This is to certify that the

thesis entitled

The Effects of the Snail Physa gyrina (Say) on the Structure of an Epiphytic Diatom Community

presented by

Nancy L. Winters

has been accepted towards fulfillment
of the requirements for

M.S. degree in **Zoology**

Major professor

Date 12 February 1980

THE EFFECTS OF THE SNAIL *PHYSA GYRINA* (SAY) ON THE STRUCTURE OF AN EPIPHYTIC DIATOM COMMUNITY

By

Nancy L. Winters

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Zoology

1980

ABSTRACT

THE EFFECTS OF THE SNAIL PHYSA GYRINA (SAY) ON THE STRUCTURE OF AN EPIPHYTIC DIATOM COMMUNITY

By

Nancy L. Winters

The purpose of this study was to determine the potential grazing role of the freshwater gastropod, Physa gyrina (Say), in structuring the diatom portion of the periphytic community. Effects of intensive snail grazing on colonized glass substrates was measured in the laboratory as: (1) periphytic biomass (ash-free dry weight), (2) diatom species diversity, and (3) alterations in numbers and numeric proportions of specific diatom genera. The response of the periphytic community two weeks after grazing ceased was also measured using the same parameters. Grazing effects were also measured in situ at lower natural snail densities.

At high densities in the laboratory P. gyrina reduced both the diatom standing crop and the species diversity, and preferentially removed Navicula. Two weeks after release from grazing pressure, the periphyton remained reduced in standing crop but not in species diversity. At the lower, natural densities of P. gyrina the diatom standing crop was increased while the species diversity was not altered.

ACKNOWLEDGMENTS

I thank Dr. Donald J. Hall for his suggestions and encouragement throughout the course of this research. Dr. Robert G. Wetzel and Dr. Donald L. Beaver offered comments on earlier drafts of this thesis. Dr. Patricia Werner gave guidance in the design and initiation of the research. I extend my sincerest thanks to Elizabeth Hutchison and Judith Soule for unending encouragement, suggestions, and comments on earlier drafts. I am especially endebted to Martin Werner. His assistance, suggestions, and enthusiastic concern have supported me throughout the course and completion of this work.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The majority of the world's lakes are small, shallow (less than 20 meters deep) bodies of water and therefore provide conditions necessary for extensive littoral development (Wetzel 1975). Littoral flora in these shallow lakes may contribute significantly to the primary productivity of the lakes. Aquatic macrophytes not only contribute to the synthesis of organic material, but also provide an enormous amount of surface area for colonization by epiphytic primary producers.

In addition, macrophytes provide structural complexity within the community which provide a niche dimension along which organisms may divide habitat space. The multitude of organisms which this habitat can support creates a potential for complex ecological interactions.

Epiphytes on the surfaces of macrophytes contribute significantly to the total primary production of many aquatic systems. Periphyton was determined to be the most important producer in shallow Borax Lake, California (Wetzel 1964).

A number of mechanisms operate to regulate both the physical structure and species composition within the periphytic community such as the surrounding water chemistry (Hutchinson 1975), the nature of the substrata whether organic or inorganic, the length of the colonization period, and the age and condition of the macrophyte

host (Round 1965). The nature and species of the macrophyte host may determine, in part, which species of epiphytes colonize the surface. Prowse (1959) found Utricularia to be preferentially colonized by Gomphonema, Najas by Eunotia, and Enhydrias by Oedogonium. Seiburth and Thomas (1973) found decaying eelgrass to be colonized initially only by Cocconeis and secondarily by other species. In a study of macrophyte-epiphyte interactions on Lawrence Lake, Michigan, Allen (1971) suggested a dissolved organic carbon "pool" is established within the marl matrix between the macrophyte host and the periphyton. He named four sources which may contribute to this carbonate-muco-organic "pool" including: (a) extracellular release from the macrophyte, (b) active excretion by the attached algae and bacteria, (c) decomposition products following autolysis of attached algae and bacteria, and (d) dissolved allochthonous and autochthonous carbon within the littoral zone. It is the chemical interactions proposed (the first three contributors listed) which may, in fact, determine macrophyte-epiphyte specificity. Further biochemical analysis is necessary to determine the extent of such specificity.

Morphology of the attachment structure influences the physical structure of the community. Epiphytes may be attached by (1) branched or unbranched stalks (e.g., Gomphonema and Cymbella), (2) tight and direct adherence to the host surface (e.g., Cocconeis), (3) a basal mucilaginous pad (e.g., Synedra and Eunotia); or (4) they may be motile within the epiphytic structure (e.g., Navicula) (Round 1965). A mat of the directly adherent diatoms either unispecific (Seiburth and Thomas 1973) or multispecific (Allanson 1973) may form a crust upon

which other epiphytes colonize. The physical structure of the epiphytic community was directly observed on Chara spp. and Potamogeton natans using scanning electron microscopy (Allanson 1973). Allanson noted a loosely woven diatomaceous component held in place by a stranded matrix formed of the gelatinous epiphytic stalks and underlain by a layer of calcite deposits.

Epiphytic community structure may be determined by length of colonization period. Whitford (1956) outlined a successional pattern for algae epiphytic on Sagittaria leaves in a hard freshwater spring in Florida. Cocconeis was found to be a pioneer species on bare leaves; Cocconeis colonization was followed by a canopy of Synedra, Gomphonema, Xenoccus, and Achnanthes; eventually these were overgrown by other diatoms, filamentous green algae and Plectonema.

Species composition within the community may be regulated by seasonal fluctuations in light and temperature. Sullivan (1977) found species diversity to be greatest in early spring when macrophyte growth was greatest and competition for space and light was least. The actual relationships between species composition and physical structure are yet to be documented.

The structure and composition of the periphytic community may also be controlled by ecological interactions with other members of the aquatic system. For example, Batrick and Strawbridge (1963) hypothesized that diatom species populations were regulated at low densities by interspecific competition and predation.

Predation or grazing may alter the community in a number of ways. The density of epiphytes has been demonstrated to be affected by grazing. For example, a population of chironomids completely depleted

the periphyton on old Typha stems by the end of the growing season (Mason and Bryant 1975). Brook (1975) attributed the increase of epiphytic algae and diatoms in the winter to a lack of predation by Tricoptera, Ephemeroptera, chironomids, and fish.

Herbivorous grazing may also alter the primary productivity of an algal community. Cooper (1973) reported that moderate grazing in microcosms by the herbivorous fish Notropis spilopterous increased net primary productivity. Flint and Goldman (1975) also demonstrated an increase in periphytic primary productivity as a result of grazing by crayfish. The amphipod, Hyallela, increased epibenthic algal productivity at densities simulating those in a natural lake (2 to 3 amphipods/20 cm^2) (Hargrave 1970a).

Grazing may alter the structure of an aquatic community by affecting diversity. Paine and Vadas (1969) suggested the sea urchin Strongytocentrotus spp. enhanced diversity in the epilithic macroalgal community. By grazing on Hedophyllum, which was the dominant species in the absence of the urchin, Strongytocentrotus indirectly allowed other algal species to persist. Species diversity is not necessarily enhanced as a result of grazing. For example, the voracious grazing of the tadpole Rana aurora decreased species diversity in a pond by removing the green algae and desmids from the periphytic community. Only after the tadpoles metamorphosed, and thereby eliminated the intense grazing pressure on the periphyton, did a secondary succession of the community occur accompanied by an increase in diversity although not comparable to the original diversity (Dickman 1968).

When a predator or grazer feeds preferentially on the competitively dominant member of the community, the diversity of that community is increased. Lubchenco (1978) demonstrated this point for the algal and Littorina littorea interactions in intertidal pools. As the snail density increased the algal density also increased. However, at high snail density algal diversity was reduced.

Grazing, as has been demonstrated, may affect community structure by altering density, productivity, or diversity. Grazing within the periphytic community is specifically of interest for three reasons. First, since periphyton is a contributor to the primary production of many aquatic environments, any alteration of the productivity is an alteration of the photosynthetic energy entering the system. Secondly, organisms which alter density may alter the physical structure of the community affecting post-grazing colonization of epiphytes. Thirdly, interactions which alter the populations within the periphytic community affect the structure of the community and affect other organisms of the littoral zone.

Physa gyrina (Say), a common freshwater gastropod, grazes on periphyton, primarily on diatoms (Clampitt 1970). Diatoms were the preponderant component of the gut contents which he studied. Periphyton is a significant contributor to the primary productivity of shallow freshwater lakes. Stockner and Armstrong (1971) reported that diatoms represent 60-70% of the epiphytic community, while in a previous study it was found that they represented 75% of the epiphytic community on Potamogeton tenufolius in Gull Lake, Michigan, a hard-water lake neighboring Lawrence Lake (Winters, unpublished). Since

diatoms are the major food of P. gyrina and since they represent between 60% and 70% of the epiphytic community, the potential role of P. gyrina in structuring the diatom portion of the periphytic community is of ecological interest. The purpose of this study was to determine the effects of grazing by Physa gyrina on the diatom portion of the periphytic community as measured by: (1) periphytic biomass, (2) diatom species diversity, and (3) alterations in cell numbers and numeric proportions of specific diatom genera. In addition, the post-grazing effects (i.e., the response of the periphytic community after grazing ceased) were measured by the same parameters. Effects were measured in situ at natural densities of snails simulating densities found in Lawrence Lake, Michigan, and under laboratory conditions at densities 20 times those found in Lawrence Lake.

THE SYSTEM

Lawrence Lake

Lawrence Lake is a small calcareous lake of glacial origin located in Barry County, Michigan (85°21'W, 42°27'N). The surface area of the lake is 4.96 ha.; the maximum depth is 12.6 meters, while the mean depth is 5.89 meters (Allen 1971). Two small inlets and one outflow maintain the water level within the lake (Allen 1971). A portion of the lake's bottom is covered with extensive marl deposits. It is the calcium carbonate-nutrient interactions which are largely responsible for the low rate of primary productivity by the limnetic phytoplankton (41.1 g $C/m^2/yr$) (Wetzel 1975), while allowing a few adapted macrophytes to dominate the primary production (87.9 g $C/m^2/yr$) of the lake (Rich *et al.* 1971). The littoral zone which extends to a depth of 6 to 7 meters is the site of the major portion (48.3%) of primary productivity of the lake (Rich *et al.* 1971). Littoral macrophytes include: *Chara* spp., *Myriophyllum heterophyllum*, *Najas flexilis*, *Nuphar* sp., *Nymphaea* sp., *Potamogeton* spp., and *Scirpus subterminalis*. These macrophytes not only function in the capacity of primary producers but also function as available hosts for epiphytic colonization and primary production. Allen (1971) found epiphytic algae on emergent macrophytes in Lawrence Lake synthesized 2.9 g $C/m^2/yr$ and epiphytes on submergent macrophytes synthesized 35.0 g $C/m^2/yr$. Since a significant contribution to the primary

productivity is made by the epiphytic algae, the littoral community of Lawrence Lake provides an ideal site to study interactions such as occur between herbivorous grazers and epiphytes which may affect the epiphytic community as a whole.

Epiphytes

The species composition of epiphytes in Lawrence Lake was followed throughout a growing season by Allen (1971). On the east shore of the lake within the Najas-Chara beds in which the substrata for this study were colonized, Allen found a meager early summer colonization by Fragilaria, Tabellaria, and Cymbella. By midsummer and early fall the Najas and Chara hosts were dominated by Gomphonema with a secondary growth of Eunotia, Cymbella, Fragilaria, and Synedra adherent to the Gomphonema. Navicula, Cyclotella, Oedogonium, Zygenema, Synedra, and Chlorella were among the dominant genera found attached with holdfasts or growing prostrate on the macrophyte surface.

Physa gyrina (Say)

Physa gyrina (Say) is a pulmonate mollusc of the Order Basommatophora and Family Physidae. Physids have secondarily returned to the aquatic environment (Barnes 1963). Therefore, they must either surface to obtain air (a frequent occurrence in shallow water) (Clampitt 1970) or obtain oxygen from the water circulated through the mantle cavity (Barnes 1963). P. gyrina is distributed in a broad array of freshwater habitats (Clark 1973). The snail burrows into soft mud as temporary ponds dry and remains buried until the water is

replenished by autumn rains (DeWitt 1955). P. gyrina is more often associated with vegetated areas than with bare rock or mud surfaces (Pip and Stewart 1976).

The life span of P. gyrina is 12 to 13 months in permanent ponds and lakes in Michigan (DeWitt 1955). Oviposition occurs in April in Michigan when water temperatures reach 10°C (DeWitt 1955) and is regulated by water temperature rather than day length (DeWitt 1967). A single individual may lay from 42 to 1839 eggs (DeWitt 1954b); after the first two days of oviposition the number of eggs laid per snail per day is reduced (DeWitt 1954a). Isolated laboratory individuals of P. gyrina laid a greater number of eggs per snail (830/isolated laboratory snail versus 653/field snail) but fewer of the eggs were successful in reaching maturity (DeWitt 1954a). Although P. gyrina is monoecious and can be hermaphroditic, individuals do not reproduce in this fashion for two successive generations (DeWitt 1954a).

Eggs may hatch from 8 to 10 days following oviposition (DeWitt 1955) but development is temperature dependent (Sankurathri and Holms 1976). Juveniles feed continuously (DeWitt 1955) within their major period of growth extending from April to June (Clampitt 1970). The often observed midsummer disappearance of mature snails has been attributed to post-reproductive mortality (Sankurathri and Holms 1976). P. gyrina may migrate to deeper water in winter as was determined for their congeners, P. integra, by Clampitt (1974) or they may undergo estivation as was determined by DeWitt (1955). In either case, their activity is diminished in winter. Snails reach sexual maturity at approximately 7 mm in length (DeWitt 1955),

except under crowded conditions when they remain smaller (Clark 1973). The life cycle begins again the following April.

P. gyrina feed by means of the radula. The radula bears a number of small teeth varying from 95 to 120 oblique teeth on each side of a larger central tooth (Clark 1973). Gut content analysis has revealed that snails feed on diatoms, green algae, detritus, vascular plant tissue, rotifers, microcrustaceans, diptera larvae, and oligochaetes, but that diatoms formed the major portion of the diet (Clampitt 1970). The assimilation efficiency of food, however, is about 4% for adult Potamopyrgus jenkinsi, another herbivorous freshwater species (Heywood and Edwards 1962) and is probably similar to the efficiency of P. gyrina.

P. gyrina can detect quantitative differences in food levels (Warner 1976) locating food either by random movement (Bovbjerg 1965) or by close range chemoreception (Townsend 1973). A group of snails will adjust their feeding densities in accord with the amount of food available (Warner 1976). Further, preferences for the macrophyte Potamogeton pectinatus have been determined by Pip and Stewart (1976) who hypothesized that P. gyrina responds to the high concentration of glucose, fructose, and other soluble carbohydrates exuded by the macrophyte.

MATERIALS AND METHODS

Two experiments were performed in this study to determine the effects of a high density of grazers (Treatment I), and the effects of grazers at densities comparable to those found in Lawrence Lake, Michigan, in late summer (Treatment II). Treatment I attempted to simulate in the laboratory the grazing pressure which could extensively impact the periphytic community for a short post-hatching period in the spring. Each individual of Physa gyrina is capable of laying up to 1800 eggs per season in masses of approximately 100 eggs each (DeWitt 1954b). The egg mortality ranges from 7-55% (DeWitt 1954b). If only one-half of the eggs in each mass survives until hatching, 50 young snails would hatch. Although adult snails are capable of moving from an area at a rate of 7 meters in 24 hours (Clampitt 1974), the young snails may not be able to move as rapidly and would be unlikely to do so until the food resource becomes limiting. Thus, a high density of young snails may impact the periphytic community extensively.

Treatment I

Four boxes of 16 glass microscope slides were suspended in Lawrence Lake, Michigan, for a two-week colonization period. The boxes were removed to the laboratory where two of the boxes of slides were placed in battery jars and were exposed to a period of snail

grazing while the remaining two boxes of slides, also placed in battery jars, were not exposed to grazing. Following the grazing eight slides from each jar were removed and analyzed for ash-free dry weight, species identification, anc cell enumeration. The eight slides remaining in each of the battery jars were returned to Lawrence Lake for a two-week recolonization period with no snail grazing. Thereafter they were removed and analyzed for ash-free dry weight, species identification, and cell enumeration. A schematic flow chart outlining the procedure for Treatment I is presented in Figure 1.

Much debate has been focused on the use of artificial substrata in the study of periphytic communities. While data of Tippett (1970) firmly denies the usefulness of glass slides on the basis of selective colonization of diatoms and reduced production, Stockner and Armstrong (1971) determined that slides and denuded substrata were comparable in the accumulation of epiphytic biomass. Sládecek and Sládecková (1964) reported "only small differences in periphyton between natural and artificial substrata." Patrick (1968) stated that within two weeks the periphyton colonized on glass was characteristic of natural communities. Glass slides are convenient as they have a known surface area and can be colonized for predetermined lengths of time. It is possible, due to their silica content, that slides may be selectively colonized by diatoms. However, since diatoms are the main consideration of this study, glass slides would pose no hindrance to colonization.

The two-week colonization period was selected for this study for several reasons. Patrick (1968) proposed two-week colonization as the

Figure 1. Treatment I schematic flow sheet.

Treatment I Schematic Flow Sheet

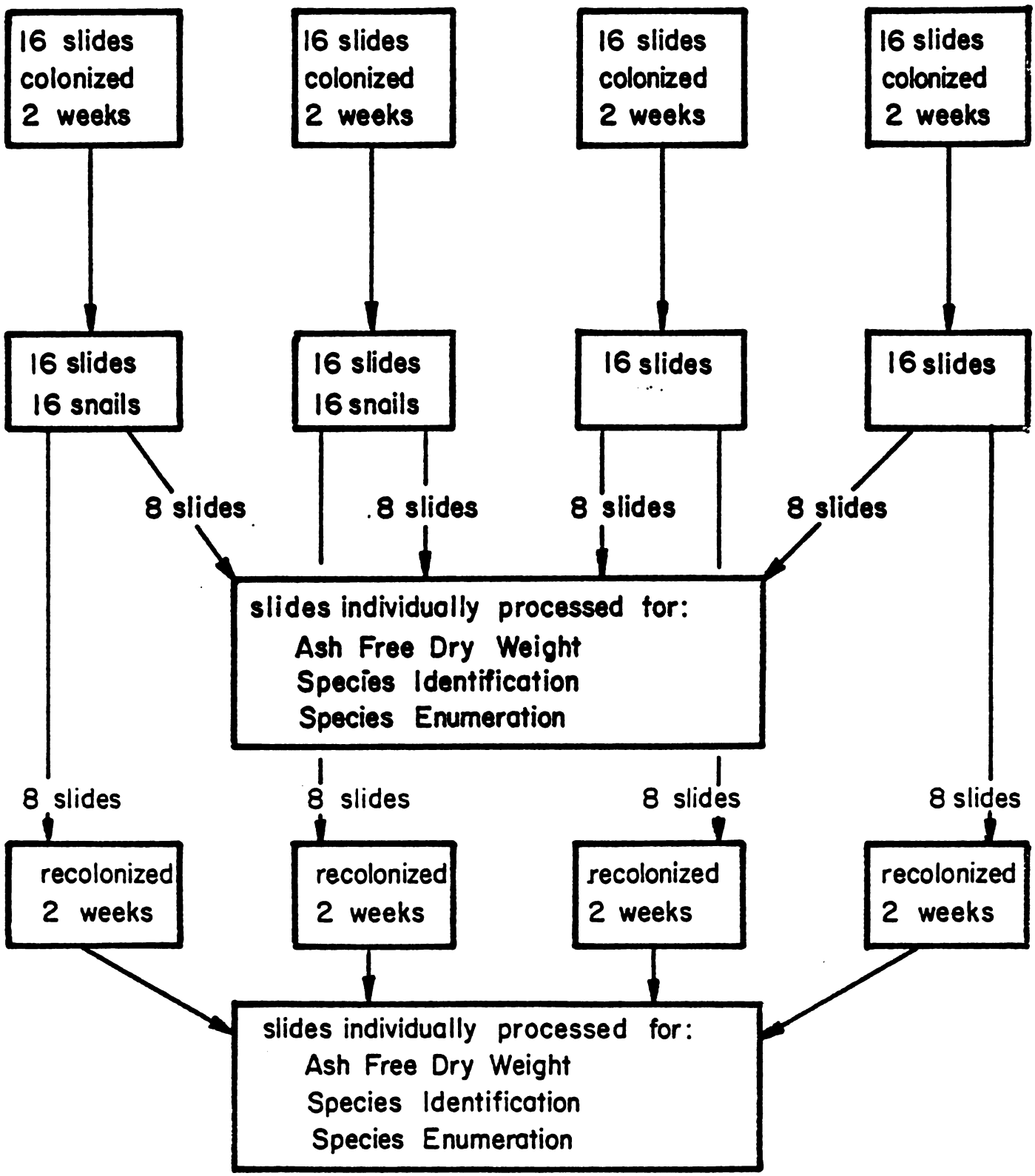

Figure 1

best interval for diatoms to settle and grow in a characteristic pattern. Castenholz (1961b) suggested that with colonization periods longer than two weeks the substrata are subject to increased predation and increased sloughing of cells. Kevern, et al. (1966) reported the rate of periphytic primary production reached a stable plateau by the 13th day of colonization of artificial substrata.

The vertical placement of the slides in the water column was determined to be most appropriate for this study as only those diatoms which are actually epiphytic would colonize vertical substrata and the amount of detritus settling on the slides would be reduced. Castenholz (1961b) reported 6 to 12 times more biomass on horizontally placed slides due to accumulation of detritus and increased ease of settlement and attachment by epiphytes. While P. gyrina feeds on detritus as well as diatoms, detritus does not represent as great a proportion of the diet as diatoms (Clampitt 1970). Detrital material is not easily categorized or quantified and was not the major focus of this study. Since it was desired that the snails graze on diatoms rather than detritus, vertical placement was deemed appropriate.

The four boxes of 16 glass microscope slides (7.6 x 2.5 x 0.1 cm) were suspended vertically 17-mm apart from an inflated bicycle inner tube between 13 and 75 cm from the sediment surface in a water column 1.75 m deep in the littoral zone of Lawrence Lake, Michigan.

The colonized slides were removed and transported to the laboratory for the exposure to grazing or control chambers. Of the four colonized boxes, two were selected randomly to be subjected to grazing by Physa gyrina (labeled boxes A and B) and the remaining two were to remain ungrazed as controls (labeled boxes C and D). The 16 slides

from each box were held vertically by grooved rubber stoppers (four slides/stopper) and placed in a two gallon battery jar filled with water from Lawrence Lake. Sixteen P. gyrina selected at random from a stock culture and measuring between 4.0 and 9.5 cm in length were placed in each of battery jars A and B. Snails had access to slides by climbing from tank bottom to stopper, then on to the slides. Slide positioning posed no difficulty in accessibility to snails. The P. gyrina had not been permitted to feed for 24 hours prior to their introduction to the battery jars. No snails were introduced to battery jars labeled C and D. The snails in jars A and B were permitted to graze between 43 and 48 hours and were then removed.

The grazing period in Treatment I was set at approximately 48 hours. Qualitative visual observations after 12, 24, and 36 hours showed that the periphyton had been disturbed little by the snails, and few grazing trails were visible. Forty-eight hours permitted the snails to acclimate and graze a relatively large portion of the periphyton without completely scraping the substrata bare. The remaining portion of periphyton served to determine selectivity for any particular diatom genus by the snails.

Eight slides from each aquarium were then randomly selected and returned to the site of colonization in Lawrence Lake for 14 days of recolonization to determine changes in species composition of the diatom community which occur post-grazing ("post-grazing effects"). The remaining 8 slides from each aquarium were processed to determine the effects of snail grazing. The surfaces of each slide were scraped using a clean glass slide and washed with distilled water into a jar. Each jar was stirred for 30 seconds, where upon a known aliquot

between 1 and 5 ml (depending on the estimated density of diatoms) was pipetted. The aliquot was then filtered onto gridded HA Millipore filters (0.45 μm pore size) and the cells preserved with Lugol's solution. Following McNabb (1960)), the filters were placed on clean microscope slides, cleared with immersion oil, air dried overnight (25°C), and made permanent with Permount^{R}. These slides were labeled and stored for later identification. Four slides from each treatment were randomly selected for species identification and enumeration. Identifications of the algae were made to genera at 400X in the case of diatoms and all other algae were grouped together. One grid (3 x 3 mm) was selected at random. Since eight slides were identified from each treatment for each replicate, any non-random distribution of algae was deemed unimportant. All diatoms within the grid were identified using Weber (1971) and enumerated. Algae classified as other algal groups represented less than 7% of the community; most of these algae were in the division Cyanophyta (e.g., Oscillatoria, Microcystis). In more densely populated grids enumeration was halted when between 500 and 1000 cells had been counted and the dimensions of the counted area determined using delineations on the microscope grid. The total surface of the filter and total dilution were then calculated.

The remaining portion (known volume 60-70 ml) of each sample in the jar was filtered onto dried (12 hours at 105°C) and weighed HA Millipore filters. The filter papers with samples were then dried for 24 hours at 105°C and weighed. They were then placed individually in crucibles which had been fired to constant weight (12 hours) at 550°C, cooled to 105°C for one hour, desiccated for 30 minutes, and weighed to

the nearest 10 μg. Filter papers in covered crucibles were heated to 550°C for three hours, cooled at 105°C for 30 minutes, desiccated for 30 minutes and weighed to the nearest 10 μg to determine ash-free dry weight.

The slides which had been returned to Lawrence Lake were removed after 14 days and were processed in the same manner as described above for species identification, enumeration and ash-free dry weight.

Treatment I was replicated five times between 7 July and 22 October 1977. Water temperatures ranged between 28°C and 12°C.

Treatment II

Nine clean glass slides positioned vertically 17 mm apart were placed in each of four boxes. The boxes were each enclosed in fiberglass screen bags (mesh size 0.46 cm diagonally). In each of two of the bags were placed five snails (Physa gyrina) ranging between 5.0 and 8.5 cm in length. The bags were suspended in Lawrence Lake in a 1.37-meter water column from 17 to 52 cm above the sediments. The bags remained in the lake for 14 days between 13 August and 27 August 1977, and were removed and processed as above for species identification, enumeration and determination of ash-free dry weight.

Determination of Snail Densities

Twenty individuals of the following macrophytes -- Myriophyllum heterophyllum, Najas flexilis, Potamogeton pectinatus, P. praelongis, and Scirpus subterminalis -- were removed from Lawrence Lake using SCUBA equipment and taken to the laboratory where determinations of surface area per unit dry weight were made using the Teepol method

(Harrod and Hall 1962). Regression equations were calculated for each species (Wagner 1978).

To determine the natural density of snails on macrophytes, 20 individuals of each of the above species were collected using SCUBA, each plant being carefully placed in a plastic bag which was sealed and floated to the water's surface. The number of all snail species was counted, the surface area of the macrophyte determined using dry weight (24 hours at 105°C) and the regressions discussed above.

Method of Data Analysis

The assumptions of normal distribution of the population and homogeneity of variance which underlie parametric statistical analyses could not be met. The effects of violated assumptions on parametric tests have not been determined (Bradley 1968); therefore, distribution-free non-parametric tests which do not make these assumptions were deemed most informative and useful.

A Krushkal-Wallis analysis of variance was used to determine the effects of time of colonization on the Treatment I data. A Friedman analysis of variance was performed to determine the overall effects of the grazing in Treatment I. To determine on which dates specifically grazing caused significant differences Mann Whitney U-tests were used. A Mann Whitney U-test was also employed in comparing grazed and non-grazed data in Treatment I. Medians, rather than means are appropriate for use with the non-parametric tests employed (Siegel 1956). Data are, therefore, presented as medians with ranges given in parentheses.

RESULTS

The Krushkal-Wallis analysis of variance was performed on each set of parameters in Treatment I to determine the effect of time of colonization. In every case the null hypothesis ($t_1 = t_2 = t_3 = t_4 = t_5$) was rejected (i.e., significant differences at P = 0.05 existed). Therefore, while Friedman analysis of variance was performed on each of the parameters to determine the overall effect of the grazing treatment, a replicate by replicate Mann Whitney U-test for the effects of grazing was used to establish on exactly which dates (replicates) the snails had a significant (P = 0.05) effect. Significant differences as determined by the Mann Whitney U-tests are denoted in tables and figures by an asterisk. The overall effects of grazing as determined by Friedman analysis of variance are those to which the text refers.

Ash-Free Dry Weight

In Treatment I the ash-free dry weight (AFDW) was found to be significantly less (Friedman analysis of variance, P = 0.05) on the grazed slides than on the non-grazed. A list of the medians, range and number of slides analyzed in each case (n) for the ash-free dry weights appears in Table 1. The information is presented graphically in Figure 2. The data indicate that a high intensity of grazing by Physa gyrina did diminish the periphytic biomass. While

Table 1. Treatment I median, range, and n = number of slides analyzed for ash-free dry weight (mg/cm^2).

Replicate	Grazed	Non-Grazed
1	0.19 (0.11 - 0.26) n = 5	0.45 (0.16 - 0.86) n = 4
2*	0.04 (< 0.01 - 0.11) n = 16	0.14 (0.06 - 0.18) n = 14
3*	0.05 (< 0.01 - 0.18) n = 16	0.16 (0.06 - 0.20) n = 16
4	0.07 (< 0.01 - 0.23) n = 16	0.08 (< 0.01 - 0.33) n = 16
5	0.03 (< 0.01 - 0.22) n = 5	0.05 (0.02 - 0.25) n = 16

*Indicates significant differences using Mann Whitney U-test P = 0.05.

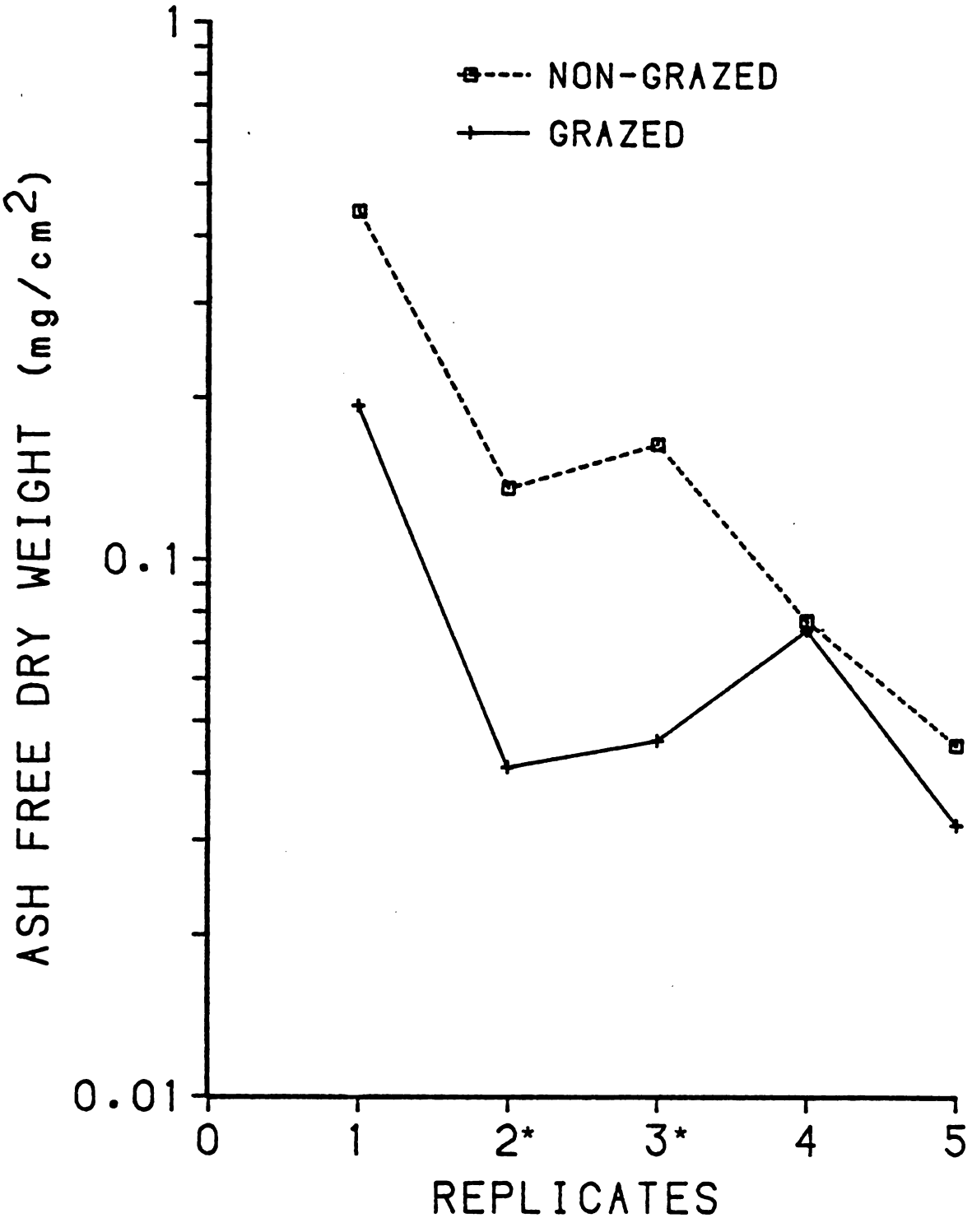

Figure 2. Ash-free dry weight plotted by replicate from Treatment I. * indicates significance using Mann Whitney U-test at P = 0.05.

the number of grazers per unit surface area was an order of magnitude higher than that determined for Myriophyllum heterophyllum in Lawrence Lake (see Table 2), it may be a realistic grazing pressure during a spring post-hatching period and prior to decreases in population from natural mortality and predation although adult snails were used rather than newborn. Data in Table 2 also indicate a range of herbivorous snail grazing pressure from a low density of 0.00083 snails per square centimeter on Najas flexilus (or 0.9 snails per plant of a mean surface area of 1078.94 cm^2) to 0.02423 individuals/cm^2 on Myriophyllum (or 17.1 snails per plant of a mean surface area of 706.54 cm^2). The snail species included not only Physa gyrina but also all of the following species: Amnicola limosa, A. lustrica, Campeloma decisum, Gyraulus deflectus, G. paruus, and Valvata tricarinate. After the slides were returned to the lake for recolonization, a significantly greater ash-free dry weight (P = 0.05) was found on the slides which were not subjected to grazing (Table 3 and Figure 3). (AFDW data from replicates 3 and 4 were accidentally burned and therefore unavailable.)

When the grazing pressure more nearly approximates that found in Lawrence Lake (see Table 2), in Treatment II the results reverse themselves. The slides in the grazed enclosures had a significantly (P = 0.05) higher ash-free dry weight (Mann Whitney U-test, P = 0.05) than the slides within the non-grazed enclosures (Table 4). The data imply that grazing by snails at natural densities enhances diatom growth.

The percent of organic matter on the slides was assumed to be constant throughout treatments. It ranged between 0.57% and 28.03%

Table 2. Median number of snails/cm^2 on Lawrence Lake macrophytes and experimental substrata.

Substratum	Date(s) Sampled		Snails/cm^2	
Myriophyllum heterophyllum	8/23/77	9/19/77	0.02423	0.01173
Najas flexilus	8/20/77		0.00083	
Potamogeton pectinatus	9/19/77		0.00531	
Potamogeton praelongus	9/17/77	9/19/77	0.00381	0.00917
Scirpus subterminalis	8/23/77		0.00253	
Glass slides	Treatment I		0.52210	
Glass slides	Treatment II		0.01431	

Table 3. Treatment I median, range, and n = number of slides analyzed for ash-free dry weight from recolonized slides.

Replicate	Grazed	Non-Grazed
1	0.90 (0.29 - 11.79) n = 5	0.98 (0.81 - 11.67) n = 4
2*	0.08 (0.02 - 0.54) n = 14	0.65 (0.28 - 0.95) n = 15
5*	0.03 (< 0.01 - 0.22) n = 13	0.12 (0.03 - 0.30) n = 16

*Indicates significant differences using Mann Whitney U-test, P = 0.05.

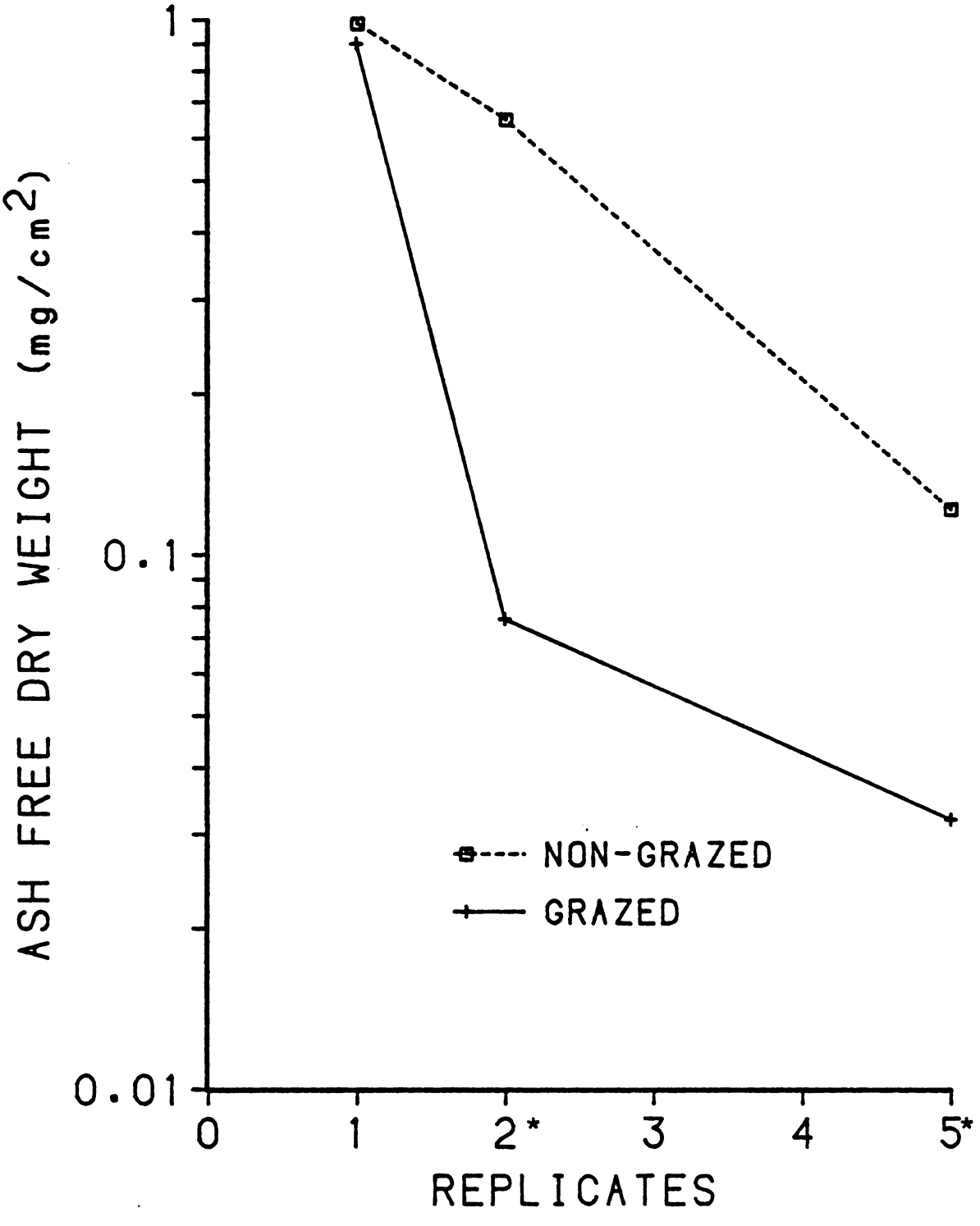

Figure 3. Ash-free dry weight plotted by replicate from Treatment I recolonized slides.
* indicates significance using Mann Whitney U-test at P = 0.05.

with a mean of 13.71%, which is lower than that reported by McIntire (1966). The discrepancy will be considered in the discussion.

Table 4. Treatment II median, range, and n = number of slides analyzed for (a) ash-free dry weight, (b) algal cells/cm^2, and (c) diversity index $H' = \Sigma\ p_i\ ln_{p_i}$

		Grazed	Non-Grazed
(a)	AFDW mg/cm^2**	0.20 (0.06 - 0.41) n = 18	0.02 (< 0.01 - 0.02) n = 17
(b)	$cells/cm^2$**	15,147 (6,797 - 17,976) n = 8	6,822 (5,155 - 10,750) n = 8
(c)	diversity	2.1878 (1.2969 - 2.5001) n = 8	2.2709 (2.1799 - 3.3058) n = 8

**Indicates grazed treatments are significantly greater than non-grazed treatments using a Mann Whitney U-test, P = 0.05.

Algal Numbers and Diversity

The slides subjected to herbivorous grazing had significantly (P = 0.05) fewer cells per unit area (Table 5 and Figure 4). After recolonization the number of algal cells had not increased to the same extent on the grazed as on the non-grazed slides (Table 6 and Figure 5). The previously grazed slides were significantly lower (P = 0.05) in the number of algal cells than the non-grazed. Because the cell numbers are not consistently significantly different on a date by date comparison using Mann Whitney U-tests the data imply that the diminished ash-free dry weight of the grazed slides may be partially due to biomass other than algae (perhaps bacteria).

Table 5. Treatment I median, range, and n = number of slides analyzed for number of algal cells/cm^2.

Replicate	Grazed	Non-Grazed
1*	32,710 (31,632-33,788) n = 2	124,852 (70,601-235,790) n = 5
2*	12,550 (4,048-29,614) n = 8	27,997 (15,260-67,788) n = 8
3	7,350 (885-26,639) n = 8	16,420 (9,475-28,138) n = 8
4	9,882 (1,833-24,104) n = 8	11,145 (1,158-79,843) n = 8
5*	1,776 (939-7,283) n = 8	36,687 (11,155-58,951) n = 8

*Indicates significant differences using Mann Whitney U-test, P = 0.05.

Table 6, Treatment I median, range, and n = number of slides analyzed for number of algal cells/cm^2 from recolonized slides.

Replicate	Grazed	Non-Grazed
1	372,061 (185,038-599,993) n = 5	303,213 (241,072-325,444) n = 5
2*	132,550 (39,324-184,614) n = 8	461,352 (135,976-960,009) n = 8
3	59,904 (21,380-412,523) n = 8	153,943 (4,272-520,277) n = 8
4	68,208 (26,604-165,532) n = 8	50,495 (30,739-147,401) n = 8
5*	26,267 (5,314-70,973) n = 8	412,967 (311,621-591,992) n = 8

*Indicates significant differences using Mann Whitney U-test, P = 0.05.

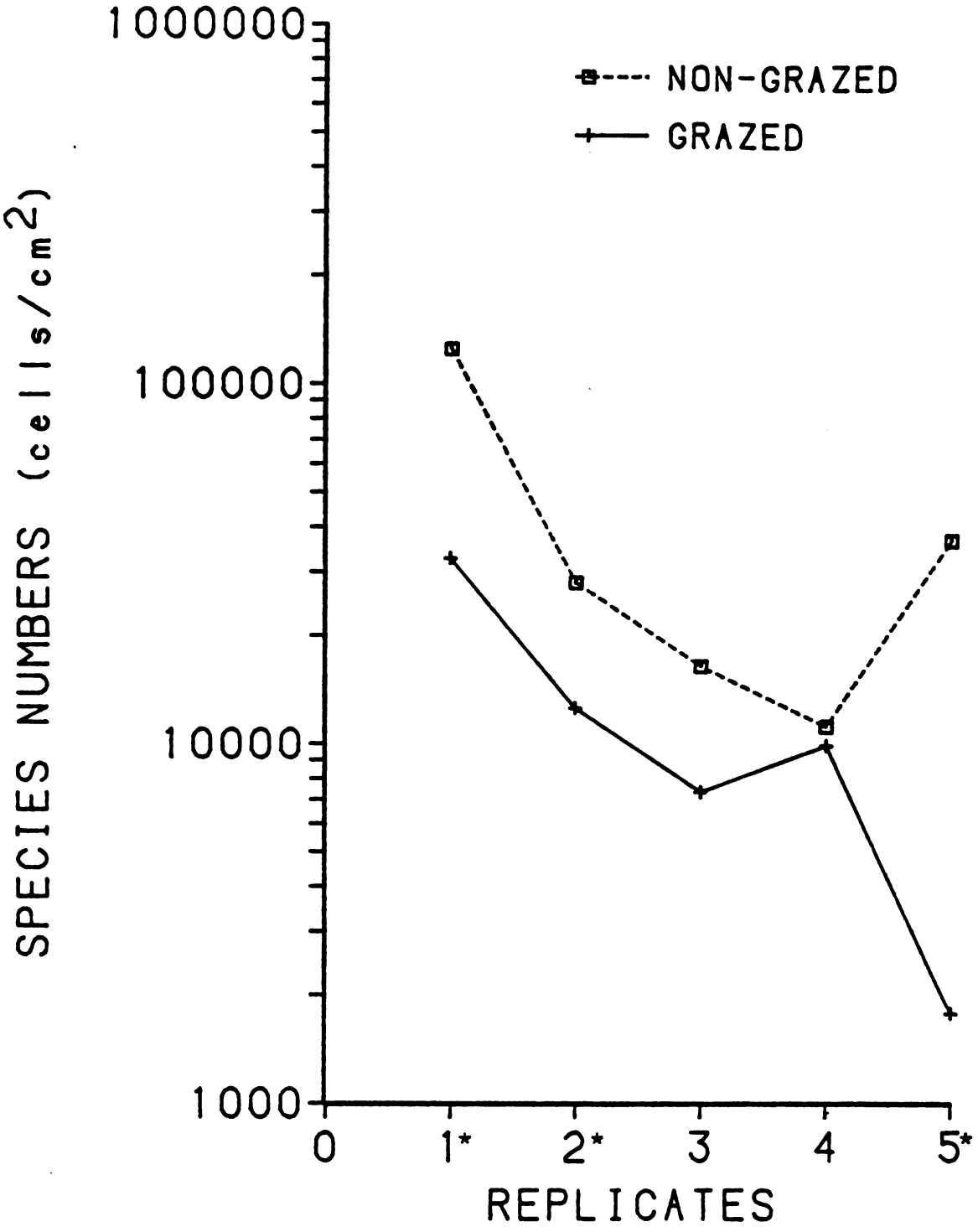

Figure 4. Species numbers plotted by replicate from Treatment I. * indicates significance using Mann Whitney U-test at P = 0.05.

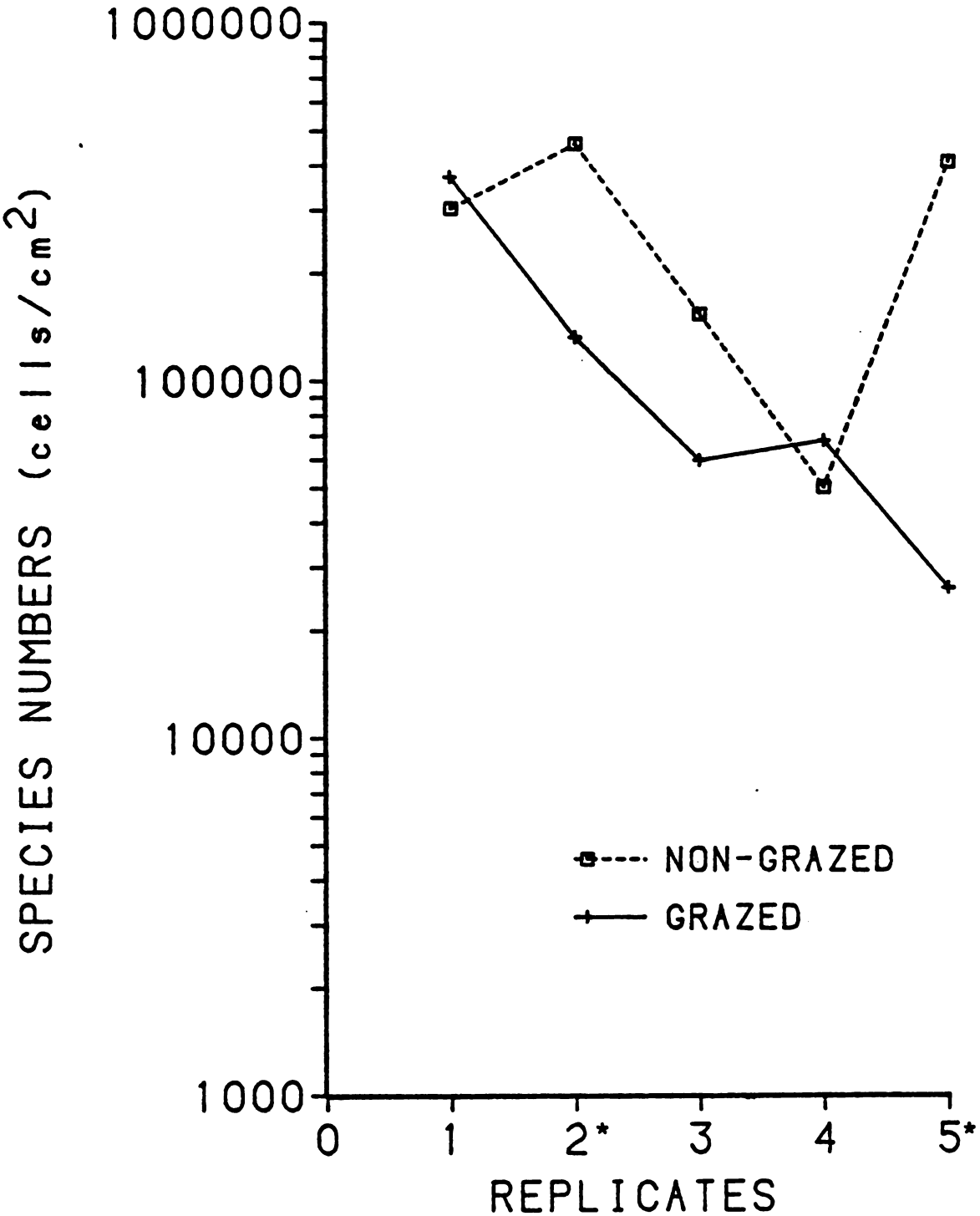

Figure 5. Species numbers plotted by replicate from Treatment I recolonized slides. * indicates significance using Mann Whitney U-test at P = 0.05.

In Treatment II the grazed slides have a significantly greater (Mann Whitney U-test, P = 0.05) number of algal cells/cm^2 and ash-free dry weight than the non-grazed (Table 4).

The Shannon Weaver Information Index (Shannon and Weaver 1949) was used to determine species diversity ($H' = \Sigma\ p_i\ ln_{p_i}$) where p_i is the proportion of all diatom species present represented by species i. Median indices were compared (Friedman analysis of variance). Physa gyrina grazing significantly decreased diversity in Treatment I (Table 7 and Figure 6) but had no effect on diversity after recolonization (Table 8 and Figure 7). Grazing had no effect on diversity in Treatment II (Table 4).

Differential Grazing

The diatom community composition was compared for each genus by calculating the percent which the genus represented of the total cell count on that slide. Comparisons between grazed and non-grazed substrata were made using a Friedman analysis of variance for Treatment I (Table 9 and Figure 8) and a Mann Whitney U-test for Treatment II. All such comparisons assume that each species represented the same proportion of the community before being subjected to the treatments. Graphical presentation of the Treatment I data is found in Figure 8.

In Treatment I Navicula was significantly lower (P = 0.05) on the grazed slides (Table 9). It is noteworthy that the percent of the girdle views (diatoms not lying with the identifying value in view) were also significantly lower in the grazed situation. The percentage of girdle views closely parallels the percentage of Navicula. It is

Table 7. Treatment I median, range, and n = number of slides analyzed for species diversity $H' = \Sigma\ p_i\ ln_{p_i}$.

Replicate	Grazed	Non-Grazed
1	1.9175 (1.7768-2.0583) n = 2	1.8991 (1.8029-1.9702) n = 5
2	1.6230 (1.2086-1.8338) n = 8	1.7569 (1.5707-1.8638) n = 8
3*	1.8280 (1.3584-2.0232) n = 8	1.9913 (1.8638-2.0988) n = 8
4*	1.6453 (1.3657-2.0134) n = 8	1.8543 (1.6232-1.9887) n = 8
5	1.1369 (0.9016-1.3134) n = 8	1.2607 (1.0723-1.4401) n = 8

*Indicates significant differences using Mann Whitney U-test, P = 0.05.

Table 8. Treatment I median, range, and n = number of slides analyzed for species diversity $H' = \Sigma\ p_i\ ln_{p_i}$ from recolonized slides.

Replicate	Grazed	Non-Grazed
1	1.6242 (1.5863-1.7124) n = 5	1.6185 (1.4343-1.7281) n = 5
2	1.3440 (0.9161-1.5977 n = 8	1.3805 (1.1816-1.6568) n = 8
3	1.5800 (1.1123-1.9167) n = 8	1.4461 (1.0274-1.8029) n = 8
4*	1.2341 (0.9984-1.4417) n = 8	1.4982 (1.0076-1.9004) n = 8
5	0.6990 (0.6282-1.0737) n = 8	0.7682 (0.6077-0.8975 n = 8

*Indicates significant differences using Mann Whitney U-test, P = 0.05.

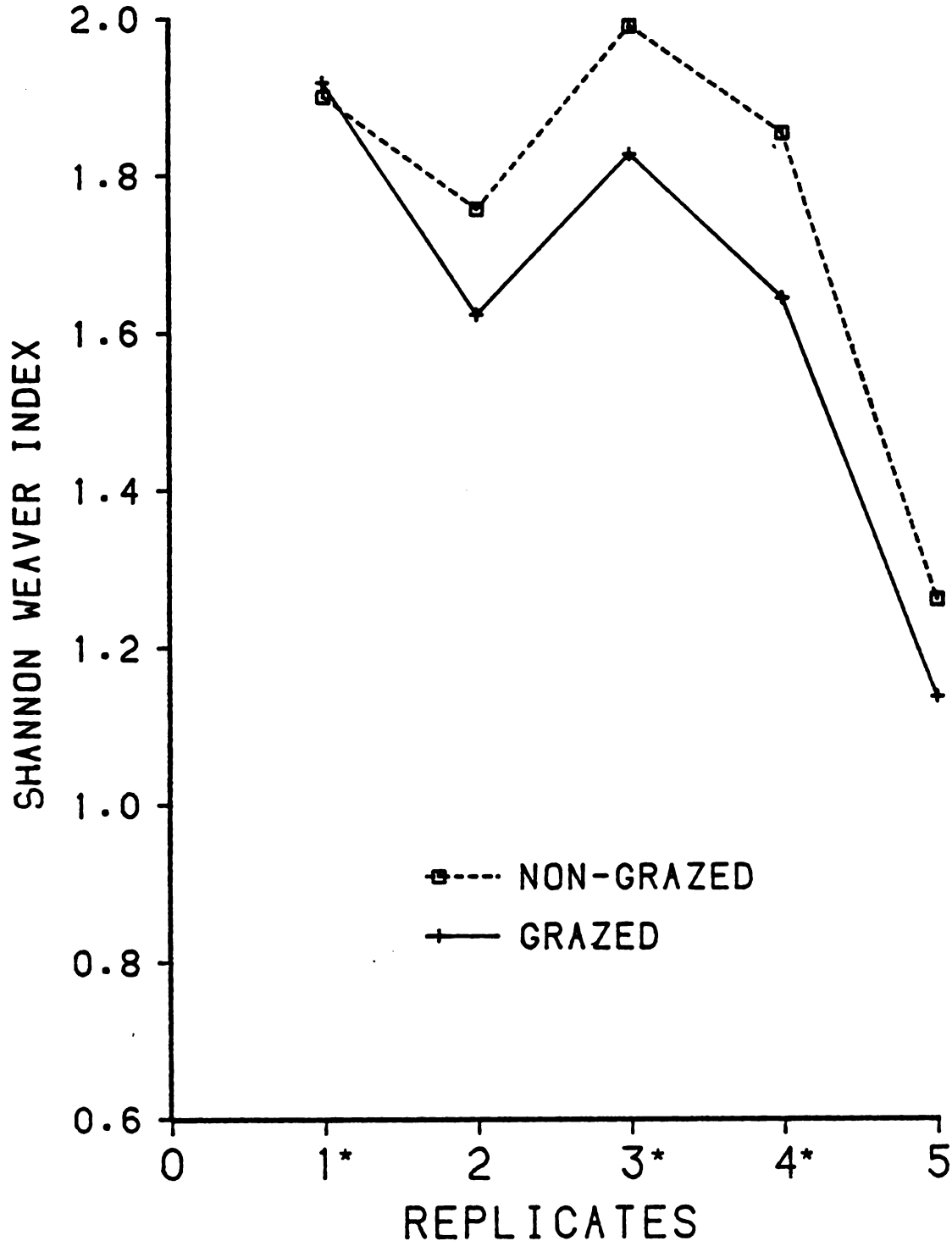

Figure 6. Shannon Weaver Index plotted by replicate for Treatment I. * indicates significant difference using a Mann Whitney U-test at P = 0.05.

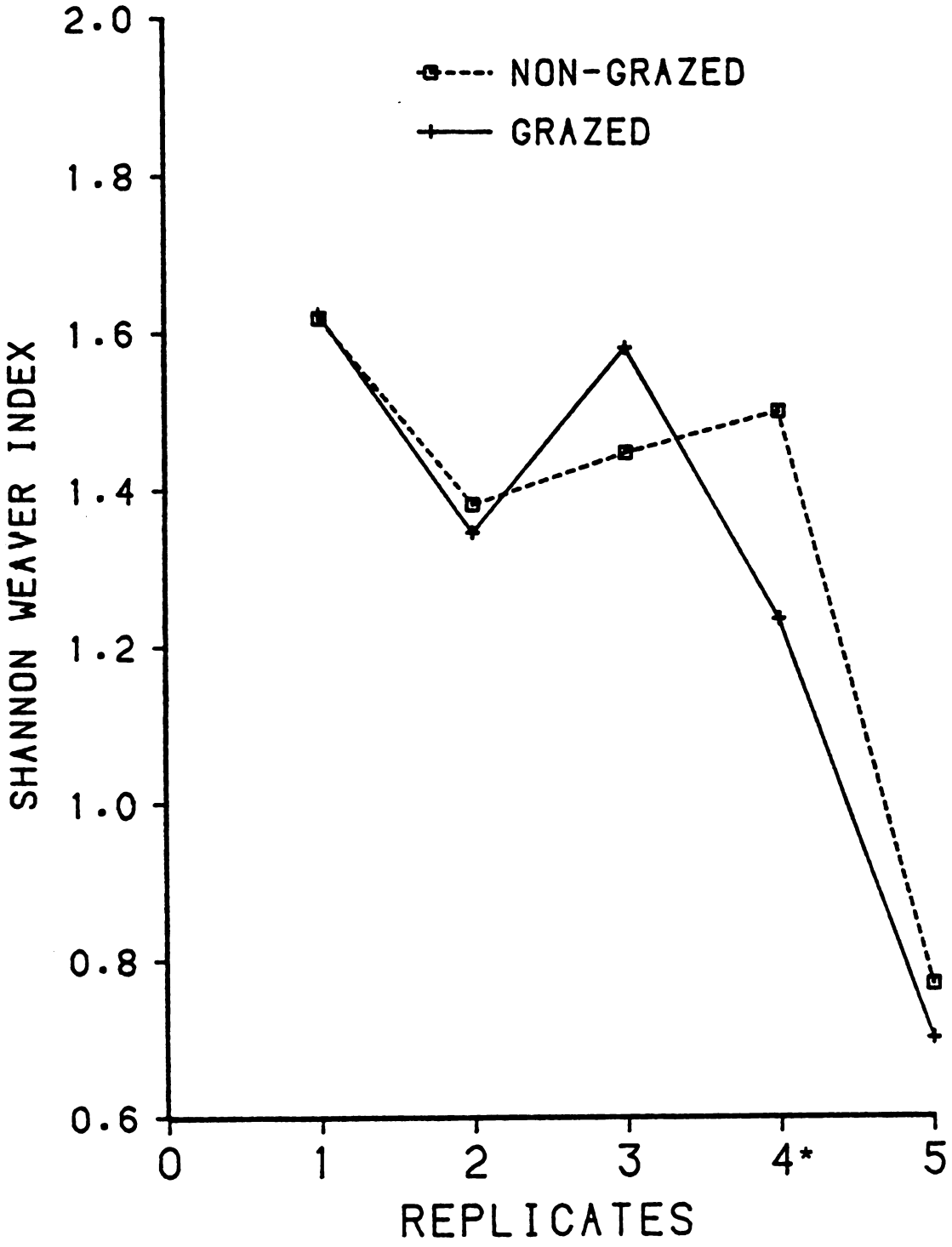

Figure 7. Shannon Weaver Index plotted by replicate for Treatment I recolonized slides. * indicates significant difference using a Mann Whitney U-test at P = 0.05.

Table 9. Treatment I median, range, and n = number of slides analyzed for the percent of the community for each major genus.

Genus	Replicate	Grazed	Non-Grazed
Achnanthes	1	32.8 (18.1-47.5) n = 2	29.3 (13.6-24.7) n = 5
	2	41.0 (25.2-53.9) n = 8	43.0 (26.9-45.4) n = 8
	3**	46.1 (30.5-65.9) n = 8	33.2 (25.0-45.3) n = 8
	4	52.2 (25.6-65.4) n = 8	37.0 (28.9-54.6) n = 8
	5	68.9 (58.6-74.5) n = 8	70.9 (66.5-74.9) n = 8
Cymbella	1	14.3 (8.2-20.4) n = 2	16.2 (14.9-22.3) n = 5
	2	7.5 (6.4-13.5) n = 8	8.7 (4.9-10.1) n = 8
	3	8.3 (3.4-11.1) n = 8	8.4 (5.9-10.8) n = 8
	4	6.0 (0.8-10.7) n = 8	6.6 (4.1-9.2) n = 8
	5	1.7 (0.0-6.3) n = 8	2.3 (1.8-4.8) n = 8
Epithemia	1	5.6 (4.2-7.0) n = 2	4.2 (1.9-8.2) n = 5
	2*	0.9 (0.2-6.5) n = 8	1.2 (0.7-2.0) n = 8
	3	5.7 (1.2-8.2) n = 8	7.1 (3.5-9.3) n = 8
	4	3.4 (1.8-8.0) n = 8	6.1 (3.9-7.7) n = 8
	5*	0.8 (0.2-2.2) n = 8	1.7 (0.9-5.1) n = 8
Eunotia	1**	4.0 (1.7-2.4) n = 2	1.0 (0.1-1.8) n = 5
	2	1.2 (0.8-4.3) n = 8	1.2 (0.6-1.9) n = 8

Table 9. (Continued)

Genus	Replicate	Grazed	Non-Grazed
Eunotia (continued)	3	3.7 (1.0-8.2) n = 8	1.4 (0.4-2.2) n = 8
	4	2.2 (0.7-4.0) n = 8	1.2 (0.4-2.2) n = 8
	5**	1.3 (0.5-1.8) n = 8	1.9 (0.9-2.3) n = 8
Fragilaria	1	2.9 (2.3-3.5) n = 2	2.6 (1.8-4.8) n = 5
	2*	1.6 (0.7-3.1) n = 8	3.4 (1.2-5.4) n = 8
	3	2.3 (0.4-6.7) n = 8	4.9 (3.8-8.2) n = 8
	4	5.5 (1.3-7.0) n = 8	3.6 (1.7-7.3) n = 8
	5*	1.2 (0.3-5.6) n = 8	4.2 (2.0-6.0) n = 8
Gomphonema	1	4.1 (4.1) n = 2	3.2 (2.1-4.7) n = 5
	2	6.0 (2.7-8.5) n = 8	5.2 (3.0-7.3) n = 8
	3	4.6 (1.9-15.5) n = 8	2.9 (1.3-4.0) n = 8
	4*	3.4 (1.5-3.8) n = 8	5.4 (2.7-9.5) n = 8
	5**	14.4 (3.4-22.9) n = 8	4.3 (3.7-8.9) n = 8
Navicula	1*	11.5 (10.9-12.2) n = 2	17.8 (16.6-22.0) n = 5
	2*	11.4 (7.0-16.1) n = 8	17.4 (12.3-19.6) n = 8
	3*	9.8 (5.4-16.6) n = 8	15.0 (12.2-20.2) n = 8
	4	11.2 (4.4-19.6) n = 8	12.9 (7.7-16.2) n = 8

Table 9. (Continued)

Genus	Replicate	Grazed	Non-Grazed
Navicula (continued)	5*	3.4 (2.1-7.6) n = 8	5.5 (4.1-7.0) n = 8
Girdle Views	1*	19.0 (13.6-24.3) n = 2	26.1 (20.9-30.6) n = 5
	2*	15.3 (9.8-20.1) n = 8	23.3 (18.5-29.9) n = 8
	3*	8.9 (4.1-17.0) n = 8	15.7 (10.6-20.8) n = 8
	4	11.9 (4.3-26.0) n = 8	17.1 (8.3-19.7) n = 8
	5*	1.0 (0.5-4.8) n = 8	3.5 (1.7-4.3) n = 8

*Indicates grazed treatments are significantly less than non-grazed using a Mann Whitney U-test at P = 0.05.

**Indicates grazed treatments are significantly greater than non-grazed using a Mann Whitney U-test at P = 0.05.

Figure 8. Percent of the community plotted by replicate for Achnanthes, Cymbella, Epithemia, Eunotia, Fragilaria, Navicula, and Girdle View of Treatment I. * indicates significant differences using a Mann Whitney U-test at P = 0.05; _____ = grazed, ------ = non-grazed.

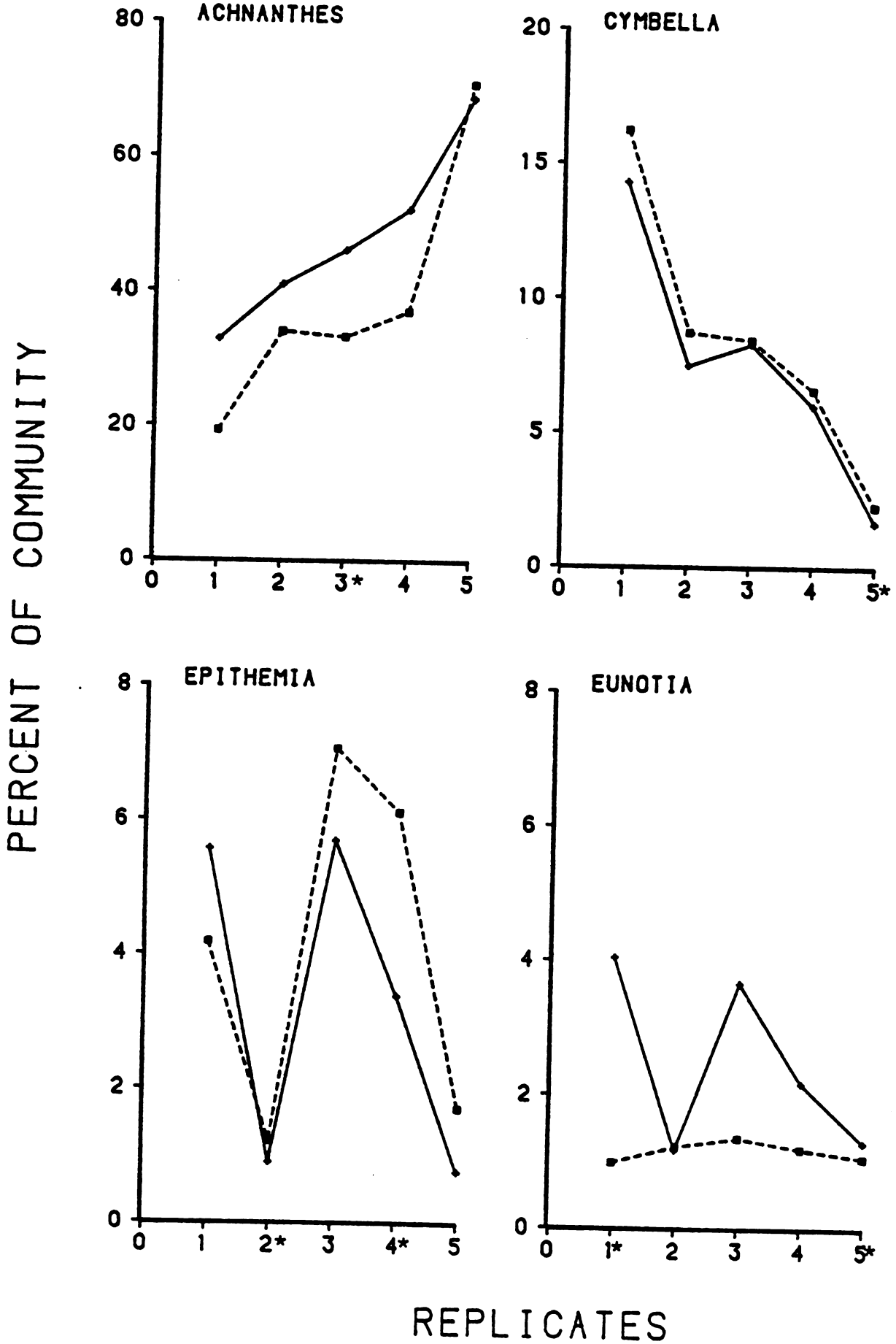
ACHNANTHES
CYMBELLA
EPITHEMIA
EUNOTIA
PERCENT OF COMMUNITY
REPLICATES
0
20
40
60
80
5
10
15
2
4
6
8
1
2*
3
3*
4
4*
5
5*
1*

Figure 8

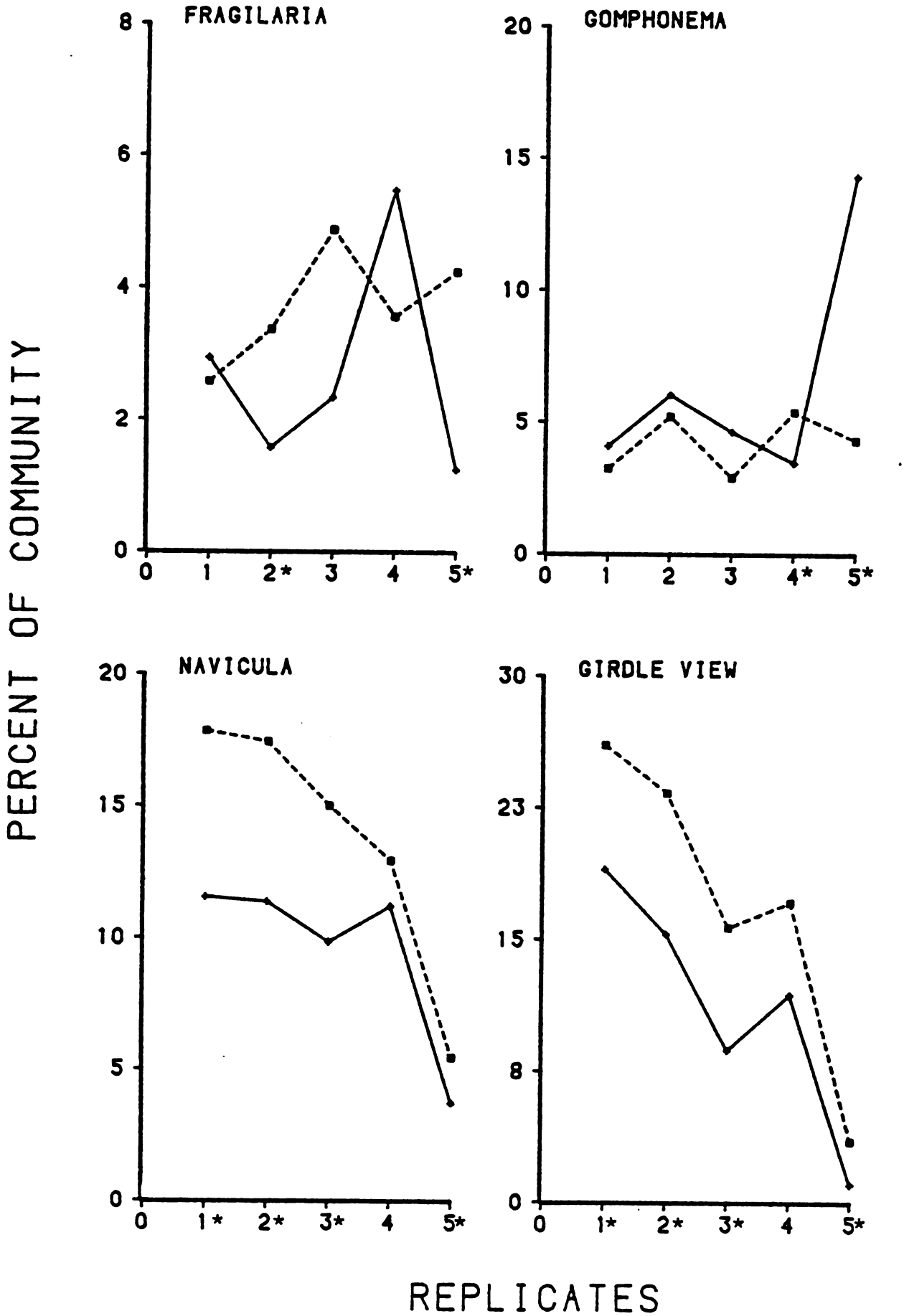

Figure 8 (Continued)

possible that the major portion of the girdle view category was, in fact, Navicula. Eunotia and Gomphonema on the contrary, were significantly higher on the grazed slides than on the non-grazed slides ($P = 0.05$). In Treatment II (Table 10) Eunotia, Fragilaria, and Gomphonema were found to be a significantly higher proportion of the community under a grazing regime.

Data from the recolonization portion of Treatment I are presented (Table 11 and Figure 9) in the same manner as data in Table 9 and Figure 8. These calculations were made to determine if grazing had any effect on recolonization. Grazing had no effect on the pattern of recolonizing by the diatoms. No statistically significant differences were found using a Friedman analysis of variance.

Table 10. Treatment II median, range, and n = number of slides analyzed for the percent of the community for each major genus.

Genus	Grazed	Non-Grazed
Achnanthes	21.1 (17.7-23.1) n = 8	16.9 (12.2-34.7) n = 8
Cymbella	9.7 (6.4-11.1) n = 8	8.2 (3.4-25.5) n = 8
Epithemia	12.6 (6.8-19.2) n = 8	13.9 (9.8-29.0) n = 8
Eunotia**	1.3 (0.5-1.8) n = 8	1.9 (0.9-2.3) n = 8
Fragilaria**	6.6 (3.9-8.6) n = 8	11.6 (7.4-13.3) n = 8
Gomphonema**	2.5 (2.0-3.8) n = 8	4.4 (2.5-8.9) n = 8
Navicula	15.9 (11.8-20.9) n = 8	13.8 (11.7-32.6) n = 8
Girdle Views	18.1 (16.4-22.1) n = 8	17.2 (15.7-40.0) n = 8

**Indicates grazed treatments are significatnly greater than non-grazed treatments using Mann Whitney U-test at P = 0.05.

Table 11. Treatment I median, range, and n = number of slides analyzed for the percent of the community each genus represents from the recolonized slides.

Genus	Replicate	Grazed	Non-Grazed
Achnanthes	1	36.7 (31.4-46.2) n = 5	44.0 (37.8-58.5) n = 5
	2	65.2 (49.2-78.8) n = 8	58.6 (41.8-67.2) n = 8
	3	56.4 (34.5-71.4) n = 8	65.1 (55.4-74.1) n = 8
	4**	69.2 (61.2-77.7) n = 8	64.5 (41.9-75.8) n = 8
	5	83.3 (70.1-85.4) n = 8	82.9 (78.3-87.5) n = 8
Cymbella	1	8.8 (5.1-9.2) n = 5	7.8 (6.5-11.4) n = 5
	2	3.9 (1.8-8.4) n = 8	4.1 (2.0-7.9) n = 8
	3**	5.6 (2.1-10.7) n = 8	3.8 (1.1-4.8) n = 8
	4	2.6 (1.6-4.5) n = 8	3.7 (1.8-5.0) n = 8
	5	0.4 (0.2-0.9) n = 8	0.9 (0.2-1.7) n = 8
Epithemia	1	1.2 (0.5-2.4) n = 5	1.6 (1.0-1.8) n = 5
	2	1.4 (0.7-2.1) n = 8	1.1 (0.4-2.7) n = 8
	3**	3.3 (1.7-4.9) n = 8	1.8 (0.6-2.6) n = 8
	4	2.8 (1.1-5.0) n = 8	3.9 (1.4-8.2) n = 8
	5	0.3 (0.0-0.5) n = 8	0.5 (0.2-1.2) n = 8

Table 11. (Continued)

Genus	Replicate	Grazed	Non-Grazed
Eunotia	1	1.0 (0.6-1.9) n = 5	0.8 (0.4-1.0) n = 5
	2**	1.2 (0.0-2.8) n = 8	0.3 (0.1-0.7) n = 8
	3	0.8 (0.2-2.4) n = 8	0.4 (0.0-1.3) n = 8
	4*	0.7 (0.3-2.4) n = 8	1.2 (0.4-5.3) n = 8
	5	0.5 (0.3-2.3) n = 8	0.4 (0.1-0.6) n = 8
Fragilaria	1	0.8 (0.2-1.6) n = 5	1.2 (1.0-1.4) n = 5
	2	0.7 (0.3-1.0) n = 8	0.6 (0.0-1.6) n = 8
	3	2.2 (0.6-3.9) n = 8	1.8 (0.0-3.7) n = 8
	4	1.9 (1.4-2.8) n = 8	2.3 (0.0-3.9) n = 8
	5*	1.9 (1.4-2.8) n = 8	2.3 (0.0-3.9) n = 8
Gomphonema	1	3.2 (1.7-4.5) n = 5	2.4 (2.0-3.6) n = 5
	2**	4.3 (1.3-6.7) n = 8	2.4 (2.0-3.6) n = 8
	3**	2.5 (1.4-4.1) n = 8	1.7 (0.7-2.3) n = 8
	4	2.0 (1.3-3.3) n = 8	2.3 (0.0-12.0) n = 8
	5**	4.2 (1.8-6.4) n = 8	1.5 (1.0-2.9) n = 8
Navicula	1	17.2 (12.9-21.1) n = 5	15.7 (10.9-17.6) n = 5
	2*	9.8 (4.5-12.3) n = 8	13.0 (8.0-20.2) n = 8

Table 11. (Continued)

Genus	Replicate	Grazed	Non-Grazed
Navicula (continued)	3	9.7 (4.3-17.6) n = 8	10.2 (5.7-14.0) n = 8
	4	4.9 (1.7-8.2) n = 8	7.1 (3.3-10.1) n = 8
	5	1.8 (1.1-12.8) n = 8	2.3 (1.1-7.2) n = 8
Girdle Views	1	21.9 (20.6-31.5) n = 5	21.0 (13.0-27.9) n = 5
	2*	9.0 (2.8-10.7) n = 8	11.4 (9.7-17.7) n = 8
	3	7.0 (3.3-18.1) n = 8	6.3 (3.5-12.6) n = 8
	4	4.3 (2.0-8.4) n = 8	5.8 (2.5-12.7) n = 8
	5	0.3 (0.0-1.0) n = 8	0.7 (0.2-2.5) n = 8

*Indicates previously grazed treatments are significantly less than non-grazed using Mann Whitney U-test at P = 0.05.

**Indicates previously grazed treatments are significantly greater than non-grazed using Mann Whitney U-test at P = 0.05.

Figure 9. Percent of the community plotted by replicate for Achnanthes, Cymbella, Epithemia, Eunotia, Fragilaria, Navicula, and Girdle Views of Treatment I recolonized slides. * indicates significant differences using a Mann Whitney U-test at P = 0.05; _____ = grazed, ------ = nongrazed.

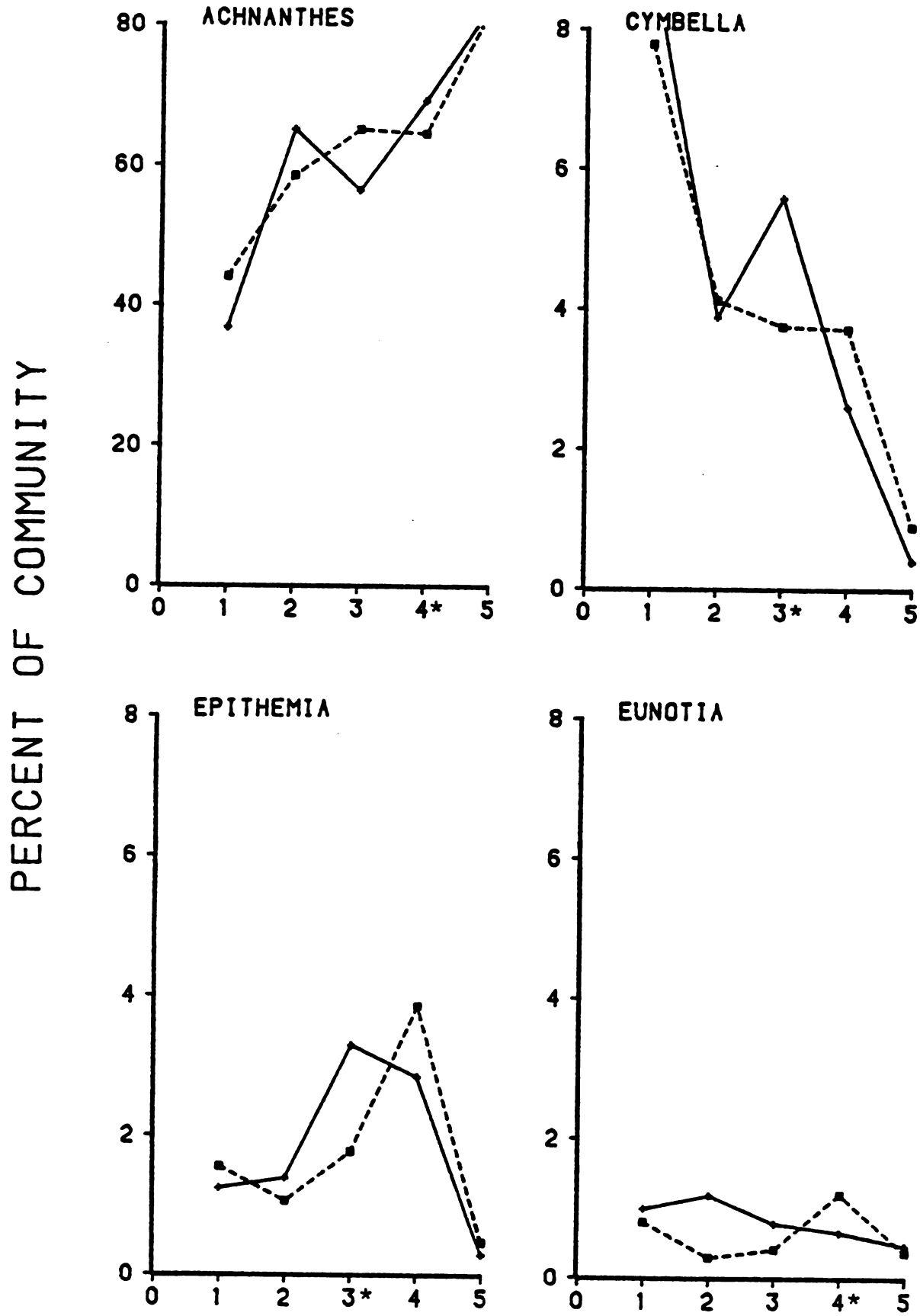
ACHNANTHES
CYMBELLA
EPITHEMIA
EUNOTIA
PERCENT OF COMMUNITY
REPLICATES
0
20
40
60
80
2
4
6
8
1
2
3
3*
4
4*
5

Figure 9

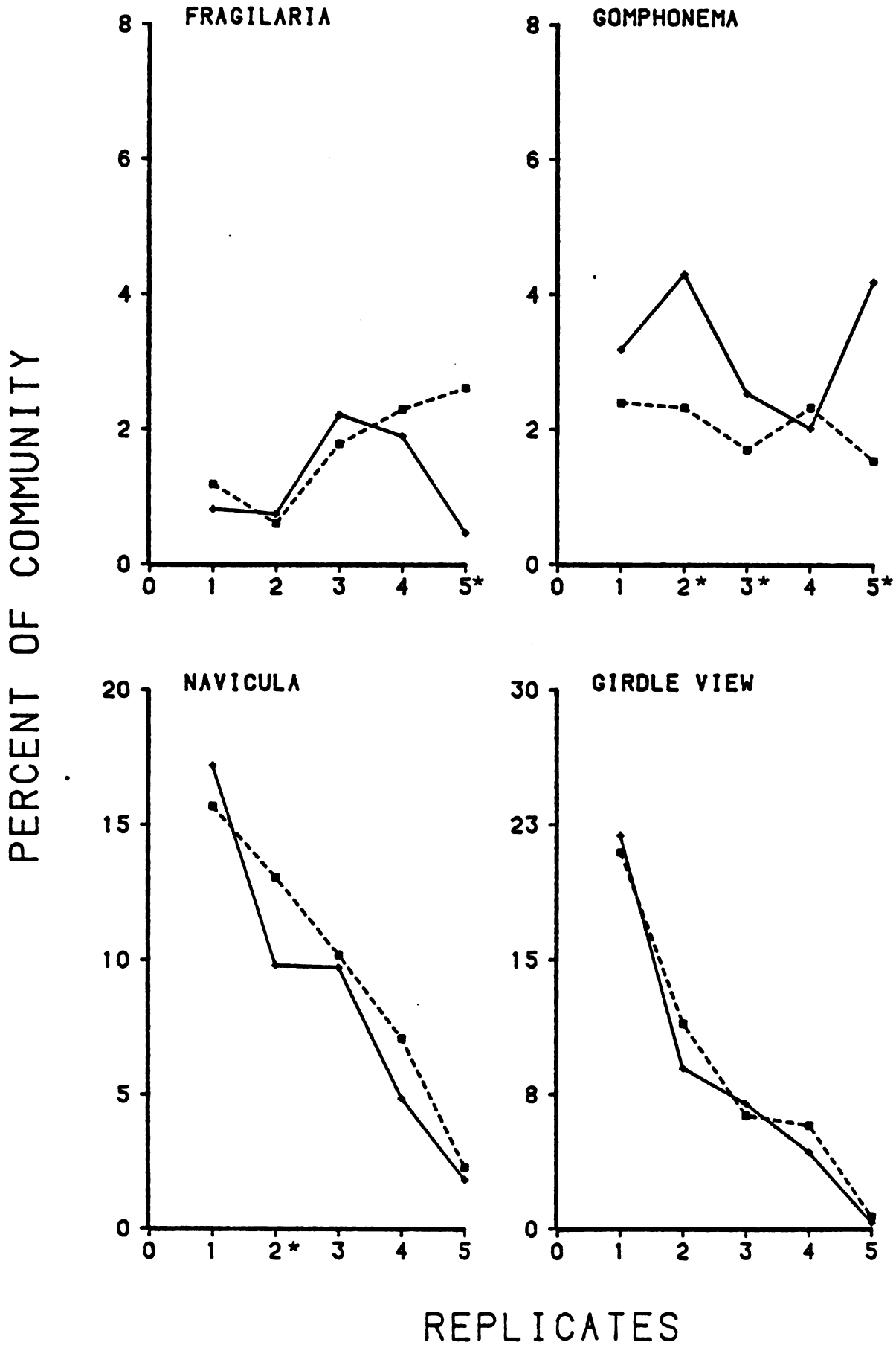

Figure 9 (Continued)

DISCUSSION

Data from Treatment I indicate that at high densities the grazing of Physa gyrina (Say) decreased the standing crop (as measured by ash-free dry weight). Mean algal cell numbers were also significantly lower when intensively grazed. In other words, over the 48 hour grazing period the epiphytes did not increase growth to compensate for lost biomass. Snail densities in Treatment I are likely comparable to snail densities (50 snails/plant) for a short post-hatching period in early spring (DeWitt 1954a) prior to dispersal. Young snails, although smaller than snails used in this study, feed continuously (DeWitt 1955) and therefore could have a similar impact as the larger snails less voracious in the laboratory. The results of this study are similar to those of Hickman and Round (1970) who found that snail grazing reduced vernal epipelic standing crop. At high densities P. gyrina may be capable of depleting a major portion of epiphytic population over a longer span of time, e.g., the growing season, as determined by Castenholz (1961a) for Littorina spp. Tadpoles have been shown to greatly reduce the epibenthic algal population before metamorphosing (Dickman 1968). High intensity grazing by snails is unlikely to persist for extended periods of time, however. As periphytic resources were depleted, increased emigration and mortality should reduce the snail population to the carrying capacity of the periphytic community. The "tadpole effect" observed by Dickman (1968)

created intense grazing pressure on the community for a relatively short time. The algal periphyton, therefore, had a temporal refuge following metamorphosis of the tadpoles during which the population could increase. This type of refuge would not be available under intense P. gyrina grazing as these snails do not leave the system.

Physa gyrina populations may also be reduced from the early spring maximum by aquatic predators such as the pumpkinseed (Lepomis gibbosus) whose diet may be composed of as much as 49% gastropods (Keast 1978), and brown bullhead (Ictalurus nebulosus) (Keast and Harker 1977), or by avian predators such as the upland plover (Bartramia longicauda) (Purchon 1968) to lower densities comparable to those found in late summer in Lawrence Lake. At lower snail densities over a longer time period competition for periphytic food would be lessened; fewer grazers would remove less of the biomass. Remaining algal cells would then have time to respond to the more moderate grazing pressure.

Grazing enhanced the growth of periphyton as shown by the ash-free dry weight and the number of algal cells per square centimeter (Treatment II). Enhancement may be caused by a number of factors. One possible mechanism is nutrient regeneration through excretion or the elimination of fecal material as Flint and Goldman (1975) suggested for crayfish. Pomeroy (1970) emphasized nutrient regeneration through fecal material as a general mechanism for increased nutrient availability and hence increased productivity. Second, senescent cells may limit other viable cells from attaining nutrient or light requirements; cropping would remove the senescent cells as suggested by Cooper (1973). Thus, light and nutrient limitation would be reduced by the removal of senescent cells. Third, cropping may

increase availability of new patches of substrata for colonization much as Pisaster opens new patches in the rocky intertidal zone for invertebrate colonization (Paine 1966). Paine and Vadras (1969) also report on opening of patches for algal colonization by the sea urchin, Strongylocentrotus. The urchin removes Hedophyllum, the dominant macroalga, and by the urchin's action open spaces are created which are available to other less competitive algae. Finally, some diatoms may pass through the digestive system undigested because of inability of the enzymes to penetrate the diatom frustrule. Nicotri (1977) suggested that diatoms with less ornamentation (i.e., fewer striae) were less susceptible to the digestive enzymes since the enzymes enter the diatoms via performations associated with ornamentation. Thus, whole live diatoms may pass through the gut surrounded by the high nutrient feces and diatom growth would thereby be enhanced. Porter (1973) suggested such a mechanism for the increased growth of some species of phytoplankton ingested by zooplankton. All of these suggested mechanisms need further investigation. Collection and culturing of fecal pellets would give some insight into this problem. Another more detailed procedure might include actually marking the precise location of grazed patches to determine if they are differentially recolonized.

After recolonization the slides previously subjected to intense grazing (Treatment I) had a significantly lower ash-free dry weight than the control slides. The median number of algal cells per square centimeter was also significantly lower on grazed slides. These data lend credibility to the hypothesis that epiphytic algae under continuous, intense grazing could not respond (i.e., reproduce) as

fast as they were cropped. However, the numbers of algal cells per square centimeter from replicates 1, 3, and 4 were not lower (using a Mann Whitney U-test) on the previously grazed slides. Consequently, this interpretation remains in question.

The percentage of organic matter found on the slides was considerably lower than that found by McIntire (1966) and Kehde and Wilhm (1972) for stream systems. The effects of increasing current were demonstrated to increase productivity of periphyton (McIntire 1966). Therefore, as lakes do not exhibit high continuous water flow rates, it is possible that productivity would be lower. A study of vertically placed glass slides in a reservoir reported a 20% accumulation of organic matter over a two to four week period (Sládecek and Sládecková 1964). These results are reasonably similar to the 13% organic matter found in this study.

Community composition is often quantified by the use of diversity indices. The Shannow-Weaver Index (Shannon and Weaver 1949) is commonly employed and is appropriate for determining species diversity and evenness of distribution within a community such as the periphyton (Pielou 1966, Wilhm 1970). Grazing significantly lowered the community diversity in Treatment I. Although not significant, the diversity indices of Treatment II also tended to be lower when grazed. After recolonization of the substrata, the diversity was not significantly lower on the grazed slides. Diversity of a community whether autotrophic or heterotrophic may be increased when the dominant competitor of the community is selectively removed by a predator, and when the other less dominant species can colonize the resultant patch more rapidly than the originally dominant species. Paine (1966) demonstrated

the validity of this principal in the rocky intertidal zone with Pisaster. Pisaster's preferential feeding on Mytilus opened space for other potential substrata colonizers which were otherwise competitively excluded by Mytilus. In another study fish in microcosms feeding selectively on Ceriodaphnia released other microcrustaceans from competitive pressure for food. The number of species which could coexist on the food source was increased by the selective removal of Ceriodaphnia; diversity was thereby increased (Neill 1975). In the same manner, the selective feeding of Strongylocentrotus on the dominant alga, Hedophyllum, permitted other epilithic algal species to become established (Paine and Vadras 1969). Conversely, the unselective browsing of the marine snail, Patella, decreased the macroalgal diversity by removing many small algal species and sporelings before they could become established (Jones 1946). Addicott (1974) determined that while the species diversity of protozoans in the leaves of the pitcher plant was reduced by predation, the species evenness was enhanced. He postulated that the abundance of species was controlled by the relative rates of increase of the various prey species rather than by the predator.

Recently Lubchenco (1978) demonstrated the importance of understanding grazer food preferences, as well as interspecific competitive relationships among the consumed species and the changing relationships between physical regimes and microhabitats. She determined that a unimodal relationship existed between algal species diversity and Littorina littorea density in rocky intertidal pools. Species diversity was highest at moderate Littorina grazing levels because the snail's preferred food was competitively dominant in the tidal

pools examined. Grazing reduced the dominant species, as in the other aforementioned studies, and allowed competitively inferior species to persist. In my study the competitively dominant species, Achnanthes, was not selectively removed by P. gyrina. Therefore, it is not surprising that species diversity was reduced in the presence of P. gyrina.

As information concerning individual genera was not apparent from the diversity indices, the percent of the community which each of the major species represented was examined. A consistent pattern is seen with Navicula which represented a significantly smaller portion of the total community on the grazed slides than on the non-grazed slides. Reduced proportions imply that Physa gyrina selectively removed this epiphyte, assuming the proportion of Navicula on grazed and non-grazed slides to be approximately equal prior to treatment. In addition, the category labeled "Girdle Views" represented a significantly lower portion of the community. I suspect that the majority of the girdle view cateogry was, in fact, Navicula, based not only on the correlation but also on the morphology of the cells. This further supports the contention of selection for Navicula by P. gyrina.

Food preferences or selectivity have been recognized in invertebrates by numerous authors. These preferences can function to structure a community. Pisaster was shown to prefer Mytilus when offered numerous two-way choices (Landenberger 1968). Douglas (1958) reported preferences for epibenthic algal species by a stream caddisfly. Calow (1973, 1974) reported a pulmonate snail, Ancylus fluviatilis, ingested a variety of periphyton but preferred the diatom

genus Gomphonema. However, due to the low density of the snails, the grazing disturbance had little effect in altering the proportion of Gomphonema in the community or the periphytic community as a whole.

Selectivity may be based on (1) nutritional value and palatability (neither of which is in the scope of this study), (2) abundance, or (3) ease of attainment. As Navicula was not the most dominant member of the community, representing from 9 to 19% of the total number of cells, while Achnanthes represented from 19 to 72%, one would suspect the snail would select Achnanthes if selection were based on abundance. Therefore, the availability hypothesis based on simple abundance is unlikely. It is more probable that Navicula is a less energetically costly food to attain. There is support for this hypothesis in the growth form of Navicula. According to Round (1965), members of the genus Navicula which are epiphytic are motile and move about, through, and on the surface of the periphyton. Other species of Navicula are reported to be stalked and attached in chains (Round 1965). Since Navicula is above the periphytic mat of diatoms, either motile or in chains, the snail would have to merely skim the surface of the mat with the radula involving less resistance to the scraping and presumedly less energy.

Other members of the periphytic community adhere more tightly to the surface of the substrata. Achnanthes is a very small, short-stalked epiphyte projecting only a small distance above the surface. While no definite trend to select against it (or ignore it) can be determined from the data, the significantly higher portion of Achnanthes on the grazed slides in replicate 3 of Treatment I, using a Mann Whitney U-test, might imply that the snails do not scrape it

off in proportion to its abundance. However, this datum point is more likely an artifact of the variation between boxes of slides.

Eunotia, on the other hand, represented a significantly greater portion on the grazed slides; it is attached via a basal mucilaginous pad which adheres to the surface of the substratum (Round 1965). Eunotia was also significantly lower in Treatment II, giving support to the idea that it is not readily available to P. gyrina. Since Eunotia also represented such a small portion of the community further study would be necessary to distinguish between abundance and ease of attainment as a reason it was not selected by P. gyrina. Fragilaria, a large stalked diatom, may be easily attained by Physa. But under less competitive conditions it was taken in less proportion than its occurrence in the community (Treatment II). Since both Eunotia and Fragilaria represented just less than 5% of the community, it is likely that variation due to structural heterogeneity (i.e., patchiness) and chance are responsible for what appears to be differential grazing.

Gomphonema is a stalked and branched diatom (Round 1965); therefore, it was potentially available to the snail. But in both Treatment I and Treatment II it accounted for a significantly greater portion of the grazed slides, implying that the snail either did not feed on it or that its growth was enhanced by the snails' presence. Such an enhancement may be due to a higher reproductive rate evolved to counteract grazing perturbations. Other diatoms are subject to the same grazing disturbances; if this were the case, it seems likely that they, too, would have responded by equivalent reproductive rates. Growth enhancement could be a response to increased specific

micronutrients found either within snail fecal material left on the slides or in slime trails which the snails leave on the substrata. Gomphonema may also be grazed but remain undigested, acquiring nutrients while in the gut; in that case, growth could be more rapid following elimination from the snail's body. Gomphonema has only a moderate amount of ornamentation. Thus the possibility exists for the snails' digestive enzymes to have less effect on it than on a more heavily ornamented species (e.g., Epithemia) as Nicotri (1977) suggested. Food is in the digestive system for three to five hours (North 1954). This length of time spent in darkness would be insufficient to kill the cell. Acquisition of micronutrients seems the most plausible explanation for differential growth by this species.

Preferences for particular diatom genera could be obtained by offering snails two-way choices of pure cultures on glass slides placed in finger bowls. A ranking of preference might well be established from this type of study. Snails may also show greater selection when not starved prior to preference feeding tests. Landenberger (1968) found the starfish, Pisaster, exhibited greater selectivity when food was not withheld prior to preference tests. Nicotri (1977) suggested that three species of marine snails and one species of periwinkle grazed more selectively and assimilated algal cells less efficiently when food was not limiting. It might, therefore, be construed that P. gyrina exhibits greater selection when food is in abundance and hunger levels are reduced. When the snails were starved (Treatment I), they fed preferentially on a species which was presumedly easy to obtain (i.e., Navicula). However, when food was abundant and snail densities were reduced, the preference

for Navicula was not observed. The snails did not feed selectively on any species in Treatment II. Instead, three species, Eunotia, Fragilaria, and Gomphonema were found in greater abundance on the grazed slides. Two of these species, Eunotia and Gomphonema, were also found in higher abundance on grazed slides in Treatment I. Possibly, these three species were avoided by the snails. Avoidance of a diatom species (Cocconeis) by a congener of P. gyrina (P. heterostrapha) was observed (Patrick 1970). Therefore, avoidance is a possibility.

The recolonization data show the response of the periphytic community after grazing. By again comparing the percent of each genus in the community, more information can be obtained than by evaluating the diversity index alone. Achnanthes accounted for a generally increased portion of the community after recolonization regardless of laboratory treatment (i.e., grazed or control). Perhaps Achnanthes was an early colonizer in the successional process on apical portions of macrophyte surfaces. As the process continued, Achnanthes may have become a proportionately less dominant member of the community. But as snails opened new patches by grazing, Achnanthes could have maintained dominance. Or perhaps this species being small in size can exploit smaller spaces and hence remain the superior competitor. In Treatment II when grazing extended over a longer period of time, while Achnanthes was a relatively smaller portion of the community, it was still the dominant species. The data do not lend support to either hypothesis.

Variation between slides and boxes of slides presented difficulty in the analysis of this study. Variation may have been reduced by increasing sample size; but analysis, especially enumeration,

became unwieldy even for the samples counted in this study. Another possible way to reduce variation would be to colonize larger glass plates, sample small sections of the plate prior to treatment, and allow snails to graze only one-half of the plate. Gut analysis might help to determine snail preferences, unless cells are differentially digested. Gut analysis might also prove valuable in analysing data from the two-way preference tests mentioned earlier. Additionally, future study might entail varying the densities of snails around natural macrophytic substrata which would be enclosed.

This study raises several issues. How important is P. gyrina in altering the structure of the periphytic community? Larger more voracious grazers such as tadpoles are capable of completely removing a major portion of periphyton during an early phase of their development (Dickman 1968). Small grazers may also change the structure of the periphytic community. For example, the mayfly nymph (Chloeon), a cyclopoid copepod, a chydorid, and a chironomid larva have been observed feeding on epiphytic algae (Allanson 1973). Hyalella azteca, an amphipod, feeds predominantly on periphytic algae (Hargrave 1970b); a ciliated protozoan reportedly feeds on diatoms (Brook 1952) of the same genera as were removed by P. gyrina in this study. These organisms as well as other gastropods influence the structure of the periphytic community. Which organisms are responsible for the major alterations in community structure has not yet been determined.

What mechanisms control diatom preferences by Physa gyrina? Is it less energetically costly to graze only diatoms not securely attached to the surface and therefore to skim only the surface of

the periphytic mat? Are certain diatoms (for instance, Gomphonema) differentially digestible; and does ingestion enhance the micro-nutrient climate surrounding the cells passing viably through the gut? From this study it appears that P. gyrina might function as to partially regulate the periphytic community by decreasing the algal population at high densities while increasing it at lower densities. Selection of Navicula, whether a preference due to palatability, digestibility, or attainability, does, in fact, alter the structure of the periphytic community. Enhancement of the growth of Gomphonema, whether the mechanism is an increased nutrient concentration provided in the gut or by the deposited fecal material, also plays a role in regulation of the heterogeneity of the periphytic community.

CONCLUSIONS

1) At high densities of Physa gyrina grazing the periphytic standing crop, the numbers of diatom cells/cm^2 of glass substrate and the community diversity were significantly reduced.
2) At high densities P. gyrina preferentially removed Navicula.
3) Two weeks after intense grazing ceased, the previously grazed substrates were significantly lower in standing crop and cell numbers. Community diversity was not lower on the previously grazed slides.
4) At lower densities snail grazing significantly increased periphytic standing crop, numbers of diatom cells/cm^2 of the substrate, and the growth of Gomphonema, Fragilaria, and Eunotia.

BIBLIOGRAPHY

BIBLIOGRAPHY

Addicott, J. F. 1974. Predation and prey community structure: An experimental study of the effect of mosquito larvae on the protozoan communities of pitcher plants. Ecology 55: 475-492.

Allanson, B. R. 1973. The fine structure of Chara spp. and Potamogeton natans from Wytham Pond, Oxford, and its significance to the macrophyte-periphyton metabolic model of R. G. Wetzel and H. L. Allen. Freshwat. Biol. 3: 535-542.

Allen, H. L. 1971. Primary productivity, chemo-organotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. Ecol. Monog. 41: 97-127.

Barnes, R. D. 1963. Invertebrate zoology. W. B. Saunders Co., Philadelphia. 632 pp.

Bovbjerg, R. V. 1965. Feeding and dispersal in the snail Stagnicola reflexa (Basommatophora: Lymnaeida). Malacology 2: 199-207.

Brook, A. J. 1952. Some observations on the feeding of protozoa on freshwater algae. Hydrobiologia 4: 281-293.

Brook, A. J. 1975. Aquatic animals aren't hungry in winter, or why Cymbella blooms beneath the ice. J. Phycol. 11: 235.

Bradley, J. V. 1968. Distribution-free statistical tests. Prentice-Hall, Inc., New Jersey. 388 pp.

Calow, P. 1973. The food of Ancylus fluviatilis (Müll), a littoral, stone-dwelling herbivore. Oecologia 13: 113-133.

Calow, P. 1974. Some observations on the dispersion patterns of two species-populations of littoral, stone-dwelling gastropods (Pulmonata). Freshwat. Biol. 4: 557-576.

Castenholz, R. W. 1961a. The effect of grazing on marine littoral diatom populations. Ecology 42: 783-794.

Castenholz, R. W. 1961b. An evaluation of submerged glass method of estimating production of attached algae. Verh. Internat. Verein. Limnol. 14: 155-159.

Clampitt, P. T. 1970. Comparative ecology of the snails Physa gyrina and Physa integra (Basommatophora: Physidae). Malacology 10: 113-151.

Clampitt, P. T. 1974. Seasonal migratory cycle and related movements of the fresh-water Pulmonate snail, Physa integra. Amer. Midl. Natur. 92: 275-300.

Clark, A. H. 1973. The freshwater molluscs of the Canadian Interior Basin. Malacology 13: 1-509.

Cooper, D. C. 1973. Enhancement of net primary productivity by herbivore grazing in aquatic microcosms. Limnol. & Oceanogr. 18: 31-37.

DeWitt, R. M. 1954a. Reproductive capacity in a pulmonate snail (Physa gyrina Say). Amer. Nat. 88: 159-164.

DeWitt, R. M. 1954b. The intrinsic rate of natural increase in a pond snail (Physa gyrina Say). Amer. Nat. 88: 353-359.

DeWitt, R. M. 1955. The ecology and life history of the pond snail Physa gyrina. Ecology 36: 40-44.

DeWitt, R. M. 1967. Simulation of egg production in a physid and a lymnaeid. Malacology 5: 445-453.

Dickman, M. 1968. The effect of grazing by tadpoles on the structure of a periphytic community. Ecology 49: 1188-1190.

Douglas, B. 1958. The ecology of the attached diatoms and other algae in a small stony stream. Ecology 46: 295-322.

Flint, R. W. and C. R. Goldman. 1975. The effects of a benthic grazer on the primary productivity of the littoral zone of Lake Tahoe. Limnol. & Oceanogr. 20: 935-944.

Hargrave, B. T. 1970a. The effect of a deposit-feeding amphipod on the metabolism of benthic microflora. Limnol. & Oceanogr. 15: 21-30.

Hargrave, B. T. 1970b. The utilization of benthic microflora by Hyalella azteca (Amphipoda). J. Anim. Ecol. 39: 427-437.

Harrod, J. J. and R. E. Hall. 1962. A method for determining the surface area of various aquatic plants. Hydrobiologia 20: 173-178.

Heywood, J. and R. W. Edwards. 1962. Some aspects of the ecology of Potamopyrgus jenkinsi (Smith). J. Anim. Ecol. 31: 239-250.

Hickman, M. and F. E. Round. 1970. Primary production and standing crop of episammic and epipelic algae. Br. Phycol. J. 5: 247-255.

Hutchinson, G. E. 1975. A treatise on limnology. III. Aquatic macrophytes and attached algae. John Wiley & Sons, Inc., New York. 660 pp.

Jones, N. S. 1946. Browsing of Patella. Nature 158: 557-558.

Keast, A. 1978. Feeding interrelations between age-groups of Pumpkinseed (Lepomis gibbosus) and comparsons with Bluegill (L. macrochirus). J. Fish. Res. Board Can. 35: 12-27.

Keast, A. and J. Harker. 1977. Fish distribution and benthic invertebrate biomass relative to depth in an Ontario lake. Env. Biol. Fish. 2: 235-240.

Kehde, P. M. and J. L. Wilhm. 1972. The effects of grazing by snails on community structure of periphyton in laboratory streams. Amer. Midl. Natur. 87: 8-24.

Kevern, N. R., J. L. Wilhm, and G. M. VanDyne. 1966. Use of artificial substrata to estimate productivity of periphyton. Limnol. & Oceanogr. 11: 499-502.

Landenberger, D. E. 1968. Studies on selective feeding in the Pacific starfish Pisaster in southern California. Ecology 49: 1062-1075.

Lubchenco, J. V. 1968. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Amer. Nat. 112: 23-39.

Mason, C. F. and R. J. Bryant. 1975. Periphyton production and grazing by chironomids in Alderfen Broad, Norfolk. Freshwat. Biol. 5: 271-277.

McIntire, C. D. 1966. Some effects of current velocity on periphyton communities in laboratory streams. Hydrobiologia 27: 559-570.

McNabb, C. D. 1960. Enumeration of freshwater phytoplankton concentrated on a membrane filter. Limnol. & Oceanogr. 5: 57-61.

Neill, W. E. 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. Ecology 56: 809-826.

Nicotri, M. E. 1977. Grazing effects of four marine intertidal herbivores on the microflora. Ecology 58: 1020-1032.

North, W. J. 1954. Size distribution, erosive activities and gross metabolic efficiency of the marine intertidal snails, Littorina planaxis and L. scutulata. Biol. Bull. 106: 185-197.

Paine, R. T. 1966. Food web complexity and species diversity. Amer. Nat. 100: 65-75.

Paine, R. T. and R. L. Vadas. 1969. The effects of grazing by sea urchin, Strongylocentrotus spp., on benthic algal populations. Limnol. & Oceanogr. 14: 710-719.

Patrick, R. 1968. The structure of diatom communities in similar ecological conditions. Amer. Nat. 102: 173-183.

Patrick, R. 1960. Benthic stream communities. Amer. Sci. 58: 546-549.

Patrick, R. and D. Strawbridge. 1963. Variation in the structure of natural diatom communities. Amer. Nat. 97: 51-57.

Pielou, E. C. 1966. The measurement of diversity in different types of biological conditions. J. Theoret. Biol. 13: 131-144.

Pip, E. and J. M. Stewart. 1976. The dynamics of two aquatic plant-snail associations. Canad. J. Zool. 54: 1192-1205.

Pomeroy, L. R. 1970. The strategy of mineral cycling. Ann. Rev. Ecol. & Syst. 1: 171-190.

Porter, K. G. 1973. Selective grazing and differential digestion of algae by zooplankton. Nature 244: 179-180.

Prowse, G. A. 1959. Relationships between epiphytic species and their macrophyte hosts. Nature 183: 1204-1205.

Purchon, R. D. 1968. The biology of the mollusca. Pergamon Press, Oxford. 560 pp.

Rich, P. H., R. G. Wetzel, and N. V. Thuy. 1971. Distribution, production and role of aquatic macrophytes in a southern Michigan marl lake. Freshwat. Biol. 1: 3-21.

Round, F. E. 1965. The biology of the algae. St. Martins Press, New York. 269 pp.

Sankurathri, C. S. and J. C. Holms. 1976. Effects of thermal effluents on the population dynamics of Physa gyrina Say (Mollusca: Gastropoda) at Lake Wabamun, Alberta. Canad. J. Zool. 54: 582-590.

Shannon, C. E. and W. Weaver. 1949. The mathematical theory of communication. Univ. of Illinois Press. 117 pp.

Sieburth, J. and C. D. Thomas. 1973. Fouling on eelgrass (Zostera marina L.). J. Phycol. 9: 46-50.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., Inc., New York. 312 pp.

Sládecek, V. and A. Sládecková. 1965. Determination of the periphyton production by means of the glass slide method. Hydrobiologia 23: 125-158.

Stockner, J. G. and F. A. J. Armstrong. 1971. Periphyton of the experimental lakes area northwestern Ontario. J. Fish Res. Bd. Canad. 28: 215-229.

Sullivan, M. J. 1977. Structural characteristics of a diatom community epiphytic on Ruppia maritima. Hydrobiologia 53: 81-86.

Tippett, R. 1970. Artificial surfaces as a method of studying populations of benthic micro-algae in fresh water. Br. Phycol. J. 5: 187-199.

Townsend, C. R. 1973. The food feeding orientation mechanism of Biomphalaria glabrata (Say). Anim. Behav. 21: 544-548.

Wagner, D. J. 1978. An investigation of some aspects of the intralake distribution of Chydorus sphaericus (Cladocera: Chydoridae). Masters Thesis, Michigan State University, East Lansing, MI.

Warner, J. S. 1976. Choice among food levels by an aquatic grazer (Physa gyrina Say). Behav. Biol. 16: 379-383.

Weber, C. I. 1971. A guide to the common diatoms at water pollution surveillance system stations. U.S. Environmental Protection Agency, National Environmental Research Center, Analytical Quality Control Laboratory, Cincinnati, Ohio. 99 pp.

Wetzel, R. G. 1964. A comparative study of the primary productivity of higher aquatic plants, periphyton, and phytoplankton in a large, shallow lake. Int. Rev. ges. Hydrobiologia 9: 1-64.

Wetzel, R. G. 1975. Limnology. W. B. Saunders Co., Philadelphia. 743 pp.

Whitford, L. A. 1956. The communities of algae in the springs and streams of Florida. Ecology 37: 433-442.

Wilhm, J. L. 1970. Effect of sample size on Shannon's formula. Southwestern Natur. 14: 441-445.