THE EFFECT OF DIFFERENT DENSITIES OF THE MAYFLY NYMPH, *Heptagenia criddlei*, ON STREAM DIATOM COMMUNITY STRUCTURE

by

Paul J. Colletti

A Thesis

Submitted in Partial Fulfillment

of the Requirements for the Degree of

Master of Science in Biology

Northern Arizona University

May 1984

Approved:

Dean W Blinn

E E Johnson

W Linn Montgomery

THE EFFECT OF DIFFERENT DENSITIES OF THE MAYFLY NYMPH, *Heptagenia criddlei*, ON STREAM DIATOM COMMUNITY STRUCTURE

A Thesis

Presented to

the Graduate Faculty

Northern Arizona University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

---

by

Paul J. Colletti

May 1984

ABSTRACT

Stream diatom community structure was examined in a laboratory stream under different densities of grazing by the mayfly nymph, *Heptagenia criddlei*. Grazer densities ranged from 0.08 to 1.50 nymphs cm^{-2} of periphyton cover in 14 experiments. Diatom cell densities were linearly proportional to grazer densities. At intermediate to high grazer densities (> 0.25 nymphs cm^{-2}), nymphs removed at least 90% of the diatom periphyton by day 10. Similarly, periphyton biomass decreased by 73% during the same time period at a density of 0.28 nymphs cm^{-2}. In contrast, experiments with grazer densities of 0.10 nymphs cm^{-2} showed no measurable change in diatom abundance, biomass, or composition after four weeks of grazing. Apparently, a threshold grazing pressure lies somewhere between 0.10 and 0.25 nymphs cm^{-2}, where densities > 0.25 nymphs cm^{-2} result in considerable removal of periphyton after one week, while densities < 0.10 nymphs cm^{-2} result in little, if any, change in diatom abundance and composition.

At intermediate to high grazer densities, the three-dimensional, overstory construction of the diatom assemblages was modified into a two-dimensional community characteristic of early successional assemblages. Diatoms composing this overstory, such as *Nitzschia dissipata, Cymbella affinis, Gomphonema ventricosum,* and *Synedra ulna,* were highly susceptible to grazing. In contrast, the relative abundances of small diatom species, like *Achnanthes minutissima, Nitzschia frustulum* var. *perpusilla,* and

Cymbella sinuata, or compressed, tightly adhering species like *Cocconeis placentula* var. *euglypta* and *Epithemia adnata*, increased. Therefore, size and mode of attachment appear to be important features in determining susceptibility to grazing.

Diatom diversity (Shannon-Weaver H′) and diatom community structure (SIMI, reported in Sullivan 1975) decreased at high grazer densities, but were unaffected at low grazer densities.

TABLE OF CONTENTS

	Page
LIST OF TABLES	ii
LIST OF FIGURES	iv
Chapter	
1. INTRODUCTION	1
2. MATERIALS AND METHODS	11
3. RESULTS	21
DIATOM CELL NUMBERS	28
PERIPHYTON BIOMASS MEASUREMENTS	36
SPECIES COMPOSITION	38
DIVERSITY, SPECIES EVENNESS, AND SIMILARITY INDICES	49
GUT CONTENT ANALYSES	57
4. DISCUSSION	59
5. SUMMARY	72
LITERATURE CITED	75

LIST OF TABLES

Table | Page

1. Nymph density and duration of the fourteen experiments conducted in Spring (May - June) 1982, Autumn (August - October) 1982, and Spring (May - June) (1983)..... 18

2. Diatom species in Oak Creek, Arizona during Spring (May - June) 1982, Autumn (August - October) 1982, and Spring (May - June) 1983..... 22

3. Dimensions of dominant diatom species in Oak Creek, Arizona..... 25

4. Density of macroinvertebrates (organisms m^{-2}) collected in riffle zone of Oak Creek, Arizona, collection site, on 7 September 1982, 18 February 1983, and 20 May 1983.... 26

5. Diatom densities (10^3 cells cm^{-2})in control and grazed channels for experiments with 0.28 and 0.31 nymphs cm^{-2} of periphyton cover..... 31

6. Diatom densities (10^3 cells cm^{-2}) in control and grazed channels for experiments with 0.49 and 0.40 nymphs cm^{-2} of periphyton cover..... 32

7. Diatom densities (10^3 cells cm^{-2}) in control and grazed channels for experiments with 0.72 and 0.71 nymphs cm^{-2} of periphyton cover..... 33

8. Diatom densities (10^3 cells cm^{-2}) in control and grazed channels for experiments with 0.10 and 0.08 nymphs cm^{-2} of periphyton cover..... 34

9. Periphyton biomass values ($g \cdot m^{-2}$) for control and grazed substrata in experiments with 0.28 and 0.08 nymphs cm^{-2} of periphyton cover..... 37

10. Relative abundances of diatom species in the guts of *Heptagenia criddlei* in grazed channels and on grazed and control substrata for experiments with 0.28 nymphs cm^{-2} of periphyton cover..... 58

LIST OF FIGURES

Figure		Page
1.	Laboratory stream used for grazing experiments.....	13
2.	Delineated periphyton squares on the upper surfaces of rocks in control and grazed channels.....	16
3.	Relationship between density of *Heptagenia criddlei* and diatom cell densities after three days of grazing.....	30
4.	Relative abundance of diatom species based on cell number for grazed and control substrata during the experiment at 0.28 nymphs cm^{-2}.	40
5.	Relative abundance of diatom species based on cell number for grazed and control substrata during the experiment at 0.71 nymphs cm^{-2}.	42
6.	Relative abundance of diatom species based on cell number for grazed and control substrata during the experiment at 0.31 nymphs cm^{-2}.	45
7.	Relative abundance of diatom species based on cell number for grazed and control substrata during the experiment at 0.08 nymphs cm^{-2}.	47

8. Diatom diversity (H′) on grazed and control substrata during experiments with 0.72, 0.71, 0.28, and 0.08 nymphs cm^{-2}..... 51

9. Diatom evenness (J) on grazed and control substrata during experiments with 0.72, 0.71, 0.28, and 0.08 nymphs cm^{-2}..... 53

10. Diatom community structure similarity (SIMI) between grazed and control substrata in the experiments with 0.28 and 0.08 nymphs cm^{-2} 56

ACKNOWLEDGMENTS

My experience at Northern Arizona University was one of tremendous growth in which several people participated. First, I would like to express my warmest appreciation for my advisor, Dr. Dean Blinn, who suggested my research project and who provided valuable time, encouragement, and guidance. His love for biology and unselfish desire to share this with others, and his ability to bring out the best in people will stay with me long after I leave NAU; I will always cherish our friendship. Dr. W. Linn Montgomery and Dr. C.D. Johnson gave helpful advice and criticism in the writing of this thesis. Mr. Gordon Cuthbertson, Mr. H.E. Graham, Mr. J.J. Callan, and Mr. Duane Short generously assisted me in modifying the laboratory stream for my research. Dr. Milton Sanderson aided in the identification of several Oak Creek macroinvertebrates. Dr. Graydon Bell helped me with the statistical analyses. Finally, my wife, Shirley, was a constant source of encouragement and love throughout my thesis program.

CHAPTER 1

INTRODUCTION

The term periphyton describes the attached community of organisms on aquatic substrata. Collins and Weber (1978) have presented a brief review of its uses. Originating in Russia, the term periphyton first specified organisms growing on objects placed in water by humans (Behning 1928, cited by Collins and Weber 1978). Eventually, the term referred to all attached microorganisms (bacteria, fungi, plant and animal) living on artificial and natural substrata (Young 1945), a meaning comparable to the German word, Aufwuchs. Another use of the term periphyton has included both the detritus and the attached living components (Cummins and Klug 1979). Recently, phycoperiphyton has been employed to characterize only the attached, benthic, algal flora (Foerster and Schlichting 1965). Diatoms are usually the predominant algal component in attached stream communities and may comprise as much as 90% of the algal assemblage (Blinn et al., 1980; Sumner and McIntire 1982; Horner and Welch 1981).

Most studies of phycoperiphyton ecology have overlooked the effects of biological interactions and have concentrated on the chemical and physical factors which determine algal abundance, composition, and distribution (Butcher 1947; Whitford 1960; Felföldy 1961; Round 1965; Hynes 1970; Moss 1973; Munteanu and Maly 1981; Horner and Welch 1981). Nonetheless, since benthic

algae are the primary food source of stream invertebrates (Chapman and Demory 1963; Hynes 1970; Coffman et al. 1971; Cummins 1974; Mann 1975), it is likely that these herbivores exert a significant impact on phycoperiphyton communities in flowing water systems.

Benthic algae are major components in the diet of stream invertebrates. For example, Coffman et al. (1971) examined the gut contents of the 75 most common macroconsumers in the autumn assemblage of a small woodland stream in Pennsylvania. The ingested foods were placed into three categories: algae (almost entirely diatoms), detritus, and animals. Algal material composed 50% or more of the ingested food in 50 of the 75 species examined.

To date, the majority of macroinvertebrates appear to be generalists (polyphagous) in their feeding (Cummins 1973) and their diets typically reflect the relative availability of food in the environment (Brown 1961; Hynes 1970; Coffman et al. 1971; Mecom 1972; Cummins 1973; Moore, 1977; Bowker et al. 1983). For example, the food habits of the trichopteran, *Glossosoma nigrior* Banks, differ markedly in two different streams. The diet of larvae from Linesville Creek (Pennsylvania), a stream characterized by an abundance of algal growth, consisted almost exclusively of algae, whereas in Augusta Creek (Michigan), detritus and detrital feeding predominated (Cummins 1973).

Therefore the classification of macroinvertbrates into functional feeding groups according to the type of food ingested may cause confusion (Cummins 1973; Cummins and Klug 1979). Moreover, a larva may feed exclusively on the stream epilithic algal community but will also ingest fine particulate organic

matter (FPOM, < 1 mm) and small animals. Therefore, it has been suggested that functional feeding classifications of stream invertebrates be based on the mode by which macroinvertebrates obtain food rather than on the food eaten. For example, invertebrate consumers have been partitioned into the following functional groups based on feeding mechanisms: shredders, collectors, scrapers, piercers, and predators (Cummins 1973). Because they depend primarily on the periphyton community, especially the epilithic algae, for their nutrition, scrapers are the major focus of this study.

Several studies of natural stream systems document marked reduction in periphyton standing crop due to grazing by invertebrate "scrapers". Douglas (1958) found a negative correlation between populations of the diatom, *Achnanthes* sp., and grazing populations of the caddis fly larva, *Agapetus fuscipes* Curtis, in a small stony stream. Periphyton biomass increased in a Canadian stream following the eradication of aquatic insects with a DDT application (Ide 1967). Using a ^{32}P material balance method, Elwood and Nelson (1972) proposed that the snail, *Goniobasis clavaeformis* Lea, limited periphyton primary production by regulating the standing crop of periphyton in a small woodland stream in southeastern U.S. Lamberti and Resh (1983) reported that the caddis fly larva, *Helicopsyche borealis* (Hagen), reduced periphyton standing crop (chlorophyll a) while increasing the algal turnover rate (O_2 evolved per unit chlorophyll a).

Due to the complexity of natural stream systems, most workers have examined the impact of grazing on periphyton standing crops

in artificial streams. Artificial streams offer greater simplicity at the expense of losing some reality characteristic of natural systems (Warren and Davis 1971). Bohle (1978) observed the depletion of periphyton cover on substrata at high grazer densities (2500-4200 larvae m^{-2}) of the mayfly nymph, *Baetis rhodani* (Pictet) in laboratory streams. The nymphs tended to aggregate on those substrates supporting large amounts of periphyton. Complete removal of the algal cover by grazers resulted in increased drift by the mayfly nymph. Eichenberger and Schlatter (1978) also noted a decrease in benthic algal biomass in outdoor river channels at high grazer densities (13,000-372,000 larvae m^{-2}) of two orthoclad midge species (family Orthocladinae).

The majority of studies of grazing on periphyton, have involved herbivorous snails. In addition to being common, herbivorous snails are typically more manageable and heartier than aquatic insect grazers. Kedhe and Wilhm (1972) observed a slight reduction in periphyton standing crop after three months of grazing (120 snails m^{-2}) by the snail, *Physa gyrina* Say, in a laboratory stream. Laboratory investigations and biological models have also indicated that the snail, *Oxytrema silicula* (Gould), has a large impact on periphyton biomass in several small woodland streams of the Willamette River valley, Oregon (McIntire 1973, 1975; McIntire and Colby 1978). Intermediate (510 snails m^{-2}) and high (1020 snails m^{-2}) grazer densities of the snail, *Juga plicifera*, caused a decline in periphyton biomass in laboratory streams (Gregory 1980). No change in periphyton biomass occurred

at low grazer densities (< 170 snails m^{-2}). Sumner and McIntire (1982) investigated the effects of light intensity, nitrate enrichment, and grazing by the same grazer on phycoperiphyton community structure in laboratory streams. They observed that snail densities of 500 m^{-2} reduced periphyton biomass by as much as 30% in a laboratory channel.

In contrast, several workers have countered that invertebrate grazing has little impact on periphyton abundance (Stockner 1971; Cummins 1973; Moore 1975, 1978; Collins et al. 1976; Stockner and Shortreed 1976). However, two of these studies were thermal spring communities which operate under very different environmental parameters than do natural stream systems (Stockner 1971; Collins et al. 1976). The other three remaining studies have relied principally upon information gathered indirectly from gut content analyses. These analyses may prove misleading because of the differential digestion rates of food items (Cummins 1973). Moreover, they frequently overlook the unknown impact of small insect instars and protozoa on periphyton assemblages.

In addition to decreasing periphyton standing crop, herbivores may also alter the species composition of a stream phycoperiphyton assemblage. Changes in the species composition may occur by means of "selective feeding." Definitions of selective feeding are confusing. Cummins (1973) contends that "true selective feeding involves the rejection of some of the available food substances." Food availability is defined as those food items which are not rejected because of physical mechanisms (ie. too small or large, mode of attachment, calcification) or

chemical properties (ie. toxins). Frequently, it is difficult to discern selective feeding from physical or chemical constraints. Regardless of the mechanisms operating, specific food items are ingested and others are not. Thus, Cummins prefers the term "restricted food intake", eliminating the question of "behavioral choice" by the grazer.

Alteration of the species composition of a stream epilithic community has often been inferred through gut content analyses (Hynes 1941, 1961; Calow 1973; Moore 1975, 1977; Gray and Ward 1979). Gut contents differing from the relative availability of food on stream substrata suggest selective feeding, leading to the inference that species composition has changed on the substrata. Frequently, herbivore guts contain a greater proportion of the diatom, *Gomphonema* spp., than surrounding substrata (Moore 1975, 1977; Calow 1973). The gelatinous, stalk-producing, *Gomphonema* spp. project prominently above the substrata, resulting in greater accessibility for herbivores. In field and laboratory experiments, Calow (1973) observed that the snail, *Ancylus fluviatilis*, ingested *Gomphonema* spp. more frequently than other diatom species. This diet selectivity was most evident in satiated snails. *Gomphonema* spp. were also dominant algal components in the diet of the mayfly nymph, *Cinygmula tarda* McD., in some subarctic streams (Moore 1977).

Several studies have reported lower amounts of the diatom, *Cocconeis* spp., in the guts of invertebrate grazers than on stream substrata (Mecom and Cummins 1964; Patrick 1970; Moore 1975, 1977). Epiphytic *Cocconeis* spp. were rarely ingested by the

isopod, *Asellus aquaticus* L. and the amphipod, *Gammarus pulex* L. and this was attributed to its compressed mode of attachment and to its upper surface extending only 3 μm above the substrate (Moore 1975). The herbivorous mayfly nymph, *Leptophlebia nebulosa* Banks, fed predominantly on the filamentous green alga, *Bulbochaete* sp., unicellular diatoms, and small chlorophyceans and chrysophytes yet was unable to ingest *Cocconeis placentula* Ehr. in the same proportion to its relative abundance on substrata in subarctic streams (Moore 1977). On the other hand, small mayfly nymphs (*Chloeon dipterum* L.) fed primarily on coccoid cells and small *Cocconeis* cells (Brown 1961). Furthermore, invertebrate grazers, *Stylaria lacustris* L. (Oligochaeta) and *Lepidostomota* sp. (Trichoptera), readily grazed on the dominant alga, *Cocconeis placentula*, permitting colonization by other diatoms in a small Ontario stream (Dickman and Gochnauer 1978).

Many invertebrates avoid filamentous algae, particularly the filamentous green alga, *Cladophora glomerata* (L.) Kütz. (Brown 1961; Moore 1975; Gray and Ward 1979). The oligochaete, *Nais elinguis* Muller, fed almost exclusively on epilithic chlorophycean unicells and pennate diatoms while ignoring all filamentous algae including *Ulothrix* and *Microspora* (Bowker et al. 1983). Calow (1973) observed that the snail, *Ancylus fluviatilus* Müller, overwhelmingly preferred diatoms over filamentous green and blue-green algae. Although *C. glomerata* was very abundant at several locations in a small Colorado stream, most aquatic insects did not feed on this alga (Gray and Ward 1979). The increased deposition of calcium carbonate on the filaments, particularly

during late autumn before senescence, and the large size of the filament cells may have inhibited grazing activity (Brown 1961; Gray and Ward 1979). Consumption of *C. glomerata* by an assemblage of mayflies, caddis flies, and dipterans increased as plants declined and fragmented (Gray and Ward 1979); presumably the disintegrating filaments were more manageable and palatable. The sparse ingestion of *C. glomerata* may have also been a result of its low energy content in comparison to diatoms and allochthonous organic matter. In spite of their abundance in the environment, *C. glomerata* and the blue-green alga, *Phormidium foveolarum* (Mont.) Gom., were absent in the diet of *Asellus aquaticus* and *Gammarus pulex* (Moore 1975). In contrast, Koslucher and Minshall (1973) observed that diatoms and *C. glomerata* were the only significant living components in diets of eight invertebrate herbivores in a northern cool-desert stream (Idaho). Moreover, the filamentous green alga, *Ulothrix*, was the dominant algal constituent in diets of the mayfly nymph, *Ephemerella* (Jones 1949), and in several trichopteran species (Mecom 1972).

Relatively few studies have directly documented alteration of species composition of phycoperiphyton communities by a stream invertebrate, i.e., quantified changes in community structure directly on the substrate. In one such study, blue-green algae, *Oscillatoria* and *Phormidium*, formed extensive mats in outdoor control (ungrazed) channels after two months, but populations of orthoclad midges prevented their establishment in another channel (Eichenberger and Schlatter 1978). By the end of the experiment (100 days), channels were cleaned of periphyton.

Other studies have worked exclusively with mollusks. Gregory (1980) observed that diatoms dominated periphyton communities in laboratory streams where moderate to heavy snail grazing was prevalent. High grazer densities resulted in the dominance of small diatom species whereas low grazer densities did not alter the community structure. Sumner and McIntire (1982) reported that at high grazer densities, the proportion of certain large, overstory diatom species like *Melosira varians* Ag. and *Synedra ulna* (Nitz.) Ehr. decreased and the relative abundance of the smaller, closely adhering species like *Achnanthes minutissima* Kütz. and *Navicula minima* Grun. increased in laboratory streams. No change in community structure occurred at low grazer densities. Similar grazing patterns have been reported for limpets in marine intertidal zones (Nicotri, 1977; Hunter and Russell-Hunter 1983) and for snails in lacustrine systems (Hunter, 1980; Kesler, 1981). In contrast, Kedhe and Wilhm (1972) reported that snails did not change the periphyton community structure in an artificial stream. However, the high water temperatures (30-34°C) resulting in decreased algal species diversity and an absence of diatoms, may have distorted their results.

In view of the limited information about the impact of insect grazing on standing crop and community structure of stream periphyton , the objectives of this study were to 1) investigate the effects of different grazer densities of the mayfly nymph, *Heptagenia criddlei* McD., on stream diatom community structure, and 2) examine the removal rates of diatoms by *H. criddlei*. Only diatoms were examined because they are more easily quantified than

other algal components and they comprise nearly 90% of the algal community in Oak Creek, Arizona (Blinn et al. 1980).

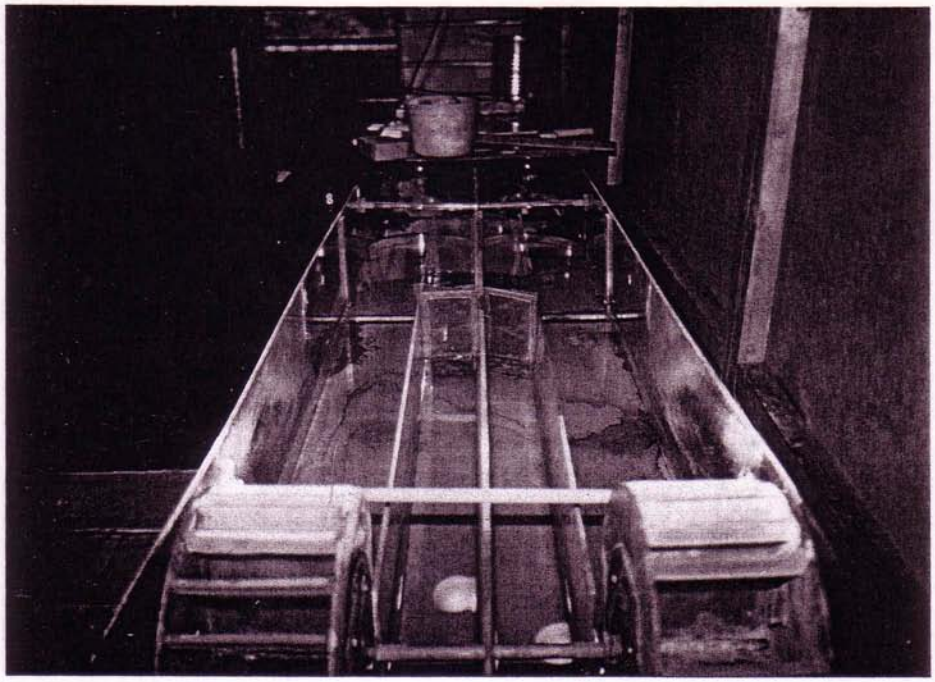
CHAPTER 2

MATERIALS AND METHODS

A closed and recirculating plexiglass laboratory stream, measuring 178 cm long, 48 cm wide, and 24 cm high, was divided into separate grazing and control (no grazers) channels (Fig. 1). Thirty eight liters of water in each channel maintained the water level at a depth of 7 cm. In each channel, a region 43 cm long and 9 cm wide was partitioned with screens. Screen mesh size was 1 mm. Small sterile stones, ranging from 1-4 cm in diameter, lined the bottom of the regions. Two adjoining paddlewheels, located at one end of the stream, maintained the current at approximately 22 $cm \cdot sec^{-2}$ within the screened off chambers. The current was measured with a Pygmy current meter. A Gro-lux lamp positioned above the channels provided 150 ft·c of illumination for the Spring and Fall 1982 preliminary trials. Spring 1983 experiments received 600 ft·c of light from four fluorescent lamps. The photoperiod consisted of alternating periods of 12 hr. light/12 hr. dark. Within any one trial, water temperature fluctuated within a 5 °C range. Including all trials, temperatures ranged from 11-21 °C, approximating water temperatures in Oak Creek at the time of the trials.

Experiments were conducted in Spring 1982 (May through June), Fall 1982 (August through October), and Spring 1983 (May through June). Water, periphyton, and nymphs of the mayfly, *Heptagenia criddlei*, were collected for the laboratory experiments in Oak

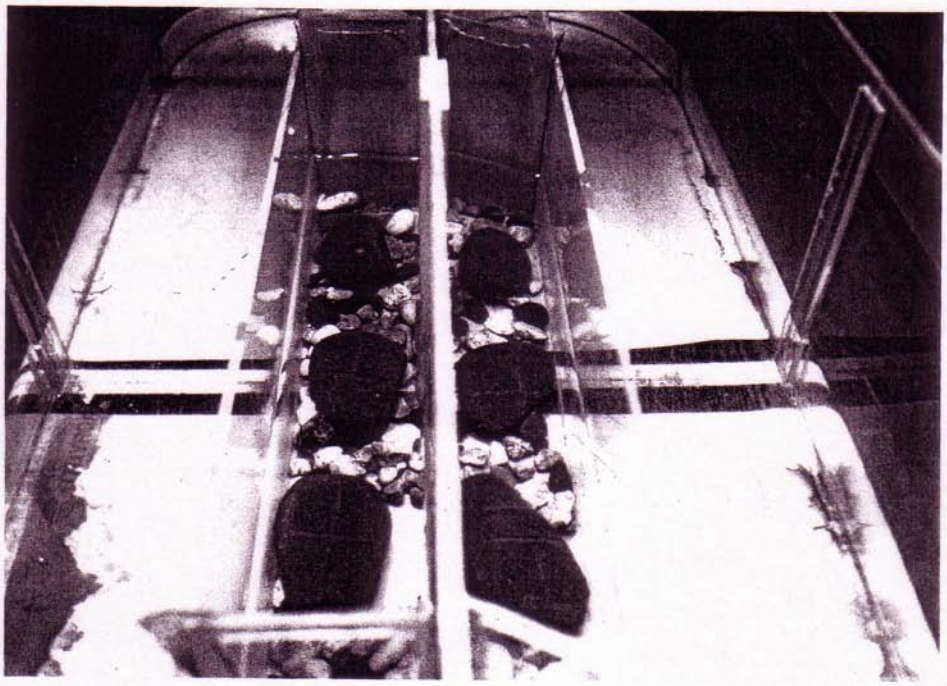
Figure 1. Laboratory stream used for grazing experiments.



Creek, 27 km south of Flagstaff, Coconino County, Arizona and 3.3 km below Pumphouse Wash. However, because of poor periphytic growth in early Spring 1983, periphyton for the experiment using 0.28 nymphs cm^{-2} of periphyton cover was collected from Wet Beaver Creek, adjacent to Montezuma Well, Yavapai County, Arizona. All diatoms identified from Wet Beaver Creek were found in Oak Creek. Nymphs of *Heptagenia criddlei* and rocks of roughly uniform size and periphytic growth were chosen and placed into separate buckets for transportation to the laboratory. Water was collected and transported in 19 liter containers. The rocks, nymphs, and water were placed in the laboratory stream within 3 hours of collection. Once in the laboratory, known areas of periphyton covering the top surface of the rocks were delineated with a razor blade and the remaining periphyton was scraped off (Fig. 2). The delineated areas ranged anywhere from 5.5 cm^2 to 12.2 cm^2. After placing in an equal number of delineated areas in both channels, a chosen number of mayfly nymphs were evenly distributed within the grazing region. Introduced mayfly nymphs ranged from 6-10 mm in length (tip of head capsule to base of caudal filaments) and their dry weights averaged 5.4 mg.

Approximately 50% of the rocks' surfaces were covered by periphyton. This arrangement seemed to mimic the patchy nature of periphyton distributions in natural streams better than other studies, where investigators have lined the entire bottom with periphytic slides or tiles (Kedhe and Wilhm 1972; Hunter 1980; Gregory 1980; Sumner and McIntire 1982).

Figure 2. Delineated periphyton squares on the upper surfaces of rocks in control and grazed channels.



Twelve preliminary experiments with different densities of grazers were performed in Spring and Fall 1982 (Table 1). Densities ranged from 0.09 - 1.50 nymphs cm^{-2} of periphyton cover. Several of the high density experiments were short because all the accessible periphyton was removed within one or two days; as a result, nymph behavior changed when food was unavailable.

In these experiments, three delineated areas of periphyton were typically removed daily from both channels and scraped clean with a razor blade. Sampling occurred on downstream rocks first and progressively moved upstream. A proportionate number of nymphs were removed with the blocks to maintain the same grazer density throughout the experiment.

Two additional experiments were performed in Spring 1983 (Table 1). These trials more closely approximated natural grazing densities of *Heptagenia criddlei* in Oak Creek, one representing a high grazing density situation (0.28 nymphs cm^{-2} of periphyton cover) and the other simulating natural grazing densities of the 6-10 mm *H. criddlei* (0.08 nymphs cm^{-2} of periphyton cover). These two trials differed from the preliminary trials in that they extended from 2-4 weeks in length, sampling occurred at greater time intervals, fresh water was exchanged every third day, and dry and ash-free dry weights of the periphyton were measured to complement taxonomic counts.

In order to determine dry and ash-free dry weights of periphyton, each removed delineated area of periphyton was partitioned equally; one half was used for taxonomic counts and the other half for measurements of biomass. Periphyton was placed

Table 1. Nymph density and duration of fourteen experiments conducted in Spring (May - June) 1982, Autumn (August - October) 1982, and Spring (May - June) 1983.

Trials (nymphs cm^{-2} of periphyton cover)	Length of experiment (days)
Spring and Autumn 1982:	
1.50	3
0.77	3
0.72	2
0.71	3
0.49	4
0.41	4
0.31	5
0.31	5
0.23	4
0.10	6
0.10	12
0.09	4
Spring 1983:	
0.28	14
0.08	28

in pre-weighed crucibles, dried to constant weight at 105°C, and roasted for one hour at 500°C in a muffle furnace (APHA 1971).

In all samples used for species determination, diatoms were oxidized by the peroxide dichromate procedure (van der Werff 1953) and permanently mounted on slides with Hyrax mounting medium. A minimum of 500 diatom frustules were counted from each of the three replicate slides for each channel. At least 100 fields (70 μm X 70 μm) were counted if thoroughly grazed substrates prevented a count of 500 cells. The size dimensions of the 14 dominant diatom species were also measured. Counts and measurements were made at 1000X magnification with a Zeiss phase contrast microscope.

The diversity (H′) of diatom assemblages was measured on each sampling date with the Shannon-Weaver equation (Pielou 1969) and evenness (J) was estimated from the ratio of H′ to H max, where H max is the diversity computed as if all taxa were equally abundant. The comparison of diatom community structure between grazed and ungrazed substrata was also determined by means of a similarity index (SIMI). This index compares the species composition and apportionment of assemblages and has been used by Sullivan (1975, 1977) in comparisons of edaphic diatom communities in salt marshes and by Tuchman and Blinn (1979) in comparisons of periphyton assemblages on natural and artificial substrata. The SIMI index is:

$$\text{SIMI} = \frac{\sum_{i=1}^{S} Pij\ Pin}{\sqrt{\sum_{i=1}^{S} Pij^2}\ \sqrt{\sum_{i=1}^{S} Pin^2}},$$

where Pij and Pin are the average relative abundances of the ith species in the jth and nth communities, and s is the number of species. Values range from 0 to 1, where 0 signifies communities with no species in common and 1 denotes identical communities.

Gut contents of nymphs removed after each sampling period, (i.e. 1, 3, 7, 10, and 14 days of the experiments involving 0.28 nymphs cm^{-2} of periphyton cover) were analyzed to determine the relative abundances of diatom species. The entire gut was dissected out and placed in a watch glass containing distilled water. After the contents were removed from the gut, they were placed in a 10 ml graduated cylinder, thoroughly shaken, and a 1 ml aliquot was pipetted into a Sedgwick-Rafter counting chamber. Three strip counts per sample were made with a Zeiss phase contrast microscope at 100X magnification.

Three replicate Surber samples were collected on 7 September 1982, and 4 were collected on 18 February 1983, and 20 May 1983 at the collection site in Oak Creek. Macroinvertebrates were preserved with AFA and later enumerated and identified to at least the ordinal level.

CHAPTER 3

RESULTS

A total of 85 species of epilithic diatoms were identified from the three sampling seasons (Table 2). Dimensions of the dominant diatom species are presented in Table 3.

The experimental design for the two Spring 1983 experiments was considerably improved over the 10 preliminary trials and the following sections will concentrate on these results. Data from the preliminary trials will be used to complement the Spring 1983 findings. Furthermore, according to the Surber collections made on 7 September 1982, 18 February 1983, and 20 May 1983 in the riffle zone of the Oak Creek collection site, the grazer densities of the Spring 1983 trials (0.08 and 0.28 nymphs cm^{-2} of periphyton cover or 267 and 1176 nymphs m^{-2}) may more closely approximate natural densities in Oak Creek (Table 4). For instance, densities of *Heptagenia criddlei* nymphs ranging between 6 and 10 mm in length averaged as high as 215 nymphs m^{-2} in the 7 September 1982 Surber collections. *Heptagenia criddlei* nymphs < 5 mm were extremely abundant in the same collection, averaging 724 nymphs m^{-2}. The trichopteran, *Glossosoma ventrale* Banks, was also abundant in the late spring and autumn collections, averaging as high as 463 nymphs m^{-2} in the 20 May 1983 collections. The stonefly nymph, *Capnia* sp. (196 nymphs m^{-2}), and a chironomid larva (223 individuals m^{-2}) were the dominant taxa in the winter collections. *Heptagenia criddlei* nymphs > 4 mm were not

Table 2. Diatom species in Oak Creek, Arizona during Spring (May - June) 1982, Autumn (August - October) 1982, and Spring (May - June) 1983.

DIVISION BACILLARIOPHYTA

Class Centrobacillariophyceae

Order Eupodiscales

Family Coscinodiscaceae

Cyclotella meneghiniana Kütz.

Melosira varians Ag.

Class Pennatibacillariophyceae

Order Achnanthales

Family Achnanthaceae

Achnanthes affinis Grun.
A. deflexa Reim.
A. lanceolata (Breb.) Grun.
A. lanceolata var. dubia Grun.
A. microcephala (Kütz.) Grun.
A. minutissima Kütz.

Cocconeis pediculus Ehr.
C. placentula var. *euglypta* (Ehr.) Cl.
C. placentula var. *lineata* (Ehr.) V. H.

Rhoicosphenia curvata (Kütz.) Grun. *ex* Rabh.

Order Bacillariales

Family Nitzschiaceae

Hantzschia amphioxys (Ehr.) Grun.

Nitzschia accedans Hust.
N. acicularis W. Sm.
N. dissipata (Kütz.) Grun.
N. filiformis (W. Sm.) Hust.
N. fonticola Grun.
N. frustulum (Kütz.) Grun.
N. frustulum var. *perpusilla* (Rabh.) Grun.
N. kützinghiana Hilse
N. linearis W. Sm.
N. palea (Kütz.) W. Sm.
N. romana Grun.
N. sigmoidea (Ehr.) W. Sm.
N. vermicularis (Kütz.) Grun.

Order Epithemiales

Family Epithemiaceae

Epithemia adnata (Kütz.) Breb.
E. sorex Kütz.
E. turgida (Ehr.) Kütz.

Rhopalodia gibba (Ehr.) Müll.
R. gibba var. *ventricosa* (Kütz.) H. & M. Perag.

Order Fragilariales

Family Fragilariaceae

Diatoma vulgare Bory

Fragilaria capucina var. *mesolepta* Rabh.
F. leptostauron (Ehr.) Hust.
F. vaucheriae (Kütz.) Peters.

Meridion circulare (Grev.) Ag.

Synedra acus Kütz.
S. delicatissima var. *augustissima* Grun.
S. goulardi Breb.
S. incisa Boyer
S. mazamaensis Sov.
S. rumpens Kütz.
S. rumpens var. *familiaris* (Kütz.) Hust.
S. socia Wallace
S. ulna (Nitz.) Ehr.
S. ulna var. *danica* (Kütz.) V. H.

Order Naviculales

Family Cymbellaceae

Amphora ovalis var. *pediculus* (Kütz.) V. H. *ex* De T.
A. perpusilla (Grun.) Grun.
A. veneta Kütz.

Cymbella affinis Kütz.
C. cistula (Ehr.) Kirchn.
C. cymbiformis var. *nonpunctata* Font.
C. mexicana (Ehr.) Cl.
C. minuta Hilse *ex* Rabh.
C. prostrata (Berk.) Cl.
C. sinuata Greg.
C. tumida (Breb. *ex* Kütz.) V. H.

Family Gomphonemataceae

Gomphoneis herculeana (Ehr.) Cl.

Gomphonema acuminatum Ehr.
G. affine Kütz.
G. augustatum (Kütz.) Rabh.
G. clevei Fricke
G. intracatum var. *vibrio* (Ehr.) Cl.
G. parvulum Kütz.
G. truncatum Ehr.
G. ventricosum Greg.

Family Naviculaceae

Amphipleura pellucida Kütz.

Caloneis bacillum (Grun.) Cl.

Navicula americana Ehr.
N. arvensis Hust.
N. cryptocephala Kütz.
N. cryptocephala f. *minuta* Boye-P.
N. cryptocephala var. *veneta* (Kütz.) Rabh.
N. descussis Ostr.
N. minima Grun.
N. pelliculosa (Breb. *ex* Kütz.)
N. pupula Kütz.
N. radiosa var. *tenella* (Breb. *ex* Kütz.) Grun.
N. tripunctata (Müll.) Bory
N. tripunctata var. *schizimoides* (V. H.) Patr.
N. zanoni Hust.

Pinnularia brebissonii (Kütz.) Rabh.

Order Surirellales

Family Surirellaceae

Cymatopleura solea (Breb.) W. Sm.

Surirella augustatum Kütz.

Table 3. Dimensions of dominant diatom species in Oak Creek, Arizona. Diatom species are listed according to increasing size.

Species	Length (µm) x	s	Range (µm)	Breadth (µm) x	s	Range (µm)
Nitzschia frustulum var. *perpusilla* (n=35)	8.6	1.8	6 - 14	2.5	0.3	2 - 3
Achnanthes minutissima (n=50)	10.4	1.8	6 - 14	2.7	0.3	2 - 3.5
Cymbella sinuata (n=51)	12.2	2.9	9 - 24	3.9	0.4	3 - 5
Cocconeis placentula var. *euglypta* (n=51)	15.0	3.5	8 - 24	9.9	2.3	6 - 18
Achnanthes lanceolata (n=51)	16.2	4.6	10 - 30	5.6	0.8	4 - 7
Navicula cryptocephala var. *veneta* (n=38)	16.8	2.0	14 - 20	4.9	0.4	4 - 5
Nitzschia kutzinghiana (n=51)	19.7	4.2	12 - 30	2.5	0.4	2 - 4.5
Cymbella affinis (n=50)	23.6	2.4	19 - 29	8.2	0.7	6 - 9
Epithemia sorex (n=40)	26.5	1.8	21 - 30	8.0	0.7	7 - 10
Nitzschia dissipata (n=52)	33.2	7.8	16 - 52	3.8	0.4	3 - 5
Epithemia adnata (n=32)	34.0	5.0	25 - 43	10.4	1.2	8 - 13
Navicula zanoni (n=42)	34.5	1.2	33 - 37	7.1	0.5	6 - 9
Gomphonema ventricosum (n=33)	42.1	7.6	39 - 48	10.9	0.5	10 - 12
Synedra ulna (n=32)	86.1	16.4	63 - 167	6.3	0.5	5 - 7

Table 4. Density of macroinvertebrates (organisms m^{-2}) collected in riffle zone of Oak Creek, Arizona collection site on three different sampling dates. Numbers represent means (x) and standard deviations (s) of three replicates for 7 September 1982 and four replicates for the latter two sampling dates.

Macroinvertebrates	7 Sept. 1982		18 Feb. 1983		20 May 1983	
	x	(s)	x	(s)	x	(s)
EPHEMEROPTERA:						
Heptagenia criddlei > 5 mm	215	(38)	0	(0)	137	(71)
H. criddlei < 5 mm	724	(136)	11	(15)	75	(38)
Epeorus (Iron) margarita	0	(0)	0	(0)	24	(18)
Baetidae sp.	75	(56)	75	(62)	151	(166)
Ephemeroptera sp.	22	(0)	57	(42)	0	(0)
PLECOPTERA:						
Capnia sp.	22	(37)	196	(125)	0	(0)
TRICHOPTERA:						
Glossosoma ventrale	205	(74)	32	(30)	463	(263)
Hesperophylax sp.	0	(0)	0	(0)	5	(11)
Helicopsyche sp.	14	(25)	3	(5)	8	(11)
Trichoptera spp. (6 species)	28	(16)	35	(42)	51	(48)
DIPTERA:						
Chironomidae sp.	0	(0)	223	(91)	62	(56)
Diptera spp. (7 species)	37	(28)	100	(55)	54	(44)
COLEOPTERA:						
Optioservus sp.	46	(23)	0	(0)	19	(5)
ODONATA:						
Odonata sp.	0	(0)	0	(0)	3	(5)
HEMIPTERA:						
Hemiptera sp.	22	(28)	0	(0)	0	(0)
ACARINA:						
Acarina sp.	0	(0)	0	(0)	3	(5)
TURBELLARIA:						
Dugesia sp.	22	(11)	0	(0)	24	(18)
OLIGOCHAETE:						
Oligochaeta sp.	0	(0)	0	(0)	3	(5)
Total	1432		732		1082	

encountered in winter collections, and numbers < 4 mm were considerably reduced.

Diatom Cell Numbers

Diatom cell densities decreased as grazer densities increased ($y = 15.8 - 4.67x$, $r = 0.83$, $p < 0.0025$) (Fig. 3). Throughout the first 7 days of the Spring 1983 trial at 0.28 nymphs cm^{-2} of periphyton cover (hereafter 0.28 experiment), diatom densities on grazed and control substrata averaged 3,372 X 10^3 cells$\cdot cm^2$ and 4,642 X 10^3 cells$\cdot cm^2$, respectively (Table 5). However, more than 90% of the diatoms in relation to the controls were removed by day 10. Similar impact on diatoms was evident within 1 to 4 days in trials with grazer densities > 0.40 nymphs cm^{-2}. Only 4 days at densities of 0.49 and 0.41 nymphs cm^{-2} were required to remove more than 90% of the diatoms (Table 6), and 93% of the diatoms were removed within 24 hours in the 0.72 experiment and 97% of the diatoms were removed within 48 hours in the 0.71 experiment (Table 7).

The effect of grazer densities ranging between 0.10 and 0.40 on diatom cell numbers exhibited more variability than the higher density trials. At these low to intermediate densities, the effect of grazing was not uniform, and cell numbers decreased only in localized regions (Table 5). However, as demonstrated in the 0.28 experiment, extension of the experiment beyond a week often resulted in the removal of most diatoms and thus, a more uniform grazing impact on all rock substrata.

At low grazer densities (< 0.10), little, if any, change in diatom densities was observed (Table 8). The large fluctuations

Figure 3. The relationship between density of *Heptagenia criddlei* and diatom cell densities (cells cm^{-2}) ($\ln x$ transformation) after three days of grazing. Each point represents a mean of three replicates.

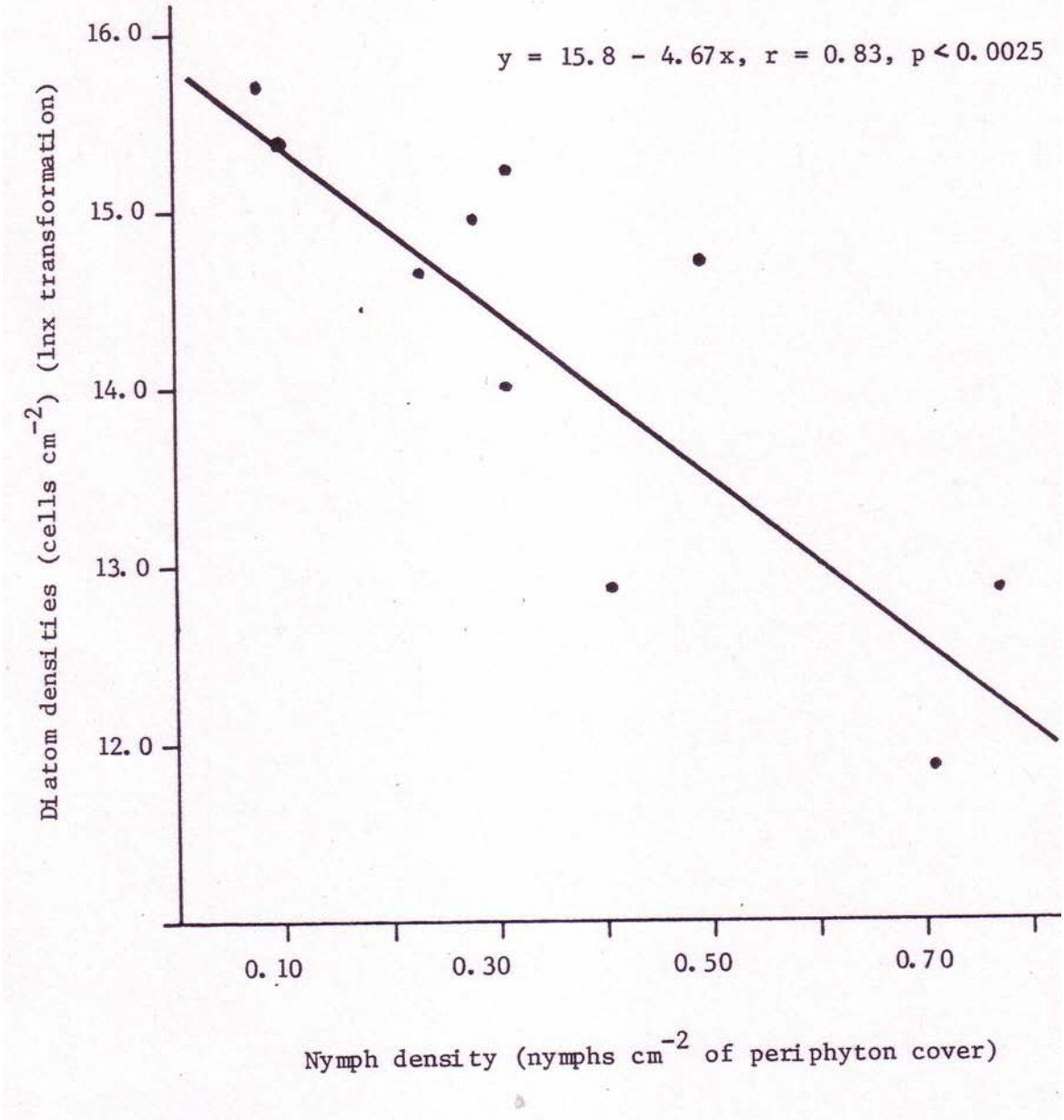

y = 15.8 - 4.67x, r = 0.83, p < 0.0025
16.0
15.0
14.0
13.0
12.0
Diatom densities (cells cm^{-2}) (lnx transformation)
0.10
0.30
0.50
0.70
Nymph density (nymphs cm^{-2} of periphyton cover)

Table 5. Diatom densities (10^3 cells cm^{-2}) in control and grazed channels for experiments with 0.28 and 0.31 nymphs cm^{-2} of periphyton cover. Numbers represent means (x) and standard deviations (s) of three replicates. Cell numbers for day 0 in grazed and control channels are from the same three replicates.

		Cells cm^{-2} of substrata				
		Control		Grazed		
Density	Day	x	s	x	s	% of cells removed
0.28	0	3,846	1,100	3,846	1,100	
	1	3,038	716	3,624	451	
	3	5,350	447	3,108	1,016	42
	7	5,539	282	3,383	547	39
	10	4,134	350	283	107	93
	14	2,977	1,219	711	732	76
0.31	0	2,817	467	2,817	467	
	1	3,754	439	3,281	670	
	2	5,943	1,197	1,992	262	67
	3	4,690	1,458	1,211	741	74
	4	3,269	564	822	872	75
	5	6,341	704	3,116	1,131	51

Table 6. Diatom densities (10^3 cells cm^{-2}) in control and grazed channels for experiments with 0.49 and 0.41 nymphs cm^{-2} of periphyton cover. Numbers represent means (x) and standard deviations (s) of three replicates. Cell numbers for day 0 in grazed and control channels are from the same three replicates.

Cells cm^{-2} of substrata

Density	Day	Control x	Control s	Grazed x	Grazed s	% of cells removed
0.49	0	5,246	1,183	5,246	1,183	
	1	3,885	1,599	4,598	1,066	
	2	2,929	411	3,985	572	
	3	3,265	386	2,475	889	24
	4	3,875	113	247	185	94
0.41	0	2,518	16	2,518	16	
	1	2,832	535	544	281	81
	2	2,765	365	1,450	215	48
	3	1,812	242	389	123	79
	4	2,006	120	230	102	89

Table 7. Diatom densities (10^3 cells cm^{-2}) in control and grazed channels for experiments with 0.72 and 0.71 nymphs cm^{-2} of periphyton cover. Numbers represent means (x) and standard deviations (s) of three replicates. Cell numbers for day 0 in grazed and control channels are from the same three replicates.

Cells cm^{-2} of substrata

		Control		Grazed		
Density	Day	x	s	x	s	% of cells removed
0.72	0	2,654	1,887	2,654	1,887	
	1	4,114	567	287	39	93
	2	4,416	2,845	338	188	92
0.71	0	3,083	528	3,083	528	
	1	4,669	1,669	952	642	80
	2	4,583	996	147	21	97
	3	3,602	1,109	142	50	96

Table 8. Diatom densities (10^3 cells cm^{-2}) in control and grazed channels for experiments with 0.10 and 0.08 nymphs cm^{-2} of periphyton cover. Numbers represent means (x) and standard deviations (s) of three replicates. Cell numbers for day 0 in grazed and control channels are from the same three replicates.

		Cells cm^{-2} of substrata			
		Control		Grazed	
Density	Day	x	s	x	s
0.10	0	4,245	841	4,245	841
	1	3,854	695	3,832	708
	2	3,652	197	3,914	616
	3	4,421	278	4,796	549
	4	4,209	580	3,756	301
	5	4,745	1,187	3,089	685
0.08	0	12,615	586	12,615	586
	3	10,293	2,422	6,602	1,655
	7	7,672	1,097	8,538	6,778
	14	8,168	687	12,687	1,014
	21	6,237	1,886	5,513	1,626
	28	6,604	2,174	7,704	2,227

of diatom cell numbers in the 0.08 experiment is due to the large variability of periphyton growth from rock to rock in Oak Creek.

Periphyton Biomass Measurements

Periphyton biomass measurements were at times highly variable but typically reflected the trends exhibited by diatom cell numbers. The ash-free dry weight (AFDW) of the initial communities in the 0.08 and 0.28 experiments averaged 51.5 and 19.0 $g \cdot m^{-2}$, respectively (Table 9). The unusually high AFDW value for the initial community in the 0.08 experiment may be a result of the large variability of periphyton distributions in natural systems. During the first week of the 0.28 experiment, periphyton biomass on grazed and control substrata averaged 31.9 $g \cdot m^{-2}$ and 30.2 $g \cdot m^{-2}$, respectively. However, after ten days of the 0.28 grazer density, the AFDW of the periphyton decreased by 73 % from the control channel value of 24.5 $g \cdot m^{-2}$ to the grazed channel value of 6.7 $g \cdot m^{-2}$. No change in AFDWs were evident at the 0.08 grazer density (Table 9). Periphyton biomass on grazed and control substrata averaged 20.7 $g \cdot m^{-2}$ and 24.5 $g \cdot m^{-2}$ respectively, for the entire experiment.

Table 9. Periphyton biomass values ($g \cdot m^{-2}$) for control and grazed substrata in the experiments with 0.28 and 0.08 nymphs cm^{-2} of periphyton cover. Values represent means (x) and standard deviations (s) of three replicates. Biomass values for day 0 in grazed and control channels are from the same three replicates.

Periphyton biomass ($g \cdot m^{-2}$)

		Control		Grazed	
Density	Day	x	s	x	s
0.28	0	19.0	3.9	19.0	3.9
	1	21.2	1.8	19.8	2.9
	3	30.6	6.8	17.1	5.6
	7	21.7	7.3	25.1	4.4
	10	24.5	6.4	6.7	2.5
	14	17.5	10.0	8.7	4.6
0.08	0	51.5	8.4	51.5	8.4
	3	31.2	5.5	19.3	1.9
	7	36.9	3.0	29.0	17.1
	14	29.6	6.1	41.1	3.5
	21	25.7	6.5	31.9	12.2
	28	27.6	9.2	38.0	12.3

Species Composition

Mayfly nymph grazing had a large impact on the epilithic diatom species composition. In the experiment with 0.28 nymphs cm^{-2}, two large diatom species, *Epithemia sorex* Kütz. (x=26.5 µm) and *Nitzschia dissipata* (Kütz.) Grun. (x=33.2 µm), together composed at least 40% of the initial diatom assemblage (Fig. 4). However, after ten days of grazing, the relative abundances of these two species and other large celled species like *Cymbella affinis* Kütz. (x=23.6 µm), *Gomphonema ventricosum* Greg. (x=42.1 µm), and *Navicula cryptocephala* var. *veneta* (Kütz.) Rabh. (x=16.8 µm), decreased considerably in relation to the control substrata. These taxa decreased by 57.1%, 88.5%, 33.0%, 79.4%, and 31.1%, respectively. On the other hand, smaller diatom species such as *Achnanthes minutissima* Kütz. (x=10.4 µm), *Nitzschia frustulum* var. *perpusilla* (Rabh.) Grun. (x=8.6 µm), *Cymbella sinuata* Greg. (x=12.2 µm), and *Achnanthes lanceolata* (Breb.) Grun. (x=16.2 µm) increased in their relative abundances by 34.3%, 65.7%, 83.2%, and 80.6%, respectively. Although relatively small in diameter, *Cocconeis placentula* var. *euglypta* (Ehr.) Cl. did not change in relative abundance.

Similar changes occurred more rapidly at greater grazer densities. In the experiment with 0.71 nymphs cm^{-2}, *N. dissipata*, *C. affinis*, and *A. minutissima* were the dominant taxa, averaging 48.2% of the control community throughout the experiment (Fig. 5). Following 24 hours of grazing, the relative abundances of the

Figure 4. Relative abundance of diatom species based on cell number for grazed (solid bar) and control (unshaded bar) substrata for five sampling dates of the experiment with 0.28 nymphs cm^{-2} of periphyton cover. The species are *E. sorex* (ES), *Nitzschia dissipata* (ND), *Cymbella affinis* (CA), *G. ventricosum* (GV), *Navicula cryptocephala* var. *veneta* (NCV), *A. minutissima* (AM), *Nitzschia frustulum* var. *perpusilla* (NFP), *Cymbella sinuata* (CS), *A. lanceolata* (AL), and *Cocconeis placentula* var. *euglypta*.

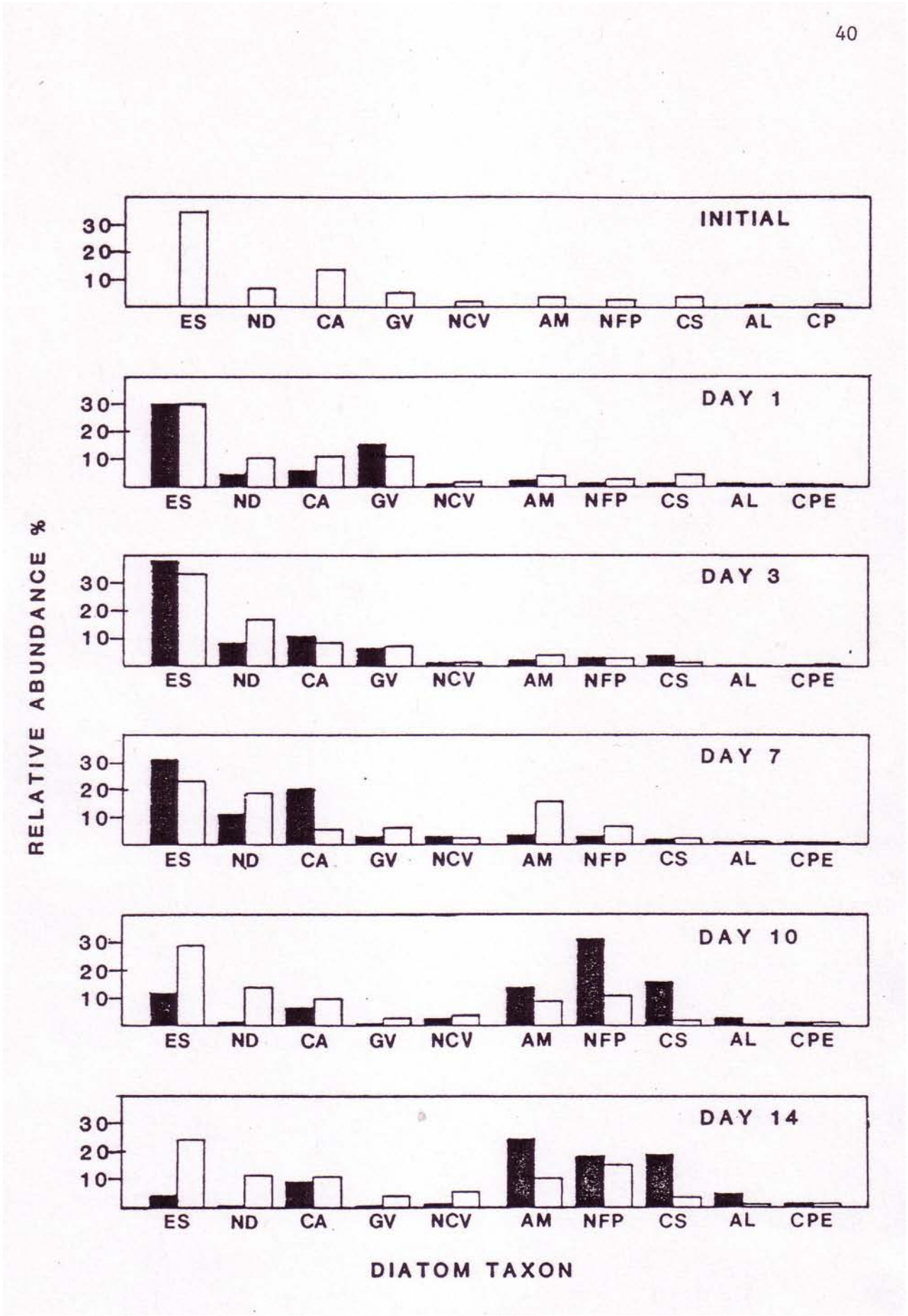
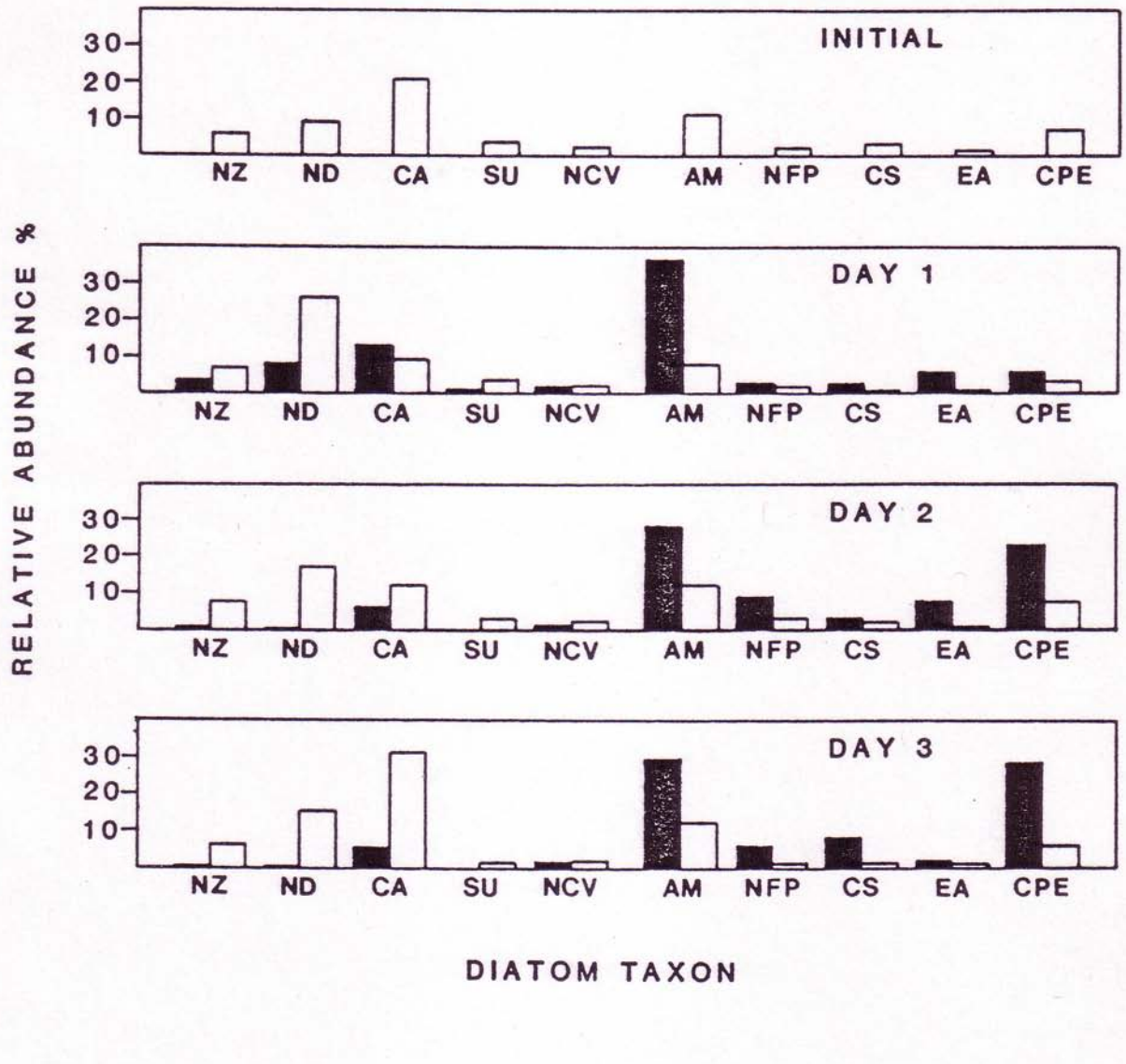

INITIAL
DAY 1
DAY 3
DAY 7
DAY 10
DAY 14
30
20
10
ES
ND
CA
GV
NCV
AM
NFP
CS
AL
CP
CPE
RELATIVE ABUNDANCE %
DIATOM TAXON

Figure 5. Relative abundance of diatom species based on cell number for grazed (solid bar) and control (unshaded bar) substrata for three sampling dates for the experiment with 0.71 nymphs cm^{-2} of periphyton cover. The species are *Navicula zanoni* (NZ), *Nitzschia dissipata* (ND), *Cymbella affinis* (CA), *S. ulna* (SU), *Navicula cryptocephala* var. *veneta* (NCV), *A. minutissima* (AM), *Nitzschia frustulum* var. *perpusilla* (NFP), *Cymbella sinuata* (CS), *E. adnata* (EA), and *Cocconeis placentula* var. *euglypta* (CPE).


INITIAL
DAY 1
DAY 2
DAY 3
30
20
10
NZ
ND
CA
SU
NCV
AM
NFP
CS
EA
CPE
RELATIVE ABUNDANCE %
DIATOM TAXON

larger species, *N. dissipata*, *Navicula zanoni* Hust. (x=34.5 μm), and *Synedra ulna* (Nitz.) Ehr. (x=86.1 μm) noticeably decreased in comparison to control substrata. Loss rates were 67.6%, 39.1%, and 85.1%, respectively. The removal of *C. affinis* was more pronounced after 48 hours, decreasing by 48%. The proportion of *A. minutissima*, *N. frustulum* var. *perpusilla*, *C. sinuata*, *C. placentula* var. *euglypta*, and *Epithemia adnata* (Kütz.) Breb. increased by 77.3%, 42.4%, 77.8%, 23.6%, and 89.1%, respectively. Once the substrata were visibly gleaned of diatoms (more than 90% diatoms removed), the mayfly nymphs decreased their activity considerably.

At the intermediate grazer density of 0.31 nymphs cm^{-2}, changes in community structure were more variable (Fig. 6). Localized grazing on some rocks resulted in decreased proportions of *C. affinis*, *N. dissipata*, *N. zanoni*, and *S. ulna* (64.3%, 59.0%, 78.2%, and 61.4%, respectively) and increased proportions of *A. minutissima*, *N. frustulum* var. *perpusilla*, *C. sinuata*, *C. placentula* var. *euglypta*, and *E. adnata* (62.7%, 93.7%, 92.9%, 57.1%, and 90.0%, respectively) after four days. However, grazing impact on the rock sampled on the fifth day was negligible and no change in community structure was evident. As demonstrated in the 0.28 experiment, extension of the trial beyond five days may have resulted in community structure alteration. At 0.08 grazer density, little or no change in diatom community structure was observed after four weeks (Fig. 7).

Although the impact of grazing on non-diatom algal components was not quantified, observations suggest that filamentous green

Figure 6. Relative abundance of diatom species based on cell number for grazed (solid bar) and control (unshaded bar) substrata for five sampling dates for the experiment with 0.31 nymphs cm^{-2} of periphyton cover. The species are *Navicula zanoni* (NZ), *Nitzschia dissipata* (ND), *Cymbella affinis* (CA), *G. ventricosum* (GV), *S. ulna* (SU), *A. minutissima* (AM), *Nitzschia frustulum* var. *perpusilla* (NFP), *Cymbella sinuata* (CS), *E. adnata* (EA), and *Cocconeis placentula* var. *euglypta* (CPE).

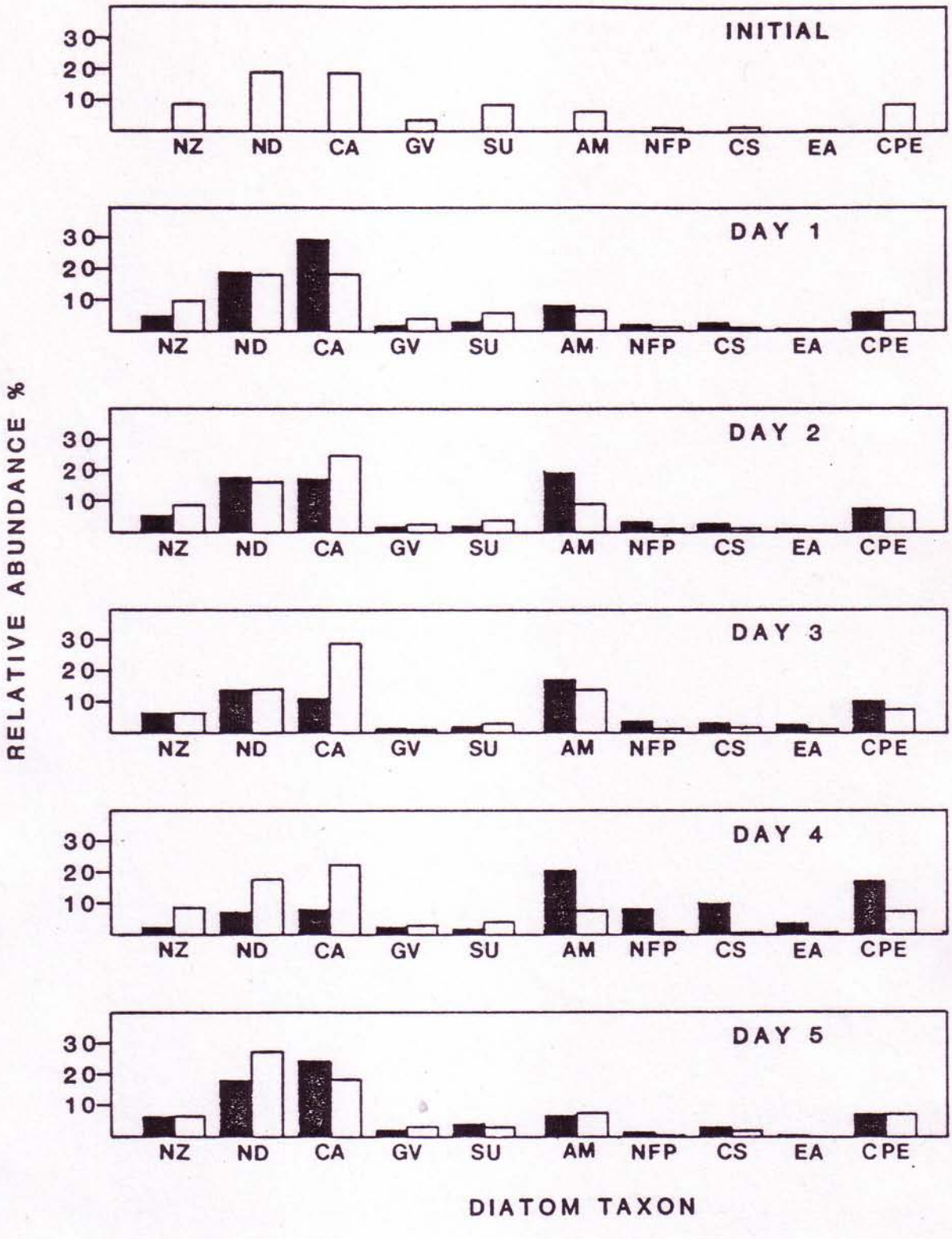
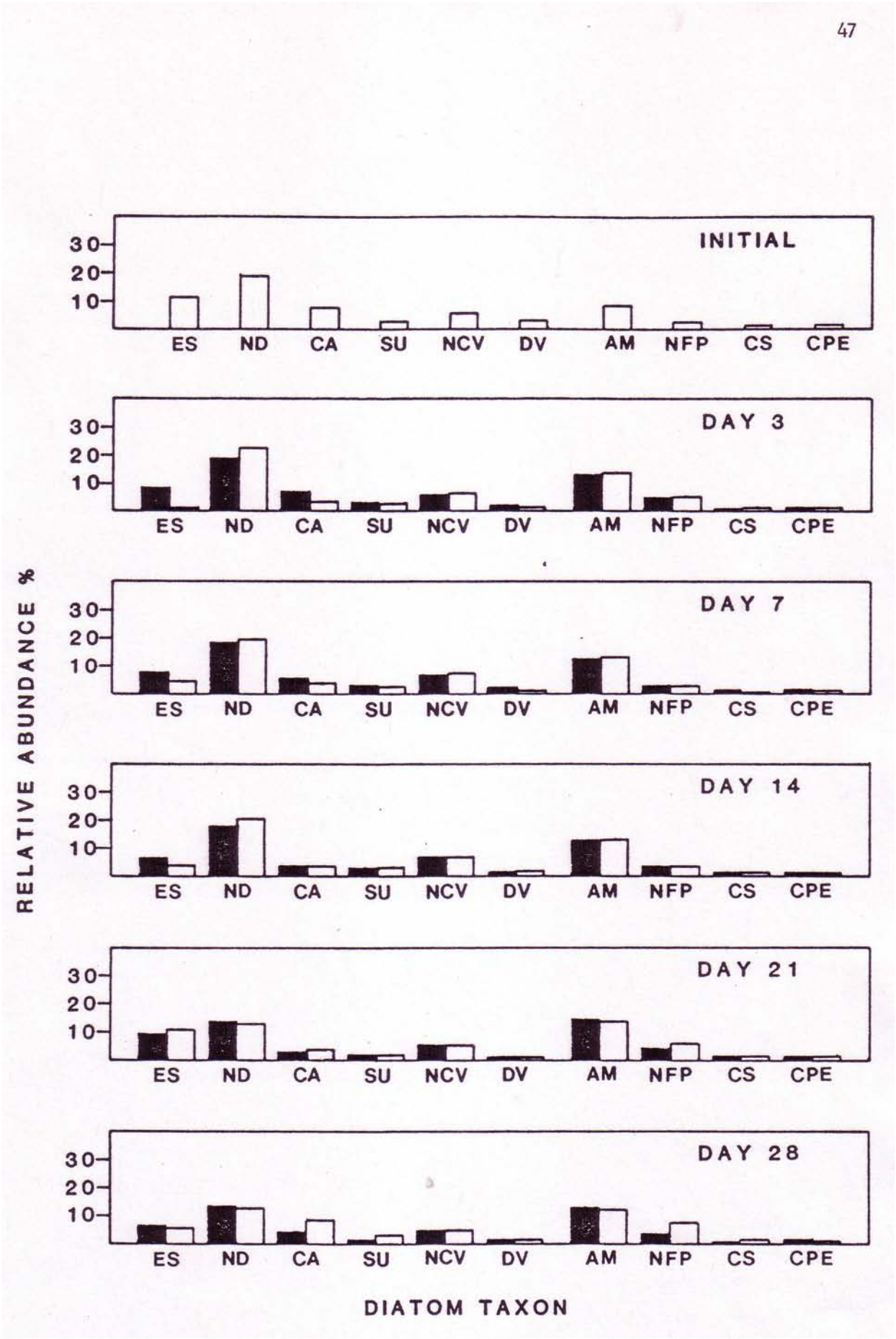

INITIAL
DAY 1
DAY 2
DAY 3
DAY 4
DAY 5
30
20
10
NZ
ND
CA
GV
SU
AM
NFP
CS
EA
CPE
RELATIVE ABUNDANCE %
DIATOM TAXON

Figure 7. Relative abundances of diatom species based on cell number for grazed (solid bar) and control (unshaded bar) substrata for five sampling dates for the experiment with 0.08 nymphs cm^{-2} of periphyton cover. The species are *E. sorex* (ES), *Nitzschia dissipata* (ND), *Cymbella affinis* (CA), *S. ulna* (SU), *Navicula cryptocephala* var. *veneta* (NCV), *D. vulgare* (DV), *A. minutissima* (AM), *Nitzschia frustulum* var. *perpusilla* (NFP), *Cymbella sinuata* (CS), and *Cocconeis placentula* var. *euglypta* (CPE).


INITIAL
DAY 3
DAY 7
DAY 14
DAY 21
DAY 28
30
20
10
ES
ND
CA
SU
NCV
DV
AM
NFP
CS
CPE
RELATIVE ABUNDANCE %
DIATOM TAXON

algae were not eaten, even after diatoms were obliterated. The mayfly nymphs did not visibly feed upon *Cladophora glomerata* and its extensive epiphytic diatom flora throughout the four day 0.49 nymphs cm^{-2} trial. In addition, the filamentous green alga, *Spirogyra* sp., was abundant in the periphyton assemblage of the experiment with 0.08 nymphs cm^{-2}, but was not found in the nymph guts throughout the four week experiment.

Diversity, Species Evenness, and Similarity Indices

Changes in diatom community structure were measured by means of diversity (H′), species evenness (J), and similarity (SIMI) indices. In the high grazer density experiments at 0.71 and 0.72 nymphs cm^{-2}, diversity decreased rapidly in 24 hours, dropping from an initial value of 2.76 to 2.31 in the 0.71 experiment and from 2.79 to 1.94 in the 0.72 experiment (Fig. 8). Similar reductions in diversity occurred by day ten in the 0.28 experiment, where control and grazed substrata H′ values were 2.43 and 2.05, respectively (Fig. 8). No change in diversity was evident in either channel during the low grazing experiment of 0.08 (Fig. 8), all values displaying < 1% variation from each other.

Species evenness (J) values range from 0 to 1, where 1 denotes the condition in which each species of a community has the same number of individuals. The evenness values of the diatom assemblages were unaffected by 0.08 and 0.28 grazer densities, all values being within 1% of each other (Fig. 9). However, slight reductions did occur in the 0.72 and 0.71 experiments (Fig. 9). For instance, evenness values for the grazed substrata of the 0.72 and 0.71 experiments averaged 5.7% and 8.3% lower than control substrata.

The similarity of community structure between grazed and ungrazed substrata was measured by the similarity index, SIMI, where 1 describes communities without any species in common and 0

Figure 8. Diatom diversity (H′) on grazed (dashed lines) and control (solid lines) substrata during experiments at 0.72, 0.71, 0.28, and 0.08 nymphs cm^{-2} of periphyton cover. Each point represents a mean of three replicates from each sampling date.

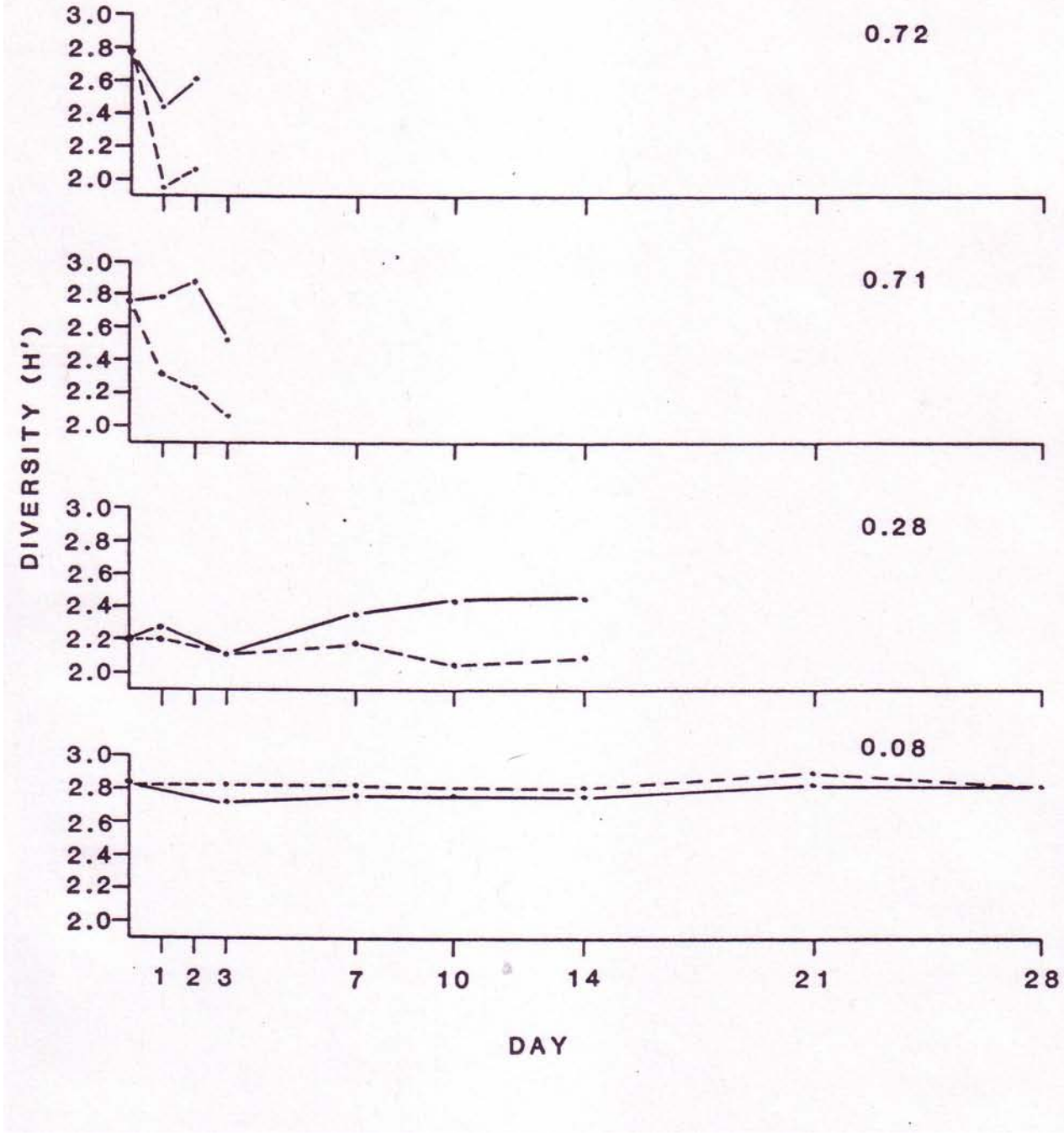
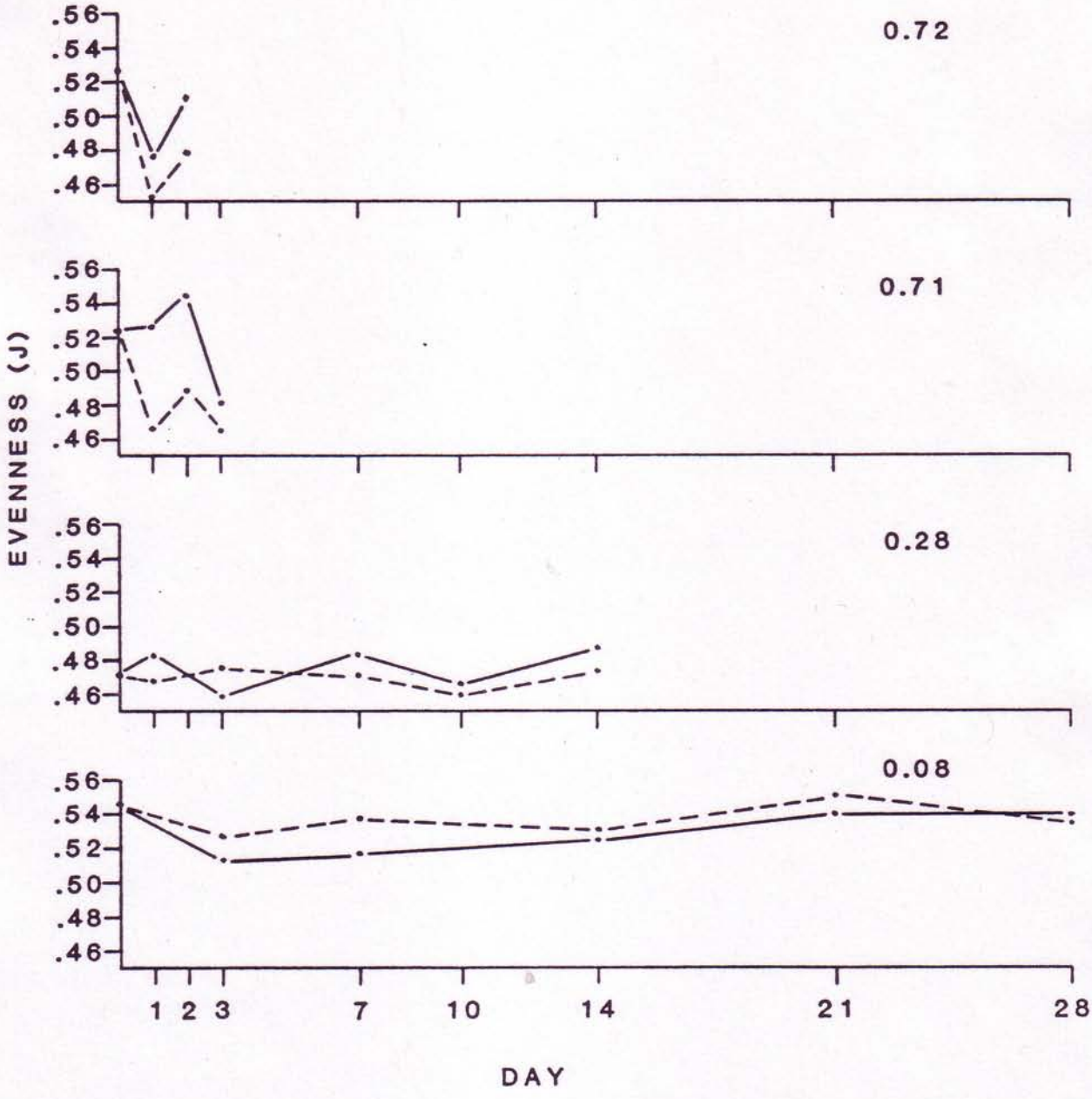
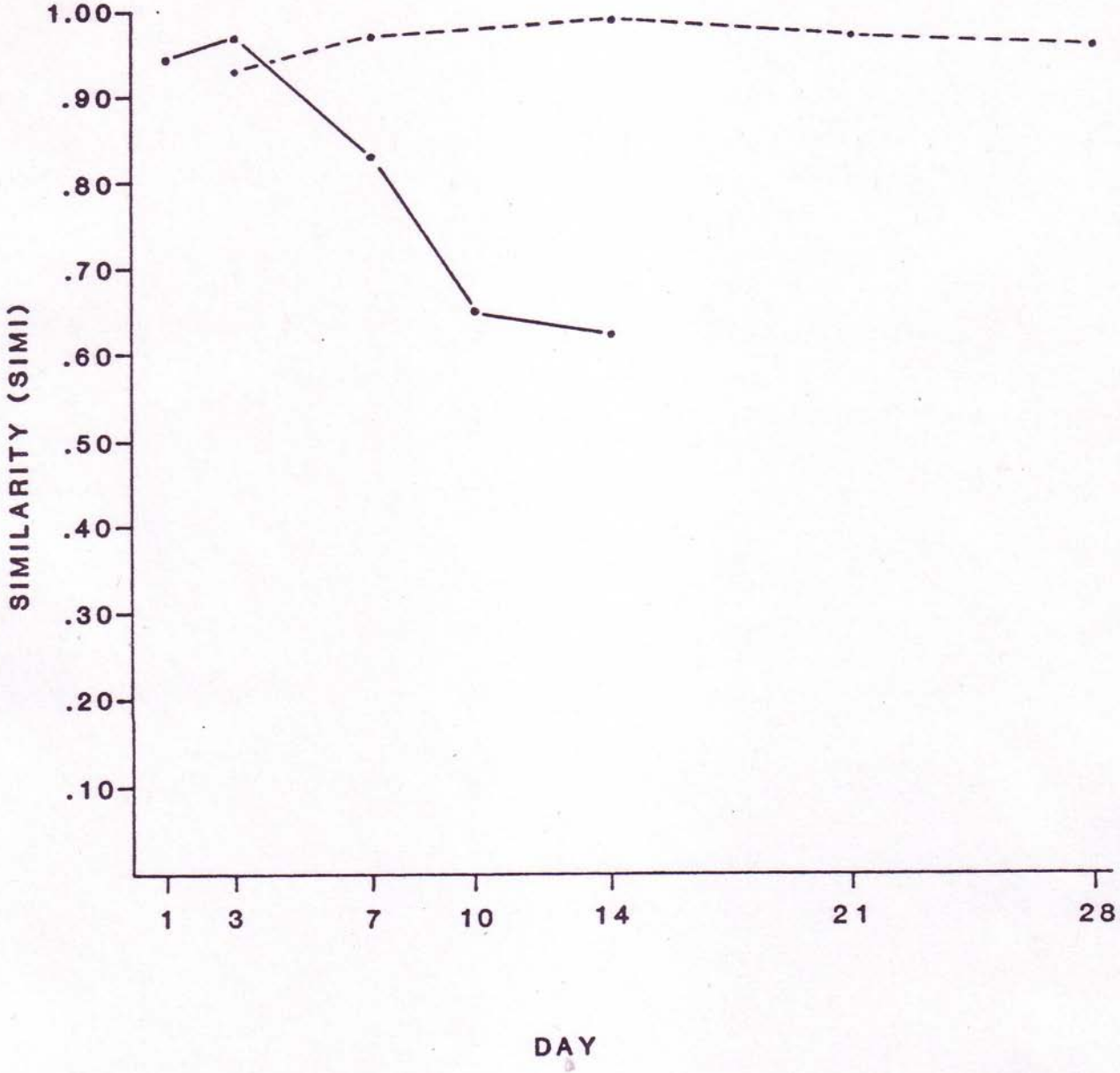

0.72
0.71
0.28
0.08
3.0
2.8
2.6
2.4
2.2
2.0
DIVERSITY (H')
1 2 3 7 10 14 21 28
DAY

Figure 9. Diatom evenness (J) on grazed (dashed lines) and control (solid lines) substrata during experiments at 0.72, 0.71, 0.28, and 0.08 nymphs cm^{-2} of periphyton cover. Each point represents a mean of three replicates from each sampling date.


0.72
0.71
0.28
0.08
EVENNESS (J)
.56
.54
.52
.50
.48
.46
1 2 3 7 10 14 21 28
DAY

represents identical communities. In the 0.28 experiment, SIMI values were initially high, greater than 0.90 (Fig. 10). However, following ten days of grazing, SIMI values decreased markedly to 0.647. SIMI values for the 0.08 grazer density were high (> 0.90) and constant throughout the experiment (Fig. 10).

Figure 10. Diatom community structure similarity (SIMI) between grazed and control substrata in the experiments with 0.28 (solid lines) and 0.08 (dashed lines) nymphs cm^{-2} of periphyton cover. Each point represents a mean of three replicates from each sampling date.


1.00
.90
.80
.70
.60
.50
.40
.30
.20
.10
SIMILARITY (SIMI)
1
3
7
10
14
21
28
DAY

Gut Content Analyses

The relative abundances of diatom species in the guts of mayfly nymphs during the Spring 1983 experiment with 0.28 nymphs cm^{-2} were mostly variable (Table 10). Since several nymphs did not have food in their guts, sample sizes were low. The proportion of a few dominant species, *Cymbella affinis, Epithemia sorex, Achnanthes lanceolata,* and *Diatoma vulgare* Bory, in the nymph guts generally reflected their relative abundances on the substrata. Although *Achnanthes minutissima* and *Nitzschia frustulum* var. *perpusilla* exhibited similar patterns through the first week, a lower proportion of these taxa were present in the gut than on the substrata during the second week. The relative abundances of *Cymbella sinuata* and *Navicula cryptocephala* var. *veneta* in the guts far exceeded the proportion of these cells on substrata during the first week of grazing. The relative abundances of the two large diatom species, *Nitzschia dissipata* and *Gomphonema ventricosum,* were slightly lower in the guts than on the substrata. The proportion of *Synedra ulna, Cocconeis placentula* var. *euglypta,* and *Nitzschia kützinghiana* ingested was highly variable. Some filamentous green algal fragments of *Chaetophora* sp. (20, 35 cells in length), *Oedogonium* sp., and *Microspora* sp., a few fragments of the blue-green alga, *Oscillatoria* sp., and *Closterium* sp., *Scenedesmus* sp., and *Coelastrum* sp. were also observed in the nymph guts.

Table 10. Relative abundances of diatom species in the guts of Heptagenia criddlei in grazed channels and on grazed and control substrata for the experiment with 0.28 nymphs cm^{-2} of periphyton cover. The numbers in the parentheses represent sample sizes.

	Cymbella affinis	Nitzschia dissipata	Epithemia sorex	Gomphonema ventricosum	Nitzschia kützinghiana	Diatoma vulgare	Synedra ulna	Navicula cryptocephala var. veneta	Achnanthes minutissima	Nitzschia frustulum var. perpusilla	Cymbella sinuata	Achnanthes lanceolata	Cocconeis placentula var. euglypta	Other diatoms
DAY 1														
gut (5)	7.1	6.6	22.8	5.7	21.0	14.3	0	8.6	4.5	1.0	9.0	0.9	1.8	2.8
grazed (3)	5.9	4.8	29.9	15.5	16.7	11.6	0	1.2	2.4	1.7	1.8	1.0	1.0	1.5
control (3)	10.9	10.5	30.1	11.1	12.3	3.4	0	2.2	4.7	2.8	4.8	0.7	0.8	1.9
DAY 3														
gut (5)	6.3	4.9	18.3	3.2	3.1	3.4	0.2	6.7	4.0	1.7	39.6	2.0	4.4	4.6
grazed (3)	10.8	8.1	38.1	7.2	11.8	6.2	1.6	1.4	2.5	3.2	3.9	0.3	0.8	3.0
control (3)	8.5	17.1	33.6	7.9	10.6	5.5	2.2	1.8	4.4	2.7	1.5	0.1	0.3	3.7
DAY 7														
gut (2)	18.0	8.5	28.2	1.7	5.8	1.2	0.2	4.2	7.5	3.4	16.0	1.3	0.5	4.9
grazed (3)	20.2	11.3	31.0	3.2	10.6	2.7	1.8	2.9	4.2	3.2	2.1	0.4	0.6	3.7
control (3)	5.8	19.3	23.4	6.5	4.5	2.1	0.3	2.1	15.6	7.0	2.5	0.8	0.5	6.2
DAY 10														
gut (3)	36.4	4.0	7.7	1.3	7.1	6.2	0.5	2.7	5.0	0.9	14.3	1.8	4.0	8.0
grazed (3)	6.7	1.6	12.4	0.7	0.4	0.4	0	3.1	14.3	32.4	16.1	3.1	0.9	1.8
control (3)	10.0	13.9	28.9	3.4	3.0	1.0	0.3	4.5	9.4	11.1	2.7	0.6	0.9	4.1
DAY 14														
gut (1)	11.7	4.3	4.8	0.2	58.6	0.2	1.7	0.7	6.5	0.4	5.2	0	1.7	3.9
grazed (3)	8.9	0.4	4.4	0.3	5.3	0.5	0.2	1.3	10.3	17.7	18.5	0	1.5	0.2
control (3)	10.4	11.6	24.4	4.0	4.3	0.5	0.2	5.5	24.4	15.0	3.4	0	1.1	2.6

CHAPTER 4

DISCUSSION

The standing crop and structure of lotic periphyton communities are determined by a number of factors including the available species pool, invasion rate, density-independent factors, parasitism, competition, and grazing pressure (Patrick 1977). However, the role of invertebrate grazing in regulating natural periphyton assemblages is not well understood. The dynamics of natural stream systems are extremely complex and it is usually difficult to differentiate the effects of grazing on periphyton *in situ* from the influence of other biological, chemical, and physical factors. Also, the generally patchy nature of periphyton distributions (Gumtow 1955; Douglas 1958; Castenholz 1961; Round 1965; Nicotri 1977; Jones 1978; Blinn et al. 1980; Tuchman and Stevenson 1980; Korte and Blinn 1983) often hinders attempts at quantification.

This study demonstrated that grazing by the mayfly nymph, *Heptagenia criddlei*, had an important effect on diatom cell densities and periphyton biomass. Diatom cell densities were linearly proportional to grazer densities. At intermediate to high grazer densities (> 0.25 nymphs cm^{-2} of periphyton cover), mayfly nymphs removed at least 90% of the diatoms by day 10. Similarly, periphyton biomass decreased by 73% during the same time period at a density of 0.28 nymphs cm^{-2}. In contrast,

experiments with grazer densities of 0.10 nymphs cm^{-2} showed no measurable change in diatom cell numbers or periphyton biomass even after four weeks of incubation. This suggests that the threshold between no impact on diatom cell numbers or periphyton biomass and a measurable change in diatom abundance or biomass lies somewhere between 0.10 and 0.25 nymphs cm^{-2}.

In extrapolating these results to densities found in Oak Creek, grazer densities were converted from nymphs cm^{-2} of periphyton cover to nymphs m^{-2} of the grazing chamber. Since periphyton distribution on natural stream substrata is typically patchy (like the periphyton distribution in my experimental channels), the conversion to nymphs m^{-2} of the grazing chamber simulates nymphs m^{-2} of a Surber collection. Accordingly, grazer densities in the experiments with 0.10 nymphs cm^{-2} of periphyton cover (260 nymphs m^{-2} of the grazing chamber) approximated mean densities of 6-10 mm *H. criddlei* nymphs in Oak Creek (215 m^{-2}). However, densities of all invertebrate species in Oak Creek were as high as 1430 m^{-2} in the 7 September 1982 Surber collections. Most of these invertebrates are periphyton grazers including small instars of *H. criddlei, Glossosoma ventrale* Banks, *Epeorus (Iron) margarita* Edmunds and Allen, a baetid species, and a few of the chironomid species. Therefore, it is conceivable that a natural grazer density of 0.28 nymphs cm^{-2} of periphyton cover (1176 invertebrates m^{-2} of the grazing chamber) is not unrealistic and that diatom assemblages are impacted in localized regions of Oak Creek. However, the grazing potential of these other invertebrate grazers is unknown and thus further study is needed.

In this study, initial periphyton assemblages were three-dimensional in construction. The three-dimensional construction of a periphyton mat results from increased competition for space and nutrients (Patrick 1977). Early successional genera, like *Achnanthes, Amphora*, and *Cocconeis*, are typically the first diatom colonizers on substrata (Hudon and Bourget 1981; Patrick 1977; Tuchman and Blinn 1979; Korte and Blinn 1983). These are small, rapidly dividing, and motile species. Cells often lie closely pressed to the substrata, forming a flat, two-dimensional community. *Achnanthes* species may also secrete short, mucilaginous peduncles to prevent "smothering" by other diatoms (Hudon and Bourget 1981). Eventually space for colonization diminishes and other diatom species that possess different adaptive strategies to evade competition become important. Species of *Synedra* and *Nitzschia* often form vertical aggregations, usually in a rosette-like fashion, by attaching to the substrate with apical mucilage pads (Round 1965; Patrick 1977; Hoagland et al. 1982). Species of *Gomphonema* and *Cymbella* usually produce short and long gelatinous stalks to project cells above the prostrate forms. Frequently, *Gomphonema* cells do not become established until a three-dimensional community is already present (Patrick 1977). Filamentous diatoms, like species of *Melosira* and *Diatoma*, may also develop, allowing large, nonmotile forms (eg. *Synedra*) to establish via entanglement (Sumner 1979). The interaction of these later successional diatom species eventually results in the development of a three-dimensional, overstory community.

This three-dimensional, overstory community was markedly altered by the grazing activity of *H. criddlei*. At intermediate to high grazer densities, nymphs changed the three-dimensional structure of the periphyton community into a two-dimensional structure characteristic of early successional seres. The diatoms composing the three-dimensional overstory of my study, such as *Nitzschia dissipata, Cymbella affinis, Gomphonema ventricosum*, and *Synedra ulna*, were highly susceptible to grazing. On the other hand, small species, like *Achnanthes minutissima, Nitzschia frustulum* var. *perpusilla*, and *Cymbella sinuata*, and prostrate forms, like *Cocconeis placentula* var. *euglypta* and *Epithemia adnata*, were less vulnerable and increased in their relative abundances. Therefore, a monolayer consisting of diatom species characteristic of early successional substrata predominated under high grazer densities.

Two hypotheses may explain the occurrence of a monolayer diatom assemblage at intermediate to high grazer densities. First, nymphs may have selected diatoms on the basis of accessibility resulting from diatom size or mode of attachment. Large, overstory species were more accessible than smaller, prostrate forms and thus were frequently removed. Second, small diatom species generally divide at a faster rate than large species (William 1964). Although the faster division rates of small diatom species may help maintain small diatom populations, large diatom species may be unable to divide at the same rate that they are being ingested.

Similar grazing patterns have been reported for snails in

laboratory streams (Sumner 1979; Gregory 1980), limpets and periwinkles in marine intertidal areas (Nicotri 1977; Hunter and Russell-Hunter 1983), and snails in lacustrine systems (Hunter 1980; Kesler 1981). For instance, the large snail, *Juga plicifera* (8-10 mm long), used by Sumner and McIntire (1982) and Gregory (1980), altered the diatom taxonomic community structure in a manner similar to *H. criddlei* in my study (i.e. grazing removed most diatoms except for small, prostrate forms such as *Achnanthes minutissima* and *Navicula minima* Grun.). However, one finding of Kesler (1981) contradicted these results. He observed that the snail, *Amnicola limosa* (Say) (2-4 mm long), significantly lowered the relative abundances of all small diatoms (< 18 µm long), except for *Cocconeis placentula*, in a Rhode Island pond. In contrast to his findings, the relative abundances of *Nitzschia frustulum* var. *perpusilla* (8.6 µm long), *Achnanthes minutissima* (10.4 µm long), *Cymbella sinuata* (12.2 µm long), and *Achnanthes lanceolata* (16.2 µm long) in my study increased considerably at high grazer densities of *Heptagenia criddlei*. Perhaps *A. limosa* is a more efficient grazer than *J. plicifera* (8-10 mm long) or *H. criddlei* (6-10 mm long) because of either its small size (2-4 mm long) or possible possession of a more efficient radula. For example, the size of particles ingested by zooplankton filter feeders is directly related to zooplankton body size (Burns 1968; Porter 1977). Possibly small molluscan species or smaller size classes of *H. criddlei* may be as efficient as *A. limosa*.

Two similarly sized diatom species of the same genus, *Epithemia sorex* (26.5 µm X 8.0 µm) and *E. adnata* (34.0 µm X 10.4

μm), appeared to possess different degrees of vulnerability to grazing. In the 0.28 experiment *E. sorex* was the dominant diatom, composing > 20% of the flora on all substrata (Fig. 4). However, within ten days, the relative abundance of this species on grazed substrata dropped nearly 60% in relation to control substrata. In contrast, the proportion of *E. adnata* on grazed subtrata increased by almost 90% after 24 hours of the 0.71 experiment (Fig. 5). Since *E. sorex* was not a dominant diatom in the other high density trials this pattern was observed to a lesser degree in those experiments. Apparently, this pattern does not result from nutrient differences between experimental channels since the proportion of both diatom species remained the same on the control substrata. Assuming that both species have similar physico-chemical requirements, it is inferred that grazing may be an important determinant for the success of either species. Possibly the slightly larger *E. adnata* has evolved a better attachment mechanism in response to grazing pressure. Nonetheless, this illustrates the subtle differences that may occur in lotic periphyton distribution and structure. Grazing, rather than a chemical or physical factor like light and temperature, may have caused the subtle difference in the relative abundances of each of these diatom species and perhaps phycologists have too often overlooked the impact that grazing has on lotic periphyton distribution and structure.

The avoidance of filamentous algae by herbivorous aquatic larvae has been documented often (Jones 1949; Brown 1961; Mecom 1972; Moore 1975, 1977; Gray and Ward 1979). Based upon casual

observations during the experiment with 0.49 nymphs cm^{-2}, *Heptagenia criddlei* also did not feed on filamentous algae. Nymphs avoided the filamentous green alga, *Cladophora glomerata*, even when it was the only food remaining. The large filaments and thick, cellulose walls of *Cladophora* (Gray and Ward 1979) probably reduce its susceptibility to the nymphs. In addition, the filamentous green alga, *Spirogyra* sp., though abundant on stream substrata, was not present in nymph guts of the experiment with 0.08 nymphs cm^{-2}. Although food was not limiting in the 0.08 trial, the nymphs probably could not manage the long, mucilaginous cells of *Spirogyra*. Small fragments of filamentous algae (e.g. species of *Chaetophora, Microspora, Oedogonium*, and *Oscillatoria*) were found in the guts of some nymphs, presumably taken up in the random scraping of the nymphs. The small size of these fragments apparently did not hinder their ingestion by the nymphs.

The avoidance of filamentous green algae despite the absence of any other food has important ecological implications. Nutrient enrichment of aquatic systems results in the gradual replacement of the diatom component with filamentous green and blue-green algae (Patrick et al. 1969; Schindler et al. 1973). Increased nutrient input into Oak Creek could have a significant effect on *Heptagenia criddlei* and possibly other aquatic inverterbrates, thereby upsetting the existing food chain.

Most studies examining the impact of invertebrate grazing on species diversity have been done in marine intertidal systems (Dayton 1971, 1975; Kitching and Ebling 1961,1967; Paine and Vadas 1969; Vadas 1968; Lubchenco 1978; Lubchenco and Gaines 1981;

Gaines and Lubchenco 1982). These studies have documented both the decrease and increase of algal species diversity because of invertebrate grazing. The effect of invertebrate grazing on species diversity in marine intertidal zones depends on several factors including herbivore food preferences, competitive ability of the plants, and grazing intensity (Lubchenco 1978). For instance, a herbivore that prefers to feed on competitively dominant taxa may, depending upon grazer densities, alter the species diversity in three different ways. First, studies have shown that at low grazer densities, the competitively dominant food items continued to outcompete other taxa (competitive exclusion), reducing species diversity (Paine 1966, 1971, 1974; Paine and Vadas 1969; Vadas 1968; Lubchenco 1978). Second, high grazer densities resulted in the overgrazing of all taxa, whether competitively dominant or inferior, reducing species diversity again (Dayton 1971, 1975; Kitching and Ebling 1961, 1967; Paine and Vadas 1969). Finally, intermediate grazer densities increased species diversity by removing the competitively dominant food and permitting other species to establish themselves (Vadas 1968; Paine and Vadas 1969; Dayton 1975; Lubchenco 1978).

Since most macroinvertebrates in lotic systems appear to be generalists in their feeding (Cummins 1973), the degree of an alga's vulnerability to grazing in lotic systems may be substituted for "herbivore food preferences" in marine intertidal zones (Sumner 1979). Sumner and McIntire (1982) reported that in a laboratory stream channel dominated by the large, overstory species (competitively dominant), *Synedra ulna, Melosira varians,*

and *Nitzschia linearis*, grazing by a snail increased species diversity. In contrast, species diversity decreased in other channels where small, non-filamentous taxa dominated. Patrick (based on unpublished laboratory data by K. Roop 1970) observed that the snail, *Physa heterostropha* Say, removed all the diatoms in a laboratory stream except for the grazer tolerant *Cocconeis placentula*; thus, species diversity decreased. Ironically, the grazing activity of the caddisfly larva, *Lepidostomota* sp., and the oligochaete, *Stylaria lacustris*, in a small Canadian stream increased species diversity by preventing *C. placentula* (competitively dominant) from dominating (Dickman and Gochnauer 1978).

Although large, overstory diatom species dominated the initial diatom assemblages in my study, species diversity did not increase at any of the grazer densities (Fig. 8). Possibly grazer densities were either too low or high; thus, a longer experiment at a moderate grazer density (between 0.10 and 0.20) might result in greater species diversity. However, a better understanding of species diversity changes is contingent upon gaining more information on such important variables as diatom species competitve abilities (Lubchenco 1978).

In my study, species diversity and evenness decreased rapidly at high grazer densities (> 0.70) (Fig.8). Similar changes in species diversity occurred after a longer time interval in the 0.28 experiment. Reduction in diatom diversity in all these experiments coincided with the removal of more than 90% of the diatoms from the substrata. Apparently, the larger, dominant

species were selected by the nymphs; thus, species diversity decreased.

The structural similarity index (SIMI) comparing grazed and control diatom communities was sensitive to changes caused by grazing. SIMI values for substrata of the 0.08 experiment indicated that there was no apparent difference between grazed and control diatom assemblages (Fig. 10). Correspondingly, SIMI values remained high through the first three days of the 0.28 experiment. However, following one week and more strikingly after ten days, the similarity of diatom community structure between grazed and control channels decreased. Diatoms more susceptible to grazing were replaced in relative abundance by the less vulnerable taxa.

Generally, the relative abundance of individual diatom species in the mayfly nymph guts of the 0.28 experiment depended on each species' vulnerability to grazing (Table 10). The relative abundance in nymph guts of species that are susceptible to grazing, like *Cymbella affinis*, *Epithemia sorex*, and *Diatoma vulgare*, approximated their relative abundances on grazed and control substrata. The ingestion of these species was unimpeded because of their large size and mode of attachment (i.e. *C. affinis* produces gelatinous stalks and *D. vulgare* forms filamentous colonies). The proportion of grazing tolerant species like *Achnanthes minutissima*, *A. lanceolata*, and *Nitzschia frustulum* var. *perpusilla* in mayfly guts and on grazed and control substrata was similar through the first week of the experiment. Perhaps some proportion of these cells were positioned in the

three-dimensional overstory and thus, were accessible to the grazers. However, once the three-dimensional community was removed (after one week), small cells lying close to the substrata became less accessible and increased in their relative abundances.

The relative abundances of other diatom species in nymph guts exhibited contradictory patterns. The relative abundances of *Navicula cryptocephala* var. *veneta* and the grazing tolerant, *Cymbella sinuata*, were greater in the guts than on the substrata. Also, the proportion of the two highly susceptible diatom species, *Nitzschia dissipata* and *Gomphonema ventricosum*, was slightly lower in the mayfly guts than on grazed and control substrata. Moreover, the proportion of the grazing vulnerable *Synedra ulna* and *Nitzschia kützinghiana* and the grazing tolerant, *Cocconeis placentula* var. *euglypta*, did not show any consistent pattern. Possibly, sample sizes were too small to obtain accurate results.

The design of my experiments was based upon the assumption that all the substrata (initial, grazed, and control) in a specific experiment were equally colonized by periphyton. However, periphyton colonization was typically uneven, sometimes varying widely from rock to rock and even at different points on a single rock. For example, the initial biomass of periphyton in the 0.08 experiment (Table 9) was considerably higher than for any of the grazed or control substrata throughout the experiment. Similarly, diatom densities fluctuated widely from rock to rock in both grazed and control channels (Table 8). These differences in periphytic growth from rock to rock are difficult to control

because of the many, often subtle, factors that regulate growth and distribution. Consequently, experimental manipulations involving periphyton are difficult and this may explain the dearth of studies exploring grazing dynamics in streams.

Further experimental problems in my study concerned the length of grazing periods and replenishment of dissolved nutrients. Most trials were less than one week in duration. This was partly due to the rapid impact of high grazer densities on the periphyton where, typically, most of the periphyton was removed within one or two days. The ensuing rise in nymph mortality and change in nymph behavior necessitated termination of these trials after most of the diatoms (> 90%) were removed. In addition, the closed nature of the laboratory stream prevented the continual replenishment of nutrients characteristic of natural streams. Moreover, it has been demonstrated that toxic trace metals become more soluble with time in closed laboratory streams and thus, inhibiting diatom growth and promoting green and blue-green algal growth (Patrick, et al. 1969). These problems were partly solved by exchanging fresh Oak Creek water every third day in the longer and improved experiments of Spring 1983 (0.28 and 0.08). Although this did not entirely simulate the natural situation, the periphyton appeared to maintain its integrity throughout these longer experiments.

My study represents a preliminary step towards understanding grazing dynamics in a stream ecosystem. Further examination of the many individual components (ie. grazers, predators, food, physical factors) that interact to regulate grazing in lotic

systems is necessary. In addition, there is a need for a greater understanding of the life history and ecology of *Heptagenia criddlei* and of the role of smaller nymphs (< 5 mm) in regulating periphyton community structure. This study demonstrates the considerable impact that one grazer may impart and justifies further exploration of the role of grazing in stream dynamics.

CHAPTER 5

SUMMARY

Stream diatom community structure was examined in a laboratory stream under different grazer densities of the mayfly nymph, *Heptagenia criddlei*. Grazer densities ranged from 0.08 to 1.50 nymphs cm^{-2} of periphyton cover in 14 experiments.

1. Diatom cell densities were linearly proportional to grazer densities. High grazer densities of the mayfly nymph (> 0.40 nymphs cm^{-2}) removed more than 90% of the diatoms within four days. Similar reductions in diatom densities occurred by day ten at an intermediate grazer density (0.28 nymphs cm^{-2}). At low grazer densities (< 0.10 nymphs cm^{-2}), little, if any, change in diatom densities was observed. Apparently, a threshold grazing pressure lies somewhere between 0.10 and 0.25 nymphs cm^{-2}, where densities > 0.25 result in considerable removal of diatoms after one week and densities < 0.10 result in little, if any, change in periphyton abundance.

2. The pattern of change in periphyton biomass was similar to what occurred with diatom cell densities. Periphyton biomass decreased by 73% by day ten in the experiment with 0.28 nymphs cm^{-2} whereas little change occurred throughout the experiment with 0.08 nymphs cm^{-2}.

3. Intermediate to high grazer densities had a large impact on the diatom physical structure and species composition. The three-dimensional overstory of the diatom assemblage was modified into a two-dimensional assemblage similar to early successional communities. The diatoms composing the three-dimensional overstory, such as *Nitzschia dissipata, Cymbella affinis, Gomphonema ventricosum*, and *Synedra ulna*, were highly susceptible to grazing, probably because of their large size or upright mode of attachment to the substrata. On the other hand, small species such as, *Achnanthes minutissima, Nitzschia frustulum* var. *perpusilla*, and *Cymbella sinuata*, and compressed, tightly affixing species like *Cocconeis placentula* var. *euglypta* and *Epithemia adnata* were less vulnerable and their relative abundances increased. Therefore, size and mode of attachment appear to be critical features in determining a diatom species' susceptibility to grazing pressure.

4. Diatom diversity (H') and evenness (J) decreased at high grazer densities (> 0.70). Similar reductions in diatom diversity occurred after a longer time period (10 days) at intermediate grazer densities. No change in diatom diversity and evenness was evident at low grazer densities (< 0.10).

5. The structural similarity index (SIMI) values for the experiment with 0.08 nymphs cm^{-2} were high (> 0.90) and constant throughout the experiment. In the experiment with 0.28 nymphs

cm^{-2}, SIMI values were initially high (> 0.90), but gradually decreased after one week of grazing.

6. Two similarly sized species of the same genus, *Epithemia sorex* and *E. adnata*, seemed to display different degrees of susceptibility to grazing. *Epithemia adnata* escaped grazing more readily than *E. sorex* through an attribute that needs to be determined. Assuming that both species have similar physico-chemical requirements, grazing may be an important determinant for the success of either species.

7. Casual observations indicate that the mayfly nymphs did not feed on the filamentous green algae, *Cladophora glomerata* and *Spirogyra* sp.

LITERATURE CITED

American Public Health Association. 1971. *Standard Methods for the Examination of Water and Wastewater.* 13th ed. Washington, D.C., American Public Health Association, 874 pp.

Behning, A. 1928. Das Lebender Wolga. Zugleich eine Einfuhrung in de Fluss-Biologie. *In* Thienemann, A. (ed.), *Die Binnengewasser V.*, Stuttgart. 162 pp.

Blinn, D.W., A. Fredericksen, and V. Korte. 1980. Colonization rates and community structure of diatoms on three different rock substrata in a lotic system. *Br. Phycol. J.* 15: 303-310.

Bohle, V.H.W. 1978. Beziehungen zwischen dem Nahrungsangebot, der Drift und der raumlichen Verteilung bei larven von *Baetis rhodani* (Pictet) (Ephemeroptera: Baetidae). *Arch. Hydrobiol.* 84: 500-525.

Bowker, D.W., M.T. Wareham, and M.A. Learner. 1983. The selection and ingestion of epilithic algae by *Nais elinguis* (Oligochaeta: Naididae). *Hydrobiologia* 98: 171-178.

Brown, D.S. 1961. The food of the larvae of *Chloeon dipterum* L. and *Baetis rhodani* (Pictet) (Insecta, Ephemeroptera). *J. Anim. Ecol.* 30: 55-75.

Burns, C.W. 1968. The relationship between body size of filter-feeding cladocera and the maximum size of particle ingested. *Limnol. Oceanogr.* 13: 675-678.

Butcher, R.W. 1947. Studies on the ecology of river, VII. The algae of organically enriched waters. *J. Ecol.* 35: 186-191.

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

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

Chapman, D.W. and R.L. Demory. 1963. Seasonal changes in the food ingested by aquatic insect larvae and nymphs in two Oregon streams. *Ecology* 44: 140-146.

Coffman, W.P., K.W. Cummins, and J.C. Wuycheck. 1971. Energy flow in a woodland stream ecosystem: I. Tissue support trophic structure of the autumnal community. *Arch. Hydrobiol.* 68: 232-276.

Collins, G.B. and C.I. Weber. 1978. Phycoperiphyton (algae) as indicators of water quality. *Trans. Amer. Micros. Soc.* 97: 36-43.

Collins, N.C., R. Mitchell, and R.G. Wiegert. 1976. Functional analysis of a thermal spring ecosystem, with an evaluation of the role of consumers. *Ecology* 57: 1221-1232.

Cummins, K.W. 1973. Trophic relations of aquatic insects. *Ann. Rev. Ent.* 18: 183-206.

Cummins, K.W. 1974. Structure and function of stream ecosystems. *BioScience* 24: 631-641.

Cummins, K.W. and M.J. Klug. 1979. Feeding ecology of stream invertebrates. *Ann. Rev. Ecol. Syst.* 10: 147-172.

Dayton, P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351-389.

Dayton, P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* 45: 137-159.

Dickman, M.D. and M.B. Gochnauer. 1978. A scanning electron microscopic study of periphyton colonization in a small stream subjected to sodium chloride addition. *Verh. Internat. Verein. Limnol.* 20: 1738-1743.

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

Eichenberger, E. and A. Schlatter. 1978. Effect of herbivorous insects on the production of benthic algal vegetation in outdoor channels. *Verh. Internat. Verein. Limnol.* 20: 1806-1810.

Elwood, J.W. and D.J. Nelson. 1972. Periphyton production and grazing rates in a stream measured with a ^{32}P material balance method. *Oikos* 23: 295-303.

Felfoldy, L.J.M. 1961. Effect of temperature on the photosynthesis of a natural diatom population. *Ann. Biol. Tihany* 28: 95-98.

Foerster, J.W. and H.E. Schlichting, Jr. 1965. Phycoperiphyton in an oligotrophic lake. *Trans. Amer. Micros. Soc.* 84: 485-502.

Gaines, S.D. and J. Lubchenco. 1982. A unified approach to marine plant-herbivore interactions. II. Biogeography. *Ann. Rev. Ecol. Syst.* 13: 111-138.

Gray, L.J. and J.V. Ward. 1979. Food habits of stream benthos at sites of differing food availability. *Am. Midl. Nat.* 102: 157-167.

Gregory, S.V. 1980. Effects of light, nutrients, and grazing on periphyton communities in streams. Ph.D. Thesis. Oregon State University, Corvallis, Oregon. 154 pp.

Gumtow, R.B. 1955. An investigation of the periphyton of a riffle of the West Gallatin River, Montana. *Trans. Amer. Micros. Soc.* 84: 485-502.

Hoagland, K.D., S.C. Roemer, and J.R. Rosowski. 1982. Colonization and community structure of two periphyton assemblages, with emphasis on the diatoms (Bacillariophyceae). *Amer. J. Bot.* 69: 188-213.

Horner, R.R. and E.B. Welch. 1981. Stream periphyton development in relation to current velocity and nutrients. *Can. J. Fish. Aquat. Sci.* 38: 449-457.

Hudon, C. and E. Bourget. 1981. Initial colonization of artificial substrate: community development and structure studied by scanning electron microscopy. *Can. J. Fish. Aquat. Sci.* 38: 1371-1384.

Hunter, R.D. 1980. Effects of grazing on the quantity and quality of freshwater Aufwuchs. *Hydrobiologia* 69: 251-259.

Hunter, R.D. and W.D. Russell-Hunter. 1983. Bioenergetic and community changes in intertidal Aufwuchs grazed by *Littorina littorea*. *Ecology* 64: 761-769.

Hynes, H.B.N. 1941. The taxonomy and ecology of the nymphs of British Plecoptera, with notes on the adults and eggs. *Trans. R. Ent. Soc. Lond.* 91: 459-557.

Hynes, H.B.N. 1961. The invertebrate fauna of a Welsh mountain stream. *Arch. Hydrobiol.* 57: 344-388.

Hynes, H.B.N. 1970. *The Ecology of Running Waters*. University of Toronto Press, Toronto, 555 pp.

Ide, F.P. 1967. Effects of forest spraying with DDT on aquatic insects of salmon streams in New Brunswick. *J. Fish. Res. Bd. Can.* 24: 769-805.

Jones, J.G. 1978. Spacial variation in epilithic algae in a stony stream (Wilfin Beck) with special reference to *Cocconeis placentula*. *Freshwat. Biol.* 8: 539-546.

Jones, J.R.E. 1949. An ecological study of thr River Rheidol, North Cardiganshire, Wales. *J. Anim. Ecol.* 18: 67-88.

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

Kesler, D.H. 1981. Periphyton grazing by *Amnicola limosa*: An enclosure-exclosure experiment. *J. Freshwat. Ecol.* 1: 51-59.

Kitching, J.A. and F.J. Ebling. 1961. The ecology of Lough Ine. XI. The control of algae by *Paracentrotus lividus* (Echinoidea). *J. Anim. Ecol.* 30: 373-383.

Kitching, J.A. and F.J. Ebling. 1967. Ecological studies of Lough Ine. *Advance. Ecol. Res.* 4: 198-291.

Korte, V.L. and D.W. Blinn. 1983. Diatom colonization on artificial substrata in pool and riffle zones studied by light and scanning electron microscopy. *J. Phycol.* 19: 332-341.

Koslucher, D.G. and G.W. Minshall. 1973. Food habits of some benthic invertebrates in a northern cool-desert stream (Deep Creek, Curlew Valley, Idaho-Utah). *Trans. Amer. Micros. Soc.* 92: 441-452.

Lamberti, G.A. and V.H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. *Ecology* 64: 1124-1135.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Amer. Natur.* 112: 23-37.

Lubchenco, J. and S.D. Gaines. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Ann. Rev. Ecol. Syst.* 12: 405-437.

Mann, K.H. 1975. Patterns of energy flow. *In* B.A. Whitton (ed.). *River Ecology*. University of California Press, Berkeley, California, 724 pp.

McIntire, C.D. 1973. Periphyton dynamics in laboratory stream: a simulation model and its implications. *Ecol. Monogr.* 43: 399-420.

McIntire, C.D. 1975. Periphyton assemblages in laboratory streams. *In* B.A. Whitton (ed.). *River Ecology*. University of California Press, Berkeley, California, 724 pp.

McIntire, C.D. and J.A. Colby. 1978. A hierarchical model of lotic ecosystems. *Ecol. Monogr.* 48: 167-190.

Mecom, J.O. 1972. Feeding habits of Trichoptera in a mountain stream. *Oikos* 23: 401-407.

Mecom, J.O. and K.W. Cummins. 1964. A preliminary study of the trophic relationships of the larvae of *Brachycentrus americanus* (Banks) (Trichoptera: Brachycentridae). *Trans. Amer. Micros. Soc.* 83: 233-243.

Moore, J.W. 1975. The role of algae in the diet of *Asellus aquaticus* L. and *Gammarus pulex* L. *J. Anim. Ecol.* 44: 719-730.

Moore, J.W. 1977. Some factors affecting algal consumption in subarctic Ephemeroptera, Plecoptera, and Simuliidae. *Oecologia* 27: 261-273.

Moore, J.W. 1978. Seasonal succession of algae in rivers. III. Examples from the Wyle, an eutrophic farmland river. *Arch. Hydrobiol.* 83: 367-376.

Moss, B. 1973. The influence of environmental factors in the distribution of freshwater algae: An experimental study. II. The role of pH and carbon dioxide-bicarbonate system. *J. Ecol.* 61: 157-177.

Munteanu, N. and E.J. Maly. 1981. The effect of current on the distribution of diatoms settling on submerged glass slides. *Hydrobiologia* 78: 273-282.

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

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

Paine, R.T. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. *Ecology* 52: 1096-1106.

Paine, R.T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15: 93-120.

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

Patrick, R. 1970. Benthic stream communities. *Am. Sci.* 58: 546-549.

Patrick, R. 1977. Ecology of Freshwater Diatoms - Diatom Communities. *In* D. Werner (ed.). *The Biology of Diatoms.* University of California Press, Berkeley, California, 498 pp.

Patrick, R., B. Crum, and J. Coles. 1969. Temperature and manganese as determining factors in the presence of diatom or blue-green algal floras in streams. *Proc. natn. Acad. Sci. U.S.A.* 64: 472-478.

Pielou, E.C. 1969. *An Introduction to Mathematical Ecology.* Wiley-Interscience, New York, 286 pp.

Porter, K.G. 1977. The plant-animal interface in freshwater ecosystems. *Am. Sci.* 65: 159-170.

Round, F.E. 1965. *The Biology of Algae*. Pitman Press, London, 269 pp.

Schindler, D.W., H. Kling, R.V. Schmidt, J. Prokopowich, V.E. Frost, R.L. Reid, and M. Capel. 1973. Eutrophication of Lake 227 by addition of phosphate and nitrate: the second, third and fourth years of enrichment 1970, 1971, 1972. *J. Fish. Res. Bot. Can.* 30: 1415-1440.

Stockner, J.G. 1971. Ecological energetics and natural history of *Hedriodiscus truquii* (Diptera) in two thermal spring communities. *J. Fish. Res. Bd. Can.* 28: 73-94.

Stockner, J.G. and K.R.S. Shortreed. 1976. Autotrophic production in Carnation Creek, a coastal rainforest stream on Vancouver Island, British Columbia. *J. Fish. Res. Bd. Can. 33: 1553-1563.*

Sullivan, M.J. 1975. Diatom communities for a Delaware salt marsh. *J. Phycol.* 11: 384-390.

Sullivan, M.J. 1977. Edaphic diatom communities associated with *Spartina alterniflora* and *S. paterns* in New Jersey. *Hydrobiologia* 52: 207-211.

Sumner, W.T. 1979. Grazer-periphyton interactions in laboratory streams. M.S. Thesis. Oregon State University, Corvallis, Oregon. 99 pp.

Sumner, W.T. and C.D. McIntire. 1982. Grazer-periphyton interactions in laboratory streams. *Arch. Hydrobiol.* 93: 135-157.

Tuchman, M. and D.W. Blinn. 1979. Comparison of attached algal communities on natural and artificial substrata along a thermal gradient. *Br. Phycol. J.* 14: 243-254.

Tuchman, M.L. and R.J. Stevenson. 1980. Comparison of clay tile, sterilized rock, and natural substrate diatom communities in a small stream in southeastern Michigan, USA. *Hydrobiologia* 75: 73-79.

Vadas, R.L. 1968. The ecology of *Agarum* and the kelp bed community. Ph.D. Thesis. University of Washington. 280 pp.

Van der Werff, A. 1953. A new method of concentrating and cleaning diatoms and other organisms. *Verh. Internat. Verein. Limnol.* 12: 276-277.

Warren, C.E. and G.E. Davis. 1971. Laboratory stream research: Objectives, possibilities, and constraints. *Ann. Rev. Ecol. Syst.* 2: 111-144.

Whitford, L.A. 1960. The current effect and growth of freshwater algae. *Trans. Amer. Micros. Soc.* 79: 302-309.

Williams, R.B. 1964. Division rates of salt marsh diatoms in relation to salinity and cell size. *Ecology* 45: 877-880.

Young, O.W. 1945. Limnological investigation of periphyton in Douglas Lake, Michigan. *Trans. Amer. Micros. Soc.* 65: 1-20.