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The taxonomic composition of benthic algal assemblages, which form the basis of the food web in many streams, is determined in part by herbivory and nutrient concentrations. The effects of grazing and nitrogen enrichment on the taxonomic structure of periphyton were investigated in two experiments, one in laboratory streams and the other in a natural stream.

Effects of grazing by the pleurocerid snail *Juga silicula* (Gould) and larvae of the limnephilid caddisfly *Dicosmoecus gilvipes* (Hagen) were investigated in a 50-day laboratory experiment. Grazing by *Dicosmoecus* at high densities (50 m^{-2}) produced assemblages with a relatively high biomass and dominated by the long, linear diatom *Synedra ulna*, and a group of small, prostrate diatoms (*Achnanthes minutissima*, *Navicula arvensis*, *Navicula minima*, and *Nitzschia fonticola*). Algal assemblages in streams grazed by *Juga* at high densities (500 m^{-2}) were characterized by low biomass and by high abundances of the cyanobacterium *Phormidium tenue* and basal cells of the heterotrichous chlorophyte *Stigeoclonium tenue*. Effects of concurrent grazing by the dissimilar

herbivores were not additive, and produced algal assemblages intermediate in biomass and of distinct taxonomic composition. Algal assemblages in mixed-grazer streams were characterized by intermediate abundances of basal cells of *S. tenue*. Assemblages in high density (50 caddisflies m^{-2} and 500 snails m^{-2}) mixed-grazer streams were dominated to a greater degree by prostrate diatoms than in intermediate density (25 caddisflies m^{-2} and 250 snails m^{-2}) mixed-grazer streams. Cobble-sized (22 x 22 x 4 cm) channel-spanning substrate blocks in intermediate density mixed-grazer streams increased substrate heterogeneity and influenced the effects of the herbivores on periphyton succession. The top substrates in these streams were characterized by high algal biomass, and algal assemblages were dominated by large, linear diatoms and by filaments of *S. tenue* and *Ulothrix*. The recessed substrates also possessed high biomass but had greater abundances of the prostrate diatoms, the filamentous cyanobacterium *Oscillatoria agardhii*, and basal cells of *S. tenue*.

Effects of nitrogen enrichment on periphyton were investigated by adding ammonium sulfate to Lookout Creek (Oregon) in the summers of 1991 and 1992. A maximum concentration of 90 μg NH_4^+-N l^{-1} was achieved in the enriched section, whereas NH_4^+-N concentrations in the non-enriched section were low (1-6 μg l^{-1}). The taxonomic composition of periphyton in the enriched section was conspicuously different from the composition of algal assemblages in the non-enriched section. Assemblages in the non-enriched section in late summer were dominated by the large diatom *Epithemia hyndmanii*, which contains nitrogen-fixing cyanobacterial endosymbionts, and by nitrogen-fixing heterocystous cyanobacteria (*Calothrix fusca*, *Calothrix* sp. 2, and *Nostoc* sp. 1). Assemblages in the enriched section in late summer were characterized by the diatoms

Rhoicosphenia curvata, *Gomphonema rhombicum*, *Gomphonema dichotomum*, and *Nitzschia oregona*, and the filamentous cyanobacterium, *Phormidium tenue*, which are often found in nitrogen-rich aquatic ecosystems.

The results of the two experiments described here demonstrate that both grazing and nutrient enrichment result in significant changes in the taxonomic composition of algal assemblages which may in turn affect the abundance and distribution of consumer organisms at all trophic levels.

Effects of Grazing and Nitrogen Enrichment on the Taxonomic Structure of Periphyton Assemblages in Lotic Ecosystems

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1. INTRODUCTION

Autotrophy by benthic algae is a significant part of primary production in many aquatic ecosystems. This is especially true in mid-order lotic ecosystems, where light is not limiting, and primary production may exceed community respiration (Minshall 1978, Vannote *et al.* 1980). Therefore, periphyton constitutes an important food resource for consumer organisms, and high turnover rates of algae imply that small standing crops can support a relatively high biomass of consumers (McIntire 1973). The quality of the algal food resource, and hence its capacity to support secondary production, depends in part on the taxonomic composition of the algal assemblage (Gregory 1983).

Many abiotic and biotic factors influence the taxonomic composition of periphyton in stream ecosystems. Abiotic factors include nutrients (Borchardt 1996), substrate composition (Burkholder 1996), substrate heterogeneity (DeNicola and McIntire 1990a), irradiance (Hill 1996), current velocity and shear stress (Stevenson 1996), timing and frequency of disturbance (Peterson 1996), and temperature (DeNicola 1996). Biotic factors include herbivory (Steinman 1996), algal export (Stevenson 1996), and autogenic changes in algal composition associated with competition and succession (McCormick 1996). These factors do not act alone, but in concert, and many studies have found interaction effects in how these various factors influence algal taxonomic composition (cf. Steinman *et al.* 1989, DeNicola and McIntire 1990b, Rosemond *et al.* 1993).

The general objectives of this thesis were to investigate how the taxonomic composition of benthic algae in lotic ecosystems was affected by concurrent grazing by dissimilar herbivores, by the interaction between concurrent grazing and substrate heterogeneity, and by nitrogen enrichment. Streams in the Pacific Northwest are often nitrogen-limited (Borchardt 1996), and two co-occurring dissimilar invertebrate grazers, the snail *Juga silicula* (Gould) and larvae of the caddisfly *Dicosmoecus gilvipes* (Hagen), are often the dominant herbivores (Furnish 1989, Li 1990). Effects of these factors were determined in two experiments, one in laboratory channels and the other in a natural stream. The first experiment (Chapter 2) studied the effects of concurrent grazing and substrate heterogeneity on algal taxonomic composition in laboratory streams. Patterns of algal taxonomic composition were compared between streams containing the caddisfly *Dicosmoecus gilvipes* (Hagen) (Trichoptera:Limnephilidae) and the snail *Juga silicula* (Gould) (Gastropoda:Pleuroceridae). The experimental design included four treatments: snails at high densities, caddisflies at high densities, snails and caddisflies concurrently at intermediate densities, and snails and caddisflies concurrently at high densities. Interactions of concurrent grazing with substrate heterogeneity also were investigated in an additional treatment by characterizing algal assemblages associated with top and recessed substrates of streams containing cobble-sized blocks and intermediate densities of snails and caddisflies. These assemblages were compared with corresponding algal assemblages in streams without substrate relief. The second experiment (Chapter 3) investigated effects of nitrogen enrichment on algal assemblages in a natural stream. Algal assemblages in different habitats in an enriched section of the stream were compared with

assemblages in a non-enriched upstream section of the same stream. Results and implications of these experiments are summarized in Chapter 4.

2. EFFECTS OF CONCURRENT GRAZING BY THE SNAIL *JUGA SILICULA* (GOULD) AND THE CADDISFLY *DICOSMOECUS GILVIPES* (HAGEN) ON THE TAXONOMIC STRUCTURE OF PERIPHYTON IN LABORATORY STREAMS

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2.1 Abstract

Relationships between the composition of benthic algal assemblages and herbivore type, herbivore competition, and substrate heterogeneity were investigated in laboratory streams. The snail *Juga silicula* and larvae of the caddisfly *Dicosmoecus gilvipes*, which are dominant herbivores in streams in Oregon and the Pacific Northwest, were either introduced into separate streams at high densities (500 m^{-2} and 50 m^{-2}, respectively), or together into the same streams at high or intermediate (250 m^{-2} and 25 m^{-2}) densities. Intermediate densities of both herbivores were also introduced together into streams which contained cobble-sized 22 x 22 x 4 cm channel-spanning substrate blocks.

At the end of the experiment, algal biomass was greatest in the "blocked" streams and least in the *Juga*-only and high density mixed streams. Algal heterogeneity was lowest in the *Juga*-only streams at the end of the experiment, intermediate in the high-density mixed streams, and high in all other streams. Periphyton succession in the *Juga*-only streams tended toward assemblages characterized by filaments of the cyanobacterium *Phormidium tenue* and basal cells of the heterotrichous chlorophyte *Stigeoclonium tenue*, whereas periphyton on the top substrates in the "blocked" streams tended toward large, linear diatoms (*Synedra ulna*) and filaments of the chlorophytes *S. tenue* and *Ulothrix*. Assemblages on the recessed surfaces of the "blocked" streams tended more toward relatively high abundances of the filamentous cyanobacterium *Oscillatoria agardhii*, small, prostrate diatoms (*Achnanthes minutissima*, *Navicula arvensis*, *Navicula minima*, and *Nitzschia fonticola*), and basal cells of *Stigeoclonium tenue*. Assemblages in the *Dicosmoecus*-only streams were dominated by prostrate

diatoms and the long, linear diatom *Synedra ulna* at the end of the experiment. In the intermediate density mixed-grazer streams, assemblages were intermediate between the snail-only and caddisfly-only streams in terms of abundances of the basal cells of *S. tenue*, and the high density streams possessed high abundances of small, prostrate diatoms. Although relative abundances of *P. tenue* and basal cells of *S. tenue* differed among treatments, estimated biomasses of these taxa appeared to be independent of the type and density of grazers.

The effects of concurrent grazing by dissimilar herbivores on algal assemblages were not additive, but produced algal assemblages intermediate in biomass and of distinct taxonomic composition. Results suggested that consumptive demand of herbivores, which is dependent on life history of the grazer and effects of the physical environment, may be as important a factor as grazer species, mouthpart types, and densities in affecting the taxonomic structure of periphyton assemblages. Substrate heterogeneity affected grazer-periphyton interactions by changing the flow regime, which altered initial algal colonization and distribution of the herbivores. The presence of herbivores did not appear to inhibit succession, but rather led to grazer-tolerant algal assemblages which were distinct from early successional assemblages.

2.2 Introduction

Herbivores affect the distribution and abundance of their food resources. Feminella and Hawkins (1995) and Steinman (1996) recently reviewed the effects of herbivores on freshwater benthic algae. Effects of herbivores on algal assemblages in

freshwater ecosystems are dependent on the density (Colletti *et al.* 1987, Swamikannu and Hoagland 1989), body size (Cattaneo and Kalff 1986, Steinman 1991), consumptive demand (Steinman 1991), and species of the herbivore (Jacoby 1987, Lamberti *et al.* 1987, Karouna and Fuller 1992), as well as on the physiognomy and taxonomic composition of the algal assemblage (Sumner and McIntire 1982, Gregory 1983, DeNicola *et al.* 1990, Gresens and Lowe 1994). The influence of such abiotic factors as irradiance (Lamberti *et al.* 1989, Steinman *et al.* 1989, DeNicola and McIntire 1991, Steinman 1992), substrate heterogeneity (DeNicola and McIntire 1991), season (Chapman and Demory 1963), and nutrient concentrations (Marks and Lowe 1989, McCormick and Stevenson 1989, Hart and Robinson 1990, Mulholland *et al.* 1991, Steinman *et al.* 1991, Hill *et al.* 1992, Rosemond *et al.* 1993, Pan and Lowe 1994) on the process of herbivory also affects algal distribution and abundance. However, only a few studies have examined the concurrent effects of two dissimilar herbivores (Hill and Knight 1988a, Feminella and Resh 1991, Kohler 1992, Pan and Lowe 1994) or the interaction between herbivores and substrate heterogeneity (DeNicola and McIntire 1991) on algal assemblages in lotic ecosystems.

The introduction of herbivores into laboratory streams (Sumner and McIntire 1982, Lamberti *et al.* 1989) or enclosures in natural streams (Hill and Knight 1987) can decrease the biomass of benthic algal assemblages during early stages of succession. However, productivity of algal assemblages may be enhanced by moderate grazing pressure (Gregory 1980), and in certain cases algal biomass may increase as a result of grazing (McCormick and Stevenson 1991a). Periphyton in later stages of succession may

reach a size that allows escape from grazing (Steinman *et al.* 1987). Herbivores also alter successional trajectories of algal assemblages, either to an assemblage that resembles an early seral stage by inhibiting establishment of later seral species (Dudley and D'Antonio 1991), or more commonly, to a distinct herbivore resistant (or tolerant) assemblage (Hart 1985, Power *et al.* 1988).

Herbivores may change the taxonomic composition of algal assemblages by direct or indirect mechanisms. Direct effects result from selective consumption of specific algal taxa (e.g., Hill and Knight 1988a). Herbivores also graze unselectively (Lamberti and Moore 1984), and indirect effects have been attributed to nutrient regeneration (Peer 1986, Sterner 1986, Mulholland *et al.* 1991), and to habitat disturbance. For example, grazing can result in an increase in light penetration in the algal mat (Lamberti and Resh 1983) or an increase in algal export (Lamberti *et al.* 1987, DeNicola *et al.* 1990). Dissimilar herbivores may produce different changes in algal assemblages. For example, Karouna and Fuller (1992) found that grazing by the caddisfly *Psilotreta* reduced the abundance of stalked diatoms such as *Gomphonema* but increased the abundance of prostrate diatoms such as *Achnanthes*, whereas grazing by the mayfly *Paraleptophlebia* increased the numbers of all diatom species but reduced the abundance of the chlorophyte *Oedogonium*. Both direct and indirect effects of grazers on algal assemblages have been attributed to herbivore species-specific differences in mouthpart morphology and feeding behavior (McAuliffe 1984b, Lamberti *et al.* 1987, Karouna and Fuller 1992), which can give rise to a "species-related gradient of grazing intensity" (DeNicola *et al.* 1990).

Previous studies involving concurrent grazing by dissimilar herbivores have generally shown that the effects are additive. Concurrent effects of larvae of the caddisfly *Neophylax* and the mayfly *Ameletus* (Hill and Knight 1988a) or the larvae of the caddisflies *Helicopsyche borealis* and *Gumaga nigricula* (Feminella and Resh 1991) in natural streams were additive in terms of reduction of algal biomass and alteration of taxonomic composition, producing algal assemblages with relatively low biomass and composed of prostrate, grazer-resistant taxa. The effects of concurrent grazing by *Helicopsyche borealis* and larvae of the mayfly *Baetis tricaudatus* also were additive in terms of suppressing algal biomass, but produced assemblages more dominated by *Cocconeis placentula* than in chambers grazed by *Helicopsyche* alone (Pan and Lowe 1994). In one set of experiments, the effects of concurrent grazing by larvae of the caddisfly *Glossosoma nigrior* and the mayfly *Baetis tricaudatus* in laboratory chambers were also additive in reducing periphyton biomass (Kohler 1992). However, in another experiment, concurrent grazing by both these species did not reduce algal biomass more than either grazer alone (Kohler 1992).

The general objective of this research was to investigate concurrent effects of two dissimilar species of herbivores on the biomass and taxonomic structure of algal assemblages in laboratory streams. We used the pleurocerid snail *Juga silicula* (Gould), which rasps the substrate with a radula, and larvae of the limnephilid caddisfly *Dicosmoecus gilvipes* (Hagen), which scrapes the substrate with its mandible and tarsal claws. *Juga silicula* and *Dicosmoecus gilvipes* are the dominant herbivores in many streams in Oregon and the Pacific Northwest (Furnish 1989, Li 1990). Specifically, the

experiment was designed to examine the following hypotheses: (1) the effects of concurrent grazing by *Juga* and *Dicosmoecus* on the biomass and taxonomic structure of algal assemblages are additive; and (2) the presence of substrate heterogeneity, by altering the flow regime and providing refuge for the algae and a patchy distribution of food resources for the herbivores, alters the pattern of plant-herbivore interactions in a system with concurrent grazing by dissimilar herbivores.

2.3 Materials and Methods

2.3.1 Laboratory Streams

The experiment was conducted in 16 fiberglass laboratory streams at the Fairplay Laboratory, Oregon State University. Each stream was 3 m long, 0.5 m wide, and 0.2 m deep, and each possessed a wetted surface area of approximately 2 m^2. A centerboard, approximately 2.5 m long, divided each stream into two channels, around which water was circulated by a motor-powered paddle wheel at a free current velocity of 10 cm s^{-1}. An overflow standpipe at one end of each stream maintained a water depth of 10 cm. Well water with a mean temperature of 12° C was introduced to the streams at an exchange rate of 1.5 l min^{-1}. Water temperature in the channels was 14 ± 1° C throughout the experiment. Nutrient concentrations in the well water were relatively high (PO_4^{3-}-P: 0.10 mg l^{-1}; silica: 19.2 mg l^{-1}; NH_4^+-N: 0.01 mg l^{-1}; NO_3^--N: 5.35 mg l^{-1}) (DeNicola and McIntire 1991). Sixteen 1000 W Metalarc lamps (Sylvania Corp.) provided light with a

mean irradiance of 425 μmol quanta m^{-2} s^{-1} at the water surface. The lamps were controlled by a set of timers that maintained a photoperiod of 10 hours light to 14 hours dark.

A surface for sampling algal assemblages was provided by lining the bottom of each stream with rows of unglazed clay tiles. The dimensions of these tiles were 7.5 cm x 7.5 cm x 1.3 cm, and each row contained three tiles between the centerboard and the side of a stream. In the non-blocked streams one tile in every other row contained a single 1 cm raised edge to provide a degree of substrate irregularity and to give the animals a refuge from the direct effects of the water flow. The streams representing the blocked-substrate treatment contained channel-spanning blocks composed of stacks built of 3 x 3 x 3 tiles that were placed on top of a primary layer of tiles. The stacks were spaced 22.5 cm apart and separated by three rows of tiles. Therefore, each block was 22.5 cm x 22.5 cm with a top surface 4 cm above an adjacent lower surface with the same surface area (DeNicola 1990). The sides of the streams were lined with larger tiles, each with the dimensions of either 15 cm x 15 cm x 1.3 cm or 15 cm x 7.5 cm x 1.3 cm.

2.3.2 Experimental Design

The experiment began on 23 April 1991 and continued for 50 days. On the first day (day 0) periphyton was scraped and brushed from rocks collected from Oak Creek, Rock Creek, the Alsea River, and the Willamette River in Benton County, Oregon. The suspension of the scrapings was mixed for 30 s in a 3.8 L Waring blender. After dilution of the mixed algal suspension, a 1.0 L subsample was added to each stream. A subsample

of the inoculum also was preserved in Lugol's solution for an analysis of species composition. Two species of herbivores, the snail *Juga silicula* (Gould) (Gastropoda:Pleuroceridae) and the caddisfly *Dicosmoecus gilvipes* (Hagen) (Trichoptera:Limnephilidae), were collected from Rock Creek (third order) and introduced into the streams on 1 May 1991 (day 8). *Juga silicula* and *Dicosmoecus gilvipes* are dominant herbivores in streams in Oregon and the Pacific Northwest (Furnish 1989, Li 1990). The snails used in the experiment were intermediate in size, ranging from 10-15 mm total shell length, and the caddisflies were mostly fourth (with occasional large third) instar larvae.

The experimental design consisted of 15 streams randomly assigned to one of five treatments. Therefore, each treatment was represented by three replications. The treatments were determined by the stocking densities of snails and caddisflies, where a 1X density was defined as either 25 caddisflies m^{-2} (50 caddisflies per stream) or 250 snails m^{-2} (500 snails per stream). The snails and caddisflies were stocked at a 10:1 ratio to account for the greater size and feeding activity of the caddisflies, and the 10:1 ratio was assumed to provide equivalent consumptive demand for each species of herbivore (G.A. Lamberti, unpublished data). Densities of the herbivores were within the range of those found in nearby natural streams (Hawkins and Furnish 1987, Li 1990). Specifically, the treatments and their acronyms were: 500 snails m^{-2} (JUGA-2X), 50 caddisflies m^{-2} (DICO-2X), 500 snails m^{-2} and 50 caddisflies m^{-2} (2X:2X), 250 snails m^{-2} and 25 caddisflies m^{-2} (1X:1X), and blocked-substrate streams with 250 snails m^{-2} and 25 caddisflies m^{-2}. The raised surfaces in the blocked-substrate streams were designated with

the acronym TOP 1:1, whereas the recessed surfaces were designated with the acronym BOT 1:1.

2.3.3 Sampling

For the taxonomic analysis of periphyton assemblages, random samples of two tiles were taken from each stream on days 7, 22, 36, and 50. The tiles then were scraped with a razor blade and brushed with a toothbrush to remove as much periphyton as possible. The scrapings were combined into one sample for each stream and immediately fixed in Lugol's solution. In the streams with the 22.5 cm x 22.5 cm blocks, two tiles were selected at random from both the raised substrates (TOP 1:1) and the recessed substrates (BOT 1:1), and the collections from the two areas were processed as separate samples. On day 7, one day before the animals were stocked, periphyton collections were combined into four samples: two samples, each representing six non-blocked streams, and two samples representing the blocked-substrate streams, consisting of one combined sample from the raised areas (TOP 1:1) and one combined sample from the recessed areas (BOT 1:1). It was assumed that these four samples were representative of the food resources available to grazers at the time the animals were introduced.

Sampling for periphyton biomass was conducted on days 22, 36, and 50. Two tiles were removed at random from each stream, and periphyton was scraped from each tile while following the same procedure described for taxonomic analysis. Biomass, expressed as ash-free dry mass (AFDM), was determined by the method described by Lamberti *et al.* (1987).

2.3.4 Counting Procedures

Each sample for taxonomic analysis was mixed with a Pyrex mortar-and-pestle tissue grinder. Several drops of the sample then were placed on a glass slide and approximately 500 algal units were counted at 500X magnification using a Zeiss compound microscope. During this count, diatoms were lumped into a single taxon, whereas taxa other than diatoms were identified to species when possible. For unicellular taxa an algal unit was a single cell, whereas for filamentous taxa an algal unit consisted of a defined length of filament. Specifically, the filament lengths were either 12.5 mm (*Stigeoclonium tenue* filaments, *Ulothrix* sp., and *Oscillatoria agardhii*) or 25 mm (*Phormidium tenue*). Filaments and basal cells of the heterotrichous green alga *Stigeoclonium tenue* were counted as distinct taxonomic units.

Diatoms were identified to species and counted separately using a subsample prepared in the following manner. The subsample was boiled in concentrated nitric acid for 30 minutes, after which approximately 1 g of potassium dichromate was added. The cleaned valves were allowed to settle for 24 hours, after which the supernatant was removed and replaced with distilled water. This process was repeated until the solution was no longer acidic. A few drops of the cleaned diatom suspension were placed on a cover slip and mounted on a slide with Cumar resin (Holmes *et al.* 1981). Five hundred diatom valves were counted at 1250X magnification. The numerical relative abundance ($N_{i,j}$) of a particular diatom species in a given sample then was calculated from the following equation:

$$N_{i,j} = D_j P_{i,j},$$

where $N_{i,j}$ was the calculated proportion of diatom species i in sample j, D_j was the proportion of diatoms in sample j, and $P_{i,j}$ was the proportion of diatom species i in the diatom count of sample j.

Biovolumes per algal unit (V_i) were calculated for each taxon using appropriate geometric formulae. The relative biovolume of a particular species in a given sample was calculated from the following equation:

$$R_{i,j} = V_i N_{i,j} \;/\; (V_1 N_{1,j} + V_2 N_{2,j} + \ldots + V_T N_{T,j}),$$

where $R_{i,j}$ was the calculated relative biovolume of taxon i in sample j, V_i was the biovolume per algal unit of taxon i, $N_{i,j}$ was the proportion of taxon i in sample j, and $(V_1 N_{1,j} + V_2 N_{2,j} + \ldots + V_T N_{T,j})$ represented the sum of $V_i N_{i,j}$ for all T taxa in sample j.

Absolute algal biomasses were estimated from the relative biovolume data and the sample biomass data. Specifically,

$$A_{i,j} = B_j R_{i,j},$$

where $A_{i,j}$ was the absolute algal biomass for taxon i in sample j, B_j was the biomass of sample j, and $R_{i,j}$ was the relative biovolume of taxon i in the sample j.

All of the variables and formulae used in the above calculations are summarized in Table 2.1.

2.3.5 Data Analysis

The numerical relative abundance data ($N_{i,j}$) were organized into a samples-by-species matrix for analysis of community structure. A similar matrix derived from the relative biovolume data ($R_{i,j}$) also was constructed. Algal heterogeneity, based

Table 2.1. List of variables and formulae used in the calculation of numerical relative abundance, relative biovolume, and absolute biomass.

Variables:

$A_{i,j}$: Absolute biomass of taxon i in sample j. Calculated from formula (3).

B_j : Biomass of sample j.

D_j : Proportion of diatoms in the count of sample j.

$N_{i,j}$: Proportion of taxon i in the count of sample j. For diatom taxa, calculated from formula (1).

$P_{i,j}$: Proportion of diatom taxon i in the diatom-count for sample j.

$R_{i,j}$: Relative biovolume of taxon i in sample j. Calculated from formula (2).

T : Total number of taxa occurring in the experiment.

V_i : Biovolume of an algal unit of taxon i.

Formulae:

(1) $N_{i,j} = D_j P_{i,j}$

(2) $R_{i,j} = V_i N_{i,j} \; / \; (V_1 N_{1,j} + V_2 N_{2,j} + \ldots + V_T N_{T,j})$

(3) $A_{i,j} = B_j R_{i,j}$

on numerical relative abundance, was expressed by the Shannon information measure (Peet, 1974).

Temporal variations in species composition and relative abundance were examined by detrended correspondence analysis (DCA), an ordination method performed by the program DECORANA (Hill 1979, Gauch 1982). In order to remove extreme outliers only those taxa which were found in at least 6 samples and also constituted at least 0.01% of the total count were included in the ordination. Results of this analysis, based on numerical relative abundance, were presented as a series of graphs illustrating mean successional trajectories for algal assemblages subjected to the different treatments.

Values of relative biovolume, algal heterogeneity, and ordination coordinates were represented by mean values (±1 SE) for the streams in each treatment on each date with n replications, where n=1 (day 0 (inoculum); day 7 (TOP 1:1 substrates and BOT 1:1 substrates)); n=2 (day 7 (non-blocked streams)); or n=3 (days 22, 36, and 50 (all streams)).

Repeated measure analysis of variance was used to test for differences in algal biomass (AFDM) in the streams of the non-blocked treatments (DICO-2X, JUGA-2X, 2X:2X, and 1X:1X) relative to the treatment effects of grazing and time. Tukeys HSD was used to test pairwise comparisons of treatment biomasses for the streams in the non-blocked treatments at the end of the experiment (day 50) (SYSTAT 1992).

2.4 Results

2.4.1 Algal Biomass

Repeated measure analysis of variance indicated that biomass was significantly affected by time ($p<0.001$), grazer type ($p<0.01$), and the interaction between time and grazer type ($p<0.01$). Mean algal biomass for all treatments increased monotonically during the course of the experiment (Fig. 2.1). At the conclusion of the experiment (day 50), mean ash-free dry mass (AFDM) ranged from 2.7 g m^{-2} in the JUGA-2X streams to 53.3 g m^{-2} on the TOP 1:1 substrates of the blocked-substrate streams (Fig. 2.1). Pairwise comparisons of mean biomass values for non-blocked streams on day 50 indicated that the mean 1X:1X treatment algal biomass was significantly greater than mean biomasses associated with the 2X:2X and JUGA-2X treatments (Table 2.2). In the JUGA-2X and 2X:2X streams only a thin layer of periphyton was evident throughout the experiment. In the DICO-2X streams large mats of periphyton and algal filaments were observed by day 36, followed by some senescence by day 50. Mean biomass in the DICO-2X streams on day 50 was greater than mean biomasses in streams of the 2X:2X and JUGA-2X treatments, although the differences were not statistically significant (Fig. 2.1 and Table 2.2).

In the blocked-substrate streams large mats of filaments were observed by day 36 on both the raised (TOP 1:1) and recessed (BOT 1:1) substrates. Mean algal biomass was greater on the TOP 1:1 substrates than on the BOT 1:1 substrates on days 36 and 50 (Fig.

Figure 2.1. Algal biomass accumulation on substrate surfaces. Values are means (±1 SE, n=3). Grazers were introduced on day 8.

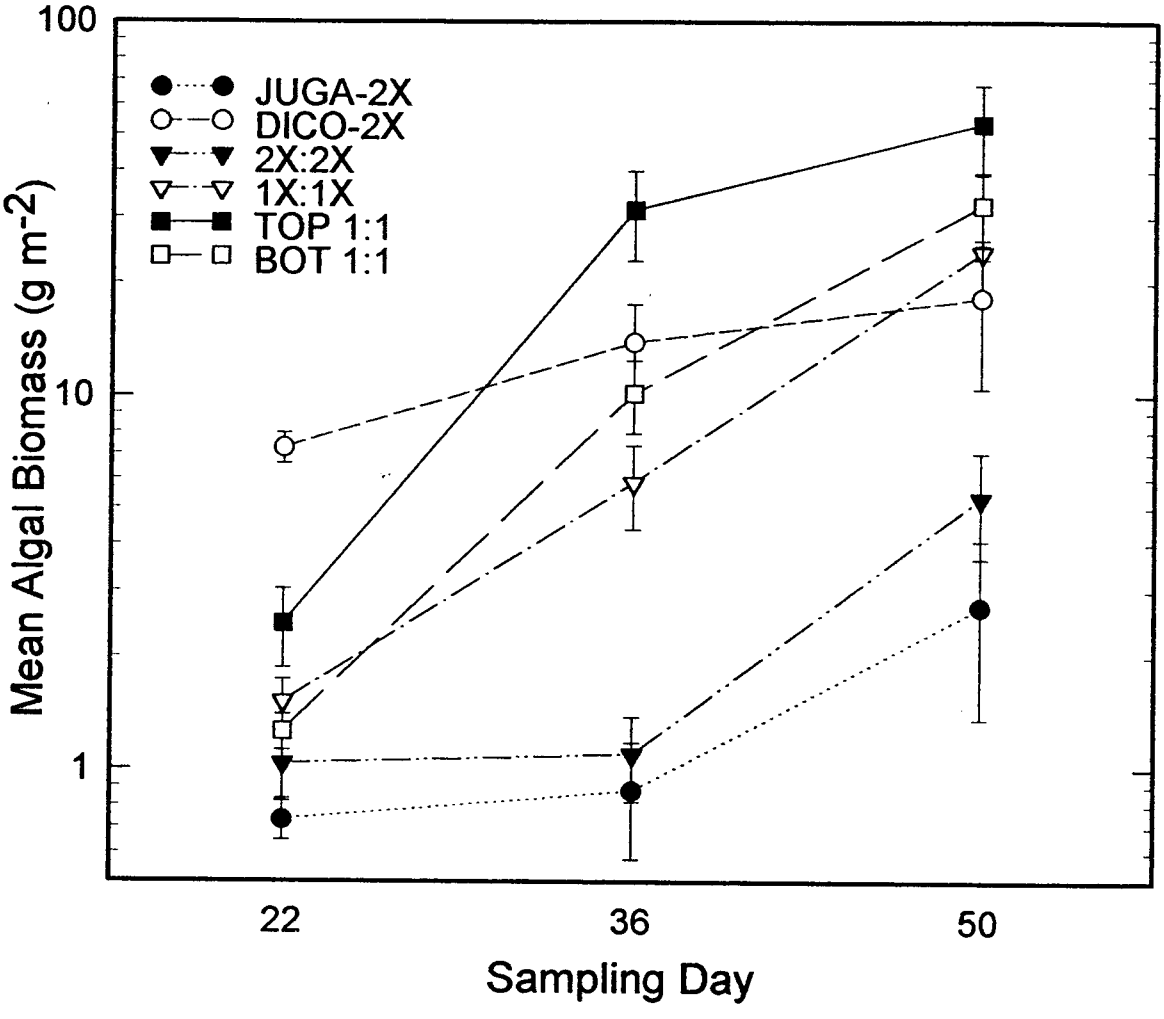
100
10
1
Mean Algal Biomass (g m-2)
JUGA-2X
DICO-2X
2X:2X
1X:1X
TOP 1:1
BOT 1:1
22
36
50
Sampling Day

Figure 2.1

Table 2.2. Tukey HSD for pairwise comparisons between means (n=3) of algal biomass (AFDM) in the non-blocked streams on day 50. Values are p-values. Asterisks (*) indicate $p<0.05$.

Treatment	JUGA-2X	2X:2X	1X:1X	Mean AFDM ($g\ m^{-2}$)
DICO-2X	0.103	0.192	0.741	18.26
JUGA-2X		0.968	0.025*	2.71
2X:2X			0.046*	5.31
1X:1X				24.18

2.1). On day 50 periphyton on the recessed substrates appeared to be more senescent than periphyton on the raised substrates.

2.4.2 Algal Taxonomic Composition

Forty-five algal taxa were observed during the experiment. Thirty-three taxa each comprised greater than 0.01% of the total count for all samples and also occurred in at least 6 samples (Table 2.3). Twelve other taxa were present in very small numbers in only a few samples prior to the introduction of grazers.

Nine algal taxa had mean relative biovolumes greater than 3.0% and collectively these nine taxa accounted for 80.8% of the mean relative biovolume over all 59 samples (Table 2.3). Of these nine algal taxa, four were diatoms (*Synedra ulna*, *Gomphonema parvulum*, *Achnanthes lanceolata*, and *Nitzschia linearis*), three were chlorophytes (*Ulothrix* sp., and *Stigeoclonium tenue* basal cells and filaments), and two were cyanobacteria (*Phormidium tenue*, and *Oscillatoria agardhii*). Four small, prostrate diatom taxa (*Nitzschia fonticola*, *Achnanthes minutissima*, *Navicula arvensis*, and *Navicula minima*), whose cell biovolumes were the smallest of the diatom taxa observed during the experiment (40-48 μm^3) (Table 2.3), collectively had a mean relative biovolume of 6.5%. The four filamentous diatoms that were observed during the experiment (*Fragilaria vaucheriae*, *Melosira varians*, *Diatoma hiemale* var. *mesodon*, and *Meridion circulare* var. *constrictum*) collectively had a mean relative biovolume of 3.4%. The relative biovolumes of the nine common taxa, the prostrate diatoms, and the filamentous diatoms during the experiment are illustrated in Figure 2.2.

Table 2.3. List of the 33 taxa included in the detrended correspondence analysis (DCA). Each of these taxa comprised greater than 0.01% of the total count and occurred in at least 6 samples. Cell biovolumes are for a single cell, except for those indicated by [a] (12.5 µm filament), [b] (25 µm filament), or [c] (coenobium of four cells). Mean relative biovolumes were calculated over all samples (n=59).

Taxon	Cell Biovolume (μm^3)	Mean Relative Bio-volume (%)
Division Cyanophyta		
Chroococcus Naegeli	2	0.21
Oscillatoria agardhii Gomont	[a]245	3.05
Phormidium tenue (Menegh.) Gomont	[b]44	4.05
Division Chrysophyta (Class Bacillariophyceae)		
Achnanthes deflexa Reim.	107	1.65
Achnanthes lanceolata (Bréb.) Grun.	274	5.72
Achnanthes minutissima Kütz.	42	1.77
Amphora ovalis Kütz.	161	0.06
Cocconeis placentula var. *euglypta* (Ehr.) Cl.	527	0.33
Cymbella minuta Hilse *ex* Rabh.	578	0.53
Cymbella sinuata Greg.	158	0.65
Diatoma hiemale var. *mesodon* (Ehr.) Grun.	979	0.42
Fragilaria vaucheriae (Kütz.) Peters.	238	2.02
Gomphonema dichotomum Kütz.	176	0.33
Gomphonema instabilis Hohn & Hellerm.	1114	0.46
Gomphonema parvulum Kütz.	421	5.83
Gomphonema rhombicum Fricke	756	0.35
Melosira varians Ag.	2163	0.97
Meridion circulare var. *constrictum* (Ralfs) V.H.	247	0.03
Navicula arvensis Hust.	42	1.85
Navicula cryptocephala var. *veneta* (Kütz.) Rabh.	154	0.03
Navicula minima Grun.	48	0.28
Nitzschia dissipata (Kütz.) Grun.	146	1.49
Nitzschia fonticola Grun.	40	2.49
Nitzschia linearis W. Smith	3523	4.95
Nitzschia oregona Sov.	143	1.31
Rhoicosphenia curvata (Kütz.) Grun. *ex* Rabh.	283	1.41
Surirella ovata Kütz.	550	0.07
Synedra rumpens Kütz.	315	0.12
Synedra ulna (Nitz.) Ehr.	4437	15.38

Table 2.3 (continued)

Taxon	Cell Biovolume (μm^3)	Mean Relative Bio-volume (%)
Division Chlorophyta		
Scenedesmus Meyen	[c]235	0.10
Stigeoclonium tenue (Ag.) Kütz		
basal cells	75	13.56
filaments	[a]383	6.01
Ulothrix Kütz.	[a]2837	22.24

Figure 2.2. Mean relative biovolumes of selected algal taxa. The acronyms of the taxa are: FIDI = filamentous diatoms (*Fragilaria vaucheriae*, *Melosira varians*, *Diatoma hiemale* var. *mesodon*, and *Meridion circulare* var. *constrictum*), PROS = prostrate diatoms (*Nitzschia fonticola*, *Achnanthes minutissima*, *Navicula arvensis*, and *Navicula minima*), OSCI = *Oscillatoria agardhii*, PHOR = *Phormidium tenue*, NILI = *Nitzschia linearis*, ACLA = *Achnanthes lanceolata*, GOPA = *Gomphonema parvulum*, STFI = filaments of *Stigeoclonium tenue*, STBC = basal cells of *Stigeoclonium tenue*, SYUL = *Synedra ulna*, and ULOT = *Ulothrix* sp. Vertical dashed line between day 7 and day 22 indicates grazer introduction on day 8. The graphs correspond to samples in the (a) JUGA-2X streams, (b) DICO-2X streams, (c) 2X:2X streams, (d) 1X:1X streams, (e) TOP 1:1 surfaces in blocked-substrate streams, and (f) BOT 1:1 surfaces in blocked-substrate streams.

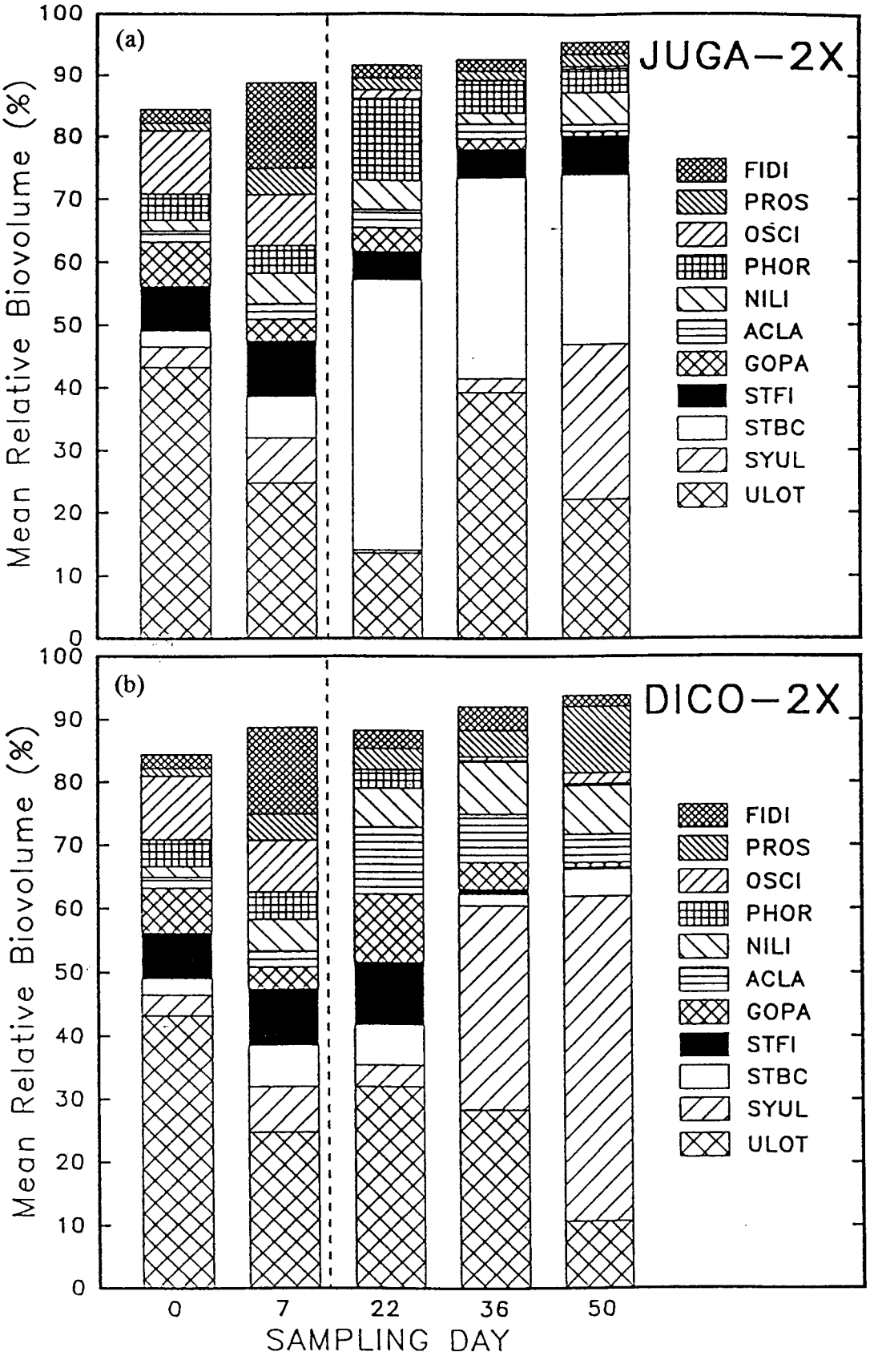
(a)
JUGA–2X
(b)
DICO–2X
Mean Relative Biovolume (%)
0
10
20
30
40
50
60
70
80
90
100
FIDI
PROS
OSCI
PHOR
NILI
ACLA
GOPA
STFI
STBC
SYUL
ULOT
0
7
22
36
50
SAMPLING DAY

Figure 2.2

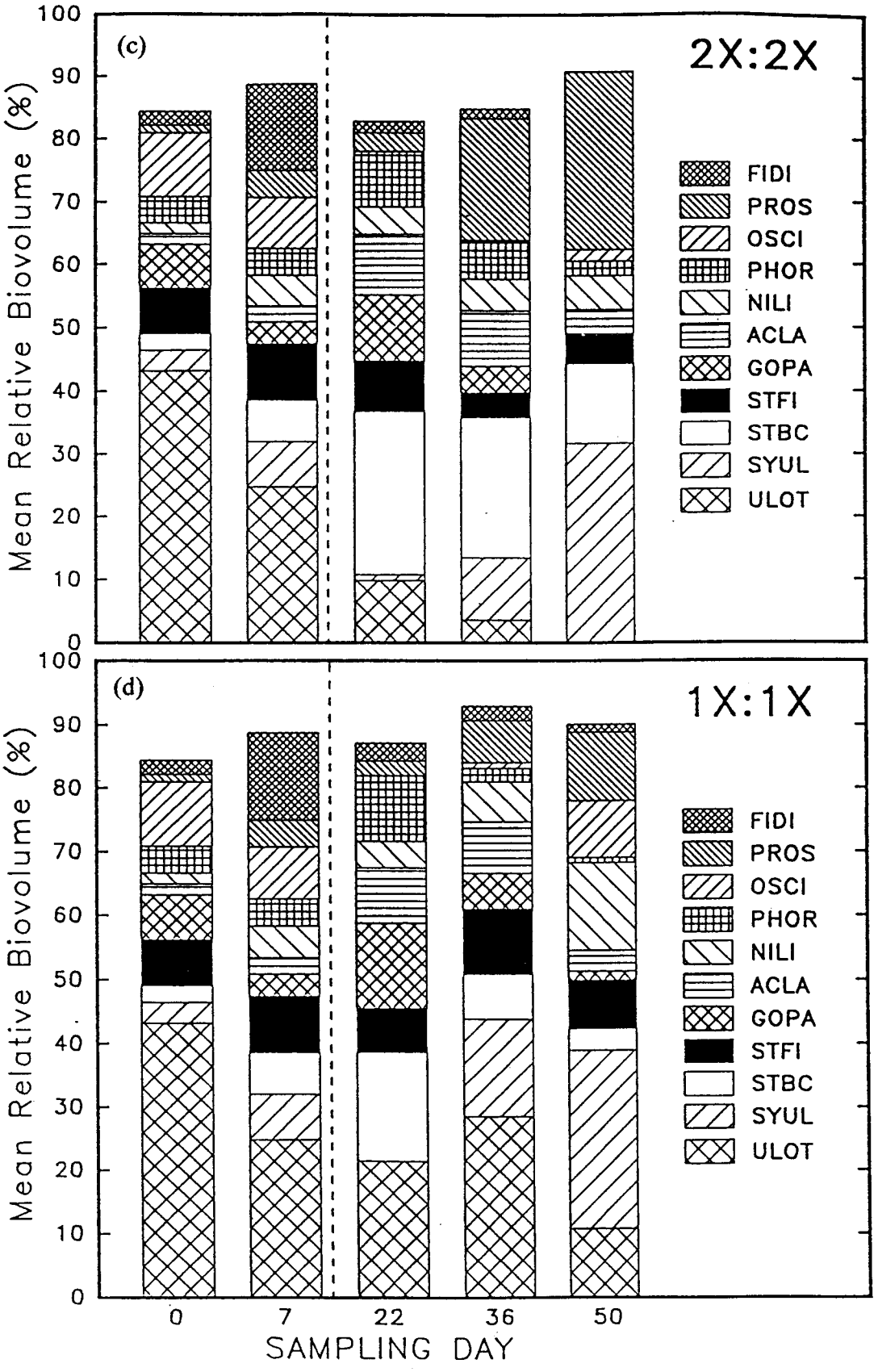

Figure 2.2 (continued)

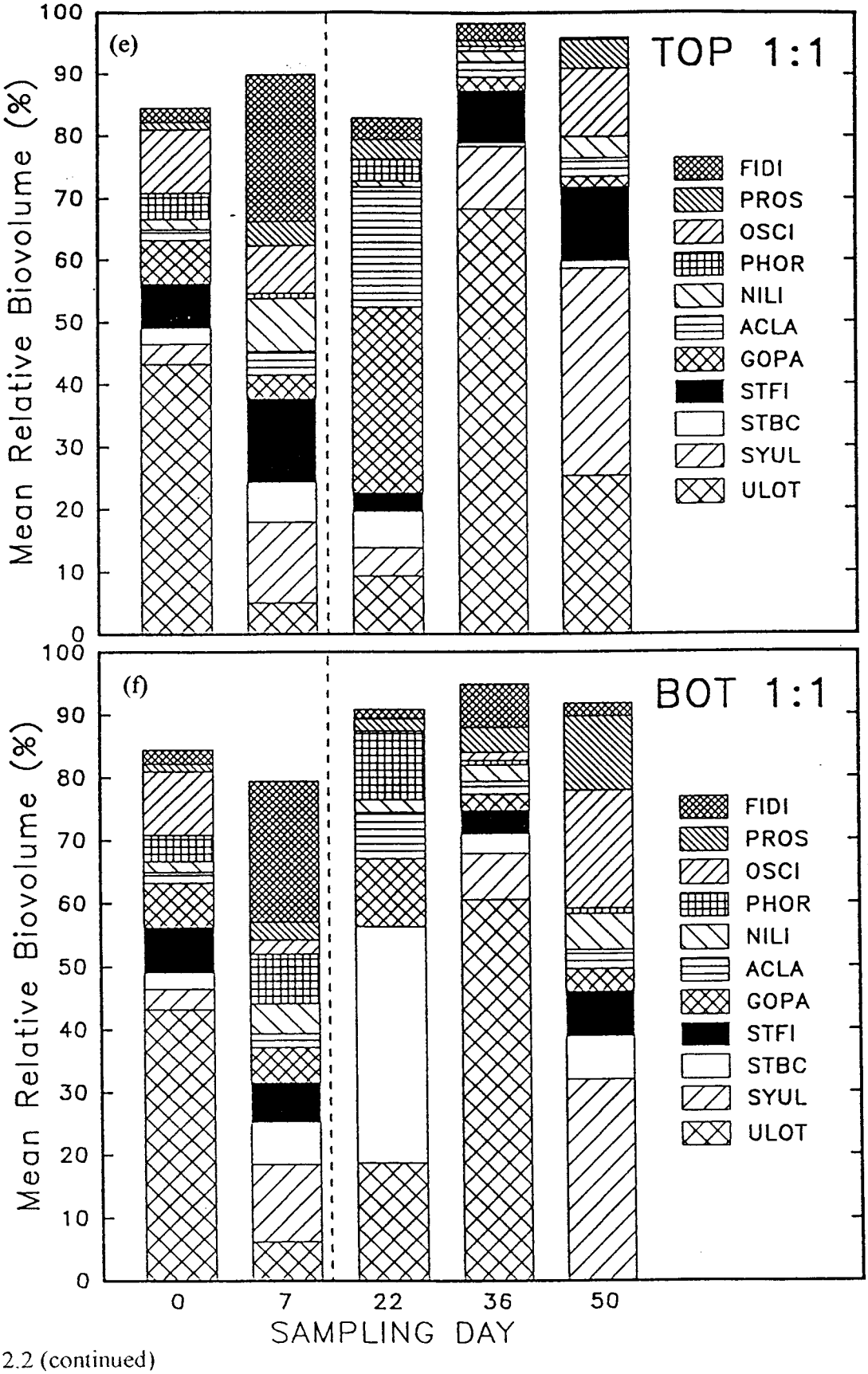

Figure 2.2 (continued)

2.4.3 Response of Algal Taxa to Grazing

Based on general response to grazing, the algal taxa could be classified into three groups, depending on which day their relative biovolumes were maximum. Relative biovolumes of the filamentous diatoms (*Fragilaria vaucheriae*, *Melosira varians*, and *Diatoma hiemale* var. *mesodon*, and *Meridion circulare* var. *constrictum*) were high only on day 7, just prior to the introduction of the grazers. Relative biovolumes of the filamentous diatoms then decreased for the remainder of the experiment (Figs 2.2a-f). Relative biovolumes of a second group of taxa (basal cells of *Stigeoclonium tenue*, the diatoms *Gomphonema parvulum* and *Achnanthes lanceolata*, the filamentous cyanobacterium *Phormidium tenue*, and, in the DICO-2X streams, filaments of *S. tenue*) increased after the introduction of grazers, reached a maximum on day 22, but then decreased for the remainder of the experiment (Figs. 2.2a-f). Relative biovolumes of a third group (*Oscillatoria agardhii*, *Synedra ulna*, the prostrate group consisting of *Nitzschia fonticola*, *Achnanthes minutissima*, *Navicula arvensis*, and *Navicula minima*, and, in the blocked-substrate streams, filaments of *S. tenue*) decreased between the introduction of grazers (day 8) and day 22, but then increased after day 22 and were maximum on day 50 (Figs. 2.2a-f). Relative biovolume of *S. tenue* filaments in the JUGA-2X, 1X:1X, and 2X:2X streams changed little throughout the experiment (Figs. 2.2a, c, and d). The filamentous chlorophyte *Ulothrix* sp. did not fit into any of these groups, and its relative biovolume decreased between the introduction of grazers and the end of the experiment in the DICO-2X and 1X:1X streams; in the other streams its maximum abundance occurred on day 36 (Figs. 2.2a-f).

Absolute algal biomasses for selected taxa after the introduction of the grazers are shown in Figure 2.3. Because algal biomass increased monotonically in all streams, any taxon whose relative biovolume increased between two days necessarily had its absolute biomass increase during the same period (e.g., *Synedra ulna*, Fig. 2.3e). In contrast, the absolute biomass of any taxon whose relative biovolume decreased between two dates after the introduction of the grazers (e.g., basal cells of *S. tenue*, the diatoms *Gomphonema parvulum* and *Achnanthes lanceolata*, and the filamentous cyanobacterium *Phormidium tenue*) could have either decreased, remained constant, or increased during that period (Fig. 2.3a-d). Although the relative biovolume of *Phormidium tenue* on any given day varied according to treatment (Figs 2.2a-f), the absolute biomass of this taxon on a given day was generally the same across treatments (Fig. 2.3a). Absolute biomass of basal cells of *Stigeoclonium tenue* exhibited a similar pattern (Fig. 2.3b). In other words, the absolute biomasses for these two taxa were generally independent of treatment. Although the relative biovolumes of these taxa decreased between days 36 and 50 (Figs. 2.2a-f), their absolute biomasses increased (Figs. 2.3a-b). Unlike *P. tenue* and the basal cells of *S. tenue*, the absolute biomasses of *Achnanthes lanceolata* and *Gomphonema parvulum* were treatment-dependent (Figs. 2.3 c-d). Although the relative biovolumes of *A. lanceolata* and *G. parvulum* in the 1X:1X streams and on the TOP 1:1 substrates decreased between days 22 and 50 (Fig. 2.2d-e), the absolute biomass of *A. lanceolata* increased and the absolute biomass of *G. parvulum* remained constant during the same period (Fig. 2.3c-d). Whereas for most taxa a reduction in relative biovolume was accompanied by an increase in algal biomass, the decrease in relative biovolume of *G.*

Figure 2.3. Absolute biomass of selected taxa on days 22, 36, and 50: (a) *Phormidium tenue*, (b) *Stigeoclonium tenue* basal cells, (c) *Achnanthes lanceolata*, (d) *Gomphonema parvulum*, and (e) *Synedra ulna*. Values are means (±1 SE, n=3). Treatments are represented by the same symbols as in Figs. 2.1, 2.4, and 2.5a. Note the logarithmic y-axes, which are scaled differently for each taxon.

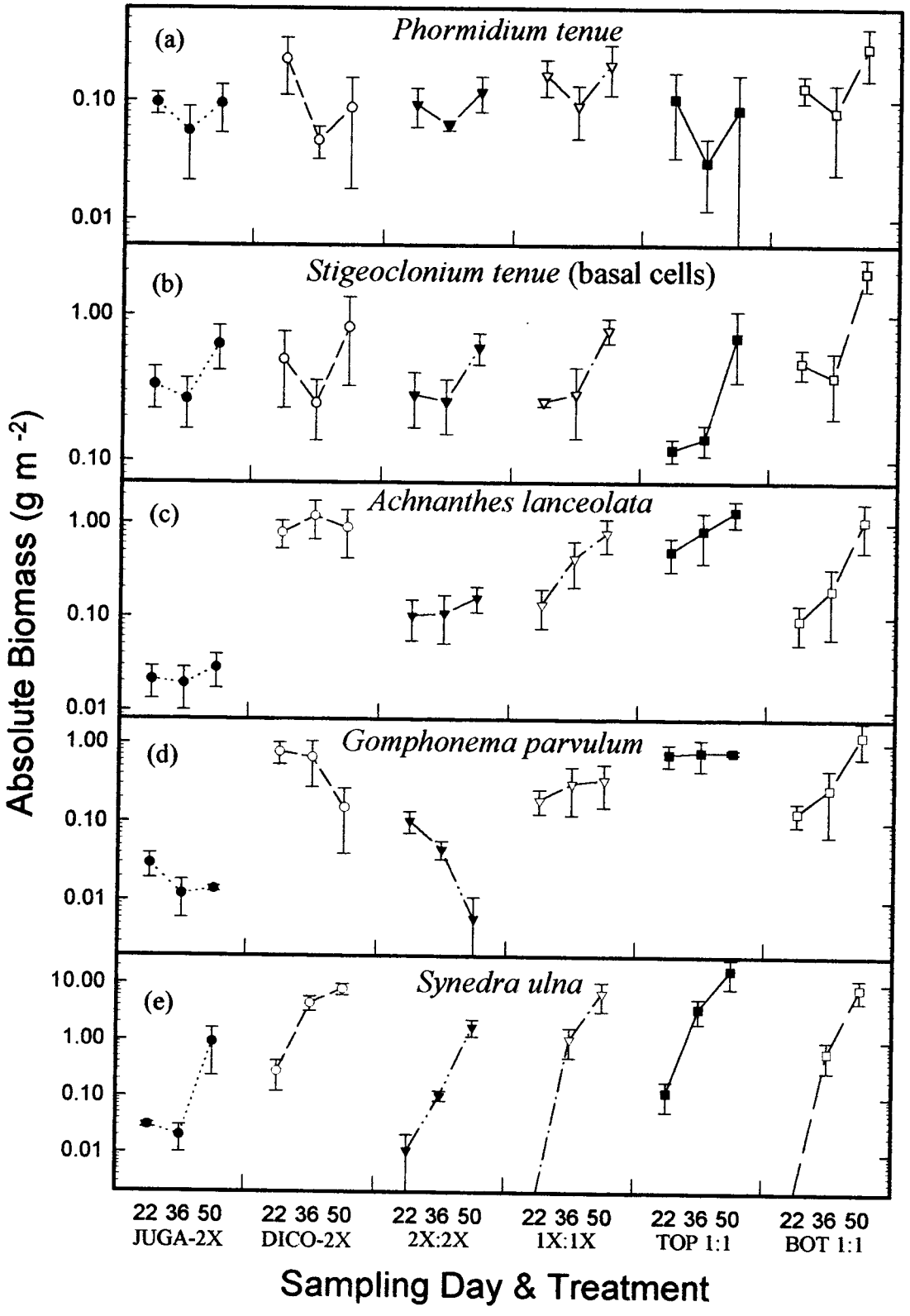
(a)
Phormidium tenue
0.10
0.01
(b)
Stigeoclonium tenue (basal cells)
1.00
0.10
(c)
Achnanthes lanceolata
1.00
0.10
0.01
(d)
Gomphonema parvulum
1.00
0.10
0.01
(e)
Synedra ulna
10.00
1.00
0.10
0.01
Absolute Biomass (g m -2)
22 36 50
JUGA-2X
22 36 50
DICO-2X
22 36 50
2X:2X
22 36 50
1X:1X
22 36 50
TOP 1:1
22 36 50
BOT 1:1
Sampling Day & Treatment

Figure 2.3

parvulum between days 22 and 50 in the DICO-2X and 2X:2X streams (Figs. 2.2b and d) represented an actual decrease in absolute biomass as well (Fig. 2.3d).

2.4.4 Algal Community Structure

Algal heterogeneity, as expressed by the Shannon information measure (H'), ranged from 1.49 on day 36 in the JUGA-2X streams to 2.66 in the DICO-2X streams on the same day (Fig. 2.4). Throughout the experiment algal heterogeneity was distributed in three levels: low (1.49-1.63), intermediate (1.89-2.04), and high (2.19-2.66) (Fig. 2.4). Before the introduction of grazers, algal heterogeneity was high in all streams, and it remained high in the DICO-2X streams and on the TOP 1:1 substrates throughout the experiment. After the introduction of grazers, algal heterogeneity dropped to the intermediate level in the 1X:1X and 2X:2X streams and was low in the JUGA-2X streams and on the BOT 1:1 substrates. Algal heterogeneity remained low only in the JUGA-2X streams, whereas on the BOT 1:1 substrates H' became high again by day 36 (Fig. 2.4). In the 2X:2X streams algal heterogeneity remained intermediate, whereas in the 1X:1X streams H' became high again by day 36. At the conclusion of the experiment algal heterogeneity was low in the JUGA-2X streams, intermediate in the 2X:2X streams, and high in the DICO-2X and 1X:1X streams, and the TOP 1:1 and BOT 1:1 surfaces in the blocked-substrate streams (Fig. 2.4).

Successional trajectories of algal assemblages, as indicated by detrended correspondence analysis (DCA), are illustrated in Figure 2.5a. Because the correspondence between sample and taxa ordinations is maximized by DCA, taxa

Figure 2.4. Heterogeneity (H') of algal assemblages. The arrow indicates time of grazer introduction (day 8).

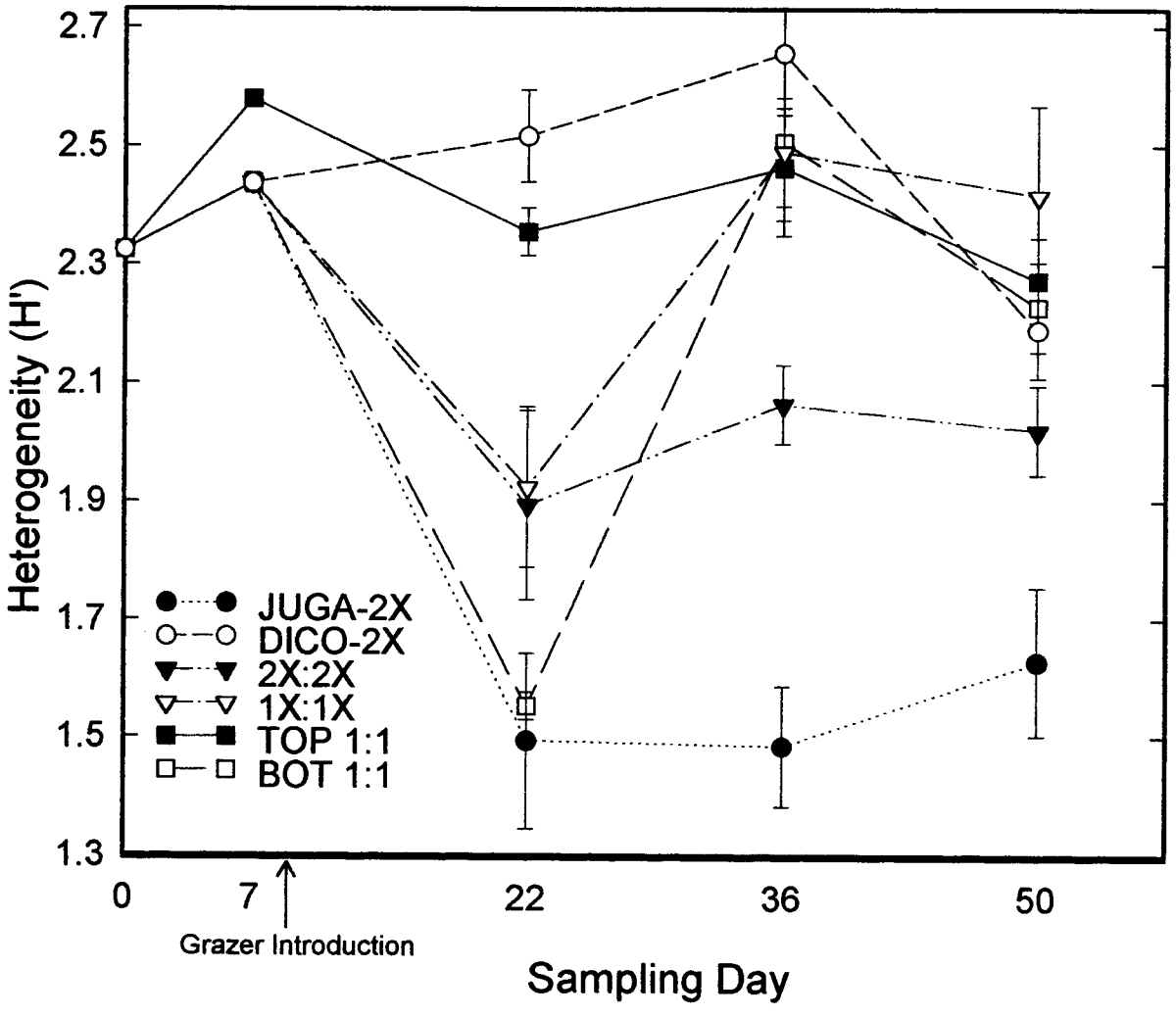
2.7
2.5
2.3
2.1
1.9
1.7
1.5
1.3
Heterogeneity (H')
JUGA-2X
DICO-2X
2X:2X
1X:1X
TOP 1:1
BOT 1:1
0
7
22
36
50
Grazer Introduction
Sampling Day

Figure 2.4

explaining a successional pattern may be determined by relating corresponding regions of the sample and taxa ordination spaces (Figs. 2.5a-b). Successional trajectories in all streams proceeded from pre-grazer assemblages characterized by 11 diatom taxa (*Cocconeis placentula* var. *euglypta*, *Cymbella minuta*, *Diatoma hiemale* var. *mesodon*, *Fragilaria vaucheriae*, *Gomphonema dichotomum*, *Gomphonema rhombicum*, *Melosira varians*, *Meridion circulare* var. *constrictum*, *Navicula cryptocephala* var. *veneta*, *Surirella ovata*, and *Synedra rumpens*) whose relative abundance decreased in all streams after the introduction of grazers (Figs. 2.5a-b). Cells of these diatom taxa possessed large biovolumes: 10 out of the 11 taxa had cells whose biovolumes were above the 40th percentile of the distribution of diatom cell biovolumes (Table 2.3), and 6 of these taxa were among the 9 largest diatom taxa listed in Table 2.3. All four filamentous diatom taxa encountered during the experiment were in this group.

The algal assemblages on the BOT 1:1 substrates and in the JUGA-2X, 1X:1X, and 2X:2X streams were placed further to the left in the sample ordination after the introduction of grazers. This pattern corresponded to the high relative abundances of *Phormidium tenue* and especially of the basal cells of *Stigeoclonium tenue* (Figs. 2.5a-b and Figs. 2.2a, c, and d). Algal assemblages in the JUGA-2X streams remained in this region of the ordination space for the duration of the experiment (Fig. 2.5a). Algal assemblages in the 1X:1X streams and BOT 1:1 substrates were placed further to the right by day 36 and downward and to the far right by day 50; this pattern indicated an increase in the relative abundance of *Synedra ulna*, *Nitzschia linearis*, *Oscillatoria agardhii*, and the small, prostrate diatoms (*Achnanthes minutissima*, *Navicula arvensis*, *Navicula*

Figure 2.5. Detrended correspondence analysis (DCA) of the sample by species matrix of the numerical relative abundance data. The associated eigenvalues are 0.349 (axis 1) and 0.180 (axis 2). See text for explanation of ordination method. (a) Successional trajectories of algal assemblages. (b) Ordination of taxa listed in Table 2.3.

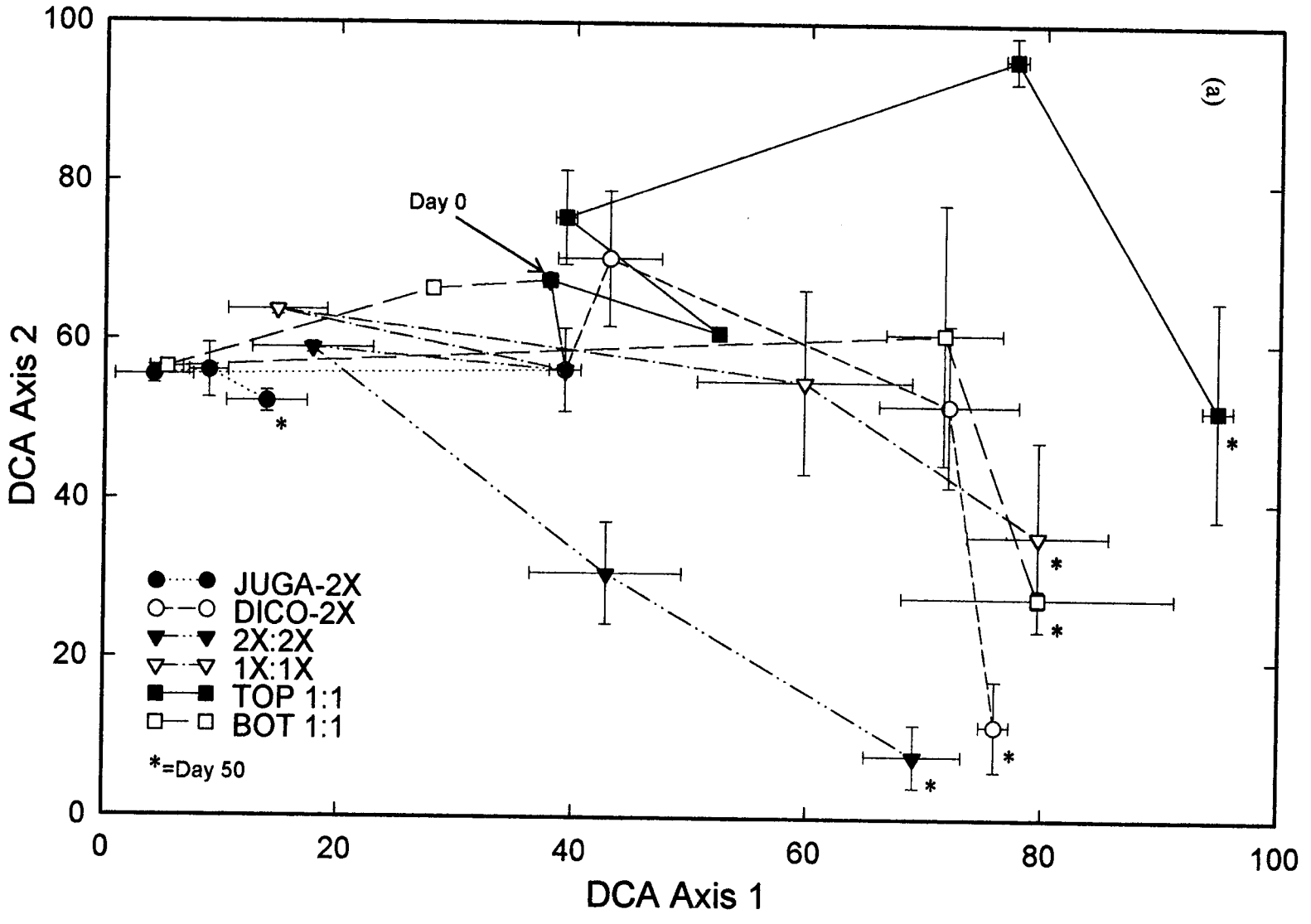
100
80
60
40
20
0
0
20
40
60
80
100
DCA Axis 2
DCA Axis 1
(a)
Day 0
JUGA-2X
DICO-2X
2X:2X
1X:1X
TOP 1:1
BOT 1:1
*=Day 50

Figure 2.5

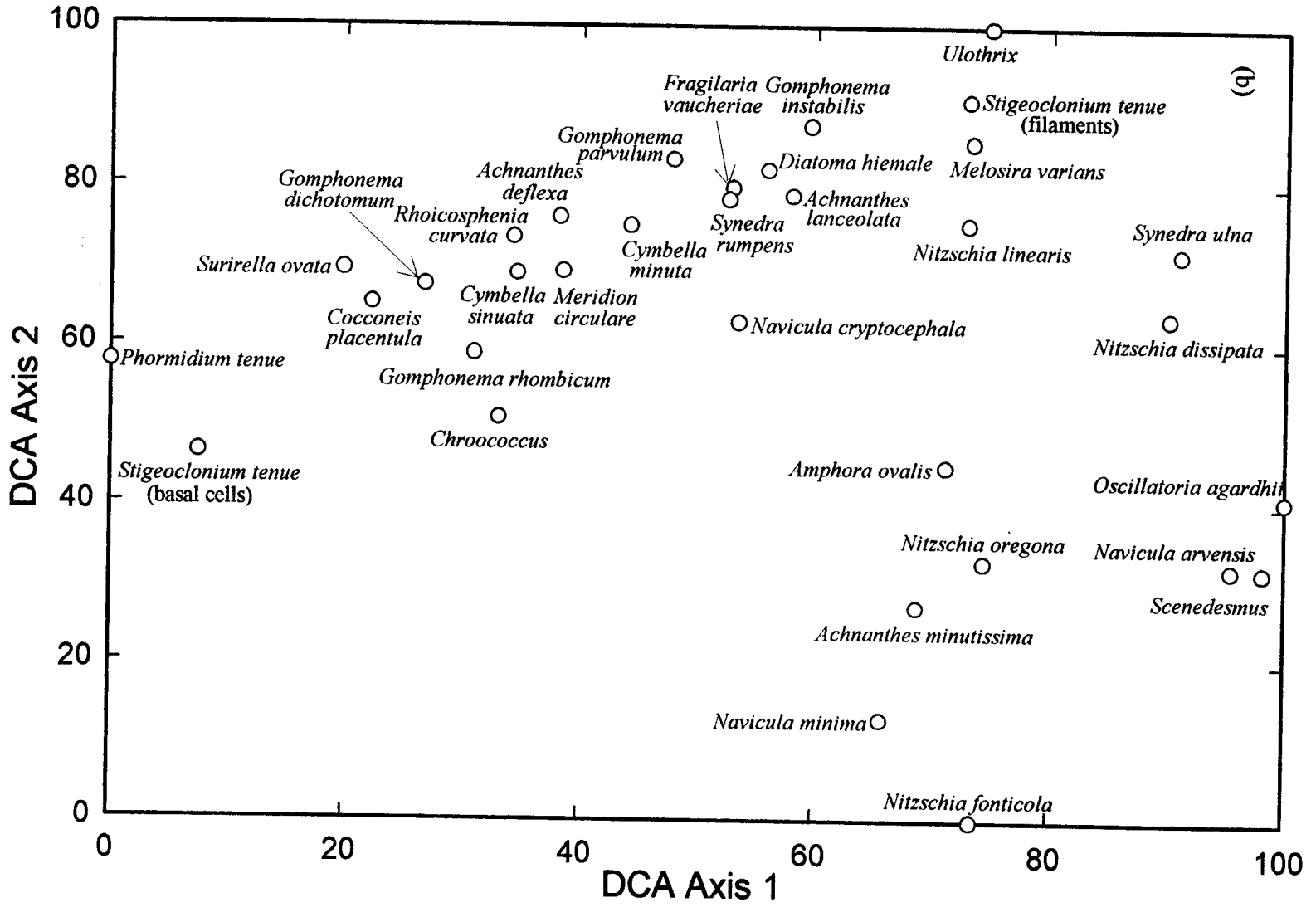

Figure 2.5 (continued)

minima, and *Nitzschia fonticola*) (Figs. 2.5a-b and Figs. 2.2c and f). Samples representing the 2X:2X streams also placed to the right and downward, but were to the left and below the BOT 1:1 substrates and 1X:1X streams on both days 36 and 50; this pattern indicated a greater relative abundance of small, prostrate diatoms and a decrease in the relative abundance of *Ulothrix*, *Phormidium tenue*, and *Stigeoclonium tenue* basal cells in the 2X:2X streams (Figs. 2.5a-b and Fig. 2.2).

On day 22, samples representing the TOP 1:1 substrates and the DICO-2X streams placed in the top-center of the ordination (Fig. 2.5a). This position signified assemblages characterized by *Achnanthes lanceolata* and *Gomphonema parvulum*, as well as a relatively low abundance of *Stigeoclonium tenue* basal cells (Fig. 2.5b, see Figs. 2.2b and e). By day 36 the DICO-2X streams and TOP 1:1 substrates placed further to the right (Fig. 2.5a). On day 36 assemblages on the TOP 1:1 substrates were represented in the upper right-hand corner of the ordination, which indicated dominance by filaments of *Ulothrix* and *Stigeoclonium tenue*. On the same day, samples representing the DICO-2X streams placed right-center in the ordination, indicating less dominance by these taxa and a greater relative abundance of *Synedra ulna*. By day 50 the trajectories of the DICO-2X streams and the TOP 1:1 substrates moved downward, which corresponded to an increase in the relative abundance of the small, prostrate diatoms and less dominance by *Ulothrix* (Figs. 2.5a-b, and Figs. 2.2b and e).

2.5 Discussion

2.5.1 Algal Successional Patterns

The major algal taxa present in the laboratory streams could generally be divided into three groups, depending on which day that their relative biovolumes were maximum: just prior to the introduction of grazers, two weeks after the introduction of grazers, or at the end of the experiment (six weeks after grazer introduction) (Fig. 2.2). The relative biovolumes of the filamentous diatoms *Fragilaria vaucheriae*, *Melosira varians*, *Diatoma hiemale* var. *mesodon*, and *Meridion circulare* var. *constrictum* were highest on day 7, just prior to the introduction of the grazers. The relative abundances of basal cells of the filamentous chlorophyte *Stigeoclonium tenue*, the cyanobacterium *Phormidium tenue*, and the diatoms *Gomphonema parvulum* and *Achnanthes lanceolata* were generally greatest on day 22, two weeks after the introduction of the grazers. Finally, the group of prostrate diatoms (*Nitzschia fonticola*, *Achnanthes minutissima*, *Navicula arvensis*, and *Navicula minima*), the long linear diatom *Synedra ulna*, and the cyanobacterium *Oscillatoria agardhii* had their maximum relative abundances at the end of the experiment, after an initial decrease following the introduction of the grazers. Thus the substrates were colonized by large, filamentous diatoms (cf. Oemke and Burton 1986) which are presumed to have high sinking rates (Stevenson and Peterson 1989) or high growth rates early in succession (McCormick and Stevenson 1991b). The addition of the herbivores into the streams led to an increase in relative abundance of *Phormidium tenue* and basal cells of *Stigeoclonium tenue* (cf. Steinman *et al.* 1987), which were then gradually replaced by

small, prostrate diatoms and *Synedra ulna* in an increasingly patchy algal mosaic (cf. Steinman *et al.* 1987, DeNicola *et al.* 1990, Pan and Lowe 1994). Pan and Lowe (1994) suggested that increases in *Synedra ulna* abundance under the influence of grazing may also be due to a high growth rate, which may result from greater efficiency in light utilization because of an erect, linear growth form. Grazing in our experiment did not lead to inhibition of succession, but rather to distinct grazer-tolerant algal assemblages. Although a possible conclusion could be that grazers facilitate succession (Connell and Slatyer 1977) in algal assemblages, the results observed may also have been affected by the lack of immigration of algal species into the laboratory streams after they were seeded with the inoculum.

2.5.2 Effect of Herbivore Type on Algal Succession

The degree to which herbivores suppress algal biomass and modify periphyton taxonomic structure increases with the density of grazers (Colletti *et al.* 1987, Swamikannu and Hoagland 1989) and also depends on differences in mouthpart morphology and feeding behavior of the animal populations (McAuliffe 1984b, Lamberti *et al.* 1987, Karouna and Fuller 1992). Such differences can generate "species-related gradients of grazing intensity" (DeNicola *et al.* 1990).

Densities of herbivores in this experiment were within the range of those found in nearby natural streams (Hawkins and Furnish 1987, Li 1990), and based on past experiments, and theoretical considerations, the intensities of grazing in the JUGA-2X, DICO-2X, and 1X:1X streams were assumed to be equivalent at the beginning of the

experiment. However, effects of the herbivores on algal assemblages in these streams differed despite this putative equality of grazing pressure. Periphyton in the JUGA-2X streams was characterized by low biomass and low heterogeneity, and by relatively high abundances of the filamentous cyanobacterium *Phormidium tenue* and basal cells of the heterotrichous chlorophyte *Stigeoclonium tenue*, whereas in the DICO-2X streams biomass was moderate with high heterogeneity, and the algal community changed to assemblages characterized by the prostrate diatoms *Nitzschia fonticola*, *Achnanthes minutissima*, *Navicula arvensis*, and *Navicula minima*, and the long linear diatoms *Synedra ulna* and *Nitzschia linearis*. With respect to macroscopic physiognomy, the JUGA-2X streams appeared to be intensely and uniformly grazed, whereas the DICO-2X streams were incompletely grazed with discrete clumps and patches of periphyton.

Several alternative explanations may account for differences between the effects of grazing by *Juga* and *Dicosmoecus* in our experiment. For example, the mouthpart morphologies of *Juga* and *Dicosmoecus* are different: *Juga* grazes periphyton by rasping the substrate with a radula and is able to remove periphyton closely appressed to the substrate (Hawkins and Furnish 1987), whereas *Dicosmoecus* scrapes the substrate with its mandibles and tarsal claws, and is often sloppy in its feeding, which leads to an increase in algal export (Lamberti *et al.* 1987, DeNicola *et al.* 1990). However, Steinman *et al.* (1987) found great similarity in algal community structure between streams with various densities of *Juga* and *Dicosmoecus*, and expressed doubts about attributing differential grazer effects on periphyton to differences in herbivore mouthpart morphology. Density-dependent effects on foraging behavior also could have caused differences in patchiness of

algal assemblages. While the rate of food consumption in the JUGA-2X and DICO-2X streams was assumed to be equivalent, the lower density of *Dicosmoecus* could have contributed to the greater patchy distribution of periphyton in the streams with *Dicosmoecus* in comparison to the streams with *Juga*. The mosaic of grazed and ungrazed patches of periphyton that occurred in the streams with *Dicosmoecus* was an assemblage with relatively high algal heterogeneity, an abundance of grazer-resistant prostrate diatoms, and large, linear diatoms, which are less grazer-resistant. However, the effects of herbivores in this experiment were in several respects opposite to the results obtained by DeNicola *et al.* (1990) in an earlier experiment conducted under similar conditions with respect to substrate, nutrients, irradiation, and identical species and densities of herbivores (Table 2.4). Therefore, differences in mouthpart morphology and density of animals do not adequately explain the different outcomes of grazing in the JUGA-2X and DICO-2X streams.

Dissimilarities in the effects of *Juga* and *Dicosmoecus* on periphyton between our experiment and the experiment by DeNicola *et al.* (1990) may have been related to differences in experimental design (Table 2.4a). Water temperature affects algal taxonomic composition directly (see review by DeNicola 1996) and has been reported to affect feeding behavior of *Juga* (Furnish 1989). The life history of herbivores also affect periphyton, as Li and Gregory (1989) found that 5th instars of *Dicosmoecus* tend to feed more than 4th instars, and that the behavior of *Dicosmoecus* also was influenced by the composition of the algal assemblage. Differences in the taxonomic composition of the algal assemblage at the time of grazer introduction can also influence the outcome of

Table 2.4. Comparison of laboratory streams grazed by either *Juga silicula* or *Dicosmoecus gilvipes* in this experiment and in the experiment by DeNicola *et al.* (1990).

(a) Difference in Experimental Conditions

Experiment	Rep-lications	Instars of *Dicosmoecus*	Water Temperature (°C)	Time of Year	Algal Inoculum	Origin of Animals
This Experiment	3	mostly 4th (some 3rd)	12-14	April-June	dominated by *Ulothrix*	Coast Range, OR
DeNicola *et al.* (1990)	1	mostly 5th (some 4th)	15-17	July-August	dominated by *Scenedesmus*	Coast and Cascade Ranges, OR

(b) Similarities in Experimental Conditions

Experiment	Density of *Juga* (snails m^{-2})	Size of *Juga* (mm)	Density of *Dicosmoecus* (caddisflies m^{-2})	Grazer Introduction (Day)	Irradiance (µmol quanta m^{-2} s^{-1})	Current Velocity (cm s^{-1})	Water Supply
This Experiment	500	10-15	50	8	425	10	Fairplay Laboratory Well
DeNicola *et al.* (1990)	500	10-15	50	9	425	10	Fairplay Laboratory Well

Table 2.4 (continued)

(c) Summary of Algal Assemblages

Experiment	Grazer	
	Juga silicula	*Dicosmoecus gilvipes*
This Experiment (day 50)	low biomass (~ 2 g m^{-2}) low heterogeneity dominant taxa: *Stigeoclonium tenue* (basal cells) *Synedra ulna* *Phormidium tenue* (on days 22-36) macroscopic physiognomy: thin layer of periphyton	high biomass (~20 g m^{-2}) high heterogeneity dominant taxa: *Synedra ulna* prostrate diatoms macroscopic physiognomy: patchy, large tufts of algae
DeNicola *et al.* (1990) (day 40)	high biomass (~20 g m^{-2}) high heterogeneity dominant taxa: *Nitzschia oregona* *Navicula minima* macroscopic physiognomy: patchy, large tufts of algae	low biomass (<5 g m^{-2}) until day 40 (~10 g m^{-2}) low heterogeneity dominant taxa: *Nitzschia frustulum* *Navicula minima* *Stigeoclonium tenue* (basal cells) macroscopic physiognomy: thin layer of periphyton

grazer-periphyton interactions in laboratory experiments (DeNicola *et al.* 1990). Therefore, because of other biotic and abiotic factors, the assumption of equivalent grazing intensity in the JUGA-2X and DICO-2X streams in our experiment may have been invalid, at least under the specific conditions of the experiment; differences in grazing intensity may provide an alternative explanation for different outcome of grazing in the JUGA-2X and DICO-2X streams. Moreover, hunger levels and subsequent feeding behavior of the animals could have been affected by times and conditions of animal storage before introduction into the laboratory streams (D.M. DeNicola, personal communication). McIntire *et al.* (1996) define food (or consumptive) demand as "the consumption rate when food is in unlimited supply and the quality of the resource is optional." Consumptive demand of herbivores, which is affected by size and stage in the life history of the animals, as well as physical conditions of the environment, may be as important a factor as grazer species, mouthpart types, and densities in affecting the taxonomic structure of periphyton assemblages.

2.5.3 Effects of Concurrent Grazing by *Juga* and *Dicosmoecus*

Two weeks after the introduction of the herbivores, periphyton in the 1X:1X streams appeared to be heavily grazed, and algal biomass and taxonomic composition were similar to that in the JUGA-2X streams; but by the end of the experiment, heterogeneity, biomass, macroscopic physiognomy, and taxonomic composition of periphyton in the 1X:1X streams were more similar to the assemblages in the DICO-2X streams. Several hypotheses may explain the effects of concurrent grazing by intermediate

densities of *Dicosmoecus* and *Juga*. The ability of *Juga* to alter the periphyton in the 1X:1X streams may have been reduced by the presence of only half the density of animals compared to the JUGA-2X streams. In addition, individuals of *Dicosmoecus* occasionally disrupted grazing by physically inhibiting contact between *Juga* and the substrate (personal observation). Therefore, interference competition may have reduced the effectiveness of grazing by *Juga*. Interference competition also has been observed between larvae of the hydroptilid caddisfly *Leucotrichia pictipes* (Banks) and larvae of the baetid mayfly *Baetis* spp. or the glossosomatid caddisfly *Glossosoma* spp. (McAuliffe 1984a). In this case, *Leucotrichia* larvae were able to exclude other species of grazers from their territories.

After the introduction of the herbivores, periphyton in the 2X:2X streams was characterized by low biomass, intermediate heterogeneity, and taxonomic composition similar to that in the 1X:1X streams and JUGA-2X streams, i.e., dominance by the diatoms *Gomphonema parvulum* and *Achnanthes lanceolata*, the filamentous cyanobacterium *Phormidium tenue*, and basal cells of *Stigeoclonium tenue*. At the end of the experiment, periphyton heterogeneity had changed little and biomass had increased slightly, and the algal assemblages were again similar to those in the 1X:1X streams, but with more prostrate diatoms and basal cells of *Stigeoclonium tenue*. Doubling the density of the herbivores clearly depressed algal biomass and heterogeneity, and directed algal succession more toward assemblages dominated by prostrate diatoms and *Stigeoclonium tenue* basal cells in comparison to assemblages in the 1X:1X streams.

Effects of concurrent grazing by high densities of *Juga* and *Dicosmoecus* on algal assemblages were not additive. If the effects had been additive, algal biomass in the 2X:2X streams should have been less than in the DICO-2X and JUGA-2X streams, with the algal assemblages consisting of only the most grazer-resistant taxa. Instead, algal biomass and heterogeneity in the 2X:2X streams were intermediate between the JUGA-2X and DICO-2X streams throughout the experiment. At the end of the experiment algal biomass in the 2X:2X streams was not significantly different from biomass in either of the single grazer streams. By the end of the experiment the 2X:2X streams possessed the highest relative abundance of the prostrate diatoms, but relative abundance of *Stigeoclonium tenue* basal cells was intermediate between the single grazer streams.

In summary, concurrent grazing by *Juga* and *Dicosmoecus* resulted in algal assemblages with a different taxonomic composition than assemblages exposed only to a single grazer. Unlike previous experiments involving concurrent grazing (Hill and Knight 1988a, Feminella and Resh 1991, Kohler 1992, Pan and Lowe 1994), the concurrent effects of *Juga* and *Dicosmoecus* were not additive. Concurrent effects of larvae of the mayfly *Ameletus* and the caddisfly *Neophylax* (Hill and Knight 1988a) or the larvae of the caddisflies *Gumaga nigricula* and *Helicopsyche borealis* (Feminella and Resh 1991) in natural streams produced algal assemblages of prostrate, grazer-resistant taxa with low biomass. Kohler (1992) found that the effects of concurrent grazing by larvae of the mayfly *Baetis tricaudatus* and the caddisfly *Glossosoma nigrior* in small, circular laboratory chambers were also additive in reducing periphyton biomass; in a third experiment, concurrent grazing by both these species did not reduce algal biomass more

than either grazer alone (Kohler 1992). Interference competition between *Juga* and *Dicosmoecus* in our experiment may explain, in part, why the concurrent effects of the grazers were not additive.

Some caution is warranted in making conclusions based on comparison of relative abundances of algal taxa among different treatments. Estimates of biomasses of individual taxa showed that the biomasses of certain taxa (*Phormidium tenue* and basal cells of *Stigeoclonium tenue*), whose relative abundances varied according to treatment, actually may have been independent of treatment (Figs. 2.3a-b). In other words, analysis of relative abundance leads to the conclusion that the different grazing treatments had differing effects on these two taxa, whereas another possible interpretation based on the biomass estimates is that these taxa were affected neither positively nor negatively by the different grazing treatments, and that variation in relative abundance in these two taxa was only an artifact caused by the changes in abundance of other species.

2.5.4 Substrate Heterogeneity and Herbivore-Periphyton Interactions

Substrate heterogeneity also influenced plant-herbivore interactions. In the blocked-substrate streams, the TOP 1:1 substrates accumulated more algal biomass than the BOT 1:1 substrates throughout the experiment. Two weeks after the introduction of the grazers, the macroscopic physiognomy of periphyton on the BOT 1:1 substrates was similar to the JUGA-2X and 2X:2X streams, with the algal assemblages characterized by low heterogeneity and by high abundance of *Stigeoclonium tenue* basal cells and *Phormidium tenue*. By the end of the experiment algal heterogeneity was high, and the

algal assemblages on the BOT 1:1 substrates were more similar to the DICO-2X, 1X:1X, and 2X:2X streams in that the relative abundances of *Stigeoclonium tenue* basal cells and *Phormidium tenue* were greatly reduced while relative abundances of *Synedra ulna*, the prostrate diatoms, and *Oscillatoria agardhii* increased. The algal assemblages on the TOP 1:1 substrates on day 22 contained relatively more *Achnanthes lanceolata* and *Gomphonema parvulum* and less *Phormidium tenue* and *Stigeoclonium tenue* basal cells than on the BOT 1:1 substrates; at the end of the experiment the algae on the TOP 1:1 and BOT 1:1 substrates were more similar. Heterogeneity of algal assemblages on the TOP 1:1 substrates was high throughout the experiment.

Because the animal densities in the blocked-substrate streams were identical to those in the 1X:1X streams, any differences in the algal assemblages between these streams can be attributed the effects of substrate heterogeneity. There were two major ways in which substrate heterogeneity influenced herbivore-periphyton interactions in the laboratory streams: 1) modification of flow regime, and 2) unequal distribution of grazers on substrate surfaces. In natural streams, substrate heterogeneity also provides herbivores refuge from predators, which increases the grazing pressure on periphyton (Power and Matthews 1983). In the laboratory streams the presence of the blocks lowered free-water velocity and thickened the laminar sublayer over the lower substrates between the blocks (DeNicola and McIntire 1990). By modifying the current regime, the blocks altered the patterns of algal colonization, so that prior to the introduction of the grazers the algal assemblages were on a different successional trajectory than assemblages in the streams without substrate heterogeneity (cf. DeNicola and McIntire 1990). On day 7, both the

TOP 1:1 and BOT 1:1 substrates had high relative abundances of filamentous diatoms (*Fragilaria vaucheriae*, *Melosira varians*, *Diatoma hiemale* var. *mesodon*, and *Meridion circulare* var. *constrictum*), which are presumed to have high sinking rates (Stevenson and Peterson 1989).

Both species of grazers were unequally distributed in the blocked-substrate streams. Throughout the experiment, *Juga* and *Dicosmoecus* individuals were much more frequently found on the lower substrates, thereby increasing the animal densities on the BOT 1:1 substrates and decreasing the animal densities on the TOP 1:1 substrates (personal observation; G.A. Lamberti, unpublished data; see also DeNicola and McIntire 1991). By altering the flow regime, the substrate blocks provided the animals with refuge from the effects of the current (Hawkins and Furnish 1987, Li and Gregory 1989, DeNicola and McIntire 1991). Presumably, increased grazing pressure accounted for the similarity on day 22 between the BOT 1:1 substrates and the JUGA-2X and 2X:2X streams and decreased grazing pressure accounted for the greater algal biomass found on the TOP 1:1 substrates throughout the experiment. However, DeNicola and McIntire (1991) found that algal taxonomic composition did not differ very much between top and bottom substrates exposed to grazing by *Juga* at high densities. In the absence of grazers, DeNicola and McIntire (1990) found that algal biomass on recessed substrates was greater than on top substrates. Despite increased grazing pressure, by the end of our experiment biomass on the BOT 1:1 substrates was greater than in any of the non-blocked streams. This may have been partially due to relatively low algal export from the BOT 1:1

substrates and a concurrent deposition of exported material from the TOP 1:1 substrates onto the BOT 1:1 substrates (personal observation).

2.5.5 Summary and Implications for Natural Streams

Effects of concurrent grazing by dissimilar herbivores produced algal assemblages of distinct taxonomic composition. Because *Juga* (Hawkins and Furnish 1987) and many other grazers (Gregory 1983) are omnivorous generalists, a shift in algal taxonomic composition caused by the herbivory by one or two dominant species of grazers may have effects throughout not only the grazing food web, but the detrital food web as well. For example, if grazing by *Dicosmoecus* were to change the quantity and quality of the food resources available to *Juga*, a subsequent shift by *Juga* to feeding on detritus could impact other detritivores, with resulting effects on higher trophic levels and nutrient cycling.

Substrate heterogeneity affected grazer-periphyton interactions by changing the flow regime, which altered algal colonization and the distribution of herbivores. Taxonomic changes, such as an increase in the relative abundance in the filamentous form of *Stigeoclonium tenue*, brought about by substrate heterogeneity and its effects on herbivory, may affect patterns of nutrient uptake and cycling by algal assemblages (see review by Mulholland 1996).

Results of our experiment also suggested that consumptive demand of herbivores, dependent upon life history of the grazer and effects of the physical environment, may be as important a factor as grazer species, mouthpart types, and densities in affecting the taxonomic structure of periphyton assemblages. Further work suggested by this study

includes investigating the effects of different life history stages of herbivores, and their interaction with environmental variables such as temperature, on the taxonomic composition of benthic algal assemblages.

2.6 Acknowledgments

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3. EFFECTS OF NITROGEN ENRICHMENT ON THE TAXONOMIC STRUCTURE OF LOTIC PERIPHYTON

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3.1 Abstract

Many streams in the Pacific Northwest are nitrogen-limited and may receive substantial inputs of nitrogen as a result of industrial and agricultural practices. We investigated the effects of nitrogen enrichment on benthic algal assemblages in a nitrogen-limited natural stream. Ammonium sulfate was added to Lookout Creek, Oregon, during the summers of 1991 and 1992. A maximum of concentration of 90 μg NH_4^+-N l^{-1} was achieved in the enriched section, whereas NH_4^+-N concentrations in the non-enriched sections were low (1-6 μg l^{-1}). Algal biomass in the enriched section did not differ from the non-enriched section, except in June 1992, when algal biomass was greater in the enriched section. Although there were no patterns in algal heterogeneity relative to nitrogen enrichment, the taxonomic composition of periphyton in the enriched section was conspicuously different than the composition in the non-enriched section. Algal assemblages in the non-enriched section in early summer were composed of large, linear or filamentous, diatoms (e.g., *Gomphoneis eriense*, *Melosira varians*, and *Synedra ulna*) and filaments of the cyanobacterium *Oscillatoria agardhii*, which are typical of early successional assemblages. In mid-summer, the algal assemblages in the non-enriched section were characterized by small prostrate forms such as the diatoms *Achnanthes lanceolata*, *Cocconeis placentula* and basal cells of the heterotrichous chlorophyte, *Stigeoclonium tenue*. In late summer, particularly in pools in 1992, the assemblages in the non-enriched section were dominated by the large diatom *Epithemia hyndmanii*, which contains nitrogen-fixing endosymbionts, and by nitrogen-fixing heterocystous cyanobacteria (*Calothrix fusca*, *Calothrix* sp. 2, and *Nostoc* sp. 1). In the enriched

section, nitrogen addition altered the successional sequence so that algal assemblages in late summer were characterized by the diatoms *Rhoicosphenia curvata*, *Gomphonema rhombicum*, *Gomphonema dichotomum*, and *Nitzschia oregona*, and the filamentous cyanobacterium, *Phormidium tenue*, which are often found in nitrogen-rich aquatic ecosystems. Because *Epithemia* may be a preferred food source for herbivores in streams, enrichment with nitrogen and the subsequent decrease in the abundance of this diatom could have important effects on energy transfer to higher trophic levels.

3.2 Introduction

Nitrogen is an essential element for living organisms. Only certain prokaryotic organisms, including many cyanobacteria (Sprent and Sprent 1990), possess the ability to reduce atmospheric, molecular dinitrogen (N_2) to ammonia (NH_3) via the process of nitrogen fixation. Consequently, other organisms must obtain nitrogen heterotrophically from the environment, and, except for the small amounts of nitrogen fixed by natural or human industrial processes, this nitrogen is ultimately supplied by nitrogen-fixing prokaryotes, either directly through symbioses or indirectly via the nitrogen cycle.

Nitrogen is supplied to stream ecosystems from either autochthonous or allochthonous inputs. Autochthonous inputs include nitrogen fixation by cyanobacteria, whereas leaf fall and woody debris provide a major source of allochthonous inputs in forested watersheds. While the relative importance of autochthonous and allochthonous inputs of nitrogen in streams is not well known and likely varies according to watershed characteristics, it has been suggested that autochthonous nitrogen fixation by

cyanobacteria may supply a significant fraction of the total nitrogen demand, particularly in streams with low concentrations of dissolved nitrogen (see review by Mulholland 1996). Although phosphorus is the limiting element in many lotic ecosystems, low nitrogen concentrations limit primary production in many streams in the Pacific Northwest (see review by Borchardt 1996).

In the last decade, a large number of studies have investigated the effects of manipulation of nutrient concentrations on benthic algae (see review by Borchardt 1996). Many of these studies employed nutrient-releasing substrates to investigate effects of nitrogen enrichment on colonizing benthic algae (e.g., in streams, see Grimm and Fisher 1986, Hill and Knight 1988, Keithan *et al.* 1988, McCormick and Stevenson 1989, Winterbourn 1990, Peterson and Grimm 1992, Rosemond *et al.* 1993, Biggs and Lowe 1994; in lakes, see Fairchild *et al.* 1985, Carrick and Lowe 1989, Marks and Lowe 1993). A few studies of benthic algae have involved larger scale nitrogen fertilization of streams (e.g., Gregory 1980, Perrin *et al.* 1987, Peterson *et al.* 1993) or addition of nitrogen into small in-stream channels (Hill *et al.* 1992); whereas other research has investigated effects of nitrogen enrichment on periphyton by comparing pristine and polluted sections of lakes (Hawes and Smith 1993), by comparing upstream and downstream sections from point source pollution in streams (e.g., Klotz *et al.* 1976, Jones 1978, Francke and den Oude 1983), and by examining periphyton along natural gradients of nitrogen concentration in streams (Mulholland and Rosemond 1992). Mulholland *et al.* (1991) and Steinman *et al.* (1991) investigated nitrogen limitation in recirculating laboratory chambers. Nitrogen enrichment studies also have been performed in streams or lakes in a variety of biomes,

including regions classified as desert (e.g., Grimm and Fisher 1986, Peterson and Grimm 1992), temperate woodland (e.g., Keithan *et al.* 1988), coniferous forest (e.g., Perrin *et al.* 1987), and tundra (e.g., Cuker 1983, Hershey *et al.* 1988, Bergmann and Welch 1990). While some studies involved solely the manipulation of nitrogen concentration, many studies have investigated the interaction of nitrogen enrichment with manipulation of other abiotic factors, including phosphorus (Fairchild *et al.* 1985, Carrick *et al.* 1988, Hershey *et al.* 1988, Keithan *et al.* 1988, Bergmann and Welch 1990, Marks and Lowe 1993, Biggs and Lowe 1994), silicon (Carrick *et al.* 1988), pH (Carrick and Lowe 1989), current velocity (Biggs and Close 1989), and irradiance (Gregory 1980, Hill and Knight 1988b, Stevenson *et al.* 1991); and with biotic factors such as grazing by invertebrates (Hershey *et al.* 1988, McCormick and Stevenson 1989, Winterbourn 1990, Hill *et al.* 1992, Rosemond *et al.* 1993, Biggs and Lowe 1994, Pan and Lowe 1994, Pan and Lowe 1995) or fish (Stewart 1987).

Some general patterns have emerged from these studies. Enrichment with nitrogen often leads to an increase in algal biomass, but in some cases, algal biomass exhibits little change, either because increases in production are transferred to higher trophic levels (Hill *et al.* 1992, Rosemond *et al.* 1993), or because some other factor limits algal production, e.g., levels of irradiance (Lowe *et al.* 1986) or grazing (Hill and Knight 1988a). Although patterns vary and depend upon interactions with other abiotic and biotic factors, species in the following genera typically increase in abundance in response to high nitrogen concentrations: diatoms such as *Achnanthes*, *Cocconeis*, *Gomphoneis*, *Gomphonema*, *Rhoicosphenia*, and *Synedra*; cyanobacteria such as *Oscillatoria*; and chlorophytes such

as *Stigeoclonium* and *Ulothrix* (cf. Fairchild *et al.* 1985, Carrick *et al.* 1988, Hill and Knight 1988, Carrick and Lowe 1989, Winterbourn 1990, Steinman *et al.* 1991, Hawes and Smith 1993, Pan and Lowe 1994). Taxa which typically decline in abundance in response to high nitrogen concentrations include the nitrogen-fixing cyanobacteria *Calothrix* (Peterson and Grimm 1992, Hawes and Smith 1993) and *Nostoc* (Hawes and Smith 1993), and diatoms of the family Epithemiaceae, which contain nitrogen-fixing cyanobacterial endosymbionts: *Epithemia* (Fairchild and Lowe 1984, Hill and Knight 1988, Steinman *et al.* 1991, Peterson and Grimm 1992, Hawes and Smith 1993, Marks and Lowe 1993) and *Rhopalodia* (Fairchild and Lowe 1984, Hill and Knight 1988, Hawes and Smith 1993, Marks and Lowe 1993).

The general objective of this research was to investigate the effects of nitrogen enrichment on the taxonomic structure of benthic algal assemblages in a natural stream. We added nitrogen during the summers of 1991 and 1992 to a nitrogen-limited coniferous forest stream with an open canopy, and compared the taxonomic structure of algal assemblages in the upstream non-enriched section with assemblages in the downstream enriched section. We examined the following hypotheses: (1) nitrogen enrichment alters the successional trajectories of benthic algal assemblages, (2) there is an interaction between time of year and nitrogen enrichment in affecting the taxonomic composition of lotic periphyton, and (3) habitat type influences the effect of nitrogen enrichment on algal assemblages.

3.3 Materials and Methods

3.3.1 Lookout Creek

Lookout Creek is a nitrogen-limited (Gregory 1980) fifth order stream located in the H.J. Andrews Experimental Forest in the Willamette National Forest, Lane County, Oregon. The stream drains a watershed of approximately 60 km^2 in the western Cascade mountains. Although much of the stream flows through old-growth conifer forest, the lower 1200 meters of the stream are not light-limited, because most of the trees are outside of the floodplain. The elevation of the section used in this study is approximately 430 m. Measurements of chemical and physical variables, such as phosphate, total phosphorus, dissolved oxygen, pH, and temperature, indicated no apparent differences between non-enriched and enriched sections (see Table 3.1).

Discharge at the mouth of Lookout Creek throughout the water years 1990-91 and 1991-92 is given in Figure 3.1. Discharge during both years was high and variable from November to the beginning of June, and then decreased during the dry season from June to the end of September. Discharge was higher in the summer of 1991 (decreasing from 1800 to 270 l s^{-1}) than in the summer of 1992 (decreasing from 540 to 190 l s^{-1}).

3.3.2 Study Design

The study area consisted of the lower 1150 m of Lookout Creek, which was divided into 32 units classified as pools, riffles, rapids, or cascades. In many analyses,

Table 3.1. Physical and chemical data for Lookout Creek. Values are means, with standard error, of samples from June through September of 1991 and 1992. Values in brackets indicate number of samples. See Table 3.2 for location of samples.

Year	Section	PO_4-P ($\mu g\ l^{-1}$)	Total P ($\mu g\ l^{-1}$)	Dissolved O_2 ($mg\ l^{-1}$)	pH	Temperature (°C)
1991	Non-enriched (Riffle-17)	13.2 ± 0.5 [5]	25.8 ± 1.4 [5]	10.09 ± 0.25 [13]	7.40 ± 0.05 [9]	13.8 ± 0.6 [13]
	Enriched (Pool-12)	13.4 ± 0.7 [5]	26.8 ± 1.2 [5]	10.16 ± 0.25 [13]	7.41 ± 0.04 [9]	13.8 ± 0.6 [13]
	Enriched (Pool-1)	14.3 ± 1.3 [4]	24.3 ± 2.3 [4]	10.31 ± 0.31 [12]	7.41 ± 0.04 [8]	14.0 ± 0.6 [12]
1992	Non-enriched (Riffle-17)	14.6 ± 0.4 [10]	25.5 ± 2.5 [2]	9.23 ± 0.33 [8]	7.40 ± 0.05 [6]	14.1 ± 1.0 [8]
	Enriched (Pool-12)	14.4 ± 0.2 [10]	28.5 ± 0.5 [2]	9.21 ± 0.30 [8]	7.38 ± 0.05 [6]	14.1 ± 1.0 [8]
	Enriched (Pool-1)	14.3 ± 0.4 [10]	30.5 ± 3.5 [2]	9.28 ± 0.23 [8]	7.35 ± 0.04 [6]	14.4 ± 1.1 [8]

Figure 3.1. Lookout Creek discharge for the water years 1990-91 and 1991-92. Discharge was measured at USGS station number 14161500, located downstream from Pool-1. Asterisks along the x-axis indicate dates of algal sampling. Note logarithmic scale of y-axis.

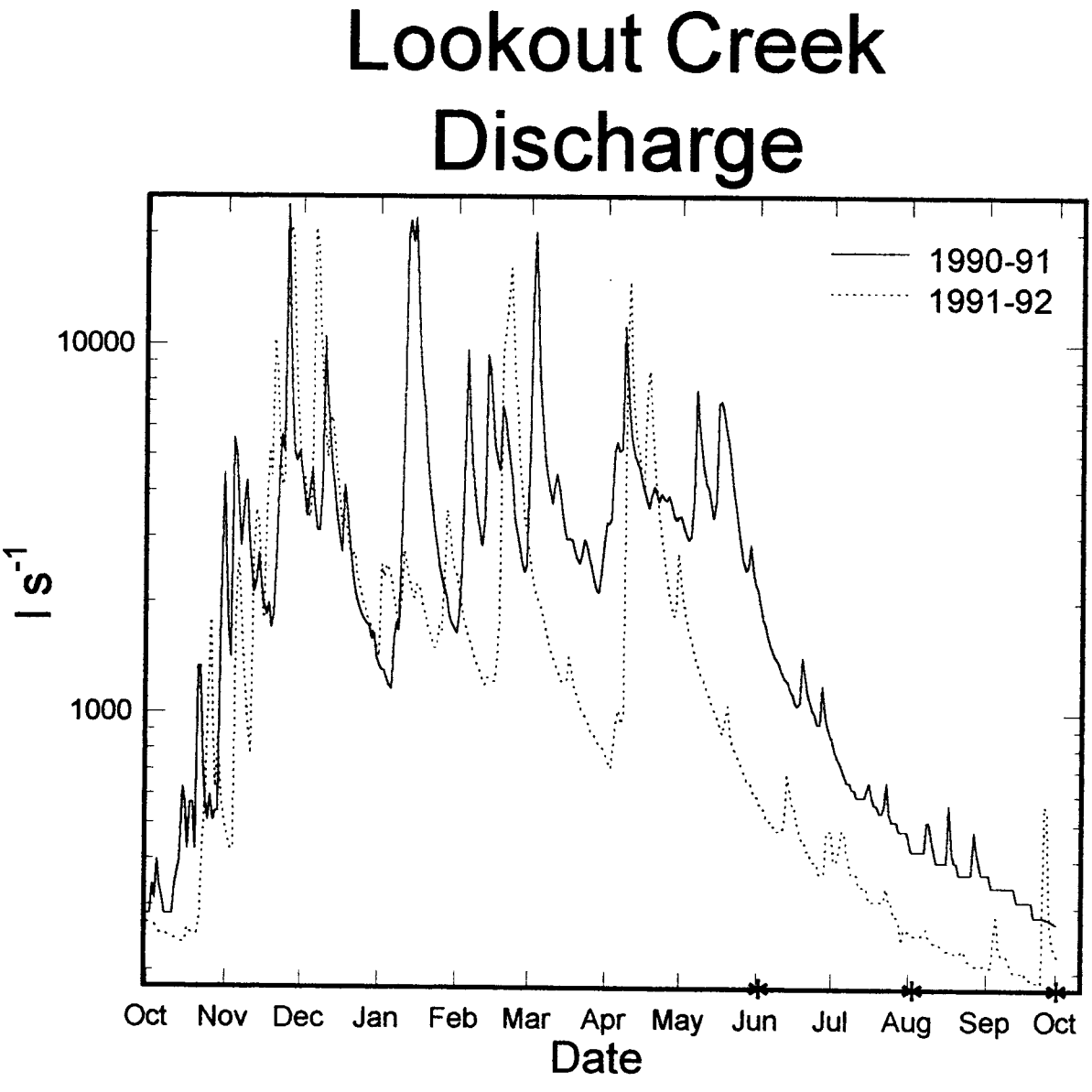
Lookout Creek
Discharge
1990-91
1991-92
10000
1000
l s-1
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Date

Figure 3.1

riffles, rapids, and cascades were considered together as "fastwater units". The lower 524 m served as the enriched section and consisted of 14 units (7 pools, 2 riffles, 3 rapids, and 2 cascades); the upper 613 m served as the non-enriched section and consisted of 17 units (7 pools, 3 riffles, 5 rapids, and 2 cascades). The units were numbered starting from 1 at the downstream end of the enriched section to 32 at the upstream end of the non-enriched section, and were labeled according to habitat type and unit number (e.g., Pool-1) (see Table 3.2). For an alternate labeling system used by other researchers at Lookout Creek, see Appendix. Samples were not collected from Riffle-17 in 1992, and the sample from Pool-16 for August 1992 was missing.

A pump-and-dripper system was used to introduce ammonium sulfate to the stream at Cascade-15 at the upstream end of the enriched section (see Table 3.2). Nutrient addition was started on 07 June 1991 and proceeded until 30 September 1991 during the first year, and in the second year the introduction commenced on 04 June 1992 and proceeded until 30 September 1992. For both years, nutrients were initially added at 25 $\mu g\ NH_4^+\text{-}N\ l^{-1}$ above background and then gradually increased over the course of the summer. In 1991 a maximum of 83 $\mu g\ NH_4^+\text{-}N\ l^{-1}$ above background was attained on 25 September, and in 1992 a maximum of 86 $\mu g\ NH_4^+\text{-}N\ l^{-1}$ above background was attained on 03 August.

3.3.3 Sampling

Algal samples from each unit were obtained three times each summer: June, August, and October. Sampling dates in 1991 were June 4-5, August 5-6, and

Table 3.2. Summary of non-enriched and enriched sections of Lookout Creek.

	Habitat Type	Unit Number	Length (m)
Non-enriched Section	Rapid	32	25.0
↓	Cascade	31	16.3
↓	Pool	30	34.0
↓	Rapid	29	21.0
↓	Cascade	28	25.0
↓	Rapid	27	31.0
↓	Pool	26	57.3
↓	Rapid	25	20.4
↓	Pool	24	46.3
↓			12.1
↓	Pool	23	41.0
↓	Riffle	22	64.3
↓			14.0
↓	Pool	21	22.8
↓			9.4
↓	Pool	20	28.3
↓	Riffle	19	42.1
↓	Rapid	18	67.0
↓	Riffle	17	12.1
↓	Pool	16	23.7
DRIPPER →→→	Cascade	15	
Enriched Section	Riffle	14	18.7
	Rapid	13	14.5
↓	Pool	12	29.4
↓	Riffle	11	68.5
↓	Pool	10	41.3
↓	Cascade	9	40.5
↓	Pool	8	27.2
↓			11.8
↓	Pool	7	18.3
↓	Cascade	6	58.3
↓	Pool	5	52.7
↓	Rapid	4	66.5
↓	Pool	3	19.4
↓	Rapid	2	18.0
↓	Pool	1	38.8

September 29, and sampling dates in 1992 were June 4, August 4, and October 4. For algal taxonomic analysis, three rocks, each approximately 10-20 cm broad, were arbitrarily selected from each unit. The rocks were selected in a stratified manner so that the lower, middle, and upper thirds of the unit, as well as the left, middle, and right thirds, were represented in the sample. The three rocks were brushed with a toothbrush to remove as much periphyton as possible, and the brushings were combined into one sample for each unit and fixed in Lugol's solution.

Algal biomass for each unit on each sampling date was estimated by the measurement of chlorophyll *a* concentration in relation to estimates of biomass:chlorophyll ratios. Concentration of chlorophyll *a* was estimated by selecting three rocks from each unit on each date and transporting them to the laboratory. Concentration of chlorophyll *a* per rock was determined by the method of Lamberti *et al.* (1987). The surface area of each rock was determined by covering the rock with aluminum foil, and the concentration of chlorophyll *a* ($g\ m^{-2}$) in the unit was calculated by dividing the concentration of chlorophyll *a* per rock by the surface area of the rock. Biomass:chlorophyll ratios (B/C ratios) were estimated for representative samples from five pools and five fastwater units in the non-enriched and enriched sections on each sampling date. Portions of the samples that were collected for taxonomic analysis (see previous paragraph) in these representative units were split into two subsamples, for which concentrations of algal biomass ($g\ ml^{-1}$) and concentrations of chlorophyll *a* ($g\ ml^{-1}$) were determined by the method of Lamberti *et al.* (1987). Biomass:chlorophyll ratios were calculated from these values, and the means of the B/C ratios for the pools and fastwater units in the enriched and non-enriched

sections on each date are presented in Table 3.3. Algal biomass (g m^{-2}) in each unit on each date was calculated according to the following equation,

$$B = C \cdot \overline{(B/C)},$$

where B was the calculated biomass (g m^{-2}), C was the chlorophyll a concentration (g m^{-2}) for the unit, and $\overline{(B/C)}$ was the mean B/C ratio for the five samples from the appropriate habitat, enrichment status, and date.

3.3.4 Counting Procedures

Each sample for taxonomic analysis was blended for approximately 30 seconds to break up clumps of algal filaments. Several drops of the sample then were placed on a glass slide, and 500 algal units were counted at 500X magnification using a Zeiss compound microscope. During this count, diatoms were lumped into a single taxon, whereas taxa other than diatoms were identified to species when possible. For unicellular taxa, an algal unit consisted of a single cell, whereas for filamentous taxa an algal unit consisted of a defined length of filament. Specifically, the filament lengths were either 12.5 µm (*Calothrix fusca*, *Calothrix* sp. 2, *Oscillatoria agardhii*, *Nostoc* sp. 1, *Stigeoclonium tenue* filaments, *Ulothrix zonata*, and *Zygnema* sp. 1) or 25 µm (*Phormidium tenue*). For the coenobic taxon *Scenedesmus* sp. 1, an algal unit consisted of a single coenobium. Filaments and basal cells of the heterotrichous green alga *Stigeoclonium tenue* were counted as distinct taxonomic entities.

Diatoms were identified to species where possible and counted separately using a subsample prepared in the following manner. The subsample was boiled in 30% hydrogen

Table 3.3. Ratio of algal biomass to chlorophyll *a* for June, August, October in 1991 and 1992. Values, expressed as $(g\ ml^{-1})/(g\ ml^{-1})$, are means of five samples. Fastwater units include riffles, rapids, and cascades.

		1991		1992	
Month	Section	Pools	Fastwater	Pools	Fastwater
June	Non-enriched	283.36	188.22	65.65	341.27
	Enriched	*229.86	*327.00	434.62	245.01
August	Non-enriched	390.08	425.07	82.72	91.24
	Enriched	341.05	333.24	145.78	77.65
October	Non-enriched	292.94	201.77	171.83	235.44
	Enriched	147.65	155.40	134.24	150.81

* No enrichment prior to June 1991

peroxide for 30 minutes, after which approximately 1 g of potassium dichromate was added. The cleaned frustules were allowed to settle for 24 hours, after which the supernatant was removed and replaced with distilled water. This process was repeated until the solution was clear. A few drops of the cleaned diatom suspension were placed on a cover slip and mounted on a slide with Cumar resin (Holmes *et al.* 1981). Five hundred diatom valves were counted at 1250X magnification. The numerical relative abundance ($N_{i,j}$) of a particular diatom species in a given sample then was calculated from the following equation:

$$N_{i,j} = D_j P_{i,j},$$

where $N_{i,j}$ was the calculated proportion of diatom species i in sample j, D_j was the proportion of diatoms in sample j, and $P_{i,j}$ was the proportion of diatom species i in the diatom count of sample j.

Biovolumes per algal unit (V_i) were calculated for each taxon using appropriate geometric formulae. The relative biovolume of a particular species in a given sample was calculated from the following equation:

$$R_{i,j} = V_i N_{i,j} \ / (V_1 N_{1,j} + V_2 N_{2,j} + \ldots + V_T N_{T,j}),$$

where $R_{i,j}$ was the calculated relative biovolume of taxon i in sample j, V_i was the biovolume per algal unit of taxon i, $N_{i,j}$ was the proportion of taxon i in sample j, and $(V_1 N_{1,j} + V_2 N_{2,j} + \ldots + V_T N_{T,j})$ represented the sum of $V_i N_{i,j}$ for all T taxa in sample j.

3.3.5 Data Analysis

The numerical relative abundance data ($N_{i,j}$) were organized into a samples-by-taxa matrix for analysis of community structure. A similar matrix derived from the relative biovolume data ($R_{i,j}$) also was constructed. Algal heterogeneity, based on numerical relative abundance, was expressed by the Shannon information measure (Peet, 1974).

Variations in taxonomic composition and relative abundance were examined by detrended correspondence analysis (DCA), an ordination method performed by the program DECORANA (Hill 1979, Gauch 1982). To remove extreme outliers, only those taxa which were found in at least 14 samples and also constituted at least 0.05% of the total count were included in the ordination. Results of this analysis, based on numerical relative abundance, were presented as a series of graphs illustrating successional trajectories for algal assemblages in each unit.

3.4 Results

3.4.1 Nitrogen

Concentrations of NH_4^+-N (ammonium) in the non-enriched section of Lookout Creek were low (less than 6 $\mu g\ l^{-1}$) throughout the summers of 1991 and 1992 (Fig. 3.2). Concentrations of NH_4^+-N in Pool-12 and Pool-1 in the enriched section were similar to values in the non-enriched section prior to nutrient introduction at the beginning of each summer. In both 1991 and 1992, concentration of NH_4^+-N in Pool-12 increased rapidly to

greater than 20 $\mu g\ l^{-1}$ after the commencement of nutrient addition and was as high as 85 $\mu g\ l^{-1}$ by the end of each summer. Concentrations of NH_4^+-N downstream in Pool-1 were less than in Pool-12 but were always greater than in the non-enriched section (Fig. 3.2). As ammonium became oxidized to nitrite and nitrate (Fig. 3.3), concentrations of (NO_2^- +NO_3^-)-N were greatest furthest downstream in Pool-1 (maximum of 55 $\mu g\ l^{-1}$) in both 1991 and 1992. Concentrations of (NO_2^-+NO_3^-)-N were always lowest in the non-enriched section, and decreased in the non-enriched section by approximately 50% between August and October in both 1991 and 1992. The magnitude of the difference in (NO_2^-+NO_3^-)-N concentrations between Pool-1 in the enriched section and Riffle-17 in the non-enriched section was much greater in the second half of the summer (after late July) in both years.

3.4.2 Algal Biomass

Algal biomass in pools ranged from 0.86 to 21.04 $g\ m^{-2}$ (Figs. 3.4a-b). Algal biomass in pools in the enriched section (right half of Fig. 3.4b) was greater than in pools in the non-enriched section (left half of Fig. 3.4b) in June and August 1992. Throughout 1991 and in October 1992 (Figs. 3.4a-b), no differences in algal biomass between the non-enriched and enriched sections were apparent. In August 1991, and in August and October 1992 (Figs. 3.4a-b), algal biomass decreased longitudinally downstream from a maximum located between Pool-7 and Pool-10 in the enriched section. For October 1991 and June 1992 there was a less obvious decrease in biomass downstream from a maximum in Pool-5 (Figs. 3.4a-b). In the non-enriched section in 1991, there was no apparent

Figure 3.2. Concentration of ammonium (NH_4^+) in Lookout Creek during (a) summer 1991 and (b) summer 1992. Ammonium sulfate was added into unit Cascade-15. Asterisks along the x-axis indicate dates of algal sampling.

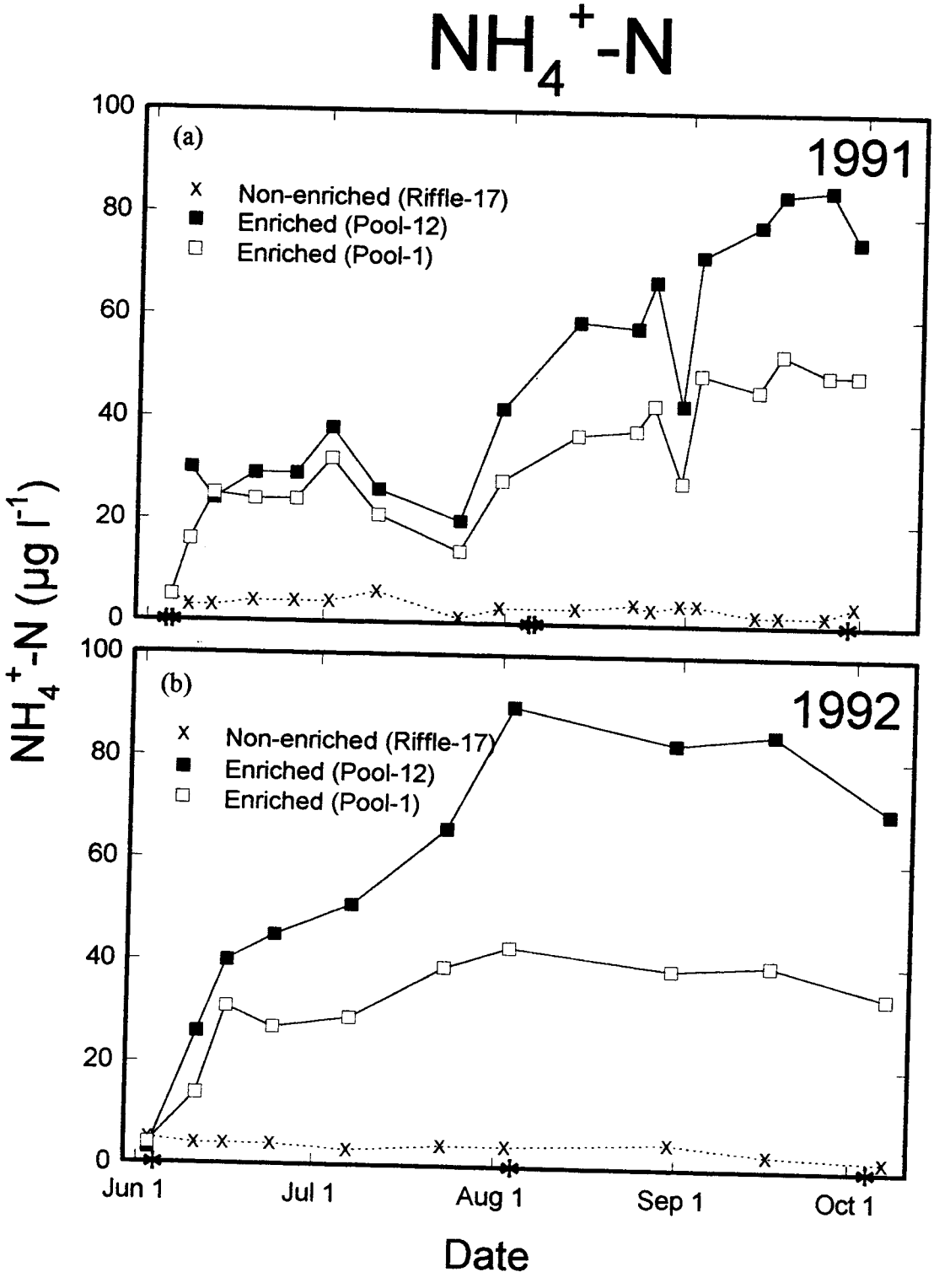
NH4+-N
(a)
1991
Non-enriched (Riffle-17)
Enriched (Pool-12)
Enriched (Pool-1)
(b)
1992
Non-enriched (Riffle-17)
Enriched (Pool-12)
Enriched (Pool-1)
NH4+-N (µg l-1)
0
20
40
60
80
100
Jun 1
Jul 1
Aug 1
Sep 1
Oct 1
Date

Figure 3.2

Figure 3.3. Concentration of nitrite (NO_2^-) plus nitrate (NO_3^-) in Lookout Creek during (a) summer 1991 and (b) summer 1992. Ammonium sulfate was added into unit Cascade-15. Asterisks along the x-axis indicate dates of algal sampling.

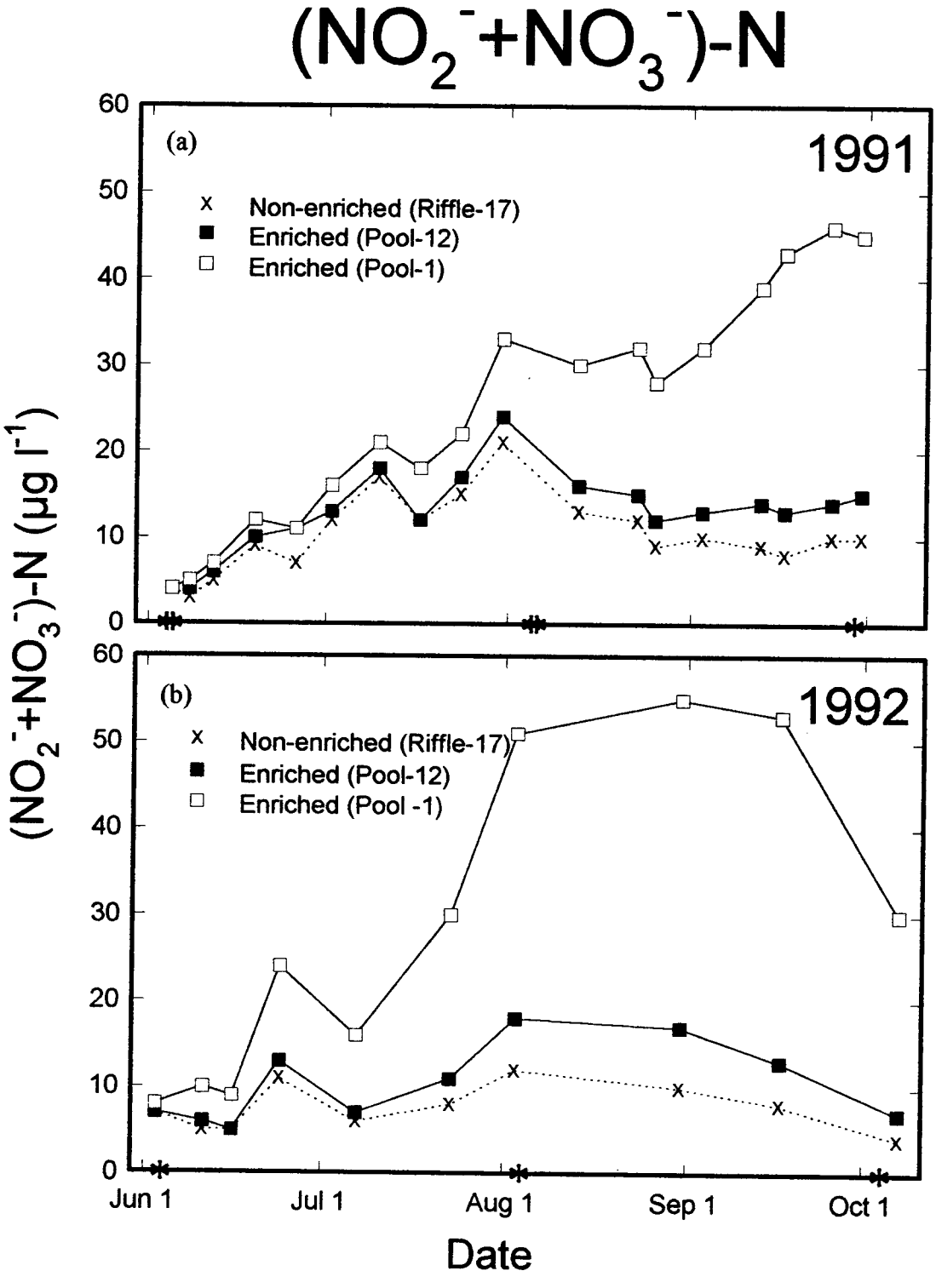
(NO2-+NO3-)-N
(a)
1991
Non-enriched (Riffle-17)
Enriched (Pool-12)
Enriched (Pool-1)
(b)
1992
Non-enriched (Riffle-17)
Enriched (Pool-12)
Enriched (Pool -1)
(NO2-+NO3-)-N (µg l-1)
0
10
20
30
40
50
60
Jun 1
Jul 1
Aug 1
Sep 1
Oct 1
Date

Figure 3.3

seasonal change in algal biomass over the summer (left half of Fig. 3.4a), but in the enriched section, algal biomass upstream from Pool-5 was maximal in August (right half of Fig. 3.4a). In 1992, algal biomass in the non-enriched section increased between June and October (left half of Fig. 3.4b), but there was no corresponding increase in biomass in the enriched section (right half of Fig. 3.4b).

In the fastwater units (riffles, rapids, and cascades) algal biomass ranged from 1.48 to 34.37 g m^{-2} (Figs. 3.4c-d). In the fastwater units in 1991, there were no obvious differences in algal biomass between the non-enriched and enriched sections, nor were there any differences seasonally (Fig. 3.4c). In 1992, there were no differences in biomass in the fastwater units between the non-enriched and enriched sections (Fig. 3.4d). In the non-enriched section in 1992, algal biomass decreased from June to August, and then increased between August and October (Fig. 3.4d). In the enriched section, algal biomass increased between August and October (Fig. 3.4d).

Ratios of algal biomass to chlorophyll (B/C ratios) used to derive estimates of algal biomass from chlorophyll *a* concentration are presented in Table 3.3. A distinct, greater than 2-fold, difference in the B/C ratios between the non-enriched and enriched sections was only present in the pools in June 1992 (greater than 6-fold difference).

3.4.3 Benthic Algal Community Structure

Fifty-four algal taxa were observed during the study. Thirty-seven taxa occurred in at least 14 samples and exhibited abundances of 0.05% or greater of the total count

Figure 3.4. Algal biomass, expressed as ash-free dry mass (AFDM), in Lookout Creek. Vertical line indicates location of nitrogen input at unit Cascade-15. Enrichment began June 1991. Graphs represent (a) Pools in 1991, (b) Pools in 1992, (c) Fastwater units in 1991, and (d) Fastwater units in 1992.

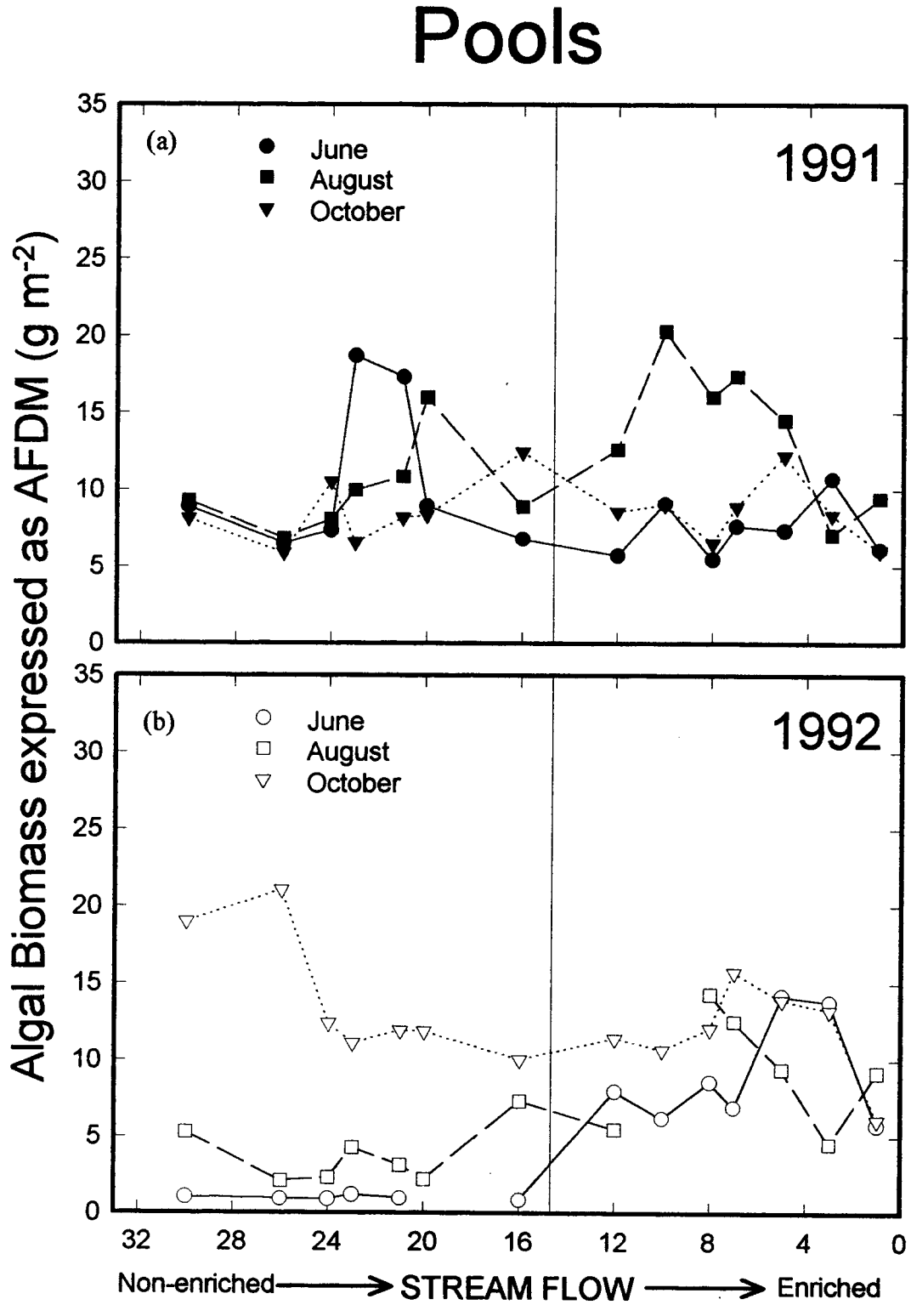
Pools
(a)
June
August
October
1991
(b)
June
August
October
1992
Algal Biomass expressed as AFDM (g m-2)
35
30
25
20
15
10
5
0
32
28
24
20
16
12
8
4
0
Non-enriched
STREAM FLOW
Enriched

Figure 3.4

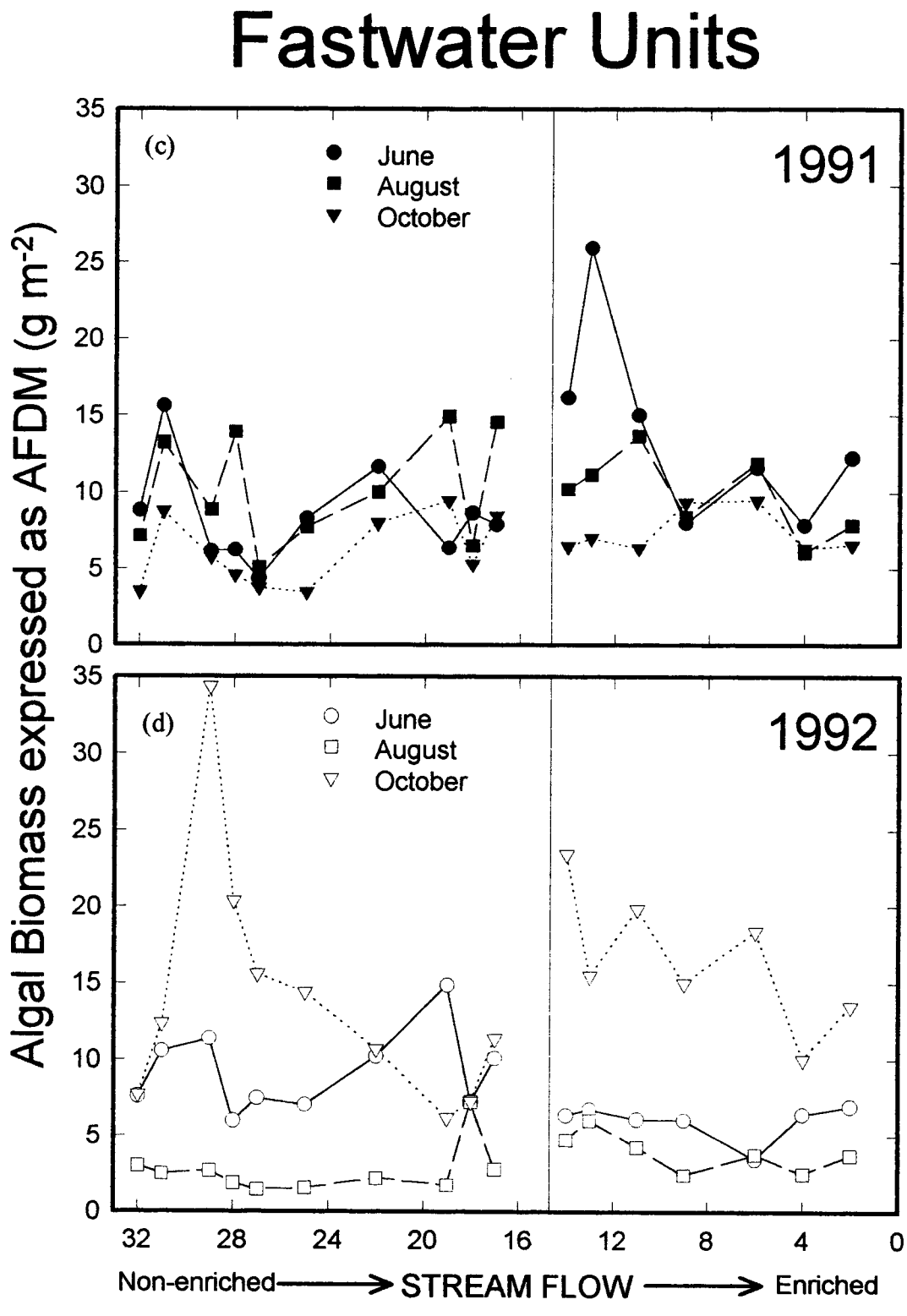

Figure 3.4 (continued)

(Table 3.4). Twenty-seven of these latter taxa were diatoms, three were chlorophytes, and seven were cyanobacteria.

Heterogeneity of algal assemblages, expressed by the Shannon diversity index (H'), ranged from a minimum of 0.87 in Pool-5 in August 1992 to a maximum of 2.83 in Pool-16 in October 1992 (Figs. 3.5a-d). In 1991 there were no apparent differences in heterogeneity in pools or fastwater units between the non-enriched and enriched sections (Figs. 3.5a and c). There were also no distinct seasonal patterns in heterogeneity in 1991 (Figs. 3.5a and c). In 1992, heterogeneity of algal assemblages was different between the non-enriched and enriched sections only in pools in August, when heterogeneity was less in the enriched section (Figs. 3.5b). In both the pools and the fastwater units in 1992, algal heterogeneity in the non-enriched section increased from June to October (left halves of Figs. 3.5b and d).

Successional trajectories of algal assemblages, as revealed by detrended correspondence analysis (DCA), are illustrated in Figures 3.6a-j. Ordination of taxa are presented in Figure 3.6k. Taxa explaining a successional pattern may be determined by relating corresponding regions of the sample and taxa ordination spaces, because the correspondence between sample and taxa spaces is maximized by DCA.

In 1991 algal assemblages in pools were initially in the right-center area of the sample ordination space (Figs. 3.6a and b), which corresponded to 10 large, mostly linear and/or filamentous, diatoms (*Gomphoneis eriense*, *Nitzschia dissipata*, *Nitzschia linearis*, *Diatoma hiemale*, *Synedra ulna*, *Hannea arcus*, *Fragilaria vaucheriae*, *Cymbella minuta*, *Melosira varians*, and *Melosira* sp. 2), filaments of the heterotrichous chlorophyte,

Table 3.4. List of algal taxa that occurred in Lookout Creek. Taxa in boldface occurred in at least 14 samples and exhibited abundances of 0.05% or greater of the total count, and were included the ordination analysis. Cell biovolumes are for a single cell, except for those indicated by [a] (12.5 µm filament), [b] (25 µm filament), or [c] (coenobium of four cells). Taxa presumed capable of fixing nitrogen are indicated by [N], and taxa whose nitrogen-fixing capability is uncertain are indicated by [N?]. Mean relative biovolumes were calculated over all samples (n=188).

Taxon	Cell Biovolume (μm^3)	Number of Samples	Mean Relative Bio-volume (%)
Division Chlorophyta			
Cosmarium sp. 1	9075	8	0.37
Scenedesmus sp. 1	[c]235	1	0.01
***Stigeoclonium tenue* (Ag.) Kütz.**			
basal cells	**75**	**187**	**6.79**
filaments	**[a]383**	**118**	**1.79**
***Ulothrix zonata* (Weber & Mohr) Kütz.**	**[a]8836**	**14**	**5.34**
zoospores	100	1	0.00
Zygnema sp. 1	[a]24544	1	0.38
Division Chrysophyta (Class Bacillariophyceae)			
***Achnanthes deflexa* Grun.**	**105**	**184**	**0.46**
Achnanthes exigua Grun.	120	1	0.00
***Achnanthes lanceolata* (Bréb.) Grun.**	**118**	**188**	**0.88**
***Achnanthes lewisiana* Patr.**	**38**	**188**	**0.41**
***Achnanthes minutissima* Kütz.**	**38**	**188**	**1.62**
***Amphora ovalis* Kütz.**	**161**	**107**	**0.05**
Caloneis bacillum (Grun.) Cl.	460	2	0.00
***Cocconeis placentula* var. *euglypta* (Ehr.) Cl.**	**571**	**188**	**10.40**
Cyclotella meneghiniana Kütz.	314	3	0.00
***Cymbella minuta* Hilse *ex* Rabh.**	**690**	**78**	**0.14**
***Cymbella sinuata* Greg.**	**265**	**107**	**0.11**
***Diatoma hiemale* var. *mesodon* (Ehr.) Grun.**	**1161**	**111**	**0.98**
***Epithemia hyndmanii* W. Sm.** [N]	**19330**	**143**	**28.46**
Eunotia pectinalis (O.F. Mull.) Rabh.	1480	9	0.02
Eunotia perpusillla Grun.	500	5	0.01
***Fragilaria vaucheriae* (Kütz.) Peters.**	**165**	**80**	**0.03**
Frustulia rhomboides (Ehr.) DeT.	5143	22	0.14
***Gomphoneis eriense* (Grun.) Skv. & Meyer**	**2579**	**134**	**2.07**
***Gomphonema dichotomum* Kütz.**	**182**	**188**	**2.47**

Table 3.4 (continued)

Taxon	Cell Biovolume (μm^3)	Number of Samples	Mean Relative Bio-volume (%)
Division Chrysophyta (Class Bacillariophyceae) (cont.)			
Gomphonema instabilis Hohn & Hellerm.	1114	1	0.00
Gomphonema parvulum Kütz.	421	16	0.01
***Gomphonema rhombicum* Fricke**	**796**	**188**	**7.38**
***Hannea arcus* (Ehr.) Patr.**	**996**	**101**	**0.59**
***Melosira varians* var. *mesodon* (Ehr.) Grun.**	**5872**	**117**	**3.10**
***Melosira* sp. 2**	**280**	**74**	**0.04**
Meridion circulare var. *constrictum* (Ralfs) V.H.	247	9	0.00
***Navicula arvensis* Hust.**	**49**	**146**	**0.04**
***Navicula cryptocephala* var. *veneta* (Kütz.) Rabh.**	**110**	**180**	**0.15**
***Navicula exigua* Greg. *ex* Grun.**	**298**	**47**	**0.02**
Navicula heufleri Grun.	471	25	0.01
***Navicula minima* Grun.**	**37**	**101**	**0.01**
Navicula viridula var. *avenacea* (Bréb. *ex* Grun.) V.H.	1444	10	0.02
***Nitzschia dissipata* (Kütz.) Grun.**	**307**	**155**	**0.41**
***Nitzschia fonticola* Grun.**	**37**	**188**	**0.11**
***Nitzschia linearis* W. Smith**	**3253**	**31**	**0.13**
***Nitzschia oregona* Sov.**	**203**	**156**	**0.46**
***Rhoicosphenia curvata* (Kütz.) Grun. *ex* Rabh.**	**403**	**188**	**6.74**
Synedra rumpens Kütz.	203	12	0.00
***Synedra ulna* (Nitz.) Ehr.**	**3824**	**124**	**3.39**
Division Cyanophyta			
***Calothrix fusca* Bornet & Flahault.** [N]	[a] **795**	**32**	**0.68**
***Calothrix* sp. 2** [N]	[a] **123**	**42**	**0.45**
Chamaesiphon incrustans Grun.	140	12	0.03
***Chamaesiphon* sp. 2**	**85**	**72**	**0.32**
***Chroococcus* sp. 1**	**2**	**188**	**0.33**
***Nostoc* sp. 1** [N]	[a] **123**	**29**	**0.29**
***Oscillatoria agardhii* Gom.** [N?]	[a] **245**	**162**	**10.08**
***Phormidium tenue* (Menegh.) Gom.** [N?]	[b] **44**	**188**	**2.28**

Figure 3.5. Heterogeneity (H') of algal assemblages in Lookout Creek. Vertical line indicates location of nitrogen input at unit Cascade-15. Enrichment began June 1991. Graphs represent (a) Pools in 1991, (b) Pools in 1992, (c) Fastwater units in 1991, and (d) Fastwater units in 1992.

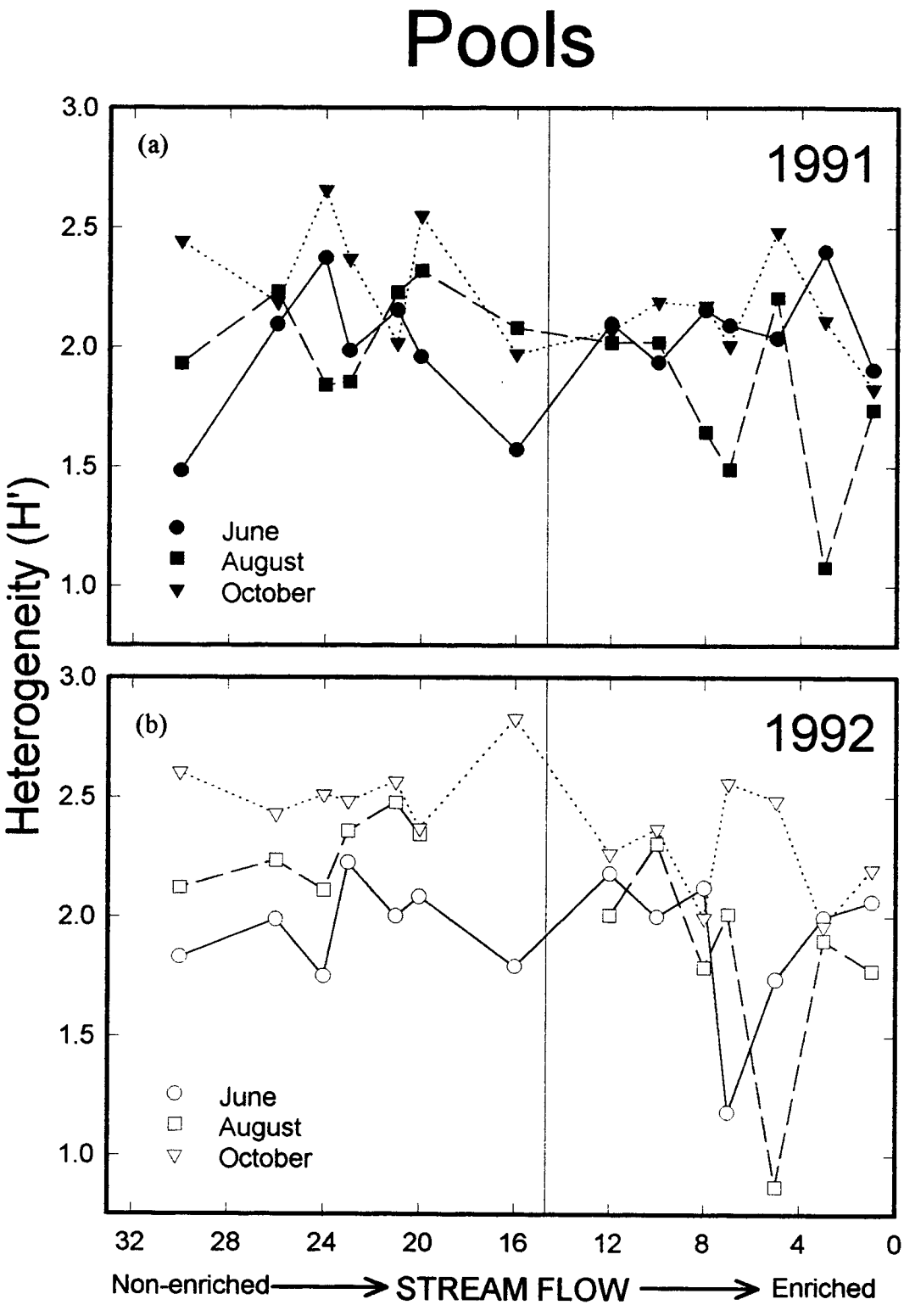
Pools
(a)
1991
(b)
1992
June
August
October
Heterogeneity (H')
3.0
2.5
2.0
1.5
1.0
32
28
24
20
16
12
8
4
0
Non-enriched
STREAM FLOW
Enriched

Figure 3.5

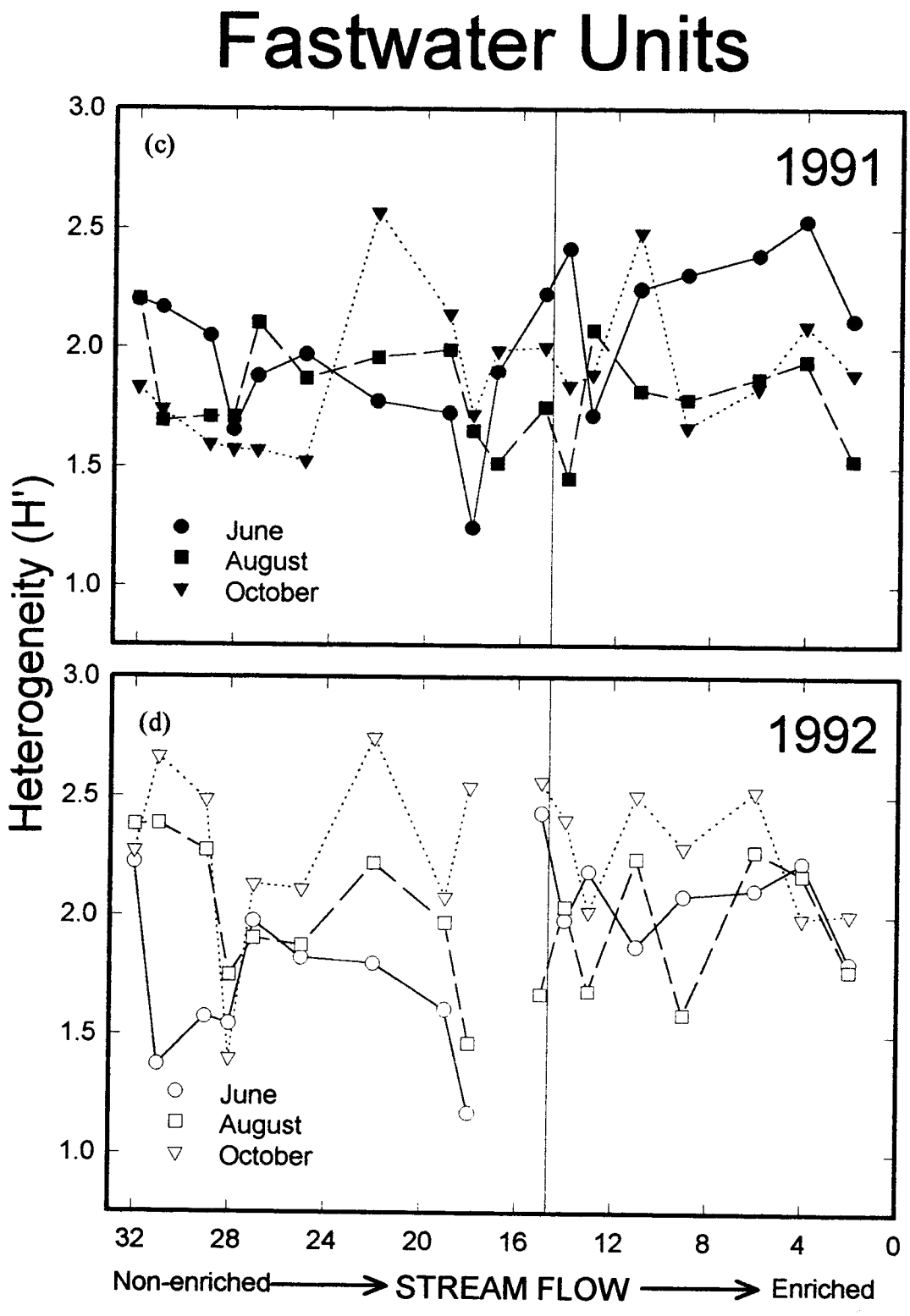

Figure 3.5 (continued)

Stigeoclonium tenue, and the filamentous cyanobacterium, *Oscillatoria agardhii* (Figs. 3.6k). Seven of these diatoms possessed cell biovolumes that were among the nine largest diatoms included in the ordination (see Table 3.4). In August 1991, algal assemblages in the pools were located in the center-bottom of the ordination space (Figs. 3.6a and b). This region was characterized by the nine smallest diatoms observed in the study (*Achnanthes deflexa*, *Achnanthes lanceolata*, *Achnanthes lewisiana*, *Achnanthes minutissima*, *Navicula arvensis*, *Navicula cryptocephala*, *Navicula exigua*, *Navicula minima*, and *Nitzschia fonticola*), two medium-sized diatoms, *Cocconeis placentula* and *Cymbella sinuata*, basal cells of *Stigeoclonium tenue*, and two cyanobacteria, *Chroococcus* sp. 1, and *Chamaesiphon* sp. 2 (Fig. 3.6k). In October 1991, pools in the non-enriched section were located slightly to the left of their position in August in the ordination, whereas pools in the enriched section were near the center of the ordination space (Figs. 3.6a and b).

In June 1992, algal assemblages in pools in both the enriched and non-enriched sections were located in the center-bottom of the ordination space (Figs. 3.6c and d). In August and October 1992, algal assemblages in pools in the non-enriched section segregated strongly at the left side of the ordination (Fig. 3.6c), a location that corresponded to three heterocystous, nitrogen-fixing cyanobacteria (*Calothrix fusca*, *Calothrix* sp. 2, and *Nostoc* sp. 1) and the large diatom, *Epithemia hyndmanii*, which contained nitrogen-fixing cyanobacterial endosymbionts (Fig. 3.6k). Relative biovolumes of these taxa were considerably greater in the non-enriched section than in the enriched section in August and October 1992, and *Epithemia hyndmanii* was relatively more

abundant in pools than in fastwater units (Table 3.5). Because *Epithemia hyndmanii* accounted for a large proportion of the total biovolume on most dates, the biovolumes of the heterocystous cyanobacteria reported in Table 3.5b appear low relative to total biovolume. However, the heterocystous cyanobacteria sometimes comprised a large proportion of the algal biovolume relative to all other (non-*Epithemia*) taxa (e.g., 29%, in pools in the non-enriched section in October 1992). Algal assemblages collected in August and October 1992 from the enriched section were positioned at the center-top part of the ordination space (Fig. 3.6d). This region corresponded to four medium-sized, mostly stalked, diatoms (*Gomphonema dichotomum*, *Gomphonema rhombicum*, *Rhoicosphenia curvata*, and *Nitzschia oregona*) and the filamentous cyanobacterium, *Phormidium tenue* (Fig. 3.6k).

Algal assemblages in the fastwater units (riffles, rapids, and cascades, Figs. 3.6e-j) exhibited a similar, although not as strongly apparent, pattern as in the pools. Algal assemblages in the fastwater units in both the non-enriched and enriched sections generally started in the right-center of the ordination space (June of both 1991 and 1992) and shifted to the center-bottom (August of both years) (Figs. 3.6e-j), which marked a shift from large, linear and filamentous diatoms and filaments of *Stigeoclonium tenue* and *Oscillatoria agardhii* to small, prostrate diatoms and basal cells of *Stigeoclonium tenue* (Fig. 3.6k). Algal assemblages in fastwater units in the non-enriched section were located closer to the left, especially the October 1992 samples, whereas assemblages in the fastwater units in the enriched section, particularly the October 1992 samples, were located closer to the center-top region (Figs. 3.6e-j) corresponding to the diatoms

Figure 3.6. Detrended correspondence analysis (DCA) of the samples by taxa matrix for algal assemblages in Lookout Creek. Successional trajectories of algal assemblages are shown in a-j, with the unit number by the June sample. The associated eigenvalues are 0.342 (axis 1) and 0.171 (axis 2). Enrichment began June 1991. The graphs correspond to (a) Pools in the non-enriched section in 1991, (b) Pools in the enriched section in 1991, (c) Pools in the non-enriched section in 1992, (d) Pools in the enriched section in 1992, (e) Riffles in 1991, (f) Riffles in 1992, (g) Rapids in 1991, (h) Rapids in 1992, (i) Cascades in 1991, (j) Cascades in 1992, and (k) ordination of taxa.

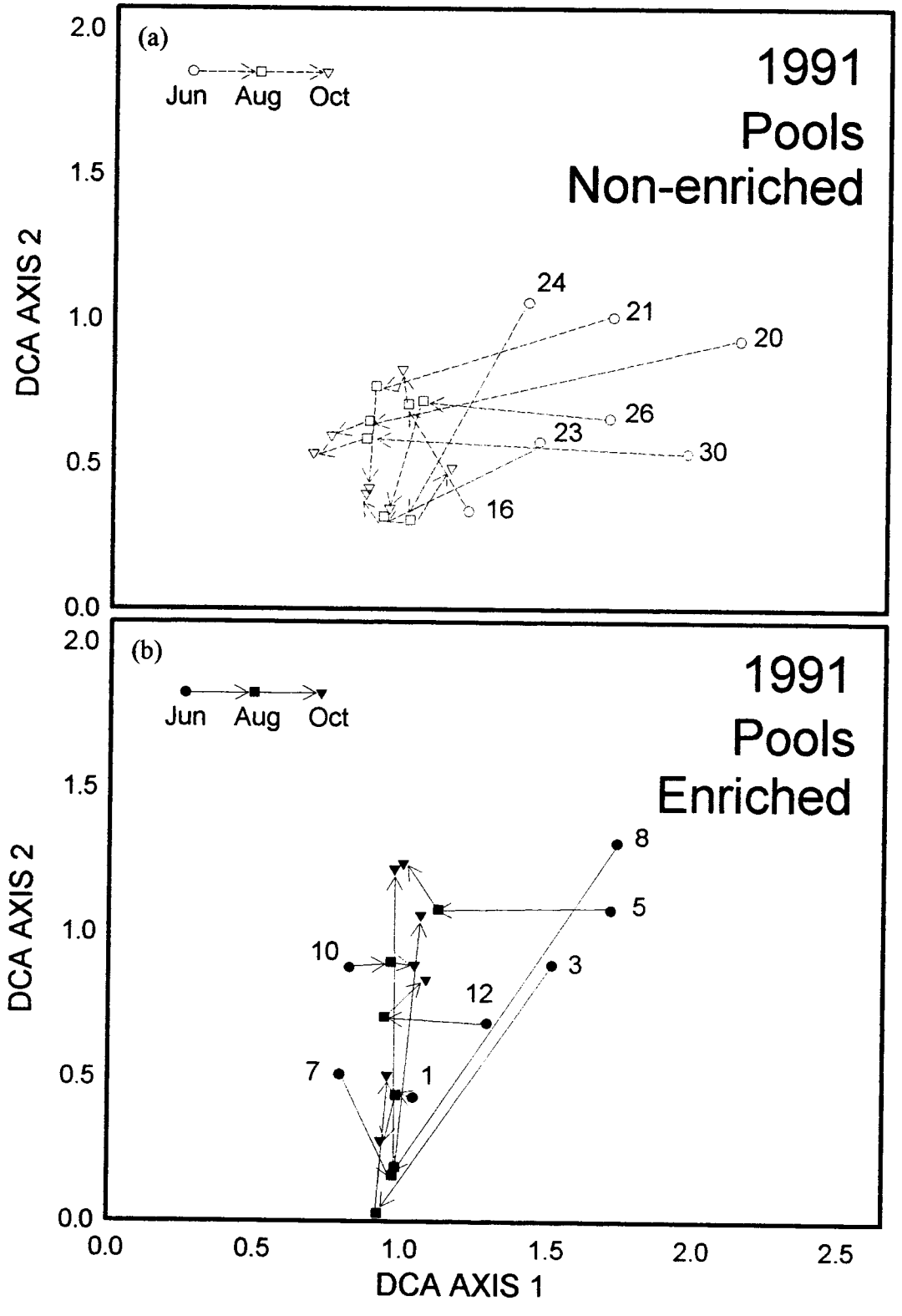
(a)
Jun
Aug
Oct
1991
Pools
Non-enriched
24
21
20
26
23
30
16
(b)
Jun
Aug
Oct
1991
Pools
Enriched
8
5
10
3
12
7
1
DCA AXIS 2
DCA AXIS 1
0.0
0.5
1.0
1.5
2.0
2.5

Figure 3.6

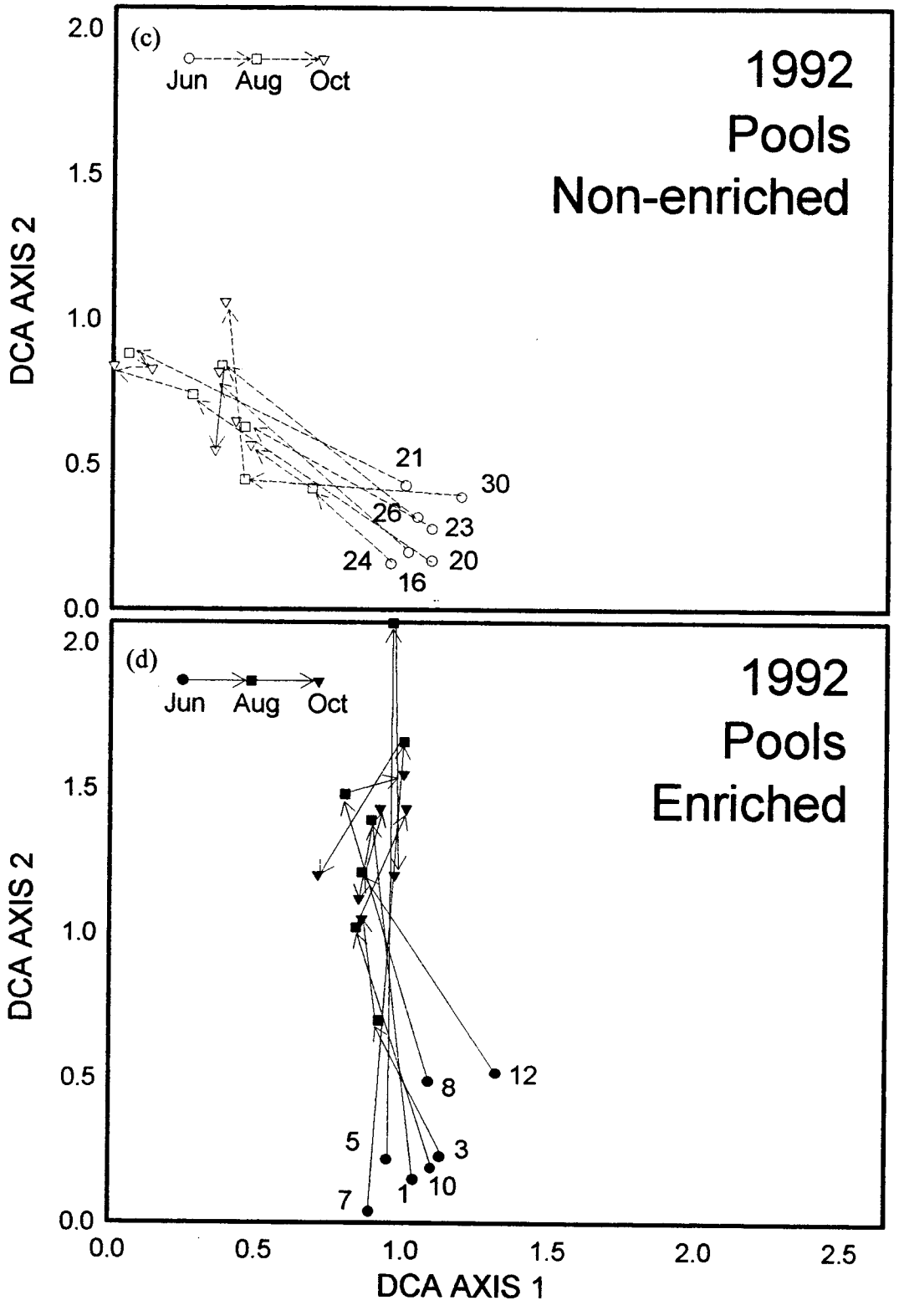

Figure 3.6 (continued)

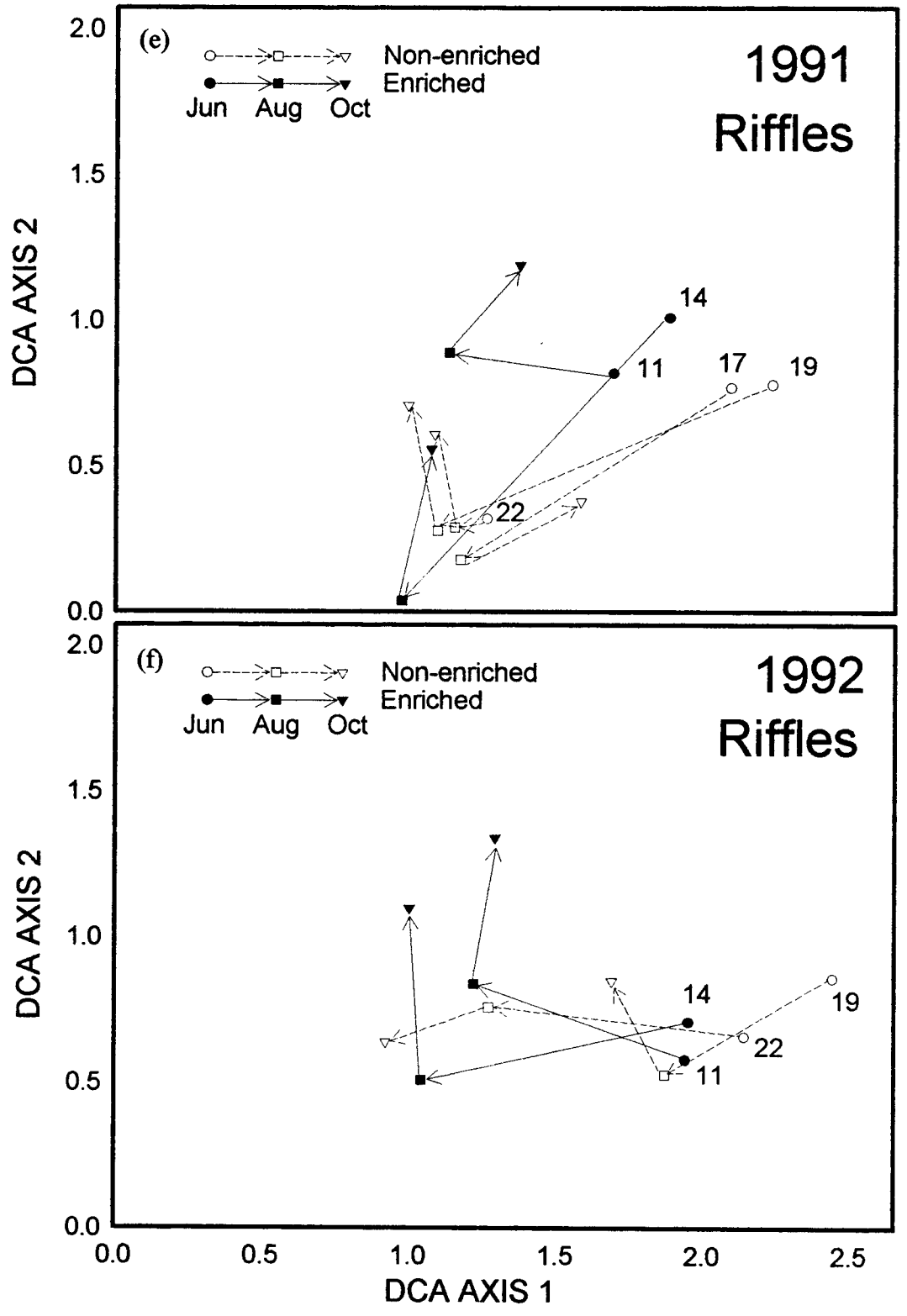

Figure 3.6 (continued)

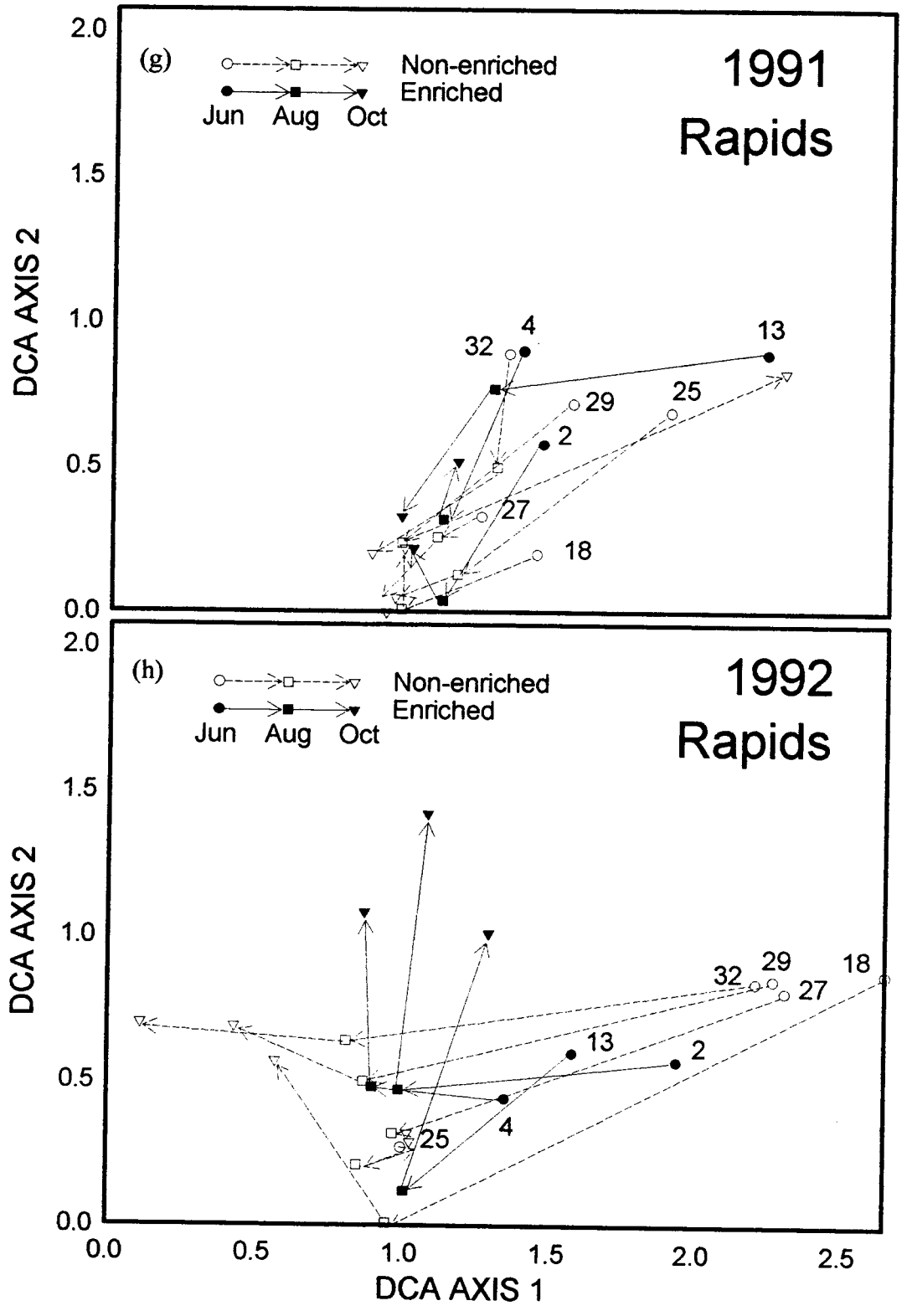

Figure 3.6 (continued)

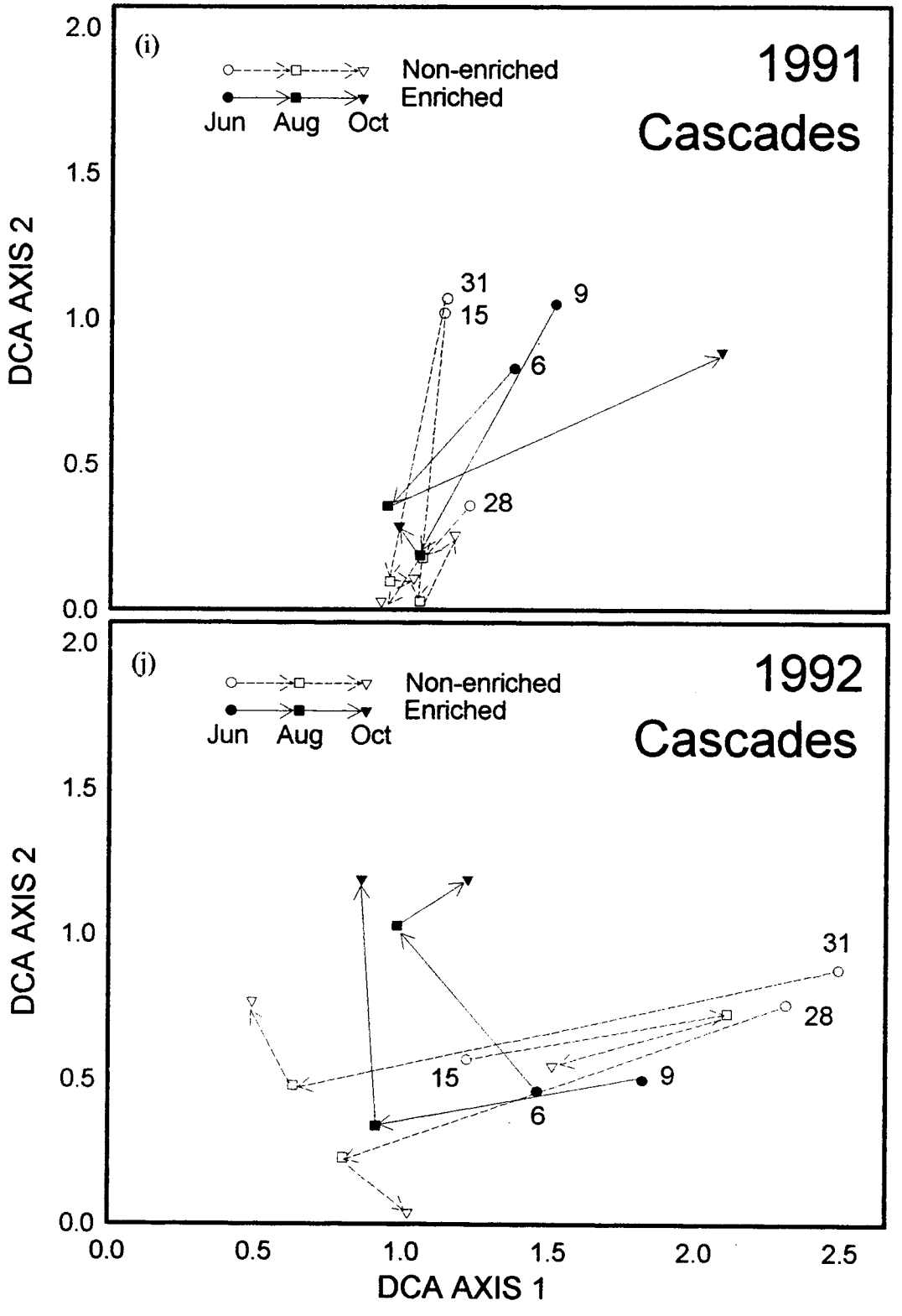

Figure 3.6 (continued)

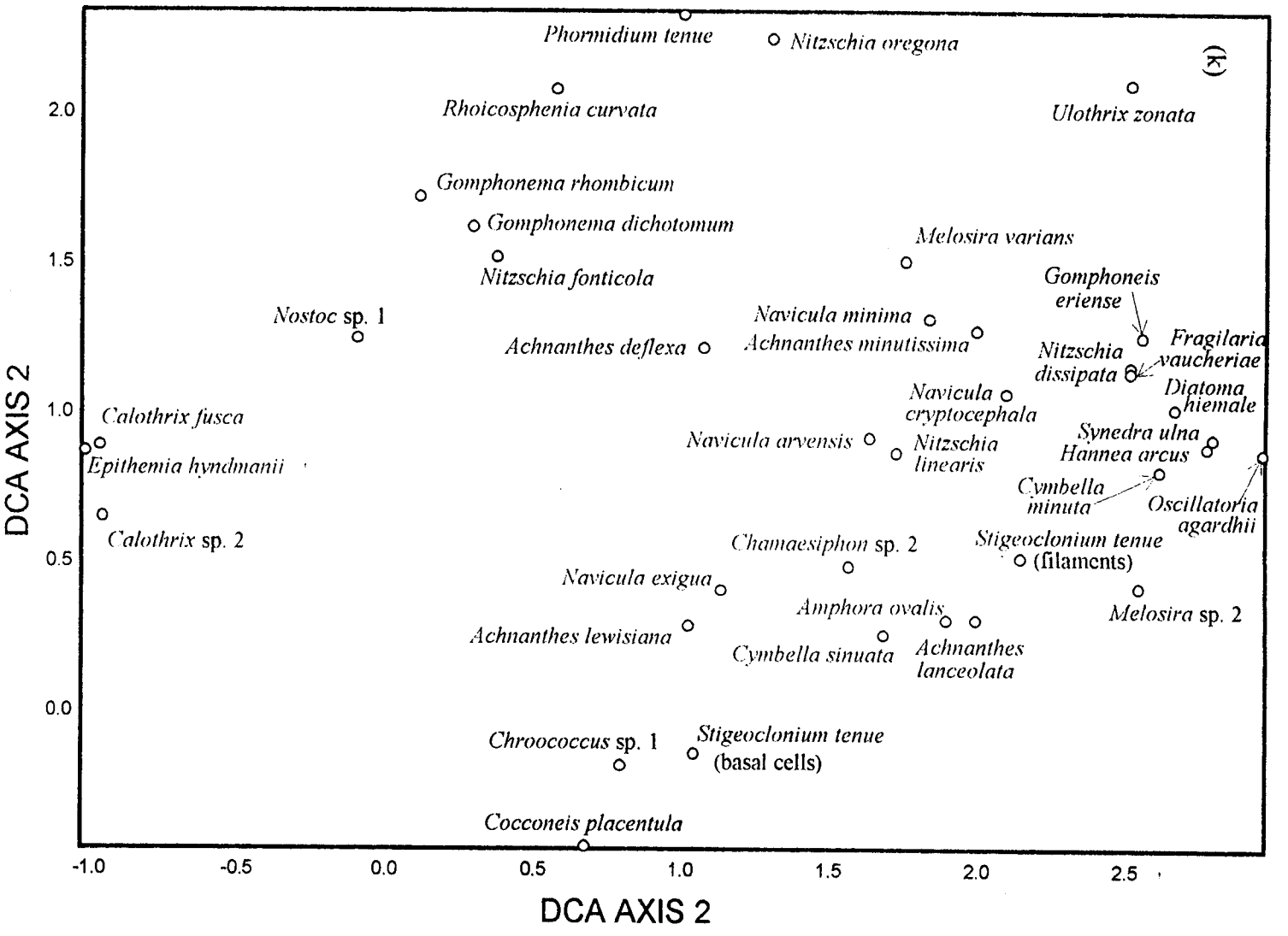

Figure 3.6 (continued)

Table 3.5. Mean relative biovolume (%) of nitrogen-fixing taxa in June, August, and October in 1991 and 1992. Fastwater units include riffles, rapids, and cascades.

(a) *Epithemia hyndmanii*

		1991		1992	
Month	Section	Pools	Fastwater	Pools	Fastwater
June	Non-enriched	7.92	8.75	46.20	10.18
	Enriched	*7.18	*2.16	34.34	6.06
August	Non-enriched	51.94	7.53	92.26	63.77
	Enriched	9.64	3.38	37.74	5.72
October	Non-enriched	64.04	31.08	91.34	64.87
	Enriched	14.36	4.11	38.54	3.90

* No enrichment prior to June 1991

(b) Heterocystous cyanobacteria (*Calothrix fusca*, *Calothrix* sp. 2, and *Nostoc* sp. 1)

		1991		1992	
Month	Section	Pools	Fastwater	Pools	Fastwater
June	Non-enriched	0.25	0.13	1.35	0.12
	Enriched	*8.51	*0.11	-	-
August	Non-enriched	5.24	0.31	2.44	1.69
	Enriched	1.04	-	1.33	-
October	Non-enriched	2.09	0.72	3.13	5.53
	Enriched	0.79	-	1.02	-

* No enrichment prior to June 1991

Gomphonema dichotomum, *Gomphonema rhombicum*, *Rhoicosphenia curvata*, and *Nitzschia oregona*, and the filamentous cyanobacterium *Phormidium tenue* (Fig. 3.6k).

3.5 Discussion

3.5.1 Algal Succession in a Nitrogen-Limited Stream

In June of both 1991 and 1992, periphyton in the non-enriched section of Lookout Creek consisted of assemblages of diatoms that were large (*Gomphoneis eriense*) and had linear (*Synedra ulna*, *Hannea arcus*) or filamentous (*Diatoma hiemale*, *Fragilaria vaucheriae*, and *Melosira varians*) morphologies, and included high relative abundances of the filamentous cyanobacterium *Oscillatoria agardhii* and filamentous chlorophytes *Stigeoclonium tenue* and *Ulothrix zonata*. The diatom taxa have high sinking rates (Stevenson and Peterson 1989) and typically appear early in benthic algal succession (DeNicola 1990, and Chapter 2). At the time of sampling, the annual wet season and period of high discharge in Lookout Creek were just beginning to abate, and therefore much of the benthic substrate had been scoured and was available for primary succession. The morphologies of these taxa allow them to colonize the substrate first, and those that attach upright to the substrate (e.g., *Synedra ulna*) have a competitive advantage in obtaining irradiance for photosynthesis (Pan and Lowe 1994). Although Lookout Creek was assumed to be nitrogen limited (Gregory 1980) and had low ammonium and nitrate concentrations in the non-enriched section (Figs. 3.2 and 3.3), these diatoms and the

filamentous chlorophytes and cyanobacteria often occur in streams with high levels of nitrogen (Hill and Knight 1988b, Peterson and Grimm 1992). This suggests that nitrogen may not have been limiting in the non-enriched section of Lookout Creek in early summer of 1991 and 1992.

Taxonomic composition of algal assemblages in the non-enriched section between June and August of both 1991 and 1992 shifted from large, linear and filamentous diatoms to small, prostrate diatoms (e.g., *Cocconeis placentula*, *Achnanthes lanceolata*, *Achnanthes lewisiana*, and *Navicula arvensis*) and basal cells of *Stigeoclonium tenue*. Whereas large, filamentous diatoms and filaments of *Oscillatoria* and *Stigeoclonium tenue* are sensitive to grazing (Chapter 2), prostrate diatoms and basal cells of *Stigeoclonium tenue* are characteristic of highly grazed algal assemblages (Chapter 2). Therefore, algal taxa that were predominant in June were replaced by grazer-tolerant taxa in July and August, suggesting that grazing was the dominant factor in determining successional trajectories in mid-summer. *Cocconeis placentula* and *Achnanthes lanceolata* are often found in streams with high concentrations of nitrogen (Winterbourn 1990), which also suggests that the non-enriched section of Lookout Creek may not have been limited by nitrogen in mid-summer of 1991 and 1992

Between August and October 1992, and to a some extent in pools between August and October 1991, taxonomic composition of algal assemblages in the non-enriched section of Lookout Creek shifted to an assemblage characterized by several heterocystous cyanobacteria (*Calothrix fusca*, *Calothrix* sp. 2, and *Nostoc* sp. 1) and dominated by the large diatom *Epithemia hyndmanii*. Heterocystous cyanobacteria such as *Calothrix* and

Nostoc are thought universally capable of fixing nitrogen (Fogg *et al.* 1973, Sprent and Sprent 1990). Several other species in the genus *Epithemia* have been demonstrated to fix nitrogen, and diatoms in the family Epithemiaceae are thought to universally contain nitrogen-fixing cyanobacterial endosymbionts (DeYoe *et al.* 1992, and references therein). The succession from nitrophilic algal assemblages to nitrogen-fixing assemblages between August and October indicates that nitrogen may be limiting in Lookout Creek only in late summer. Concentrations of nitrogen in streams are often low when discharge is low (Lohman *et al.* 1991). Consistent with this pattern, the abundances of the nitrogen-fixing taxa in Lookout Creek were greater in 1992, when discharge was much lower than in 1991. Concentrations of NH_4^+-N and (NO_3^- + NO_2^-)-N were lower in the non-enriched section in 1992 than in 1991, and there was a 50% decrease in (NO_3^- + NO_2^-)-N concentration between August and October in both 1991 and 1992.

Diatoms with nitrogen-fixing cyanobacterial endosymbionts appear to have a competitive advantage in nitrogen-poor habitats (Lowe *et al.* 1984, Fairchild *et al.* 1985, Hill and Knight 1988b, Peterson and Grimm 1992, Hawes and Smith 1993, review by Borchardt 1996). Steinman *et al.* (1991) found that two species of *Epithemia*, *E. adnata* and *E. turgida*, were more abundant in recirculating laboratory chambers, where concentrations of nitrogen became more depleted than in once-through chambers. High abundances of *Epithemia* and the closely related genus *Rhopalodia*, which also contains nitrogen-fixing cyanobacterial endosymbionts (DeYoe and Bullerjahn 1989), have been associated with nitrogen-poor streams or lakes in a variety of locations around the world, including England (Biswas 1978), Saudi Arabia (Whitton *et al.* 1986), New Zealand

(Hawes and Smith 1994), the Canadian Arctic (Moore 1980), and, in the American West, in Arizona (Crayton and Sommerfeld 1979), California (Hill and Knight 1988a), Montana (Bahls and Weber 1988), and Utah (Rushforth and Brock 1991, Yearsley *et al.* 1992). *Nostoc* (Moore 1980, Ward 1985) and *Calothrix* (Peterson and Grimm 1992) also have been found to be relatively abundant in streams and lakes with low levels of inorganic nitrogen. *Calothrix* has been reported to intensify nitrogen fixation when nitrogen concentrations are low (Savela 1983).

3.5.2 Effects of Nitrogen Enrichment on Succession

In 1991, the taxonomic structure of periphyton in the enriched section was similar to that in the non-enriched section, i.e. consisting of linear and filamentous diatoms, and filamentous chlorophytes and cyanobacteria in June, and shifting to prostrate diatoms in August and October. At the beginning of summer in 1992, algal assemblages were dominated more by the prostrate diatoms than in 1991. After June 1992, there was a strong shift in algal assemblages in the enriched section, particularly in the pools, to diatoms such as *Rhoicosphenia curvata*, *Gomphonema dichotomum*, *Gomphonema rhombicum*, and the filamentous cyanobacteria *Phormidium tenue*.

Nitrogen enrichment had a pronounced effect on the taxonomic composition of algal assemblages in Lookout Creek. The addition of nitrogen to the stream altered the successional trajectories of algal assemblages by allowing the development of assemblages dominated by nitrophilic taxa and by inhibiting the formation of a late summer assemblage dominated by nitrogen-fixing taxa. Other studies that investigated nitrogen enrichment in

lakes (Fairchild *et al.* 1985, Carrick and Lowe 1989, Hawes and Smith 1993, Marks and Lowe 1993) and streams (Hill and Knight 1988b, Peterson and Grimm 1992) have found similar patterns. In general, nitrogen-fixing taxa such as heterocystous cyanobacteria (*Anabaena*, *Calothrix*, *Nostoc* and *Tolypothrix*) and diatoms containing cyanobacterial endosymbionts (*Epithemia* and *Rhopalodia*) were more abundant in control (nitrogen-poor) samples, whereas certain diatoms (*Achnanthes*, *Cocconeis*, *Cymbella*, *Gomphoneis*, *Gomphonema*, *Rhoicosphenia*, and *Synedra*), filamentous chlorophytes (*Stigeoclonium* and *Ulothrix*) and non-heterocystous cyanobacteria (*Oscillatoria*) were more abundant in nitrogen-enriched samples. DeYoe *et al.* (1991) suggested that epithemiacean diatoms with cyanobacterial endosymbionts would be at a competitive disadvantage in situations where nitrogen is not limiting, because the growth rates of these diatoms would be relatively lower because of the energetic expense in supporting the endosymbionts.

3.5.3 Nitrogen Fixation in Filamentous Non-Heterocystous Cyanobacteria

Among filamentous non-heterocystous cyanobacteria, some species apparently can fix nitrogen, whereas other species within the same genera do not have the capacity to fix nitrogen. Two filamentous, non-heterocystous cyanobacteria were found in Lookout Creek, *Oscillatoria agardhii* and *Phormidium tenue*. *P. tenue* exhibited a pattern of high abundance in the enriched section, especially in August and October 1992, whereas *O. agardhii* only exhibited a pattern of high abundance in the enriched section early in the summer. Neither Fogg *et al.* (1973), nor Sprent and Sprent (1990) include *Phormidium* among their lists of nitrogen-fixing genera, and *P. laminosum* has been reported not to fix

nitrogen (Fresnedo and Serra 1992). In fact, *P. laminosum* has been tested for use in bioreactors to remove nitrate and nitrite from wastewater (Garbisu *et al.* 1994). However, de la Lanza Espino (1986) reported nitrogen fixation in sediments containing *P. tenue* in a Mexican lagoon, and Paling *et al.* (1989) reported nitrogen fixation in *Phormidium* mats in Western Australia. Moreover, several strains of *Oscillatoria* were reported to fix nitrogen (Fogg *et al.* 1973, Sprent and Sprent 1990). The patterns of abundance of *Phormidium tenue* and *Oscillatoria agardhii* in our study suggest that the populations of these species in Lookout Creek probably do not fix nitrogen.

3.5.4 Algal Biomass and Heterogeneity

In 1991, there were no changes in algal biomass or heterogeneity in the non-enriched section between June and October. However, in 1992 there was an increase in algal biomass and heterogeneity in the non-enriched section from June to October. In the enriched section, there were no discernible patterns of algal heterogeneity, and algal biomass was greater in the enriched section than in the non-enriched section only in pools in June and August 1992. It is difficult to explain these patterns from the algal taxonomic data alone. The lack of a dramatic increase in algal standing crops in the enriched section may have been due to an increase in grazing and secondary production (see modeling by McIntire *et al.* 1996). The increase in algal biomass in October 1992 in the non-enriched section may have been related to a decrease in grazing associated with qualitative changes in the algal food resource. Assemblages in those samples were dominated by the diatom *Epithemia hyndmanii* and the cyanobacteria *Calothrix fusca*, *Calothrix* sp. 2 and *Nostoc*

sp. 1. Cyanobacteria are thought to be of poor food quality and are often avoided by grazers (Gregory 1983). However, several studies suggest that *Epithemia* is preferentially grazed by herbivores. Hill and Knight (1988a) found that most of the depletion of algal biomass from grazing by the caddisfly *Neophylax* spp. and the mayfly *Ameletus* sp. was due to preferential grazing upon *Epithemia* sp. 1, and Blinn *et al.* (1989) found that *E. adnata*, *E. argus alpestris*, and *E. sorex* were preferentially grazed by the limpet *Ferrissia fragilis*. Hill and Knight (1987) observed a significant decrease in the biovolume of *Epithemia* sp. 1 in samples grazed by the mayfly *Ameletus validus*, although *Epithemia* sp. 1 actually increased in relative abundance in response to grazing.

3.5.5 Implications

Many studies analyze algal community structure by grouping algae into categories based on taxonomic considerations (e.g., diatoms, chlorophytes, cyanobacteria) (cf. Tilman *et al.* 1986). Because species within each of these taxonomic groups may have widely divergent morphologies, metabolisms, and life histories, lumping species into groups based on taxonomy may obscure important patterns (Benke *et al.* 1988). The existence of nitrogen-fixing diatoms, non-nitrogen-fixing cyanobacteria, and heterotrichous chlorophytes justifies a functional approach (cf. Steinman *et al.* 1991).

Taxonomic changes caused by nutrient addition could have profound effects throughout the food web. For example, Blinn *et al.* (1989) found that the limpet *Ferrissia* "preferentially grazed" on *Epithemia*. Pronounced decreases in the abundance of this alga in cases of nitrogen addition could strongly affect populations of herbivores. Therefore,

effects of nutrient addition on secondary production may be driven less by an increase in primary production, and more by qualitative changes in food sources related to taxonomic changes in the algal assemblage. Based on stream modeling, McIntire *et al.* (1996) hypothesize that "if an increase in a limiting nutrient generates a decrease in algal food quality below a threshold value, grazer production decreases with an increase in algal productivity, a response that has indirect effects on the processes of shredding, collecting, and predation." Furthermore, the fact that certain primary producers have the capability to fix nitrogen implies that there should be more qualitative differences in the effects of nitrogen enrichment on stream periphyton than in the case of phosphorus enrichment, because there is no process in the phosphorus cycle that is comparable to nitrogen fixation.

3.6 Acknowledgments

We thank Linda Ashkenas, Stan Gregory, and Gary Lamberti for their assistance with various aspects of the experiment, and for providing the algal biomass data and the chemical and physical data for Lookout Creek. We also thank Jo Miller of the USGS for providing the discharge data for Lookout Creek. This research was supported by grants BSR-8907968 and BSR-90-11663 (LTER) from the National Science Foundation.

4. SUMMARY AND CONCLUSIONS

Benthic algae are important primary producers in most aquatic ecosystems. Periphyton constitute an important food resource for consumer organisms, and high turnover rates of the algal biomass imply that small standing crops can support a relatively high biomass of consumer organisms (McIntire 1973). The quality of the algal food resource, and hence its capacity to support secondary production, depends in part upon the taxonomic composition of the algal assemblages (Gregory 1983). Studies presented in this thesis investigated the effects of a biological factor, grazing by invertebrate herbivores, and a chemical factor, enrichment with nitrogen, on the taxonomic composition of algal assemblages.

The experiment reported in Chapter 2 in this thesis indicated that grazing can modify algal assemblages by altering the successional sequence and promoting a transition from upright, filamentous, and stalked forms (e.g., *Synedra ulna*, *Fragilaria vaucheriae*, *Gomphonema* spp., filaments of *Stigeoclonium tenue*, *Oscillatoria* sp.) to prostrate forms (e.g., *Achnanthes minutissima*, *Navicula minima*, *Nitzschia fonticola*, *Phormidium tenue*, basal cells of *Stigeoclonium tenue*), a pattern that is consistent with the results of other recent studies (see reviews by Feminella and Hawkins 1995, Steinman 1996). Furthermore, this experiment demonstrated that concurrent grazing by dissimilar herbivores generated assemblages that were qualitatively different than assemblages grazed by a single species of herbivore. However, the results reported here differed from the outcome of several recent studies involving concurrent grazing by dissimilar herbivores (Hill and Knight 1988a, Feminella and Resh 1991, Kohler 1992, Pan and Lowe 1994).

These studies found that the effects of concurrent grazing were usually additive, whereas the results in Chapter 2 suggested that algal assemblages concurrently grazed by *Dicosmoecus gilvipes* and *Juga silicula* produced assemblages of intermediate biomass and unique taxonomic composition. Furthermore, the imposition of substrate heterogeneity influenced the outcome of grazer-periphyton interactions. The substrate blocks changed the successional sequence of algal assemblages directly by modifying the flow regime, and indirectly by providing the animals with a refuge from the current, which resulted in unequal distribution of grazers on the substrate surface.

Results from the laboratory experiment (Chapter 2), in comparison with the results reported by DeNicola *et al.* (1991), suggested that the life history stages of invertebrate grazers may be as important as other factors, such as herbivore species, mouthpart morphology, and density, in determining the effect that grazers have upon the taxonomic composition of algal assemblages. Li and Gregory (1989) reported that feeding behavior differed among instars of *Dicosmoecus gilvipes*, and that grazer behavior also was influenced by the composition of algal assemblages. To my knowledge, however, there have been no experiments which have examined the effects of different life history stages of a species of grazer upon the taxonomic composition of algal assemblages.

Results from the enrichment study reported in Chapter 3 are consistent with the results of several recent experiments involving nitrogen enrichment (Fairchild *et al.* 1985, Hill and Knight 1988b, Carrick and Lowe 1989, Peterson and Grimm 1992, Hawes and Smith 1993, Marks and Lowe 1993). Algal assemblages composed of nitrogen-fixing taxa (e.g., diatoms in the Epithemiaceae, such as *Epithemia* and *Rhopalodia*, which contain

cyanobacterial endosymbionts, and heterocystous cyanobacteria such as *Anabaena*, *Calothrix*, and *Nostoc*) are often found in nitrogen-poor waters. With the addition of nitrogen these taxa are replaced by diatoms (e.g., *Rhoicosphenia curvata*, *Gomphonema* spp.) and non-heterocystous cyanobacteria (e.g., *Phormidium*, *Oscillatoria*). When nitrogen is not limiting, epithemiacean diatoms with cyanobacterial endosymbionts will be at a competitive disadvantage because the growth rates of these diatoms are relatively lower as a consequence of the energy costs in supporting the endosymbionts (DeYoe *et al.* 1991).

Because species of *Epithemia* are often dominant in aquatic ecosystems where nitrogen is limiting, enrichment with nitrogen and the subsequent reduction in abundance of this diatom can have a pronounced effect on higher trophic levels. Several herbivores appear to selectively ingest *Epithemia* (Hill and Knight 1987, Hill and Knight 1988a, Blinn *et al.* 1989), suggesting that a decrease in abundance of *Epithemia* may have a significant influence on algal food quality. Results from stream modeling (McIntire *et al.* 1996) suggests that if the addition of a limiting nutrient causes a decrease in algal food quality, then an increase in algal production may be accompanied by a decrease in grazer production, which can have effects on higher trophic levels.

Results from the enrichment experiment indicated that a functional, rather than taxonomic, classification of periphyton may be more useful to stream ecologists in assessing the role of algal assemblages in streams. A similar approach has been used with stream invertebrates for two decades (Cummins 1973), and a functional classification of benthic algal assemblages based on growth forms (e.g., prostrate, upright, stalked, and

filamentous) also has emerged (cf. Hoagland *et al.* 1982). However, Benke *et al.* (1988) warned that "most stream organisms have been placed in rather broad functional groups with little attention being given to the potential for variation in ecological strategies that may occur among subgroups." For example, in Chapter 3, I have grouped a number of small diatoms in the genera *Achnanthes*, *Navicula*, and *Nitzschia* into a "grazer-resistant prostrate group". However, taxa in this group spread from bottom to top of the center area of the species ordination (Fig. 3.6k), which indicated variation within this group in terms of response to nitrogen enrichment. The relevance of nitrogen-fixing diatoms, non-nitrogen-fixing cyanobacteria, and heterotrichous chlorophytes to the interpretation of the experiments justifies a functional approach, and emphasizes the importance of choosing functional groupings that are appropriate for the investigation.

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APPENDIX

APPENDIX

ALTERNATE DESIGNATION OF UNITS IN LOOKOUT CREEK

	This Thesis	Alternate Designation
Non-enriched	Rapid-32	R 29 M
Section	Cascade-31	C 28 M
↓	Pool-30	P 27 M
↓	Rapid-29	R 26 M
↓	Cascade-28	C 25 M
↓	Rapid-27	R 24 M
↓	Pool-26	P 23 M
↓	Rapid-25	R 22 M
↓	Pool-24	P 21 M
↓		S 20 M
↓	Pool-23	P 19 M
↓	Riffle-22	I 18 M
↓		S 17 M
↓	Pool-21	P16 M
↓		S 15 M
↓	Pool-20	P 14 M
↓	Riffle-19	I 13 M
↓	Rapid-18	R 12 M
↓	Riffle-17	I 10 M
↓	Pool-16	P 9/11 M
DRIPPER →→→	Cascade-15	C 8 M
Enriched	Riffle-14	I 7 M
Section	Rapid-13	R 6 M
↓	Pool-12	P 5 M
↓	Riffle-11	I 1* M
↓	Pool-10	P 11 B
↓	Cascade-9	C 10 B
↓	Pool-8	P 9 B
↓		S 8 B
↓	Pool-7	P 7 B
↓	Cascade-6	C 6 B
↓	Pool-5	P 5 B
↓	Rapid-4	R 4 B
↓	Pool-3	P 3 B
↓	Rapid-2	R 2 B
↓	Pool-1	P 1 B