between control and grazed microcosms

Category	Day 117			Day 160		
	Control		Grazed	Control		Grazed
Chara	4.57		3.67	5.15	*	9.09
Filamentous algae	11.79	*	1.41	6.96	*	1.10
Periphyton	1.41		0.96	11.23	*	6.23
Blue-green algal colonies	0.0		0.0	2.36	*	0.48
Total	17.95	*	6.32	25.70	*	19.39

Table 3. Phosphorus distribution (grams, phosphorus) within various compartments of the microcosms on days 117 and 160. An asterisk signifies statistically significant differences ($\alpha = 0.10$) between control and grazed microcosms

Compartments	Day 117		Day 160	
	Control	Grazed	Control	Grazed
Chara	0.0852	0.0658	0.0995 *	0.1621
Filamentous algae	0.2322 *	0.0396	0.1371 *	0.0256
Periphyton	0.0192	0.0131	0.1134	0.1122
Blue-green algal colonies	0.0	0.0	0.1085 *	0.0221
Total plants	0.3366 *	0.1185	0.4585 *	0.3221
Sediment surface	2.8683	2.1860	3.2896	3.5732
Water column	0.0007 *	0.0016	0.0009 *	0.0018
Amphipods				0.0581
Total community phosphorus			3.7674	3.9469

DISCUSSION

Chemical and Biological Patterns of the Microcosm

General patterns of the parameters measured were quite similar in both grazed and control microcosms, despite the fact that the magnitude of the parameters were often significantly different (Figures 2-16). All of the inorganic nutrients measured (orthophosphate, ammonia, nitrite, and nitrate) decreased sharply during the early phase of the experiment (day 0 to day 60). This dramatic initial decrease was the result of biotic assimilation at a rapid rate before any of the inorganic nutrients became limiting. Whittaker (1961) described this phenomenon for inorganic phosphorus (in the form of P^{32}) introduced into aquatic microcosms. He determined that rapid inorganic phosphorus removal resulted directly from its assimilation by plants. Furthermore, radioactive phosphorus in the organic form also declined in the water column of Whittaker's microcosms during early phases (day 18-46) of that experiment. The decline of organic phosphorus was attributed to the gradual loss of plants from the water column due to death, subsequent sinking, and incorporation into other parts of the system, particularly the benthic community. The decline of inorganic and organic phosphorus during early phases of the present study (Figures 2 and 3) sharply parallel the situation described by Whittaker (1961). The same explanation may apply to the sharp initial decline of inorganic nitrogen components (Figures 4, 5, and 6).

Following the initial decline of inorganic nutrients was a gradual increase through time in all of the nutrient concentrations, except

ammonia. The most plausible explanation for this phenomenon is that internal nutrient cycling became important in the systems as nutrients were released a) from decomposing plant material (Harrison and Mann 1975; Barsdate et al. 1974), b) from the developing macrophyte community, (McRoy et al. 1972; Twilley et al. 1977) and c) in the grazed systems, by the heterotrophs (Johannes 1968; Pomeroy 1970).

Alkalinity and conductivity decreased at a rapid rate during the early phase of this experiment, similar to the decrease of the nutrients (Figures 7 and 8). Alkalinity is commonly defined as the total titratable base when using a strong acid. Total alkalinity includes the following ions in most natural waters:

$$\text{Total Alkalinity} = (HCO_3^-) + 2(CO_3^{2-}) + (OH^-) + (NH_3) + (H_2PO_4^-) + 2(HPO_4^{2-}) + 3(PO_4^{3-}) + B(OH)_4^- - H^+$$

and (H^+) can be neglected for a pH greater than 4 (Goldman et al. 1972). The rapid initial decrease in alkalinity must have resulted in a decrease of one or more of these ions. Orthophosphate and ammonia concentrations did decrease sharply during the same period that alkalinity decreased (Figures 2, 4, and 7). However the decrease in alkalinity was three orders of magnitude greater during this phase of the experiment, therefore, the decrease in the nutrients cannot sufficiently explain the drop in total alkalinity. A few algae (mostly blue-green algae) and some macrophytes use HCO_3^- and perhaps even CO_3^{2-} directly as their carbon source (Goldman et al. 1972). The dominant autotrophs in the microcosms during this period were periphytic and phytoplanktonic species; it is unlikely that this mechanism

of carbon removal can explain the dramatic drop in alkalinity. A third mechanism seems most plausible. Generally plants preferrentially use free CO_2 as their carbon source (Goldman et al. 1972; Wetzel 1975). As CO_2 is removed from water in which the $CO_2 + HCO_3^- + CO_3^{2-}$ buffering system had been in chemical equilibrium, $CaCO_3$ precipitates to reestablish the equilibrium by releasing more CO_2 from the carbonate system. In water with a pH between 7 and 9, as in the experimental microcosms (Table 4), $Ca(HCO_3)_2$ is the dominant inorganic carbon species (Wetzel 1975). The equilibrium reaction which releases CO_2 with a concurrent formation, and possibly precipitation, of $CaCO_3$ is as follows:

$$Ca(HCO_3)_2 \rightarrow CaCO_3 + CO_2 + H_2O$$

The pH increased from 8.28 to 8.64-8.74 in these microcosms between day 17 and day 46 (Table 4). This pH increase supports the conclusion that biogenic precipitation of $CaCO_3$ was the major mechanism leading to the sharp decrease in alkalinity during the early stage of this experiment.

Conductivity values are the reciprocal of the resistance water had to electron flow. In common bicarbonate-type water conductivity increases or decreases are closely proportional to alkalinity values, since the important ions are those of the carbonate system (Wetzel 1975). Thus one would expect parallel trends of decrease in these parameters, as is the case in this study.

Table 4. pH values of the microcosm water on various days. An asterisk denotes statistically significant differences (α = 0.10) between control and grazed microcosms

Day	pH Value		
	Control		Grazed
17	8.28		8.28
46	8.64		8.74
61		lost	
142	9.00	*	8.61
154	8.99	*	8.74

The net productivity to respiration ratio (NP:R) was greater than or equal to one throughout the entire 160 days of the experiment (Figure 12). When NP:R equals one, biomass stops accumulating in the system and the community can be said to be "stable" or "mature" (Byers 1961; Cooke 1967; Odum 1971). Apparently the microcosms in this experiment had not reached the level of plant biomass which they were capable of supporting. Structurally more simple microcosms reportedly reached a NP:R of unity from 60 to 80 days (Odum 1976; Cooke 1967).

Sediment metabolism was a subset of total system metabolism in this experiment. Percent contribution of the sediment to the total gross and net productivity and respiration is presented in Table 5. Initially the sediment contributed more to total system metabolism than during later stages of the experiment. Sediment net productivity probably became less important because of sediment shading due to the developing macrophytic community. The contribution of the sediment surface respiration remained a substantial part of total system respiration throughout the experiment. The implication is that the sediment surface remains an active site of decomposition as the experiment progressed, as was the case in other studies (e.g. Harrison and Mann 1975; Fenchel 1970; Hargrave 1970b).

The use of polyethelene as a cover to reduce oxygen diffusion in the whole system analysis introduced error due to oxygen diffusion through the polyethelene. By using the equation found in Lebovits (1966) it was determined that the maximum error due to diffusion was 0.30%. In all metabolic analyses conducted the error caused by oxygen diffusion was considered insignificant, so a correction was not made.

Table 5. Percent contribution of sediment surface to whole system metabolic rates. Notice that whole system and sediment surface metabolic analyses were not performed on same days, so percent contributions are approximate

Day of Analysis		Net Productivity		Respiration		Gross Productivity	
Whole Surface	Sediment Surface	Control	Grazed	Control	Grazed	Control	Grazed
26	29	26.7	11.4	217.0	128.2	87.4	48.9
55	57	40.2	35.4	58.8	41.2	47.7	39.6
77	78	0	16.8	68.6	64.2	20.0	34.3
98	96	12.2	14.3	47.5	75.2	24.2	35.6
107	111	21.9	15.5	47.1	54.7	30.6	29.5
135	138	23.1	0	24.8	30.3	12.0	15.5
155	158	7.5	0.5	31.6	30.2	16.2	11.7

Effects of Grazing

The major objective of this research was to investigate the response of an aquatic ecosystem to the activities of the amphipod, Hyalella azteca. Water chemistry, community metabolism and plant community structure were studied in order to assess the grazer's impact on the microcosm system. Chemical parameters measured were orthophosphate, total phosphorus, ammonia, nitrite, nitrate, alkalinity and conductivity. Net productivity and respiration of both the whole system and the sediment surface were used as indicators of the effect of the grazer on community metabolism. Alterations of the autotrophic community composition by H. azteca were determined on the basis of relative proportion of biomass represented by each of the plant categories (i.e. periphyton, blue-green algal colonies, green filamentous algae and macrophytes). The three general groupings of potential grazer effect will be discussed in the order presented above.

Chemical Analysis

With the exception of ammonia inorganic chemical concentrations (Figures 2, 4-6) were consistently higher in grazed microcosms relative to the controls. A tenable explanation for this phenomenon exists. As the amphipod ingested organic matter in the form of plant material, it egested both inorganic nutrients, and particulate material which was more easily degraded by microbial decomposers to inorganic nutrients. Direct release of inorganic nutrients has been demonstrated for a wide variety of aquatic macroinvertebrates (e.g. Flint and Goldman 1975; Johannes 1965; Rigler 1956; Hargrave and Geen 1968). The effect of

grazing organisms in manipulating particulate organic material to increase the rate of inorganic nutrient release by the microbial community is also well documented in the literature (e.g. Barsdate et al. 1975; Fenchel 1972; Harrison 1977; Harrison and Mann 1975; Lopez et al. 1977).

Inorganic phosphorus levels were higher on every sampling date in the grazed microcosms (Figure 2). It is well established that inorganic phosphorus assimilation by autotrophs is very rapid in freshwater systems. For example, Rigler (1961) added radioactive phosphorus (P^{32}) to lake water contained in polyethylene bags and found that 97% of the P^{32} was taken up by the phytoplankton within thirty minutes (see Hutchinson and Bowen 1950; and Whittaker 1961 for similar results). Despite the rapid phosphorus assimilation capabilities of autotrophs, the plants in the grazed microcosms did not assimilate inorganic phosphorus as rapidly as it was made available to them because of the amphipods activities, as evidenced by Figure 2. The differences between control and treatment means in Figure 2 reflect the amount of inorganic phosphorus released which had not been reassimilated by the autotrophs and decomposers of the systems. In fact, the amount of inorganic phosphorus excreted by the amphipod population on day 160 was calculated for every microcosm. The mean amount of PO_4-P excreted per microcosm per hour was 125 µg (s.d. ± 76) or 3000 µg per day. This predicted excretion rate is based on regression equation constructed by Lamarra (unpublished) correlating aquatic organism weight to excretion rate. The predicted excretion rate of the amphipod population is much greater than would be suggested by the maximum mean concentration

difference of 9 $\mu g \cdot l^{-1}$ (or 238 µg per microcosm) inorganic phosphorus measured between grazed and ungrazed microcosms (Figure 2, day 148). From these calculations, it is apparent that the amphipod population is excreting phosphorus into the environment at a rate exceeding the subsequent reassimilation by other biota in the system.

Ammonia was the only inorganic nutrient which was not altered in concentration by the amphipods' activity. Ammonia is a major excretory product of many aquatic animals (Wetzel 1975). It is therefore rather surprising that the amphipod population did not significantly increase ammonia levels. In fact, an equation constructed by Lamarra (unpublished) predicts the mean amphipod population in the microcosm would excrete 845 µg NH_3-N per hour on day 160. Most of the excreted ammonia is probably rapidly converted to nitrite then to nitrate by nitrifying bacteria. Most algae and macrophytes use nitrate rather than ammonia as their nitrogen source, except in alkaline situations (Wetzel 1975). Conditions of high oxygen content and moderate pH values existed in the microcosms, which is ideal for nitrification (Wetzel 1975). Perhaps the rate of conversion of ammonia by the nitrifying bacteria was sufficient to compensate for the ammonia excretion rate of the amphipod. It should be noted that unlike the other chemical parameters measured, ammonia levels did not increase over time in the microcosms, again this is probably due to rapid conversion by nitrifying bacteria.

The nitrite levels were significantly higher on days 100 and 159 in the grazed microcosms (Figure 5). Higher nitrite concentrations in the treatments might be a reflection of nitrification of excreted

ammonia as discussed in the previous paragraph. The nitrate level was also higher on day 159 in the grazed microcosms (Figure 6). Apparently, nitrate was being produced at a faster rate, relative to its assimilation by autotrophs, in the grazed microcosms. More substantial information about the role of grazing organisms on the nitrogen cycle might be gained in a future experiment similar to the present study.

Alkalinity and conductivity values were higher in grazed microcosms (Figures 7 and 8), although the differences were not statistically significant which makes any interpretation speculative. The fact that pH values were greater in the grazed microcosms late in the experiment (Table 5) suggests alkalinity values may have been maintained at a higher level by the amphipods activities. The NP/R ratio was less during this time in the grazed, relative to control, systems (Figure 12); therefore more CO_2 was released (via respiration) relative to its utilization (photosynthesis) in the grazed systems. The greater amount of free CO_2 in the grazed system might have resulted in less precipitation of $CaCO_3$, thus a higher alkalinity relative to the controls.

Based on inorganic nutrient data, the initial ratio of phosphorus to nitrogen was 1 to 160. Plants roughly require one part phosphorus to every seven parts nitrogen (Vallentyne 1974). Since phosphorus or nitrogen most often limit primary production in freshwater systems (Wetzel 1975) phosphorus was very likely the limiting nutrient in the microcosm systems.

Community Metabolism

Gross productivity of control and grazed microcosms was never significantly different for either the whole system or the sediment surface (Figures 9 and 13). Thus the grazer did not effect the system in a way that would alter the magnitude of gross productivity. This has been reported to be the case in other grazer studies, both in terrestrial and aquatic systems (e.g. Hazell 1967; Kehde and Wilhm 1972). Furthermore, it has been implied that since grazers may not alter the level of gross productivity, they have a minimal effect on the system (e.g. Grodzinski et al. 1966). Analyses indicate gross productivity, alone, may not be a reliable criterion to measure grazer effects.

Whole system analysis. The components of gross productivity are net productivity plus respiration (Ryther 1956). For whole system measurements, net productivity levels were not significantly different between control and grazed microcosms on any date. However, there appears to be a consistent trend for net productivity to be greater in control microcosms following amphipod addition to the treatment microcosms (Figure 10). Similarly, although there was only one day when a significant difference in respiration existed between control and grazed microcosms, mean respiration levels were consistently greater (or equal) in the grazed systems relative to controls (Figure 11). It is by adding net productivity and respiration together and thus having the differences between control and grazed systems cancel that a similar rate of gross productivity was realized for both controls and grazed systems in this study.

To further investigate possible changes in metabolic patterns caused by the amphipods' activities a net productivity to respiration ratio (NP:R) was calculated. This ratio is plotted against time in Figure 12. The amphipod did change metabolic patterns significantly as measured by this ratio, particularly during the latter third of the experiment. The net productivity to respiration ratio was significantly lower for grazed microcosms on four of the five final sampling dates. Therefore plant biomass accumulated at a greater rate in non-grazed systems, although gross productivity rates were the same as those measured in grazed systems. This will be discussed in greater detail later.

Sediment surface analysis. As stated previously, grazing amphipods did not significantly alter gross primary productivity levels of the sediment surface (Figure 13). However, net productivity and respiration levels were altered by the grazer, with the same general trends appearing as in the whole system analysis. Net productivity was higher in control micrososms, and respiration was greater in grazed microcosms (Figures 14 and 15). Gross productivity to respiration ratios were significantly lower in grazed microcosms during the latter portion of the experiment (Figure 16).

Byers (1963) found that a grazing snail had the effect of decreasing productivity to respiration ratios in a set of aquatic microcosms. In two separate in situ grazing experiments involving amphipods (Hargrave 1970) and crayfish (Flint and Goldman 1975), a decreased P to R ratio resulted when the grazer was at relatively high densities. These results support the contention that gross productivity values, alone, do not adequately reflect the impact a grazer has on its system.

Autotrophic Community Measurements

Total plant biomass. Since whole system net productivity to respiration ratios were consistently greater than one (except for grazed systems on day 133), biomass apparently accumulated for both grazed and ungrazed microcosms throughout the experiment. Confirming this supposition is the fact that total plant biomass estimates were significantly greater on day 160 than on day 117 for control and grazed microcosms (Table 2). It should be mentioned that periphyton biomass was probably underestimated on day 117. The slides used for this estimation of periphyton biomass on day 117 were placed in the microcosms two weeks after the experiment had started. Also, the slides only represented a portion (35%) of the vertical axis of glass available for periphyton colonization. Since a periphyton density gradient developed along the vertical axis of the microcosm (periphyton was most dense near top and least dense near the water-sediment interface of the microcosms), the slides may not have adequately represented periphyton biomass. However, relative values of periphyton in grazed and control microcosms are likely reliable and therefore the data are included here. Even with a more accurate estimate of periphyton biomass on day 117, total plant biomass would be less on day 117 than on day 160. Thus direct biomass measurements support the conclusion based on NP to R ratios that biomass was accumulating in both grazed and control microcosms.

At the termination of the experiment, the mean plant biomass per grazed microcosm was 19.4 g, while mean plant biomass of the ungrazed controls was 25.7 g. Plant biomass was 25% lower in the grazed system.

Other studies have established that invertebrate aquatic grazers can substantially reduce the standing crop of the autotrophic community (Brock 1967; Dickman 1968; Mason and Bryant 1975; Flint and Goldman 1975).

Productivity to biomass ratio. Mean gross productivity to biomass ratios for grazed and ungrazed systems are listed in Table 6. On both day 117 and day 160 this ratio was significantly greater for grazed microcosms relative to controls using a one-tail t-test ($\alpha = 0.10$). This situation was expected since grazers often increase the rate or production of the organisms they consume even while reducing the standing crop (McNaughton 1979; Mattson and Addy 1975). This can be attributed to increased nutrient levels due to excretion and other grazer activities (Johannes 1968; Pomeroy 1970) or by causing the grazed community to be dominated by younger, physiologically more active individuals (Barsdate et al. 1974; Harrison 1977).

The gross productivity to biomass ratio measured "maintenance efficiency" of the autotrophic community (Cooke 1967; Odum 1969). In stable communities, which are presumably at a later stage of succession, the ratio would be expected to be low. The autotrophs present in such a system have a relatively longer turnover period and slower growth rates (Odum 1969). Also typical of such a situation is nutrient limitation (Wright 1960; Findenegg 1965). Plants lacking the essential nutrients will necessarily become less productive.

As stated previously, the gross productivity to biomass ratio was significantly greater for the grazed microcosms on both day 117 and 160. Thus the grazer, H. azteca, maintained a more photosynthetically

Table 6. Gross production to plant biomass ratios on days 117 and 160. An asterisk denotes a statistically significant difference ($\alpha = 0.10$) between control and grazed microcosms. Units are $mgO_2/l \cdot hr \cdot g$ biomass

Day	Control		Grazed
117	1.54	*	3.37
160	1.27	*	2.07

active plant community. The grazer certainly made inorganic phosphorus more available to the autotrophs, as attested to by the significantly higher orthophosphate levels in the grazed microcosms (Figure 2). In fact, as mentioned previously, the predicted orthophosphate excretion rate for the mean amphipod population in the microcosm on day 160 was 9 mg per day. Direct investigation to determine whether a plant community developed in the grazed microcosms which were physiologically more active were not made during this experiment.

Plant community composition. Plant community composition was dramatically different in the control and grazed microcosms on days 117 and 160 (Table 2). Attention will be focused on day 160 because a more reliable representation of the actual plant community was attained on that date since plant categories (except for periphyton) were analyzed in total. As day 160 is discussed note that data from day 117 closely parallel data from day 160.

Chara attained a mean biomass of 9.0 g in the grazed microcosms compared with only 5.2 g in the controls. Thus, although mean total plant biomass was significantly greater in the controls (25.7 g in controls to 19.4 g in grazed) Chara reached a higher biomass in the grazed systems (Table 2). More striking still is the fact that Chara represented more than 50% of the total plant biomass in the grazed and less than 20% in the control microcosms (Figure 17). Macrophytes in general are not consumed by aquatic invertebrate grazers (Porter 1977). H. azteca in particular does not ingest Chara (Hargrave 1970; Cooper 1965). In fact, in this experiment the grazer actually stimulated Chara to produce higher biomass. Perhaps the more readily

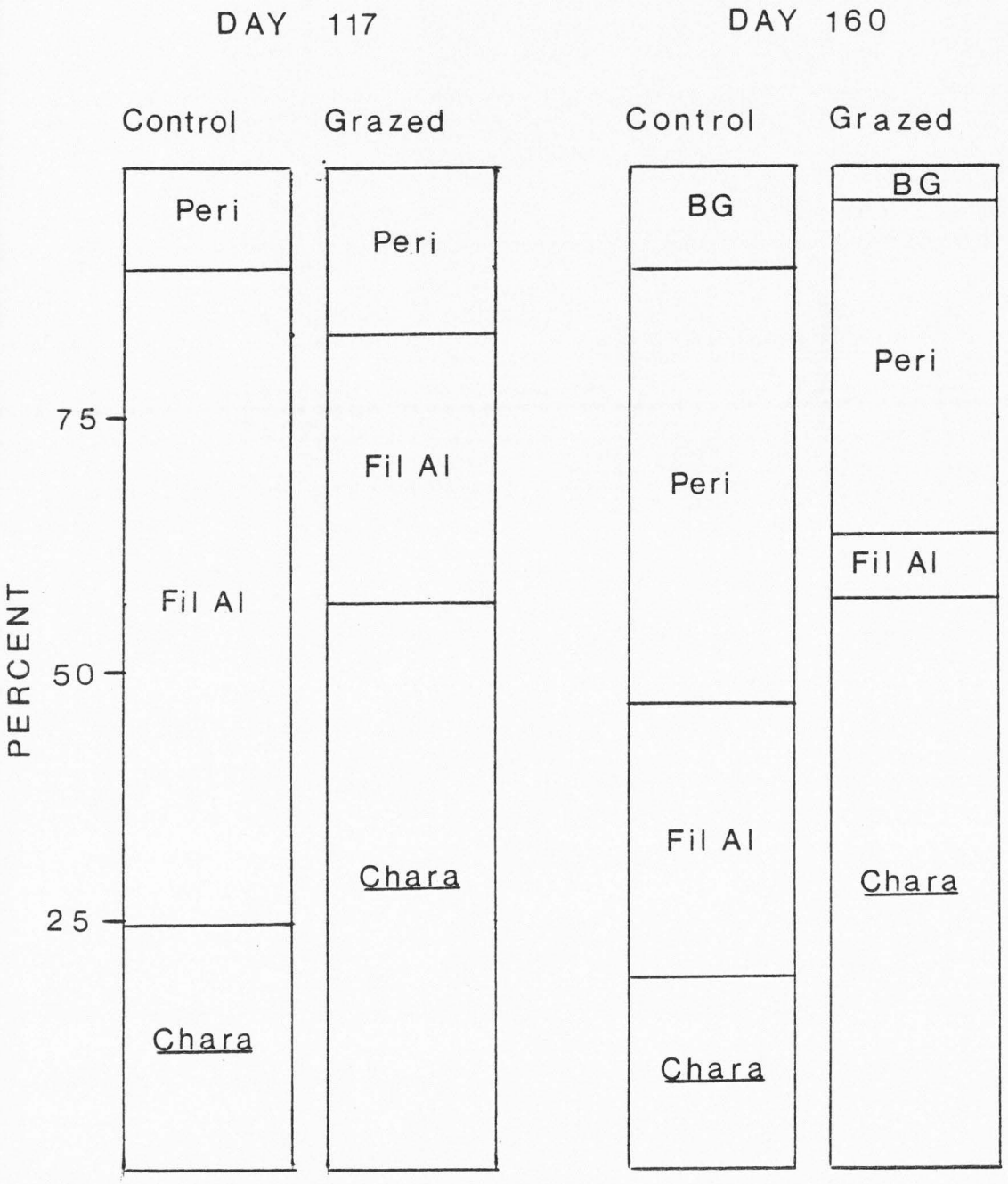

Figure 17. Plant community composition on days 117 and 160. Each plant category (Chara; Fil Al = filamentous algae; Peri = periphyton; BG = blue-green algal colonies) is represented as the percent of its biomass to total plant biomass.

available nutrients in the grazed microcosms allowed Chara to grow at a faster rate as in the case with algae (e.g. Ryther et al. 1958; McAllister et al. 1961). While other autotrophs were consumed, Chara could utilize the nutrients released by their oxidation because Chara was a persistent form (i.e. not reduced by grazing). Chara is a macroalga which can absorb nutrients almost equally well by all of its parts (Littlefield and Forsberg 1965). Most other macrophytes are vascular plants which absorb and translocated from 60 to 90% of the phosphate from their roots to their shoots (Bristow and Whitcombe 1971). Therefore, Chara growth was very likely stimulated by the increased nutrients levels in the water column of the grazed microcosms. Secondly, perhaps the grazer released Chara from competition for light. H. azteca is known to feed on epiphytes growing on host macrophytes (Hargrave 1970; Cooper 1965). It was demonstrated that filamentous algae growing among the Chara were significantly reduced by the grazer (see Table 2). Reduction of the filamentous and epiphytic algae would certainly allow more light to reach the Chara. The mechanism by which Chara became more dominant in the grazed systems merits further investigation.

Filamentous algal biomass was 530% lower in the grazed microcosms. H. azteca was often observed feeding on filamentous algal strands during the experiment. In several of the microcosms with high amphipod populations the amphipods completely eliminated filamentous algae. Apparently the algae grew at a lower rate than its removal rate by the amphipods. Periphyton biomass was also significantly lower (70%) in the grazed systems. However, it should be noted that periphyton

maintained a substantial population in all the microcosms although it was heavily grazed. Apparently the periphyton population was able to sustain high removal rates due to its high biotic potential (Wiegert and Owens 1971).

Blue-green algae had not colonized the microcosms prior to treatment initiation. Without the activities of the grazer this algal category grew to represent 9.9% of the total community compared to only 3.4% with the amphipod (Figure 17). The grazer inhibited the growth of blue-green algae, although observation indicated that H. azteca did not consume blue-green algal colonies. In summary the autotrophic community composition in the microcosms was significantly altered by the presence of the grazer, H. azteca. This magnitude and type of change in plant community composition due to grazing has been observed by Lubchenco (1978) in marine intertidal pools and by Hazell (1967) for a short-grass prairie community in Oklahoma.

Phosphorus Distribution

As previously stated, phosphorus was very likely the most critical nutrient to autotrophic productivity in the aquatic microcosms. It is unlikely that carbon, hydrogen or oxygen were ever limiting in the system. The initial inorganic nitrogen to phosphorus ratio was 160 to 1, thus nitrogen was probably not limiting. No information was taken for micronutrients, but it is assumed they were present in sufficient quantities for normal plant growth. Since phosphorus was probably the most critical element, a phosphorus distribution was used to analyze differences between grazed and control microcosms (Table 3). Attention will be focused on day 160 because data on that date were

most complete; however, parallels in trend exist on day 117. The total community phosphorus includes all phosphorus in the system which was available to the biota. Notice that only the sediment surface (rather than total sediment phosphorus) is included in this analysis. Early in the experiment an oxidized microzone developed in all of the microcosms. Therefore, it is unlikely that deep sediment phosphorus was available to the community (Mortimer 1941; 1942). The amount of total community phosphorus in the control (3.76 g) and grazed (3.95 g) microcosms was not significantly different, indicating direct comparisons between grazed and control conditions are reliable (Table 3).

In the grazed microcosms Chara incorporated significantly more phosphorus than in ungrazed systems. Phosphorus incorporated in filamentous algae, blue-green algal colonies and the summation of phosphorus of all plant categories were greater in the controls. These results would be expected based on the plant biomass analysis discussed previously (see Table 2). It is interesting that the periphyton populations in the control and grazed microcosms contained nearly the same amount of phosphorus, although periphyton biomass was significantly greater in the controls. The reason for this will be discussed below. Total phosphorus in the water column was significantly greater in the grazed microcosms. This was true for all dates analyzed beyond day 100 (see Figure 3). There were no significant differences between phosphorus levels at the sediment surface. The phosphorus distribution analysis of grazed and ungrazed systems indicated that the amphipod caused a significant redistribution of phosphorus in the microcosms, particularly between the plant categories.

Phosphorus content of plants. Table 7 contains the mean percent of phosphorus in the various plant categories for treatment and control microcosms. Note, blue-green algal phosphorus content is a lumped measurement (control plus treatments), since it was absent in most of the grazed microcosms. Filamentous algae contained a significantly higher proportion of phosphorus in the treatment microcosms. Also periphyton in the treatments contained a substantially higher percent of phosphrous, although the difference was not significant. The greater amount of phosphorus per unit of periphyton biomass in the grazed systems explains why the significantly lower biomass of periphyton in these systems on day 160 contain nearly the same amount of phosphorus. Mason and Bryant (1975) found a higher phosphorus concentration in periphyton grazed on by chironomids. Their explanation was that the chironomids increased the phosphorus turnover rate to an extent that the periphyton could assimlate phosphorus at a greater rate. Phosphate absorption rates of aquatic plants are roughly proportional to phosphate concentrations in the water (Gerloff, 1969). Thus plants exposed to higher orthophosphate levels often have higher phosphorus content in their biomass, due to what has been termed "luxury consumption" of freely available nutrients. This phenomenon explains the increased concentration of phosphorus in filamentous algae (and perhaps periphyton although the difference was statistically significant) in the grazed system of this study.

Table 7. Phosphorus content of plants on day 160, as a percent of plant dry weight. An asterisk denotes a statistically significant difference ($\alpha = 0.10$) between control and grazed microcosms

Plant Category	Percent Phosphorus			
	Control		Grazed	Combined
Chara	1.93		1.74	
Filamentous algae	1.97	*	2.34	
Periphyton	1.01		1.50	
Blue-green algal colonies				1.58

Relevance of Research to Natural Systems

There are dangers in directly applying results obtained from artificial systems, such as the microcosms used in the research, to natural ecosystems (e.g. King in press). Perhaps the information obtained in this study which is least reliably extrapolated to "real" systems is the magnitude of impact the grazer had on the system. It is possible that in a natural system the effect of Hyalella azteca would be "dampened" by factors, including: 1) reduction of amphipod population numbers due to predation, climatic factors, etc., 2) increased solar energy available to plants, and 3) nutrient input from other systems (i.e. not strict reliance by autotrophs for nutrients on internal cycling). Of these factors it seems as though the first is particularly important. In this study the mean population of amphipods on day 160 was 60% higher than the estimated density of Marion Lake, British Columbia (Hargrave 1970b). It should be considered, however, that in natural systems other grazers may partially compensate for this difference in population density.

The results of this research illustrate some of the impacts grazing organisms may have on their system and suggest some mechanisms of the grazer's effects. For example, a grazer may change the plant community composition by selective removal of certain plant types, releasing resources such as space, solar energy and nutrients to other plants which are resistant to grazing. The research also identified parameters effective in assessing grazer (and possibly other disturbances) impact on their system. For instance, productivity to respiration, or to biomass ratios were more informative than parameters

such as productivity or respiration alone in this study. Finally, this research can be used to initiate other scientific questions which can be investigated in a natural system setting; such as, quantitatively, how important are animals to internal nutrient cycling in aquatic systems?

CONCLUSIONS

1. Inorganic nutrient levels were higher in the grazed microcosms, with the exception of ammonia concentrations. The elevated nutrient levels did not directly reflect the levels predicted for by excretion rate calculations of the amphipod populations.
2. The grazing activities of Hyalella azteca did not significantly alter the level of gross productivity in the microcosms.
3. The presence of the amphipod did alter the pattern of production as reflected by reduced productivity to respiration ratios of the whole system and sediment surface in the grazed microcosms.
4. The ratio of gross productivity to autotrophic biomass was significantly greater (118% on day 117 and 64% on day 160) in the grazed microcosms relative to ungrazed controls.
5. Hyalella azteca significantly altered the plant community. Total plant biomass was 25% less in the grazed systems on day 160. Chara was 75% greater, filamentous algae 84% less, periphyton 42% less, and blue-green algal colonies biomass 80% less in the grazed systems relative to the controls.
6. The amphipod grazer significantly altered the distribution of phosphorus in the microcosms. The plants incorporated 30% more phosphorus in the controls while the water column contained 51% more phosphorus in the grazed systems.

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APPENDIX

Table 8. Mean concentrations (and standard deviations) of chemical parameters measured in microcosms*

Day	Orthophosphate Concentration (µg/l)		Day	Total Phosphorus Concentration (µg/l)	
	Control	Grazed		Control	Grazed
10	58.75 (17.19)	66.15 (19.95)	10	108.25 (23.92)	115.92 (20.54)
52	1.95 (0.82)	2.45 (0.81)	52	45.33 (8.08)	47.00 (9.17)
69	3.98 (1.46)	3.51 (1.95)	68	17.60 (6.07)	16.89 (3.76)
86	2.95 (1.85)	4.41 (1.06)	86	27.58 (4.97)	27.29 (4.11)
107	5.78 (2.68)	8.69 (7.88)	100	33.90 (7.17)	45.57 (11.23)
114	7.45 (1.28)	8.20 (2.42)	133	28.13 (8.26)	59.49 (34.61)
132	4.45 (2.60)	10.81 (7.61)	155	33.15 (11.13)	66.98 (34.48)
149	6.23 (4.21)	15.07 (10.13)			
156	5.43 (1.05)	11.91 (7.95)			
	Ammonia (µg/l)			Nitrite (µg/l)	
18	253.13 (88.02)	327.08 (110.38)	18	3,990 (490)	4,190 (420)
50	80.00 (41.07)	69.92 (15.62)	50	1.54 (0.41)	1.35 (0.45)

* Numbers in parentheses are standard deviations

Table 8. Continued*

Day	Ammonia (Cont.) Concentration (µg/l) Control	Grazed	Day	Nitrite (Cont.) Concentration (µg/l) Control	Grazed
69	76.25 (21.35)	59.86 (13.97)	69	1.80 (0.66)	1.49 (0.75)
85	41.03 (16.49)	33.48 (5.34)	86	3.98 (0.56)	3.99 (1.26)
100	35.38 (8.31)	45.33 (19.98)	100	2.09 (0.80)	2.66 (0.72)
113	31.95 (3.86)	40.08 (24.45)	154	2.15 (0.00)	4.92 (2.55)
141	38.03 (6.93)	36.32 (5.30)		Nitrate (µg/l)	
149	31.20 (5.37)	36.17 (9.54)	19	7,380 (3,230)	5,230 (1,440)
156	38.28 (3.08)	39.44 (5.31)	50	6.75 (8.41)	4.00 (28.62)
	Conductivity (µmhos/cm)		69	6.80 (2.39)	6.15 (3.46)
17	552.47 (11.09)	551.64 (8.88)	86	7.70 (1.41)	5.57 (2.26)
46	358.97 (7.18)	355.72 (16.94)	154	14.94 (1.92)	18.05 (3.72)
76	324.55 (11.73)	327.28 (23.14)		Alkalinity (mg/l)	
142	209.16 (35.06)	218.60 (49.00)	17	220.25 (9.96)	223.60 (4.02)
154	217.70 (29.82)	229.66 (36.62)	46	132.60 (4.76)	128.42 (9.47)

* Numbers in parentheses are standard deviations

Table 8. Continued *

Day	Alkalinity (Cont.) Concentration (mg/l)	
	Control	Grazed
61	127.63 (8.69)	118.40 (12.89)
142	119.38 (14.03)	132.18 (13.32)
154	112.50 (13.40)	125.17 (16.74)

* Numbers in parentheses are standard deviations

Table 9. Whole system metabolic measurements (and standard deviations) of microcosms*

Day	Gross Productivity Intensity ($\mu g\ O_2 \cdot l^{-1} \cdot hr^{-1}$)		Day	Net Productivity Intensity ($\mu g\ O_2 \cdot l^{-1} \cdot hr^{-1}$)	
	Control	Grazed		Control	Grazed
26	284.74 (140.73)	452.45 (140.48)	26	192.17 (139.85)	305.00 (128.77)
59	398.29 (102.75)	390.16 (72.56)	59	237.50 (45.00)	248.33 (71.90)
62	561.55 (99.07)	608.90 (128.01)	62	320.25 (28.05)	340.42 (87.66)
77	358.96 (90.81)	363.12 (105.08)	77	228.75 (66.88)	228.75 (53.65)
83	320.28 (77.54)	417.46 (180.01)	83	206.82 (58.15)	257.20 (108.24)
98	576.69 (435.18)	517.21 (432.69)	98	380.77 (238.55)	312.18 (241.71)
107	713.73 (309.16)	696.94 (382.78)	107	466.67 (189.66)	449.31 (234.69)
113	865.92 (275.90)	807.71 (335.87)	113	562.00 (156.27)	526.67 (166.20)
126	934.54 (376.64)	967.79 (405.41)	126	608.33 (238.92)	565.28 (267.02)
133	999.43 (132.97)	1051.46 (403.68)	133	578.00 (85.26)	517.33 (197.80)
141	1081.37 (118.41)	1030.98 (340.37)	141	616.67 (68.53)	562.35 (175.53)
148	1093.75 (260.40)	1278.47 (275.07)	148	633.33 (123.14)	672.22 (108.73)
155	1200.12 (216.77)	1216.58 (220.47)	155	777.80 (107.27)	732.94 (124.16)

* Numbers in parentheses are standard deviations

Table 9. Continued*

Day	Respiration Intensity ($\mu g\ O_2 \cdot l^{-1} \cdot hr^{-1}$)		Day	Net Productivity to Respiration Ratios	
	Control	Grazed		Control	Grazed
26	91.07 (24.68)	147.45 (36.52)	26	2.20 (1.76)	2.17 (1.09)
59	160.79 (62.91)	141.83 (20.60)	59	1.58 (0.40)	1.79 (0.55)
62	241.30 (73.23)	268.48 (49.40)	62	1.40 (0.33)	1.27 (0.25)
77	130.21 (53.94)	134.37 (58.66)	77	2.18 (1.42)	1.94 (0.76)
83	113.46 (26.18)	160.26 (80.00)	83	1.85 (0.41)	1.81 (0.68)
98	195.91 (197.16)	189.24 (197.63)	98	4.02 (3.46)	3.15 (2.64)
107	247.06 (127.84)	247.71 (160.34)	107	2.07 (0.81)	2.16 (0.94)
113	303.92 (120.56)	303.03 (181.14)	113	1.93 (0.28)	2.90 (3.02)
126	326.21 (137.74)	402.51 (146.60)	126	1.89 (0.08)	1.38 (0.31)
133	421.43 (52.95)	534.13 (218.63)	133	1.37 (0.11)	1.00 (0.21)
141	464.71 (68.19)	468.63 (173.68)	141	1.34 (0.18)	1.25 (0.24)
148	460.42 (138.00)	606.25 (171.40)	148	1.42 (0.19)	1.14 (0.16)
155	422.32 (104.83)	483.63 (81.09)	155	1.90 (0.33)	1.52 (0.14)

* Numbers in parentheses are standard deviations

Table 10. Sediment surface metabolic measurements (and standard deviations) of microcosms

Day	Gross Productivity Intensity ($\mu g\ O_2 \cdot cm^{-2} \cdot hr^{-1}$)		Day	Net Productivity Intensity ($\mu g\ O_2 \cdot cm^{-2} \cdot hr^{-1}$)	
	Control	Grazed		Control	Grazed
29	5.24 (0.95)	4.89 (0.67)	29	1.08 (0.91)	0.91 (0.45)
57	4.00 (1.40)	3.25 (1.25)	57	2.01 (1.14)	1.85 (1.28)
78	1.51 (0.65)	2.87 (1.62)	78	-0.37 (0.66)	0.81 (0.85)
96	2.94 (1.18)	3.60 (1.47)	96	0.98 (0.88)	0.94 (1.06)
111	4.60 (0.55)	4.33 (1.60)	111	2.15 (0.31)	1.47 (1.08)
138	2.72 (0.66)	3.10 (1.81)	138	0.30 (0.39)	-0.12 (1.43)
158	4.16 (0.88)	2.95 (1.35)	158	1.22 (0.77)	0.07 (1.10)
	Respiration Intensity ($\mu g\ O_2 \cdot cm^{-2} \cdot hr^{-1}$)			Net Productivity to Respiration Ratio	
29	4.16 (0.56)	3.98 (0.39)	29	1.27 (0.23)	1.23 (0.14)
57	1.99 (0.77)	1.23 (0.36)	57	2.25 (1.05)	2.77 (1.25)
78	1.88 (0.32)	1.99 (1.00)	78	0.81 (0.39)	2.01 (2.10)
96	1.96 (0.46)	2.66 (0.55)	96	1.47 (0.39)	1.33 (0.32)
111	2.45 (0.51)	2.85 (0.69)	111	1.91 (0.23)	1.49 (0.31)

Table 10. Continued

Day	Respiration Intensity ($\mu g\ O_2 \cdot cm^{-2} \cdot hr^{-1}$)		Day	Net Productivity to Respiration Ratio	
	Control	Grazed		Control	Grazed
138	2.43 (0.28)	3.05 (0.97)	138	1.11 (0.16)	0.92 (0.49)
158	2.93 (0.51)	2.96 (0.65)	158	1.43 (0.27)	0.99 (0.34)

* Numbers in parentheses are standard deviations

Table 11. Amphipod numbers for the individual grazed microcosms on day 160

Microcosm Number	Amphipod Number
2	1,003
3	1,182
5	110
6	324
7	182
8	689
9	380
10	933
11	883
12	725
15	704
16	158

Mean number = 608

Standard deviation = 364

Table 12. Equations used to predict various attributes of the amphipod populations

1. Head measurement to wet weight

$$WW = 6.04 \times 10^{-7} (H.M.)^{2.63} \quad (r^2 = 0.95)$$

2. Head measurement to dry weight

$$DW = 9.7396 \times 10^{-7} (H.M.)^{2.0951} \quad (r^2 = 0.95)$$

3. Head measurement to phosphorus content

$$P(\mu g) = 8.09 \times 10^{-2} (H.M.)^{2.34} \quad (r^2 = 0.79)$$

4. Wet weight to excreation rate (Lamarra, unpublished)

   (a) orthophosphate

   $$PO_4\text{-}P \ (\mu g/hr) = 1.5955 \ (WW)^{0.3158}$$

   (b) ammonia

   $$NH_3\text{-}N \ (\mu g/hr) = 11.2553 \ (WW)^{0.3227}$$