EFFECTS OF GRAZING BY THE OLIGOCHAETE, *Aeolosoma*, ON DETRITAL AND PERIPHYTIC ASSEMBLAGES

by

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(ABSTRACT)

The effects of grazing by the small oligochaete, Aeolosoma, on periphyton assemblages of different algal composition and on unconditioned detritus were examined. Natural water and periphyton inoculum were collected from a littoral environment and used to construct laboratory microcosms. Changes in algal community composition, microbial respiration, and structural indices (Chlorophyll a, protein, and carbohydrate) were measured in grazed and ungrazed cultures through time in 2 to 12 d experiments.

Grazed cultures after 10 to 12 d had dissimilar algal community compositions in both the early and late summer periphytic assemblages as measured by Pinkham and Pearson's Index of Similarity (B). Changes resulted from stimulation (Green coccoids, thin green filaments) and suppression (certain diatoms) of individual algal taxa, and not from the dramatic shifts in community composition and structure effected by macroinvertebrate grazing.

Grazing stimulated food quality (P/C) of periphytic assemblages without changing overall biomass. Bacterial ^{14}C-glucose respiration was significantly less in grazed cultures despite higher bacterial biomass estimates with grazing. A mucus-mediated aggregation response was observed in Aeolosoma only when placed in cultures containing unconditioned detritus. Aggregates supported a heterotrophic community with greater P/C content than unaggregated detritus.

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INTRODUCTION

The small freshwater oligochaete Aeolosoma is a common representative of the aquatic meiofaunal community. Defined as benthic metazoans less than 2 mm (Fenchel and Jorgenson 1977), meiofauna are often overlooked in field collections due to their small size and disintegration upon normal fixation procedures. Given their rapid reproductive rates and high densities (4 d and 62500 individuals/m^2 for Aeolosoma; Newman 1975, Fomenko 1980), a potentially signi ficant gap in our understanding of energy flow in aquatic systems presently exists due to inaqeduate consideration of meiofaunal dynamics.

Recent work has shown that meiofaunal activity may increase both microbial activity and energy flow to higher trophic levels. Tenore et al. (1977) found that the presence of a nematode-dominated meiofauna doubled the net incorporation of Zostera detritus by the polychaete, Nephthys. Hargrave (1970), Lopez et al. (1977), and Morrison and White (1980) showed that grazing by amphipods, organisms which are slightly larger than meiofauna but occupy a similar niche, increases microbial (algal and bacterial) biomass and activity.

The feeding habit of Aeolosoma represents a potential mechanism for the stimulation of microbial growth. Worms

aggregate fine detritus and other small particles by secreting copious amounts of mucus (Newman 1975, pers. obs.), an excellent growth substrate for both autotrophic and heterotrophic organisms. Connor and Quinn (1984) found that limpet mucus stimulated algal growth. Oceanic macroaggregates, many of which are recognizable as abandoned mucus webs, have up to 10^4 greater bacterial and protozoan densities than surrounding sea water. (Caron et al. 1982). Mucus electrostatically attracts dissolved organic compounds (Ross and Craig 1980), which may be the mechanism for increased microbial growth since it would facilitate exposure of the organism to organic substrates.

Aeolosoma is primarily found in the littoral region of lentic sytems (DiPersia 1979, Pomenko 1980). This habitat is a major contributor to the total production and metabolism of lakes (Wetzel 1979). Depending on lake geomorphology and corresponding littoral development, algal growth on sediments, rocks, and macrophytes in this zone can account for half of the system's primary production (Wetzel 1964). Hargrave (1973) showed that sediments decreased in oxygen consumption with increasing water depth. This higher heterotrophic activity in shallow, littoral sediments is partially a result of the bulk of macrophytic production entering decomposer food chains while most phytoplankton production passes through pelagic

grazing food chains. The sediments and periphyton-covered structures of the littoral zone in which Aeolosoma feeds are focal points of heterotrophic and autotrophic production in lakes. Potential stimulatory effects of its grazing, therefore, may significantly alter overall lentic production.

The high nutritional value of oligochaetes makes any study of their ecology relevant to higher trophic levels. Oligochaete dry weight is approximately 40-50% protein, making them more readily digestible than all other benthic macrofauna (Chekanovskaya 1981). A dietary switch from herbivory to carnivory in later development stages is a common feature of many aquatic insect life histories (Anderson and Cummins 1979). An oligochate supplement to the diet of a detritivorous caddisfly larvae reduced development time and increased mature larval weight (Anderson 1976). Aeolosoma represents an abundant and rapidly reproducing source of animal tissue for littoral organisms.

The objective of this study was to examine structural and functional changes in periphyton communities caused by Aeolosoma grazing. Laboratory experiments were conducted to determine if: 1) grazing altered algal community composition and bacterial activity, 2) the effects of grazing on algae depended on the type of periphytic

assemblage, 3) Aeolosoma differentially ingested certain types of algae, and 4) mucus-associated aggregates produced by Aeolosoma stimulated microbial growth. The results of this work should reveal the particular effects of Aeolosoma grazing and increase general understanding of the importance of meiofaunal grazing.

LITERATURE REVIEW

Habitat and Feeding Habits

Oligochaetes of the family Aeolostomatidae are small (body length 0.1 to 5.0 mm) worms characterized by colorless or colored (red, orange, yellow, green, and blue) spherical epidermal corpuscles from which the family name is derived (from Greek ailos = variegated). Most species of the family reproduce asexually through pygidial budding (Chekanovskaya 1981). Given favorable conditions in nature they can reproduce rapidly to capitalize on available food resources (Bringham et al 1982). In laboratory culture, Aeolosoma headlayi reproduces every 4 days (Newman 1975). Aeolosoma's broad, ciliated prostomium, a unique feature among oligochaetes, functions in food gathering and locomotion. Singer (1978) concluded that it allowed for reduction in septa and body musculature, decreasing respiratory energy requirements and allowing for greater reproductive efficiency.

The seven species of Aeolosoma which comprise the family are found among muddy sands and higher vegetation in slow moving (<0.3 m/sec) or standing water. DiPersia (1979) collected various Aeolosoma species in Argentina among filamentous algal beds, aquatic macrophytes (Azolla caroliniana, Salvinia herzogii, Glyceria multiflora) and

the algal crusts on Ampullaria gastropod shells. Aeolosoma is most common on Myriophyllum among aquatic macrophytes in north temperate lakes (Krecker 1939). Pomenko (1980), in a study of the oligochaete fauna of the Dneiper River Basin in Russia, reported densities of A. travancorense up to 62500 individuals/m^2 in slightly muddy sand, and of A. hemprichi up to 7160 inds/m^2 on higher aquatic vegetation. The latter species was also collected from muddy sands and periphyton-covered rocks in the littoral zones of reservoirs in the Dneiper Basin. Singer (1978) collected Aeolosoma from dead leaves, bark, and algal mats. He disregarded species delineation, concluding that temporal and spatial variation among individuals made such attempts impossible. Aeolosoma hemprichi is often found in aeration tanks and trickling filters of biological sewage treatment plants (Solbe 1975).

Few feeding habit studies of freshwater oligochaetes have been conducted. Most texts state that fine detritus, algae, and other microorganisms are important food sources for small oligochaetes such as Aeolosoma (Meglitisch 1972, Barnes 1980). A few quantitative studies have examined oligochaetes slightly larger than Aeolosoma. Harper et al. (1981) found that the oligochaete Nais variabilis assimilated radiolabelled bacterial biomass. The abundance of littoral Nadidae of 1.5-18 mm size was correlated with

food availability (diatoms and fine detritus) and temperature (McElhone 1978). Bowker et al. (1983) reported a spring population maximum in a lotic Nadidae species which coincided with a periphytic diatom peak. Unicellular chlorophytes, naviculoid diatoms (predominantly Nitzschia), and Synedra accounted for 91.5 % of the algae in the guts of these oligochaetes. They ingested cells up to 196 um in length and 24 x 10^3 um^3 in volume, and discriminated against colonial and filamentous algae. Two Nadidae species,Arcteonais lomondi (8-10 mm) and Uncinais uncinata (5-18 mm), in small shallow Canadian lakes ingested 57 diatom species and 3 chlorophyta species ranging in size from 9-250 um (Moore 1981). Algae accounted for 57-75% by volume of ingested material in the summer and 10-22% in the winter. The guts of Lumbriculus variegatus and Rhyacodrilus sodalis, larger oligochaetes ranging in size from 10-90 mm in length, contained 70-85% diatoms in the summer and predominantly bacteria in the winter when algae are less abundant (Moore 1978). The proportion of food items in the gut was equal to the proportion in the environment, except the mucilaginous bluegreen algae Nostoc was never ingested. Based on these studies of similar oligochaetes, Aeolosoma probably feeds predominantly on bacteria, detritus, diatoms, and certain green algae with little selectivity. There may be some behavioral or morphological negative

selection of blue-green and filamentous algae. Due to its smaller size, Aeolosoma may be more limited then other oligochaetes in the range of algae that it can ingest.

Oligochaetes do show significant physiological selection of algae and bacteria. Bowher et al. (1985) found that Nais elinguis digested diatoms much more readily than green algae. After gut passage, 31 % of ingested Nitzschia cells were lysed compared to 0.1% of the ingested Scenedesmus cells. Cells of the latter in faeces were still viable. Strait (1978) reported similar results using radiolabelled algae fed to the nadid Stylaria lacustris. Incorporation efficiencies of 34% for Nitzschia and 2% for Scenedesmus were calculated. Oligochaetes probably do not have the cellulase activity necessary to readily digest the cell walls of green algae. Physiological divergence between oligochaetes may be a mechanism for niche separation (Calow and Calow 1975). Brinkhurst and Chua (1969) concluded that three sympatric species of tubificid oligochates partition microhabitat resources through species specific physiological selection of different bacterial types. Enzymatic scope, therefore, is an important component of oligochaete nutrition, and may represent a mechanism for passive negative selection of certain prey items.

Changes induced by oligochaete grazing are not well understood. Cattaneo (1983) correlated epiphytic biomass

declines with increased oligochaete and chironimid densities. He concluded that grazing was the cause of epiphytic declines because biomass failed to decrease in areas exclosed from grazing. It seems unlikely that oligochaetes could crop the large algal species which dominate a mature epiphytic community. As discussed, even larger oligochaetes have not been shown to ingest significant amounts of filamentous algae. Chironimids do ingest filamentous algae (Mason and Bryant 1975), and may be more responsible for epiphytic declines. It seems more reasonable that oligochaete density peaks with epiphytic dieback because the senescent community provides a more readily available food source.

Grazing Effects

The stimulatory effect of earthworm grazing on soil fertility and decomposition has been known since Darwin's (1881) classic work. Recent studies have investigated the similar effects grazers have on both autotrophic and heterotrophic production in aquatic systems.

In situ grazing of periphyton by macrofauna decreases algal biomass while increasing algal turnover. Grazing by caddisfly larvae (Lamberti and Resh 1983), snails (Hunter 1980, Kesler 1981), dipteran larvae (Robbles and Cubit 1981), and tadpoles (Dickman 1968) decrease algal standing

crops relative to ungrazed periphyton, largely due to a reduction in filamentous algal biomass. The resulting algal community has higher turnover (Lamberti and Resh 1983) and primary productivity (Flint and Goldman 1975). Grazing by macroinvertebrates, therefore, maintains periphyton in a rapidly reproducing state of low biomass.

Both algal biomass and productivity can be reduced by intense grazing pressure resulting from abnormally high grazer density or absence of alternative feeding substrates. Tadpoles grazing in shallow impoundments without extensive periphyton development reduced phytoplankton primary production (Seale 1980). Photosynthetic activity of periphyton in artificial streams devoid of coarse particulate matter decreased with natural field densities of snails (Mulholland et al. 1983). Algal production was stimulated by normal crayfish (Flint and Goldman 1975) and amphipod (Hargrave 1970) densities, but was decreased at grazer densities above ambient levels.

Hunter (1980) hypothesized that decreased algal species diversity and higher Chlorophyll a (Chl a)/g dry wt of periphyton grazed by snails was a result of grazing selection pressure for an early successional community. Ecological succession is an orderly process of community development resulting in a state of maximum biomass and species diversity (Odum 1969, Colinvaux 1975). Hoagland et

al. (1982) characterized a successional sequence in periphyton assemblages colonizing glass slides into three stages: an initial organic coating of bacteria, an intermediate community of low profile diatoms, and a final upperstory of long-stalked and large rosette diatoms and filamentous algae. Based on this successional model, the diatom-dominated community that results from grazing may be viewed as an early successional community, supporting Hunter's hypothesis. Higher Chl a/ g dry wt in grazed systems may not be entirely caused by the loss of slower growing organisms of larger biomass indicative of late successional stages. It may also result from the reduction in the three-dimensionality of the community with concomitant decrease in entrapment of inorganic particles (Kesler 1981).

Protozoan grazing of bacterial cultures has been shown to effect the same changes in bacterial cultures as macroinvertebrate grazing causes in periphyton: reduced biomass and increased activity. Ciliate grazing of detritus cultures significantly reduces bacterial numbers (Barsdale et al. 1974). McCambridge and McKeekin (1980), utilizing cyclohexamide to selectively inhibit eukaryotes, found that Escherichia coli densities increased if grazing pressure was removed within the initial 2 days of culture inoculation but were unaffected if grazing pressure was

removed after that time. Detritus cultures grazed by a natural assemblage of protozoans have increased decomposition rates (Fenchel 1977). Sherr et al. (1982) reported increased glucose uptake rates in microflagellate grazed bacterial cultures. The grazed detrital bacterial community has higher overall activity despite reduced biomass, indicating increased metabolic activity in those organisms not removed by grazing.

Johannes (1965) concluded that protozoan grazing maintained bacteria in a state of "physiological youth". This was partly attributed to faster and more complete regeneration of inorganic phosphate in grazed systems due to increased cell lysis. Barsdale et al. (1974) found that bacteria rapidly cycle phosphorus (turnover time as low as 2 min) in pure culture, and concluded that increased phosphorus cycling in grazed systems was the result of rather than the cause of higher bacterial activity. However, phosphorus does seem more readily available in grazed sytems. Morrison and White (1980) reported decreased levels of alkaline phosphatase activity, an enzyme microorganisms produce in response to limiting phosphorus levels, in amphipod-grazed leaf litter. Microflagellate grazing increased degradation of the mineral poor theca of Peridinium cells, but did not affect degradation of the mineral rich protoplasm (Sherr et al. 1982).

It is well known that cropping of a density-dependent population increases its productivity by reducing competition. Such is obviously the case with detrital bacterial assemblages, but the precise mechanism responsible for reduced competition is unknown. These data lead to two hypotheses for decreased competition between bacteria with protozoan grazing: microturbulence which would replenish limiting nutrient levels in the immediate environment of the cell and reduced density of bacteria which would increase resource availability per bacterial cell.

Detritivore grazing increases not only overall activity but also biomass of benthic microflora. Natural densities of the deposit feeding amphipod Hyallela azteca increased both the algal production and bacterial respiration of sediment cores after 48 hr feeding incubations (Hargrave 1970). Elevated microbial biomass and activity with amphipod (Fenchel 1970) and bivalve (Newell 1965) feeding were attributed to reduction in particle size of the food with a corresponding increased surface area for microbial colonization. Production of fecal pellets may also contribute to increased microbial biomass with grazing (Hargrave 1976). Fecal material produced by the freshwater snail Limnaea browsing on soft mud sediments and periphyton consumed more oxygen than the intact communities (Hargrave 1972). Hargrave (1970) found that feces showed a

decrease in organic content in the dark, probably due to leaching of soluble dissolved organic compounds, but showed an increase in the light, probably as a result of autotrophic production. Feces of the marine shrimp, Paleomonetes, showed a decrease in organic content at low dissolved nutrient concentrations, but an increase in organic content at higher concentrations, reflecting the incorporation of soluble compounds into microbial biomass (Johannes and Santoni 1966). Organic carbon accrual on feces obviously depends on the ratio of autotrophic and heterotrophic organisms present and the nature and amount of organic matter in the substrate and in solution.

The relative assimilation of prey items will also affect microbial growth on fecal material. The growth of mucilaginous-sheathed algae which survive passage through the intestinal tract of Daphnia was increased above that of uningested cells (Porter 1976). This effect may be a result of the unassimilated algae's utilization of high nutrient concentrations within the gut. Porter (1973) delineated three types of algae affected by zooplankton grazing: 1) algae which are not ingested, 2) algae which are ingested and digested, and 3) algae which are ingested and not digested. The first type was unaffected in 4 day grazing experiments, while the second type was suppressed, and the last type was stimulated. The relative assimilation of prey

items, therefore, will also affect organic accural on fecal material.

Amphipod grazing of oak leaves (Morrison and White 1980) and Spartina litter (Lopez et al. 1977) increased ATP content of the detritus without reduction in particle size or accumulation of fecal material. Increased microbial biomass and net activity despite removal of organisms through grazing suggests that the microbes which survive feeding greatly increase their growth rates. Morrison and White (1980) found that respiration, lipid biosynthesis, and poly-b-hydroxybutyric acid (PHB) (an endogenous storage polymer unique to procaryotes) synthesis increased per unit of microbial biomass, supporting Johannes' theory that grazing maintained bacteria in a state of physiological youth. Bioturbation may also increase bacterial activity by facilitating enzymatic exposure to organic substrates, a process potentially limiting in soil decomposition (Greenwood 1968).

In summary, grazing by macroinvertebrates and protozoans increases both microbial biomass and productivity. Increased productivity results from decreased competition between cells that escape predation, grazing selection pressure for more rapidly reproducing individuals, and enrichment of organisms which survive passage through the gut. The physical activity associated

with grazing by some larger organisms, such as particle fragmentation, bioturbation, and fecal production, increases the carrying capacity of the detrital environment, allowing for increased bacterial and algal biomass. Grazing by Aeolosoma, like other forms of grazing, should increase microbial productivity. The effects of meiofauna, organisms between protozoans and macroinvertebrates in both size and trophic state, on microbial biomass and community structure are more difficult questions. Meiofauna cause physical modification of their environment (mucus and fecal production, bioturbation, particle fragmentation) which may increase microbial biomass as seen with some macroinvertebrates. Yet meiofauna grazing represents a different selection pressure than macroinvertebrates on algal composition due to a smaller size range of prey species.

MATERIALS AND METHODS

General Methods

Aeolosoma were purchased from Carolina Biological Supply Company (Burlington, North Carolina). Stock cultures were kept in 13 cm diameter glass culture bowls at 20 ^{o} C in a Sherer Model Cel 4-4 Environmental Chamber (Sherer Division, Kysor Industries Corporation, Marshall Michigan). Photoperiod was set at 16 L:8 D, with a light intensity of approximately 70 ft-c (General Electric 20 W Cool White Deluxe Fluorescent bulbs). Culture media was a mixture of 19 parts dechlorinated tapwater and 1 part trout chow suspension. The latter was prepared by blending 3 g of trout chow (Trout Chow #3, Ralston-Purina Co., St. Louis, Missouri) in 200 mls of dechlorinated tap water. This mixture was autoclaved and passed through cheese cloth to remove large particulates. All dechlorinated tapwater used was adjusted to 180 mg/L hardness through addition of $NaHCO_3$, KCl, $MgSO_4$, and $CaSO_4$ to match test water hardness.

All experiments were conducted in Fisher 100 x 15 mm plastic petri dishes at the same temperature and light conditions under which stock cultures were maintained. Sampling from these petri dishes was conducted in the following manner. The bottom of each plate was scraped with a razor blade to remove attached organisms. Dislodged

contents were transferred to screw top test tubes and homogenized. Aliquots were removed from tubes between mixings for dry weight, chlorophyll a (chl a), protein, carbohydrate, and ^{14}C-glucose respiraton analysis. Dry weight was analyzed using the methods of the American Public Health Association (APHA et al. 1985). Chl a samples were extracted in acetone for 24 hrs in a dark refrigerator, and analyzed fluorometrically (APHA et al. 1985). Protein was extracted at 80 ^{o} C in 0.5N NaOH for 10 min twice and once additionally at 95 ^{o} C to increase recovery of protein from green and blue-green algal cells (Reusch 1981). Protein was measured using the microbiuret method with bovine serum albumin as a standard (Ithaki and Gill 1964). Carbohydrate was determined spectrophotometrically, using the sulfuric acid-phenol method (Herbert et al. 1971).

Microbial ^{14}C-glucose respiration was measured by a modification of the method of Williams and Askew (1968). A trace amount of glucose (0.5 ug/l) was added to 125 ml Erlenmeyer flasks containing 5 ml of sample. The flasks were mixed, sealed, and incubated in the dark to prevent photosynthetic uptake of $^{14}CO_2$. Formaldehyde-killed controls were run to account for abiotic $^{14}CO_2$ production. Samples were acidified after 1 hr with 2 ml 6N H_2SO_4. $^{14}CO_2$ was absorped on phenylethylamine saturated filter papers in

the head space of the flasks for 12 hr. Filters were then placed in 10 ml of cocktail (4 g PPO and 0.1 g POPOP liter^{-1} toluene) for 12 hr, and subsequently counted on a Beckman LS-3150 T liquid scintillation counter.

Aliquots were also removed for examination of algal community composition. After 1:10 dilution with 37% formaldehyde, 0.1 ml of sample was placed in a Palmer-Maloney cell and viewed at 400X magnification with a Zeiss binocular microscope. Diatom indentifications were verified in samples cleaned with $K_2Cr_2O_7$, mounted in Hyrax, and viewed under 1250X magnification. Cell counts were converted to biovolumes to more accurately express taxon importance on a biomass basis. Biovolumes were calculated for each algal taxon utilizing mensuration formulae for solids similar in shape to cells (Beyer 1981). Measurement of at least 10 cells were taken of each taxon of variable size, and at least 3 cells of each taxon of uniform size.

Test water used for all experiments was collected from Shadow Lake, located on Shadow Lake Rd. west of US Route 460 in Montgomery County, Virginia. This shallow, eutrophic, 2 acre impoundment supports a dense growth of macrophytes (particularly Potamogeton) and the macroalgae Chara. Water was taken from a depth of 1 m in a 20 L plastic carboy and later filtered through 0.45 um membrane filters. A slurry of Shadow Lake periphyton was made for

inoculating laboratory microcosms. This slurry was prepared from conditioned allochthonous detritus (leaves), Potamogeton, and Chara collected in a 300 ml jar filled with ambient water. This mixture was shaken vigorously by hand and with a Vortex to dislodge attached organisms. The contents were then filtered through a 106 um mesh to remove large particulates and macroinvertebrates. The resulting suspension was placed on a magnetic stirrer and replicate aliquots were placed into petri dishes containing filtered lake water. All dishes were immediately examined under 60X magnification with a Wild M5 dissecting microscope. Inoculum contained detrital particles, algae, protozoans, rotifers, nematodes, chironimidae larvae, copepods, and Aeolosoma. The last three groups were removed from dishes to reduce the impact of their unequal distribution among replicates.

Other procedures conducted can be better addressed through separate examination of the individual experiments performed. The effects of grazing by Aeolosoma were studied in four periphyton communities: 1) an early summer assemblage, 2) a late summer assemblage, 3) a laboratory conditioned assemblage, and 4) an undeveloped community composed mainly of refractory detritus.

Early Summer Assemblage

Water and periphyton were collected as described above on June 29, 1985. To compensate for the low soluble nutrient levels in most lake water (Rigler 1964), filtered water was enriched with 0.5 mg/l PO_4 and 0.5 mg/l NO_3 as K_2HPO_4 and $NaNO_3$, respectively. Twenty-four petri dishes (test chambers) received 15 mls of enriched water, 40 mg of finely divided (0.45-53 um) natural detritus, and 0.5 ml of inoculum. The detritus was collected from the aerobic layer of littoral sediments, dried, reseived, and weighed out into test chambers. Collection and set up of test chambers occurred the same day.

Cultures were allowed to condition for 1 week, at which time ten Aeolosoma were introduced in 0.5 ml of water to each of twelve randomly selected test chambers. Worms were first transferred from stock cultures to glass petri dishes containing dechlorinated tapwater to decrease concomitant addition of biomass and nutrients to the test chambers. An equivalent amount of transfer water (0.5 ml) was added to all control test chambers to further reduce bias caused by nutrient and biomass introduction with the worms.

At 2, 5, and 10 d four chambers of both treatments were sampled and analyzed for dry weight, Chl a, protein, carbohydrate, and algal community composition as discussed above. Vertical center scans of successive Palmer-Maloney

cells were taken until 500 algal cells were counted. Chl a, protein, and carbohydrate were calculated on a mg dry wt basis to correct for unequal evaporation in the test chambers and resulting variance in the density of cells in aliquots of equal volume. Differences between treatments at each sampling were tested using a student's t test. Data for all sampling days were analyzed using an analysis of variance (ANOVA) model with grazing and sampling day as class variables. Percent biovolumes were calculated for 23 algal taxa identified. These numbers were arcsine transformed and similarly analyzed by t tests and ANOVA. Duncan's multiple range test was used to determine if Chl a, protein, carbohydrate, protein/carbohydrate ratio, and %biovolume means differed between grazed and ungrazed cultures by sampling days.

Because Aeolsoma is so small (0.5 ug dry wt/worm) (Newman 1975) their inclusion in grazed culture samples would not have significantly biased protein or carbohydrate results. Based on protein and carbohydrate estimates of 40 % of dry wt and 20 % of dry wt, respectively, worm biomass would constitute less than 1 % of protein and carbohydrate levels measured in cultures (Chekanovskaya 1981).

Algal species diversity was calculated for each replicate using Simpson's D diversity index (Simpson 1949):

$$= \quad n_i (n_i - 1)/n(n-1)$$

where n_i equals the number of individuals in the ith species from a population sample, n equals the number of individuals in a population sample, and S equals the number of species in the population. Values range from 0 to 1.0. Simpson (1949) defined D as a measure of the concentration of classification or the probability that two individuals chosen at random will belong to the same group. Simpson's D value is one of the few indices suitable for aquatic ecosytems (Washington 1984). Indices were arcsine transformed to normalize the data and analyzed with ANOVA as above.

Pinkham and Pearson's Index of Similarity (B) was calculated for the means of dominant algal taxa for both treatments at each sampling date as follows:

$$= 1/k \quad \text{Min } (X_{ia}, X_{ib}) / \text{Max } (X_{ia}, X_{ib})$$

where X_{ia} and X_{ib} are the number of individuals in the ith taxon for samples a and b, respectively, and k is the number of different taxa in the two samples. This index provides more reliable analysis of data than indices that examine either species occurences or abundances since it compares both factors (or species composition) simultaneously (Pinkham and Pearson 1976).

Late Summer Assemblage

The previous experiment was repeated later in the summer with minor modification. Water and inoculum were

collected as described above. Twenty petri dishes received 15 ml of similarly enriched water, 1 ml of inoculum, and 5 ml of a detrital slurry. The latter was made by collecting the top aerobic layer of littoral sediments and filtering through a 53 um mesh. The resulting suspension was sampled as described above.

Cultures were allowed to condition for 10 d after which 4 were sacrificed for measurement of dry weight, ^{14}C-glucose respiration, and algal species composition. Ten worms were added to half of the remaining cultures as in the first experiment. After 6 and 12 d, dry weight, ^{14}C-glucose respiration, protein, carbohydrate, and algal species composition were measured in four test chambers from each treatment. Algal counts were made by scanning a segment of the Palmer-Maloney cell that contained atleast 500 cells. The height of the segment was recorded with the stage micrometer and used to calculate the area of the segment:

$$\text{Area} = R^2 \cos^{-1} R\text{-}h/R - (R\text{-}h)\ 2Rh\text{-}h^2$$

where R is the radius of the Palmer-Maloney cell and h is the heigth of the segment. The fraction, area counted/total area of Palmer-Maloney cell, multiplied by the volume of the cell (0.1 ml), yields um^3 algal biovolume/ml. Differences in test chamber volumes were accounted for by multiplying this value by the ratio of total volume in test

chamber/area of test chamber bottom.

Algal cell density and ^{14}C-glucose respiration for both treatments on 6 and 12 d were analyzed by ANOVA. Protein was detectable only on day 12 so protein, carbohydrate, and P/C ratio were analyzed for day 12 with student's t tests. Algal %biovolumes were also calculated, arcsine transformed, and analyzed by ANOVA. Simpson's diversity index (D) and Pinkham and Pearson's index of similarity were calculated for day 0 and for both treatments 6 and 12 d. B was calculated using algal densities, a better measure of relative taxon importance than cell counts.

At 6 and 12 d, five randonmly selected worms were removed from each grazed replicate immediately before sampling, and examined for gut contents. Worms were transferred to algal-free water, pipetted onto glass slides, and flattened with a coverslip. All algae found in food boli within the disaggregated worm mass were enumerated. An Ivlev's electivity index was derived for algal taxa using:

$$= r_i - p_i / r_i + p_i$$

where r_i was the percent biovolume in the diet and p_i was the percent biovolume in the environment for each algal taxon. Values between 0.1 and 1 indicate positive election while values between -0.1 and -1 indicate negative

selection. Intermediate values indicate neutral or non-selection (Kohler and Ney 1982). This index has recently been criticized for tending to bias toward predator selection, and may be particularly unreliable when examining food items with a low r_i or p_i (Strauss 1979, Kohler and Ney 1982). Interpretation of electivity indices will be done with the above limitations in mind.

Laboratory Conditioned Assemblages

This experiment was conducted to repeat analyses of the effects of grazing on the bacterial community. The periphyton slurry collected in late September was kept under labaoratory conditions described above for 4 wks. Then the inoculum was refiltered through 106 um mesh and 5 ml aliquots were introduced to 8 petri dishes containing 20 ml of lake prepared as above. Test chambers were allowed to condition for 10 d at which time 10 Aeolosoma were placed into each of 4 randomly selected chambers.

After 10 d cultures were sampled for analysis of ^{14}C glucose respiration, bacterial biomass, and dry weight. The latter measurements were taken as above. Bacterial biomass was estimated by enumeration of colony forming units (CFU) on spread plates containing 1/4 strength Difco nutrient agar (Difco Laboratories, Detroit, Michigan). Dilutions of 1/10, 1/100, 1/1000, and 1/10000 were made from culture

aliquots, and examined with a dissecting microscope after 3 d incubations under experimental temperature and light conditions. ^{14}C glucose respiration analysis was performed as above with slight modification. Three 3 ml aliquots were withdrawn from each replicate and placed into 25 ml Erlenmeyer flasks. An equivalent amount of labelled glucose, 0.5 ug/L, was added to all flasks as above. Additional unlabelled glucose was added to achieve concentrations of 0.5, 1, and 20 ug/L. Cultures were incubated for 1.5 hours.

Dilution of radiolabelled glucose should decrease ^{14}C glucose respiration at higher concentrations due to competition between labelled and unlabelled glucose at uptake sites. The rate of solute uptake mediated by cell membrane transport systems should follow typical enzyme kinetics as described by the Michaelis-Menton equation:

$$v = V_i (S) / K_m + S$$

where v is the velocity at a given substrate concentration S, V_i is the maximum velocity attained when uptake sites are continually saturated with substrate, and K_m is a rate constant equal to the substrate concentration when v is 1/2 V_i. Lower K_m values indicate higher affinity of the uptake system for the substrate (Kepes 1963). Uptake of solutes by environmental bacterial assemblages approximates Michaelis-Menton kinetics (Wright and Hobbie 1966, Stanley and Staley

1977). Seasonal decreases in V_i and K_m in response to decreasing substrate availability reveal the plasticity of microbial enzyme systems (Stanley and Staley 1977). Comparison of enzyme kinetics between treatments in this experiment should reveal the effects of grazing on bacterial glucose transport systems.

Duncan's multiple range test was performed on the means of respiration at each concentration for both treatments. Differences in CFU/mg dry wt and glucose respiration/CFU at 0.5 ug/l between treatments were analyzed with student's t tests.

Unconditioned Detritus

Detritus was collected as described above in late September, and seived through a 106 um mesh. Material was dried at 90 ^{o} C to lyse live cells, soaked in distilled water for 24 h to leach out dissolved labile compounds, redried, and reseived through 106 um mesh. Periphyton slurry was collected as above in mid-November on the day of experimental set-up. Fifteen ml of unenriched lake water, 4 ml of slurry, and 40 mg of detritus were added to 12 test chambers. Immediately after inoculation, 10 Aeolosoma were added to eight of the cultures. After 2 d all cultures were sampled for Chl a, protein, carbohydrate, and dry weight. Four grazed and four control cultures were homogenized and

sampled as above. Mucus associated aggregates were removed from the remaining four grazed cultures before homogenization. The petri dish was placed on a dissecting microscope with bottom illumination and gently agitated. Aggregates were defined as those clumps of detritus that remained intact after agitation. No such clumps appeared in control cultures subjected to the same procedure. Aggregates were withdrawn from the cultures with a pipette and placed into a watch glass. Examination under the microscope revealed that 90% of the worms were removed from culture dishes with the aggregates. Worms were removed and the volume of each sample was brought to 4 mls before sampling. Due to the small amount of aggregated material only dry weight and chl a were analyzed for those samples. Unaggregated material from those same cultures were sampled for dry weight, chl a, protein, and carbohydrate. Duncan's Multiple Range tests and student's t tests were performed on means of all measurements and treatments (Sokal and Rohlf 1981).

RESULTS

Comparison of Early and Late Summer Assemblages

One of the purposes of this study was to determine the effect of grazing on two distinct periphyton communities; early and late summer assemblages. Biovolume means for all sampling in both experiments were examined to determine whether the two communities were substantially different in composition (Fig. 1).

Diatoms dominated both the early (69% of the total algal biovolume) and late (58%) summer assemblages. Synedra and Fragilaria accounted for 2/3 of the diatom biovolume in the early summer assemblage; Nitzchia, Gomphonema, Cocconeis, and Rhopalodia comprised the remaining third. Diatom composition in the late summer assemblage was distinctive. Synedra biovolume constituted over half of the diatom biovolume. Cymbella, Gomphonema, Fragilaria, Cocconeis, and naviculoids were the other diatoms present in significant numbers.

Non-diatom composition was also different between experiments. Coccoid green algae contributed 24% and 4% to the total biovolume in the early and late summer assemblages, respectively. Cosmarium and Pediastrum were the only coccoid green algae identified to genus. The remaining coccoids, which accounted for most of this

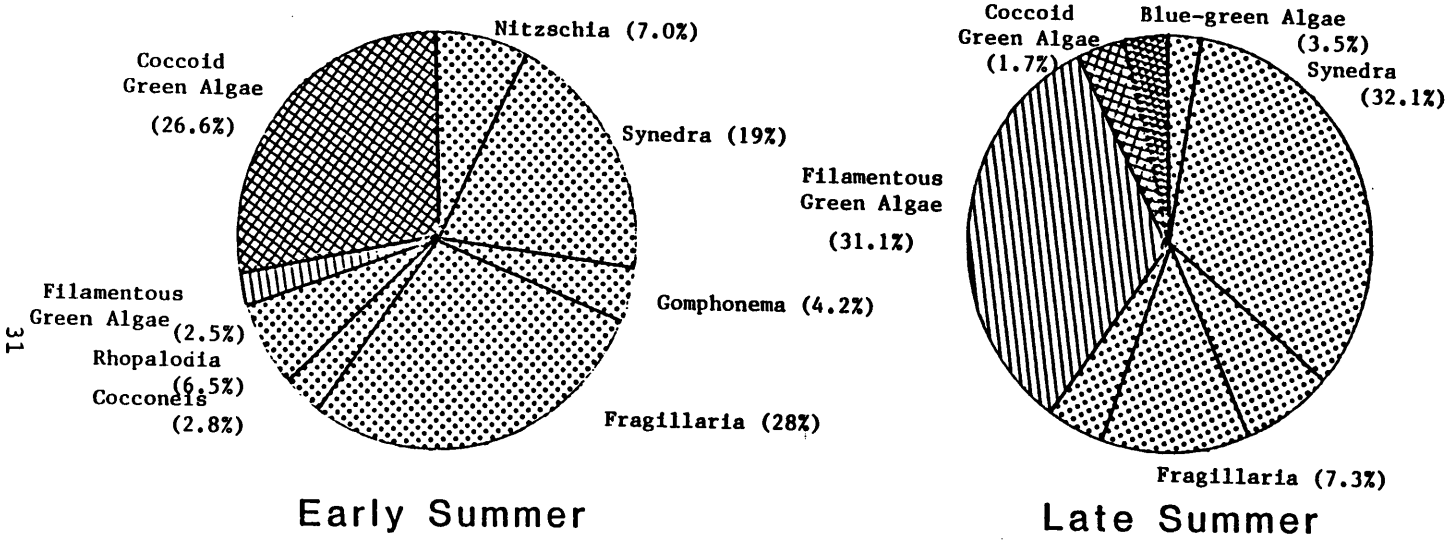

Figure 1. Comparison of algal community composition between early and late summer laboratory assemblages. Numbers represent mean % biovolume of taxon in both grazed and ungrazed treatments for all sampling days. Stippled area=diatom biovolume, single lines=filamentous algae, cross-hatched=coccoid green algae, triangles=blue-green algae

group's biovolume, were identified by the presence or absence of a mucilaginous sheath. Filamentous green algae were a major component of the late summer assemblage (30% of total bioviolume), but was a relatively insignificant part of the early summer assemblage (2.5%). Two species were identified, Mougeotia and Oedogonium. A distinction was made in the former between filaments of large (120 um x 20 um) and small (110 um x 2.5 um) cell size. These probably represent two species of Mougeotia since clonal cultures grown under laboratory conditions usually have constant cell width (Hoshaw 1968). Anabaena comprised 3.5% of the biovolume in the late summer assemblage, and was the only blue-green alga present in significant numbers in either experiment.

Early Summer Assemblage

The effect of grazing on algal and overall biomass changed over the course of the experiment. Chl a/mg dry wt in grazed cultures was greater at day 2 ($p=0.02$), but was slightly less than that in control cultures by day 10 (Fig. 2). Protein levels showed the same trend between treatments (Fig. 3). Grazed cultures contained more protein/mg dry wt at day 5 ($p=0.01$), but slightly less at day 10. Significant interaction terms in ANOVA analysis of chl a ($p=0.001$) and protein (0.0573) confirm the dependence of grazing effect

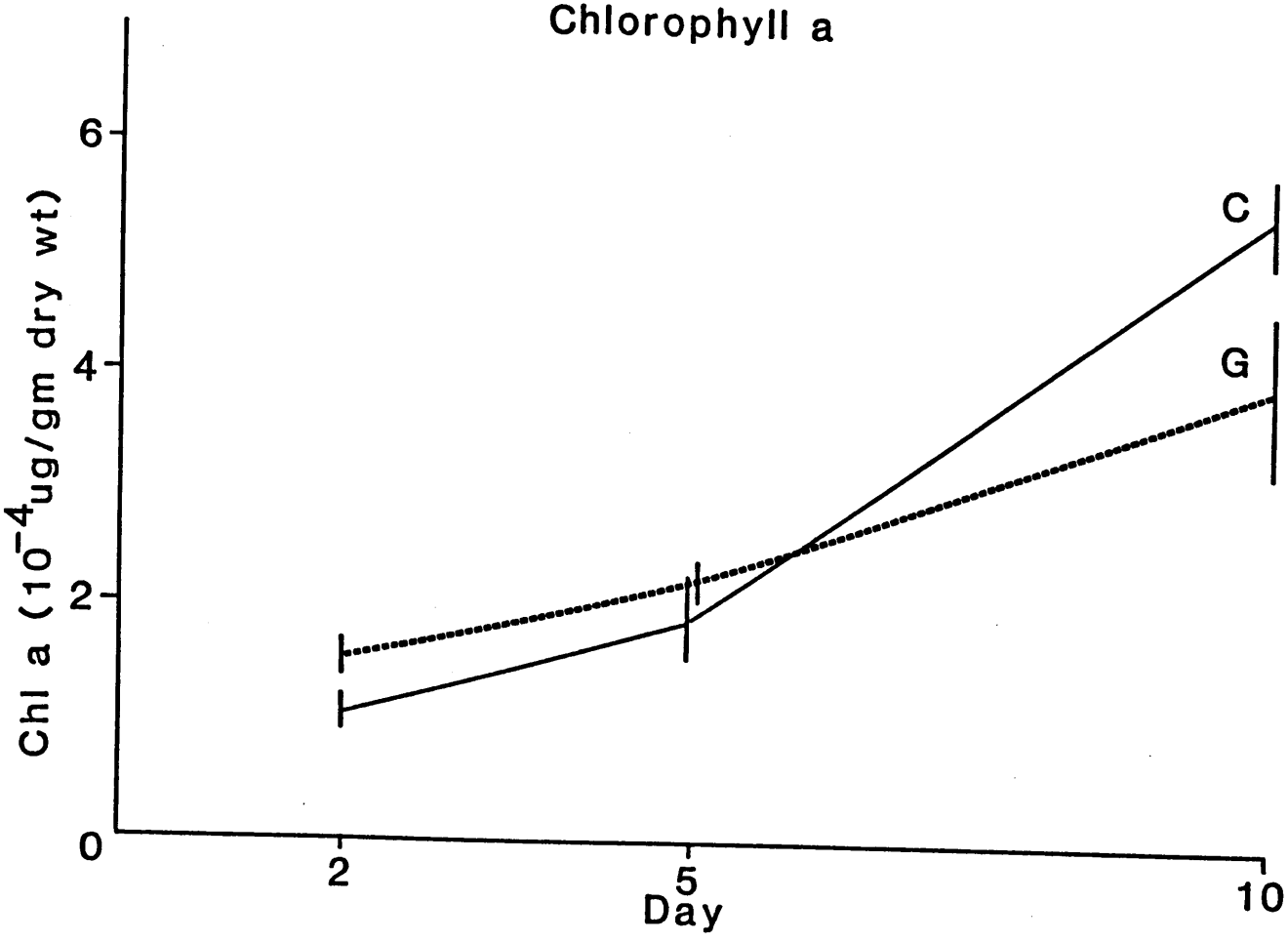

Figure 2. Chlorophyll a content of grazed (broken line) and control (solid line) over time. Error bars represent standard error of four replicates. All values for early summer periphytic assemblage.

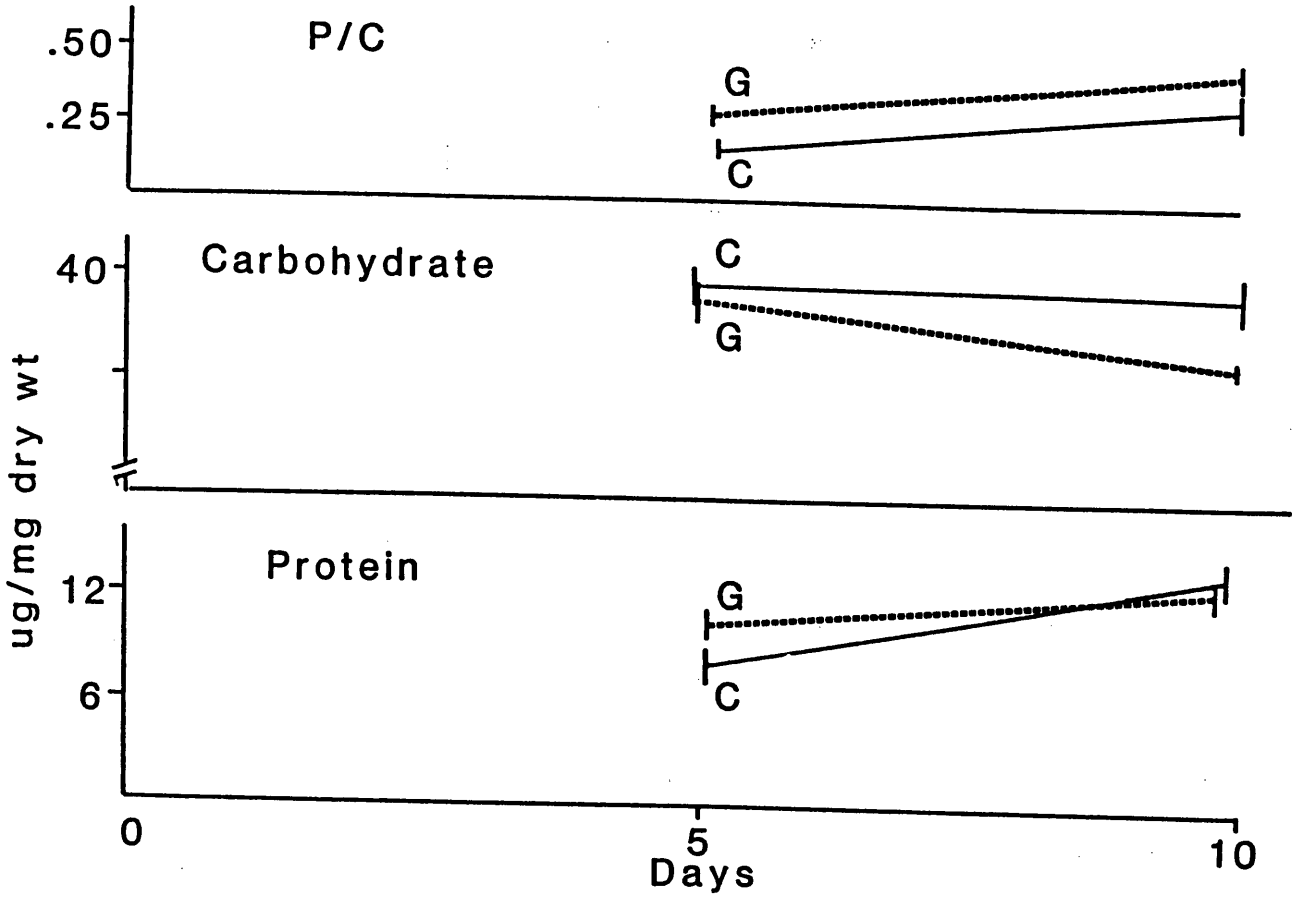

Figure 3. Protein, carbohydrate, and protein/carbohydrate content of grazed (broken line) and control (solid line) over time in the early summer assemblage. Error bars represent standard error of four replicates.

upon biomass on time (Sokal and Rohlf 1981). Protein/ carbohydrate ratio was greater with grazing ($p=0.02$) due in part to a significant reduction ($p=0.01$) in the carbohydrate content of grazed cultures at day 12 (Fig. 3). The ratio also increased with time ($p=0.0003$), probably as a result of the high carbohydrate content of detritus present at the beginning of the study. Protein ($p=0.0097$) and chl a ($p=0.0001$) increased with time, reflecting the net growth of periphyton communities during the course of the experiment.

Grazed cultures at day 10 had the most dissimilar algal community composition as revealed by a dendogram plot of Pinkham and Pearson's similarity index (Fig. 4). This divergence was mainly due to a four-fold reduction in Nitzchia ($p=0.0056$) and a three-fold increase in mucilaginous-sheathed green coccoid algal ($p=0.0341$) in grazed cultures (Figs. 5 and 6). Rhopalodia was also greater in grazed cultures at day 10 ($p=0.043$). The two algal species which accounted for over half the biovolume, Fragilaria and Synedra, showed no overall response to grazing. The interaction term for Fragilaria was significant ($p=0.0386$), reflecting its higher %biovolume at day 5 ($p=0.045$), but decreased %biovolume at day 10 (Fig. 7). The same trend of greater grazing effect with time resulted in significant interaction terms for naviculoids

Algal Community Comparison

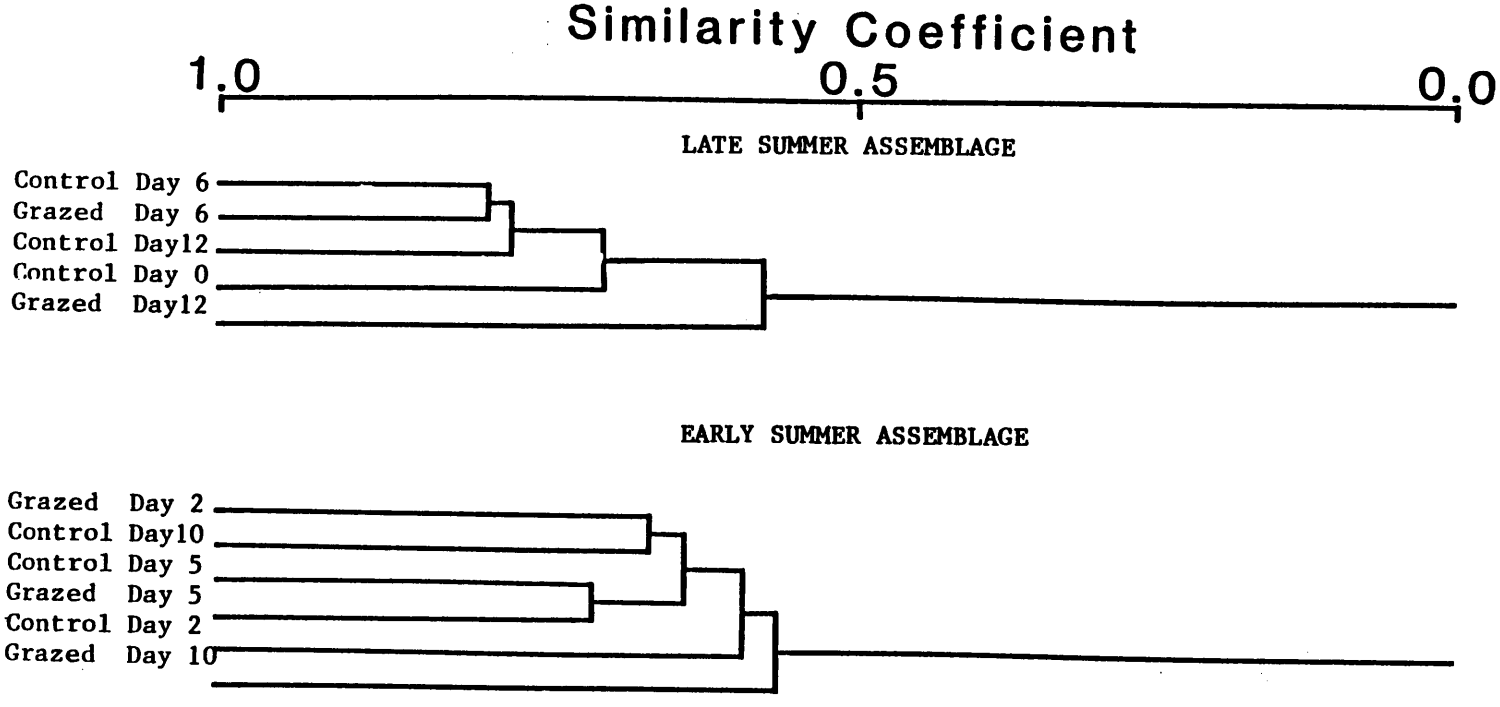

Figure 4. Dendogram plot of Pinkham and Pearson's Index of Similarity for algal community composition of all samplings in each assemblage.

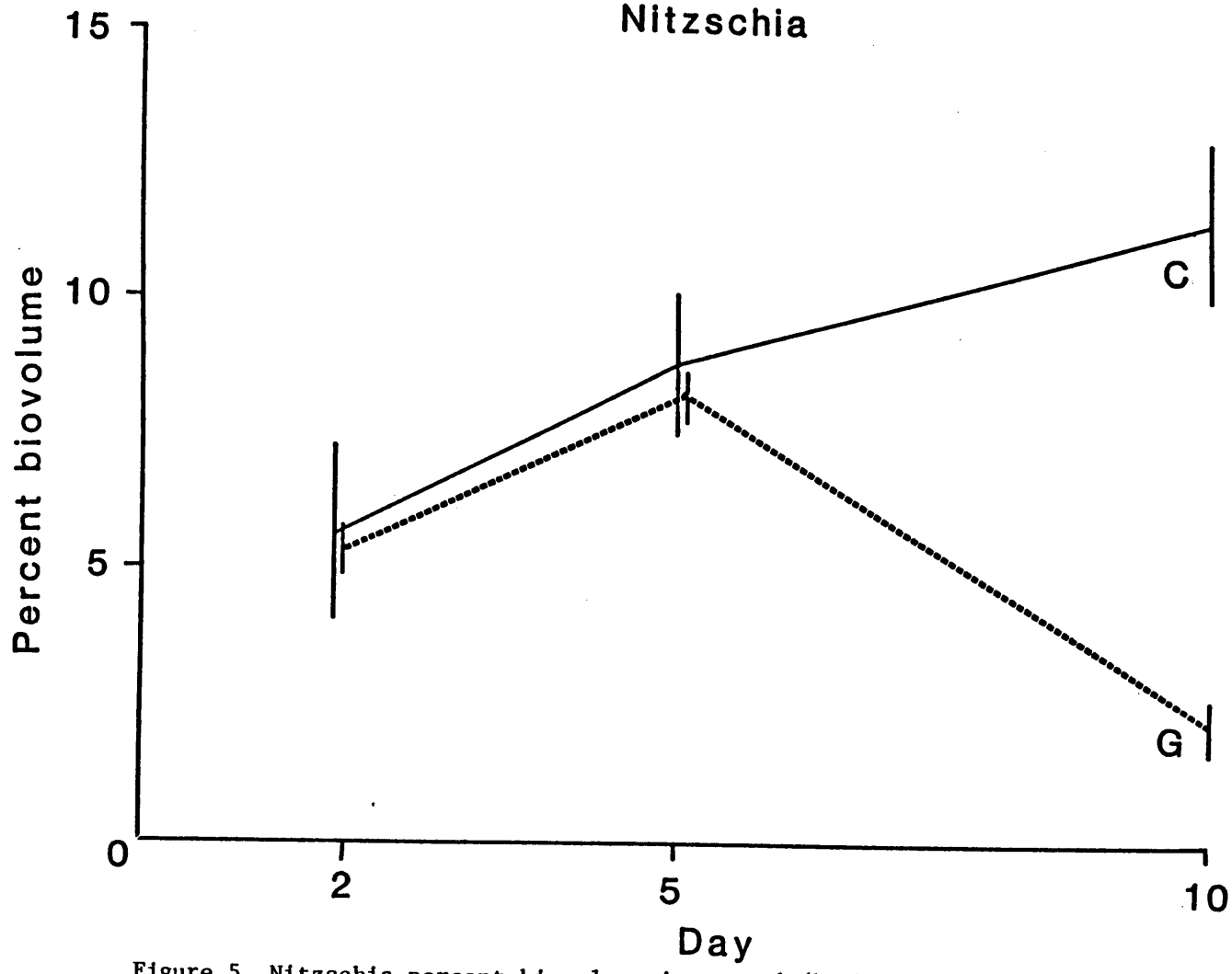

Figure 5. Nitzschia percent biovolume in grazed (broken line) and control (solid line) cultures over time in the early summer assemblage. Error bars represent standard error of four replicates.

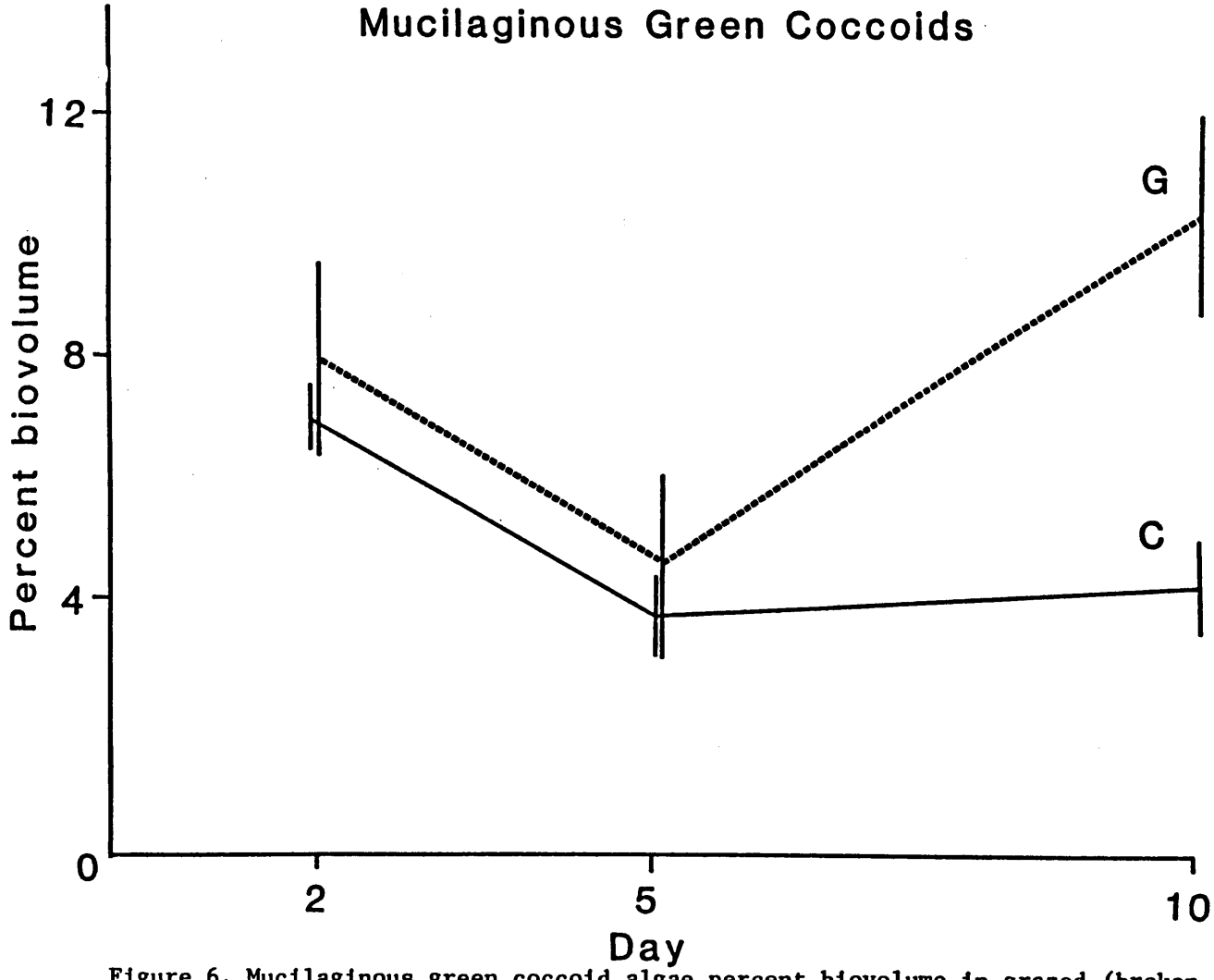

Figure 6. Mucilaginous green coccoid algae percent biovolume in grazed (broken line) and control (solid line) cultures over time. Error bars respresent standard error of four replicates. All values for early summer assemblage.

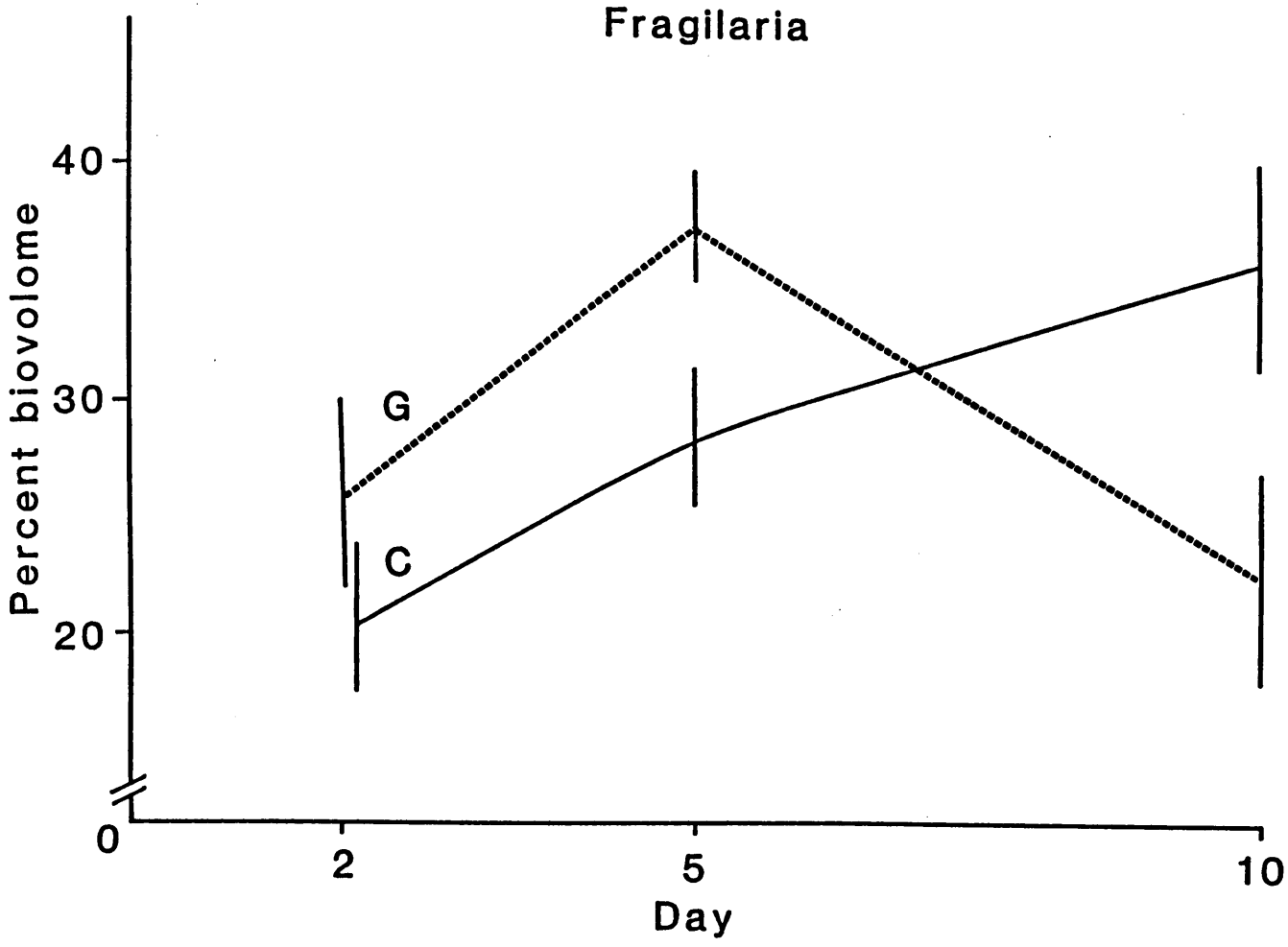

Figure 7. Fragillaria percent biovolume in grazed (broken line) and control (solid line) cultures versus time. Error bars represent standard error of four replicates. All values for early summer assemblage.

(p=0.0015) and Nitzchia (p=0.0019) (Figs. 5 and 8). Significant interaction was present for Gomphonema % biovolume due to a reduction in control cultures between days 5 and 10 (Fig. 9). Grazed Gomphonema % biovolume remained at a constant level (3%) throughout the experiment which was significantly less than control at day 2 (p=0.005) and day 5 (p=0.0046).

The species diversity of the early summer algal community was unaffected by grazing. Indices of both treatments decreased from a maximum (0.33) at day 2 to a minimum (0.24) at day 5, then increased to an intermediate value (0.27) at day 10.

Late Summer Assemblage

Algal biomass, as measured by total algal biovolume density, was not influenced by time or grazing. This uniformity in total algal biovolume caused similar results in density and %biovolume analyses of individual algal taxa. Total protein was slightly below detection limits at day 6. Protein (p=0.054) and protein/carbohydrate ratio (p=0.0596) were greater in grazed cultures on day 12. Increased protein content of cultures through time without corresponding increases in algal biovolume indicate an increase in non-algal microbial biomass. This is supported by a significant increase in ^{14}C glucose respiration rates with time (p=0.0001). Rates were also significantly greater

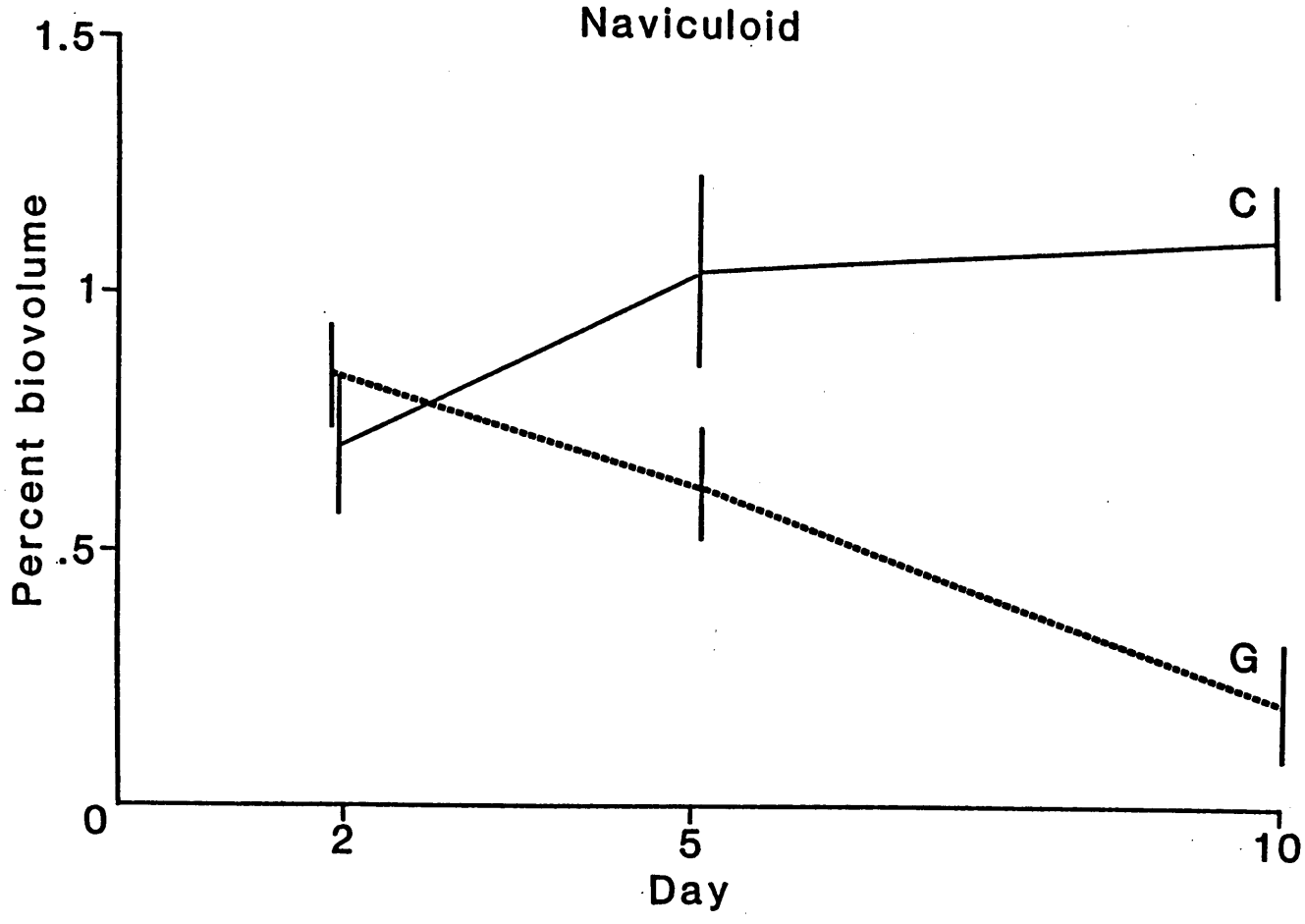

Figure 8. Naviculoid percent biovolume in grazed (broken line) and control (solid line) versus time. Error bars represent standard error of four replicates. All values for early summer assemblage.

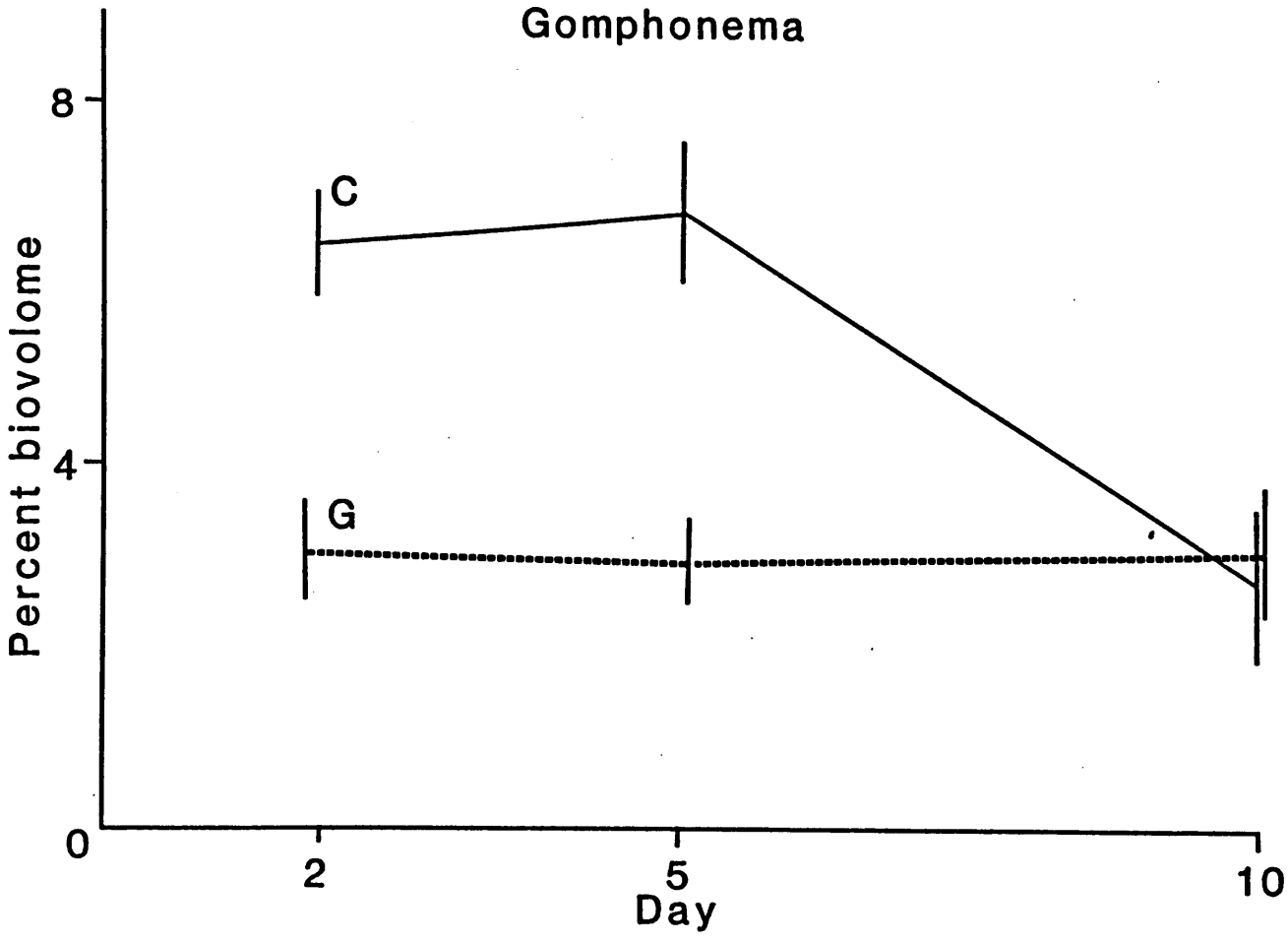

Figure 9. Gomphonema percent biovolume in grazed (broken line) and control (solid line) cultures versus time in early summer assemblage. Error bars represent standard error of four replicates.

in control cultures (p=0.0005) despite greater microbial biomass estimates for treatments at day 12 (Fig. 10).

As in the first experiment, grazed cultures at the last sampling day had the most dissimilar algal composition (Fig. 4). This separation was a result of decreased densities of three diatom taxa and increased densities of two green algal taxa in grazed cultures. Synedra densities were similar in both cultures at day 6, but had decreased sharply in grazed cultures by day 12 (Fig. 11). The interaction term for Synedra %biovolume was significant (p=0.0473), reflecting the different effect of grazing with time. Gomphonema (p=0.0105) and Cymbella (p=0.0229) densities were significantly less in grazed cultures. Divergence occurred by day 6 and was relatively constant through day 12 (Figs. 12 and 13). Density of small Mougeotia was twice as high in grazed cultures at both day 6 and 12, and showed a significant positive response to grazing (Fig. 14). Significant differences were not present between treatments when total filamentous algal density was analyzed. Green coccoids were also greater in grazed cultures (Fig. 15).

The diversity of the late summer algal assemblage was significantly higher in grazed cultures (p=0.024). Diversity indices remained low and constant (approximately 0.080) in control cultures, but increased gradually with

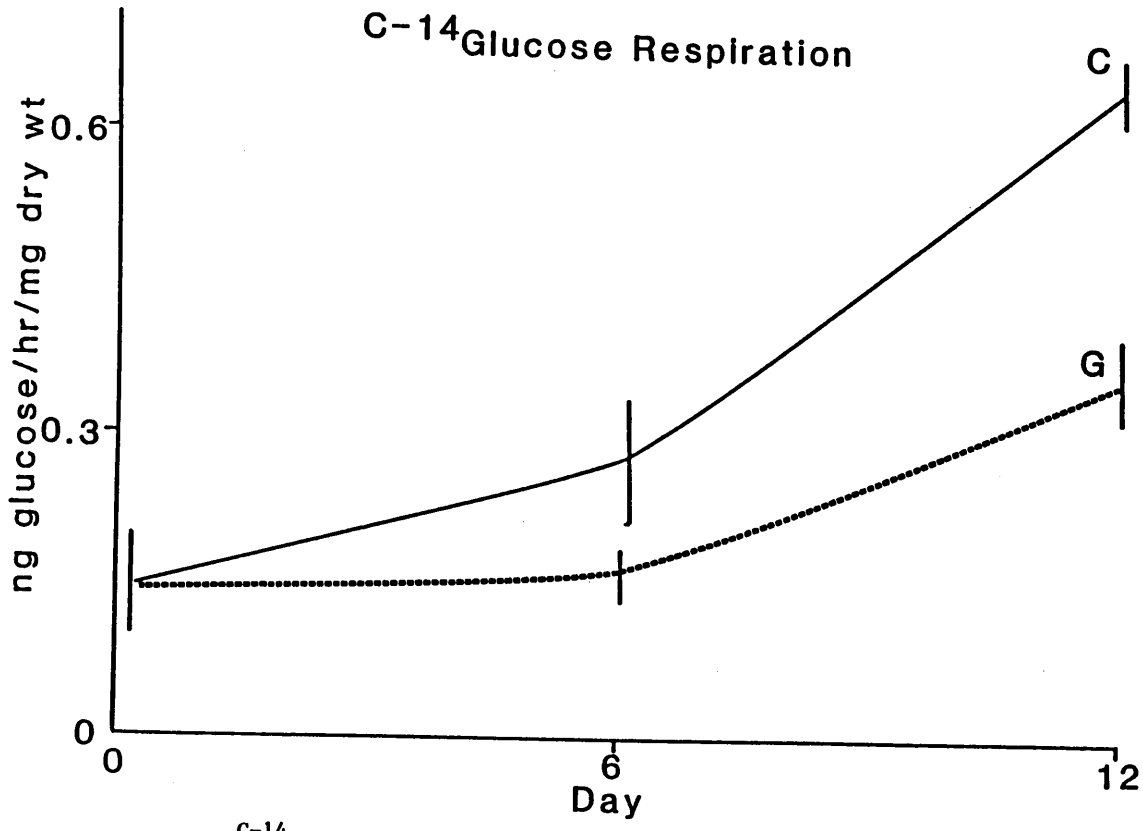

Figure 10. $^{C-14}$Glucose respiration in grazed (broken line) and control (solid line) cultures over time in late summer assemblage. Error bars represent standard error of four replicates.

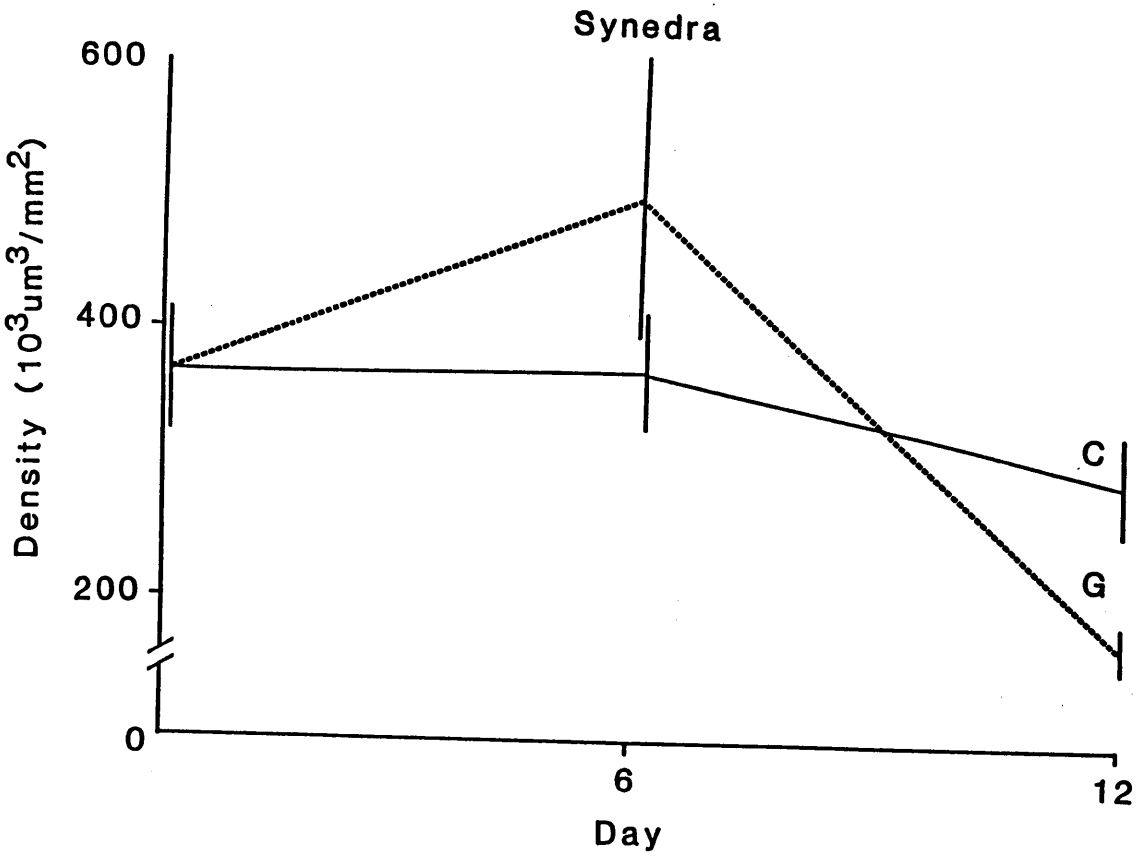

Figure 11. Syndera biovolume density in grazed (broken line) and control (solid line) cultures versus time in the late summer assemblage. Error bars represent standard error of four replicates.

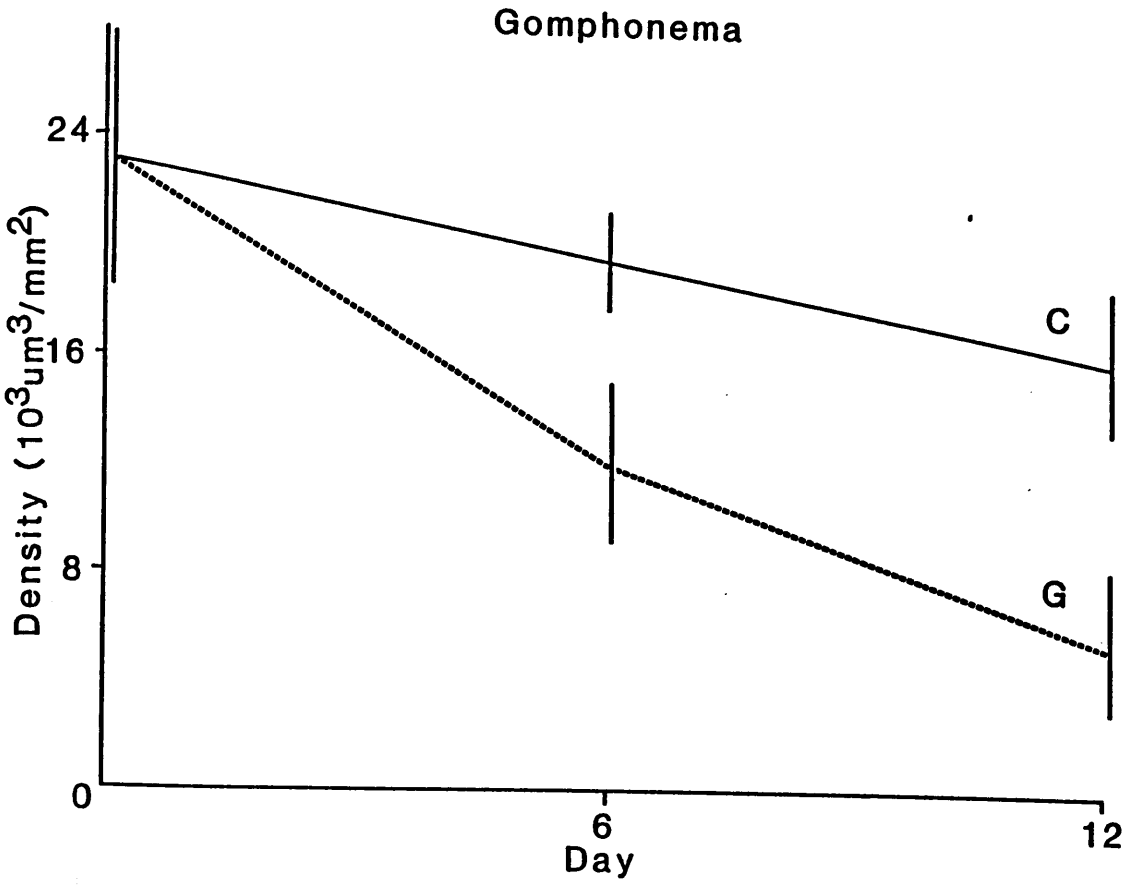

Figure 12. Gomphonema biovolume density in grazed (broken line) and control (solid line) cultures versus time in the late summer assemblage. Error bars represent standard error of four replicates.

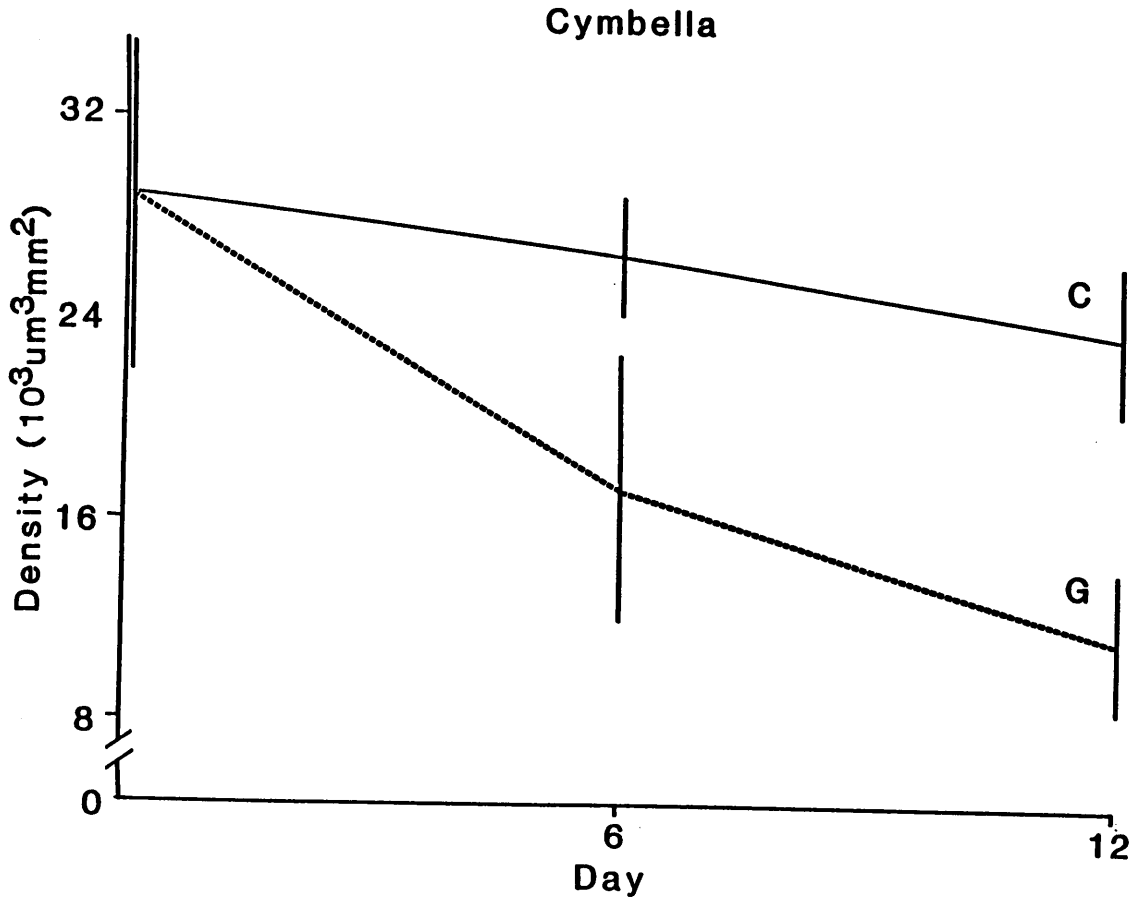

Figure 13. Cymbella biovolume density in grazed (broken line) and control (solid line) cultures versus time in the late summer assemblage. Error bars represent standard error of four replicates.

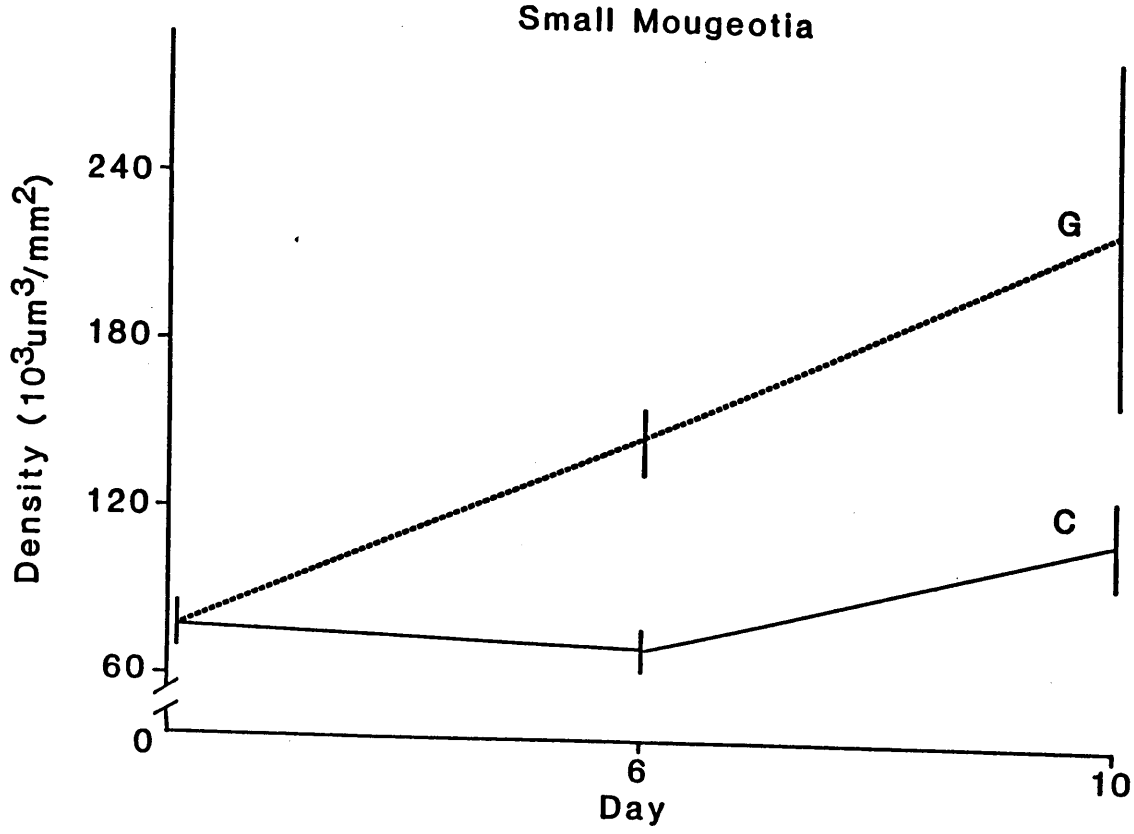

Figure 14. Small Mougeotia biovolume density in grazed (broken line) and control (solid line) cultures versus time in the late summer assemblage. Error bars represent standard error of four replicates.

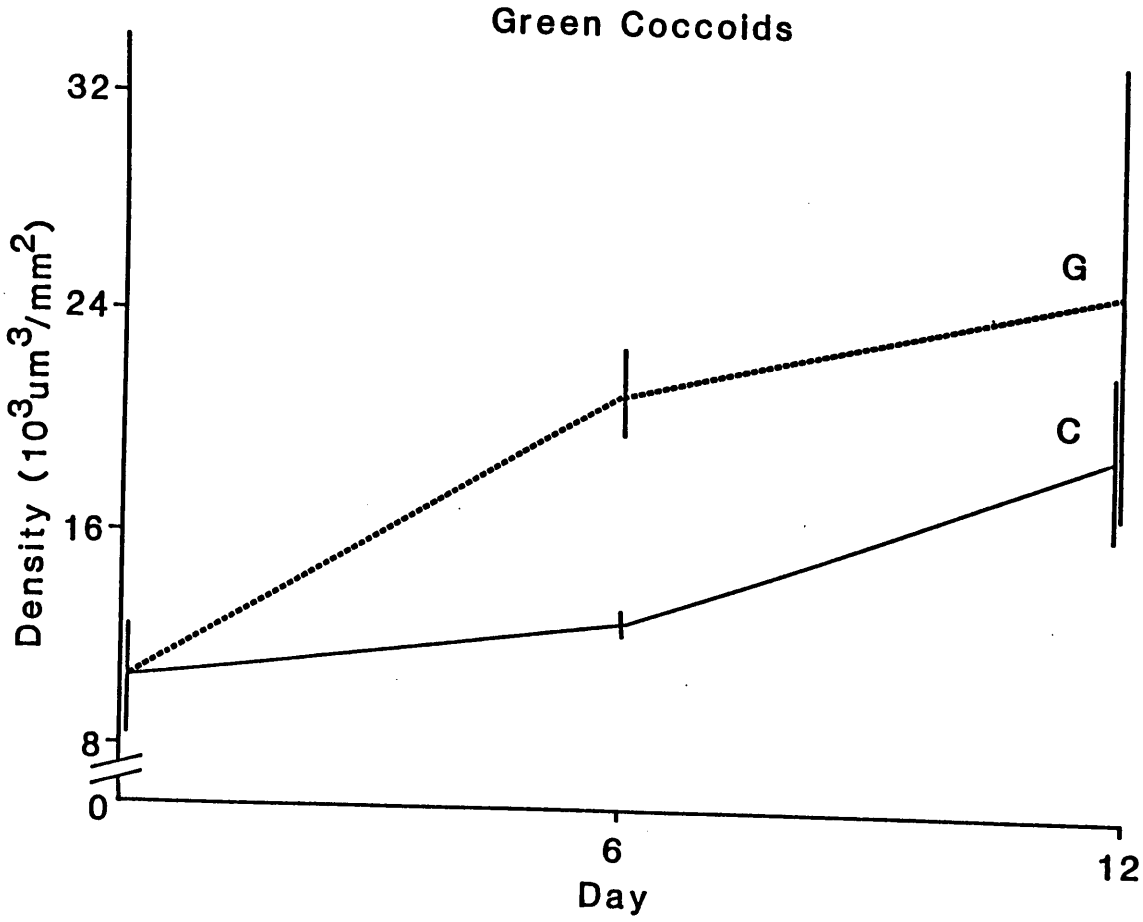

Figure 15. Green coccoid biovolume density in grazed (broken line) and control (solid line) cultures versus time in the late summer assemblage. Error bars represent standard error of four replicates.

time in grazed cultures to 0.092 at day 12.

Results from gut analysis of Aeolosoma are presented in Table 1. Large Mougeotia and Synedra accounted for 68.7 and 61.6 % of algal biovolume in the guts of Aeolosoma examined at days 6 and 12, respectively. Small Mougeotia and the other dominant diatom taxa accounted for most of the remaining algal diet. The largest cells ingested were Mougeotia filaments 320 um in length, Synedra cells 240 um in length, and Fragilaria chains 60 um square.

Ivlev's electivity indices varied with algal taxa and time (Table 1). The blue-green and green filamentous alga, Anabaena and small Mougeotia, respectively, were negatively elected on both day 6 and day 12. The former was rarely found in the gut. Large Mougeotia filaments, however, were positively elected on both days. Gomphonema and Cymbella also were positively elected on both days. Aeolosoma negatively elected Synedra, Nitzchia, naviculoids, green coccoids, and mucilaginous green coccoids on day 6, but neutrally or positively elected these taxa on day 12. Fragilaria was neutrally elected on both days.

Laboratory Conditioned Detritus

Results of the examination of grazing effect on the bacterial community are summarized in Table 2. Bacterial numbers, as estimated by CFU's, were significantly greater

Table 1. Analysis of Algal Diet of *Aeolosoma*
I = Ivlev's electivity index; r_i = % of the algal diet each taxon represents based on biovolume.

	Day 6		Day 12	
Algae	I	r_i	I	r_i
Cymbella	.19	3.9	.47	3.7
Gomphonema	.40	3.8	.66	2.3
Fragilaria	.10	6.5	.04	6.4
Synedra	-.22	29.3	-.03	20.3
Naviculoids	-.38	2.0	-.14	1.6
Nitzchia	-.23	0.3	.12	0.5
Large Mougeotia	.60	39.4	.38	41.0
Small Mougeotia	-.36	4.4	-.52	7.0
Oedogonium	-.22	0.8	-.10	0.0
Coccoid Green Algae	-.44	0.7	.06	2.9
Mucilag. Green Coccoids	-.15	0.4	.38	1.1
Anabaena	-1.00	0.0	-1.00	0.1

Table 2 Results of Examination of Grazing Effect on Bacterial Community

Numbers represent means (standard deviations) of three or four replicates. P values correspond to student's T tests. Letters reflect results of Duncan's multiple range tests, means with same letter are not significantly different.

	Biomass (CFU/mg dry wt)	^{14}C glucose respiration (10^{-9} ug glucose/hr/CFU)
Control	4968 (979)	6.8 (1.9)
Grazed	10500 (2352) (p=0.027)	3.4 (0.8) (p=0.023)

^{14}-C glucose respiration (10^{-4} ug glucose/hr/mg dry wt)

[Substrate]	Control		Grazed	
0.5mg/l	A	.344 (.047)	A	.290 (.031)
1.0mg/l	A A	.283 (.056)	B	.225 (.027)
20.0mg/l	A A	.273 (.041)	B B	.226 (.029)

in grazed cultures (p=0.027), while glucose respiration/CFU at 0.5 mg/l glucose was significantly less in grazed cultures (p=0.023). Trends in glucose respiration/mg dry wt over increasing substrate concentrations cannot be examined because the data does not conform to the expected kinetic response. Alteration in incubations times are probably necessary to prevent substrate limitation or bacterial turnover.

Unconditioned Detritus

Mucus-associated aggregation by Aeolosoma was only seen in cultures containing unconditioned detritus. Aggregating response was not displayed in the previous three experiments when Aeolsoma grazed well-developed periphyton communities.

Results of grazing effect on unconditioned detritus are presented in Table 3. Overall, grazed and control cultures contain similar quantities of chl a, pheophytin, protein, and carbohydrate. Differences are present when delineation is made between aggregated and unaggregated material within grazed cultures. Mucus-aggregated material contained significantly less chl a/mg dry wt and significantly more pheophytin/mg dry wt than control cultures, combined grazed cultures, and unaggregated material. Protein/mg dry wt and P/C ratio were

Table 3 Grazing Effect on Unconditioned Detritus

Numbers represent means (standard deviations) of three or four replicates. P values correspond to student's T tests. Letters reflect results of Duncan's Multiple Range tests, means with same letter are not significantly different.

	Chl a (10_{-4} ug/mg dry wt)		Pheophytin (10_{-4} ug/mg dry wt)	
Grazed	3.30 (0.22)	A A	0.80 (0.09)	A A
Unaggregated	3.18 (0.18)	A A	0.79 (0.06)	A A
Control	3.10 (0.19)	A	0.82 (0.08)	A
Aggregated	2.75 (0.25)	B	1.13 (0.14)	B

	Protein (ug/mg dry wt)		Carbohydrate (ug/mg dry wt)		P/C	
Control	10.89 (2.93)	A A	16.13 (1.18)	A A	0.70 (.245)	A A
Grazed	7.96 (0.25)	AB B	16.46 (1.60)	A A	0.49 (.057)	AB B
Unaggr.	7.05 (0.70)	B	18.61 (2.45)	A	0.38 (.046)	B
	p(G-U)=.054				p(G-U)=.030	

significantly less in unaggregated material relative to combined grazed material, indicating that these measures were greater in aggregated material.

DISCUSSION

Protein/carbohydrate ratio was greater in grazed cultures in both the early and late summer asssemblages. Increased P/C ratio reflects a shift from an autotrophic to a heterotrophic community because bacteria have 4-5 times more protein/dry wt than algae (Moore and Potter 1976). Changes in P/C ratio may also result from shifts within the algal community. Harg et al. (1973) found that P/C ratios of phytoplankton varied with algal composition and physiological state. Dinoflagellates and green algae have lower P/C ratios than diatoms due to the cellulose content in their cell walls. Diatoms have highly variable P/C ratios depending on their physiological state. Rapidly reproducing populations store less glucan and have higher P/C ratios than stationary populations. Since the relative abundances of green algae and diatoms were similar between treatments in both experiments, higher P/C ratios in grazed cultures probably resulted from low glucan levels in the grazed diatom community or increased bacterial biomass.

Grazed cultures did not have significantly lower chla/protein ratio in the early summer assemblage, so increased P/C ratio probably resulted from low glucan levels in grazed cultures. In fact, P/C ratio was greater in grazed cultures despite a significant increase in mucilaginous green coccoid algae which would decrease P/C

ratio. Grazed cultures did not have significantly higher algal biomass in either experiment, so high algal production inferred by low glucan levels reflect the greater turnover rate and not the faster accural of biomass in the diatom-dominated algal assemblage.

In the late summer assemblage total algal biovolume densities did not differ between treatments, but protein content of grazed cultures was greater at day 12. This suggests that grazing stimulated bacterial biomass, which might be partly responsible for increased P/C ratio with grazing.

These results differ from the effects reported for grazing of periphyton by larger invertebrates. While macroinvertebrate grazing stimulates algal turnover and productivity and decreases algal biomass (Lamberti and Resh 1984, Flint and Goldman 1975), this work shows that Aeolosoma grazing may increase turnover without reduction in biomass. This effect has potential two-fold significance. First, the epiphytes and littoral algae on which Aeolosoma commonly feeds contribute significantly to overall lake primary production (Wetzel 1964, Cattaneo and Kalff 1980). Accordingly, increases in their turnover can increase littoral and total carbon fixation. Secondly, higher P/C ratio of periphyton has been correlated to increased grazer growth rates (McMahon et al 1974). They

concluded that above a minimal level of total carbon, protein content of periphyton is more important than available biomass in supporting herbivore growth and reproduction. Grazing by Aeolosoma increased P/C ratio without reducing biomass, and, therefore, can be seen as an aid to macroinvertebrate grazer production.

A shift toward a bacteria-dominated community with correspondingly higher P/C content may be the benefit that balances the energy expenditure of mucus production by Aeolosoma. When presented with unconditioned detritus of low food quality, Aeolosoma produces mucus which aids in forming aggregates in which the organism feeds. These aggregates contain less chl a but more pheophytin a per unit dry weight than unaggregated detritus. These data probably reflects the intense grazing pressure within aggregates. Hallegraff (1981) identified pheophytin a as the dominant breakdown product of chl a in the guts of zooplankton. Aggregates probably have increased protein/unit dry wt and P/C content because unaggregated detritus contained lower values for these two measures than combined (aggregated and unaggregated) grazed detritus. Mucus-associated aggregates, therefore, support a heterotrophic community of increased food quality.

The mechanism for increased heterotrophic biomass in aggregates probably results from consolidation of fecal ma-

terial within a mucus framework. Nutrients and labile organic compounds generated through lysing of some grazed cells would be concentrated at high levels on feces, especially given the low assimilation of algae by Aeolosoma (Bowher et al 1985, Strait 1978). Electrostatic attraction of leached compounds from feces by mucus (Ross and Craig 1980) would aid in maintaining high organic content within aggregates. These high levels in surrounding media are conducive for organic accrural on feces by stimulating microbial growth (Johannes and Santoni 1966). The aggregating response of Aeolosoma, therefore, may be viewed as a means for stimulating bacterial growth. The comcomitant improvement in food quality offsets the energy expenditure of mucus production. This tradeoff must be worthwhile to Aeolosoma only when food quality of substrate is very poor since the aggregating response was not displayed toward conditioned detritus.

Grazing by Aeolosoma effected significant changes in the algal composition of both the early and late summer periphytic assemblages. As discussed, the two assemblages were structurally distinct. The former was composed of green coccoids and diatoms and the latter was composed of filamentous algae and diatoms. Since Aeolosoma can ingest all algal taxa present in both experiments it is reasonable to expect its grazing to have similar impact on periphyton

regardless of algal composition.

Changes induced by Aeolosoma grazing were not analagous to the drastic shifts in periphytic algal composition accompanying macroinveretebrate grazing (Robbles and Cubit 1981, Lamberti and Resh 1984). Abundance and diversity were not reduced as reported for snail-grazed periphyton (Hunter 1980), reflecting the lack of change in the successional state of the algal community. Rather, individual taxa within general taxonomic groups were stimulated or suppressed by grazing, effecting more subtle changes in periphyton composition.

Suppression of many diatom taxa seemed to be density dependent. Significant ANOVA interaction terms for Nitzschia, naviculoids, and Fragillaria in the early summer assemblage, and Synedra in the late summer assemblage, resulted from increased grazing effect over time. These temporal changes coincided with increasing biovolume of cropped taxa or increasing biovolume of non-digestible taxa. Reductions probably result not from active preference for these algae by Aeolosoma, but from increased contact between the algae and Aeolosoma. The oligochaete's suction feeding mechanism and its relatively small oral opening probably result in a percentage success rate of ingestion each time it passes over a certain algal cell. Success rates would depend on cell size and structure. Given more

frequent contact with a certain algal taxa the relative ingestion rate of that alga would increase. More frequent contact would result from increased taxon density or concentration of grazing due to avoidance of non-ingestible forms (blue green filaments, long green filaments, large mucilaginous coccoid aggregates).

Prey selectivity data for the late summer assemblage support this hypothesis. Synedra was negatively elected on day 6, but neutrally elected on day 12 when small Mougeotia and Anabena, both highly avoided taxa, comprised significantly more of the algal biovolume. Figure 16 illustrates the same trend in overall community prey selectivity. The percentages r_i and p_i were plotted for all dominant algal taxa and a regression line was calculated for days 6 and 12. A slope of 1, where the percentage of algae in the gut and the environment are equivalent, indicates no electivity. Both regression lines were significant, but R^2 values are not high enough to perform statistical tests between coefficients. The general trend of decreased electivity at day 12 is apparent. This result would be expected if grazing pressure was concentrated due to increased non-ingestable algal biovolume.

In both the early and late summer assemblages grazing reduced biovolume of the stalked diatom Gomphonema. Significant decreases were observed 2 days after

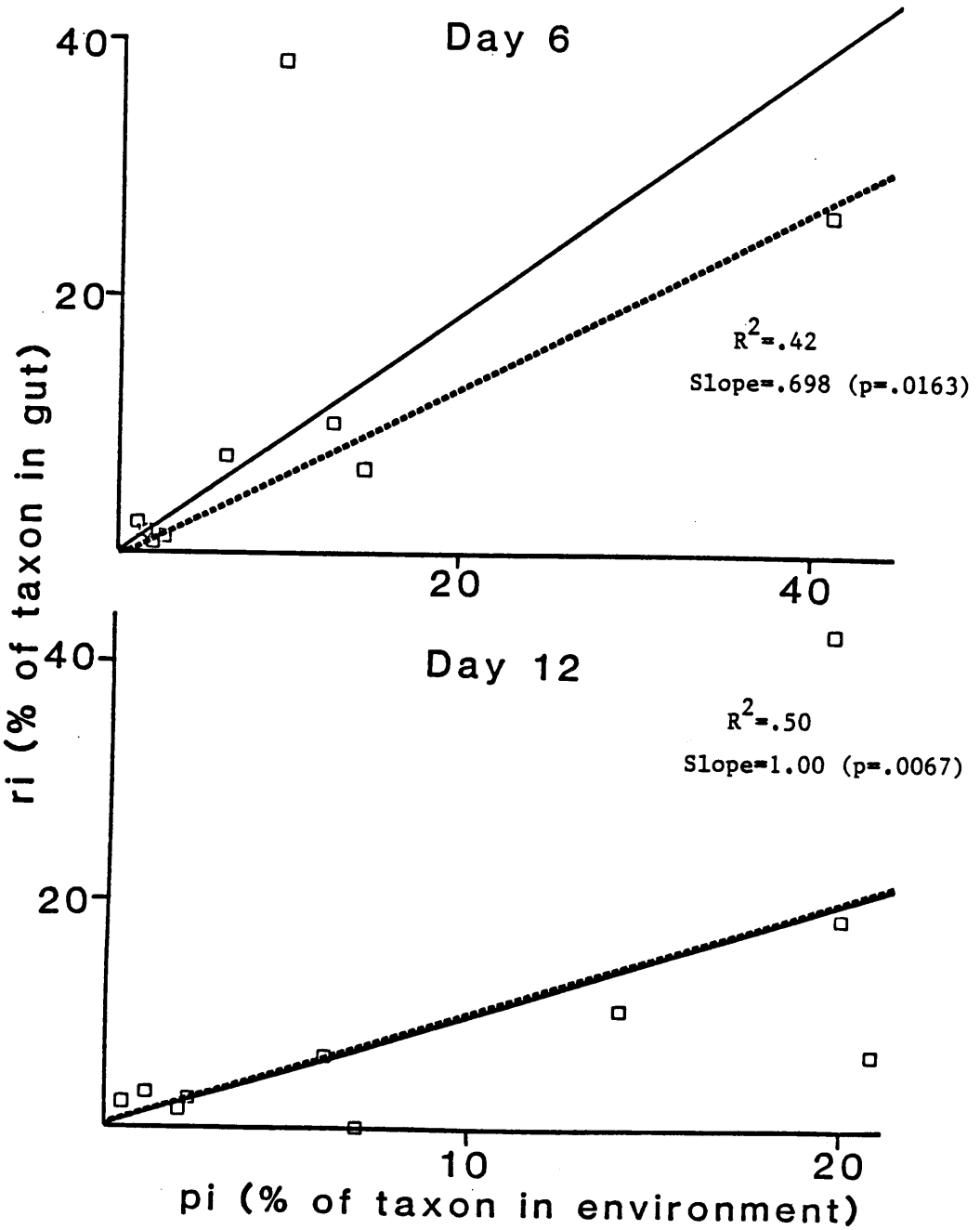

Figure 16. Plot of the % of each algal taxon in the gut (r_i) of Aeolosoma vs. the % of that algal taxa in the environment (p_i) for day 6 and 12. Percentages based on algal biovolumes. Solid line represents a line of slope 1, broken line represents regression line for data. P value corresponds to test for significant regression.

introduction of grazing pressure. When another stalked diatom, Cymbella, was present in significant numbers in the second experiment its biovolume was also reduced in grazed cultures. Both these algae were positively elected, reflecting Aeolosoma's potential preference for stalked diatoms. Positive election of stalked diatoms may be due to their upright, exposed position or the nutritional value of their stalk (Huntsman and Sloneker 1971).

The effects of grazing on another upright algal type, Mougeotia, were not as distinct. While overall filamentous algal biovolume was unaffected by grazing, small Mougeotia biovolume was twice as great in grazed cultures. Small Mougeotia filaments were negatively elected, while large Mougeotia filaments were positively elected. The latter was the dominant component of Aeolosoma's algal diet, accounting for 6 times more of the ingested algal biovolume than small Mougeotia. Dissimilar ingestion rates may be the result of increased filament growth rate in small Mougeotia. Because Aeolosoma does not possess hard mouthparts for shearing or cutting, filament length may be the critical factor controlling the susceptibility of Mougeotia to ingestion. If small Mougeotia filaments grew more quickly under culture conditions then it would be relatively more difficult to ingest than large Mougeotia.

Grazing by Aeolosoma also stimulated coccoid green

algal biovolume, although results were contradictory. In the early summer assemblage only mucilaginous green coccoid biovolume was greater in grazed cultures, while in the late summer assemblage only non-mucilaginous green coccoid biovolume was stimulated by grazing. Mucilage production may facilitate passage through the gut, which would stimulate growth through utilization of high nutrient concentrations in the gut and the feces (Porter 1973, Porter 1976). Non-mucilaginous green algae such as Scenedesmus are viable in the feces of similar oligochaetes (Strait 1978, Bowher et al. 1985), indicating that mucilage may not be neccessary to render green algae indigestible.

The majority of green coccoid algae in the guts of Aeolosoma seemed unaffected by ingestion, but a few cells appeared half digested; cell walls and cytoplasm were partially dissolved. Digestion of refractory algae may be enhanced by reingestion of cells. This would account for the occurrence of a small percentage of partially digested cells and the different results between experiments. Green coccoid algae were likely to be reingested more rapidly in the early summer assemblage since their biovolume constituted almost 10 times more of the algal community than in the late summer assemblage. Intense grazing pressure caused by increased reingestion may have favored mucilage production to further protect cells from

digestion. Regardless of the exact mechanism, grazing stimulated green coccoid algal biovolume in both experiments.

Grazing also stimulated the growth of the diatom Rhopalodia when it was present in the first summer study. Rhopalodia contains a symbiotic blue-green algae whose nitrogen fixation (Floener and Bothe 1980) may be the cause of Rhopalodia's positive response to increased phosphorus concentrations (Fairchild et al. 1985). It is doubtful that the diatom's increase was a result of higher phosphorus concentrations in grazed cultures because blue-green algae did not increase with grazing. If Rhopalodia is undigestible by Aeolosoma then it might be stimulated through utilization of high phosphorus concentrations in the gut. Blue-green algae, as discussed, are rarely ingested and would be excluded from such a stimulus.

Lower glucose respiration rates in grazed cultures may be a result of the grazed bacterial assemblage's exposure to high nutrient levels inside the gut and on the feces of Aeolsoma. Lower nutrient concentrations in control cultures may have caused induction of transport enzymes in the non-grazed bacterial community, thereby enabling more efficient utilization of nutrients like glucose by those communities. Similar oligochaetes display differential digestion of separate bacterial types (Brinkhurst and Chua 1969).

Bacteria which survive passage through the gut, and which have the least chance of enzyme induction due to exposure to high substrate concentrations, should increase in numbers relative to digestable types.

These findings contradict other studies which report a positive response of heterotrophic activity to grazing. The long term, static nature of this study may be the cause for these different results. In situ studies would involve greater mixing of grazed substrate with ambient water that prevents fecal accumulation (Morrison and White 1980). Other laboratory studies involved shorter grazing incubations (48 hrs) which may have decreased selection pressure for bacteria able to utilize high glucose concentrations in the gut (Hargrave 1970). It is interesting to note that with increased grazer density glucose respiration declined. Decreased bacterial biomass with excessive grazing was given as the potential reason for this trend, but this study suggests that greater selection pressure for undigestible organisms may be partly responsible.

CONCLUSIONS

1) Grazing by Aeolosoma increased food quality of periphytic assemblages as measured by greater protein/carbohydrate ratio. Higher protein content probably resulted from stimulation of bacterial biomass and selection for rapidly reproducing diatom populations.

2) Grazing by Aeolosoma caused equivalent changes in algal community composition in early and late summer periphytic assemblages. Differences resulted from stimulation and reduction of individual algal taxa without the dramatic shifts in community composition and structure effected by macroinvertebrate grazing.

3) Aeolosoma ingested all algal taxa in the early and late summer assemblages except the blue-green filament, Anabaena. Densities of many diatom species were reduced in grazed cultures after initial increases, suggesting a density-dependent grazing effect. The stalked diatoms, Gomphonema and Cymbella, were positively elected by Aeolosoma and negatively affected by grazing. Green coccoid algae, which were not visibly digested by Aeolosoma, were stimulated by grazing in both assemblages, possibly due to their utilization of high gut and fecal nutrient concentrations. Filaments of the green algae, Mougeotia, of 20 um cell width were positively elected by Aeolosoma and

accounted for 40% of ingested algal biovolume in the late summer assemblage. Mougeotia filaments of 2.5 um cell width were negatively elected and constituted only 4-7% of ingested algal biovolume.

4) A mucus-mediated aggregation response was observed in Aeolsoma only when placed in cultures containing unconditioned detritus. Aggregates contained a heterotrophic community with greater protein/carbohydrate content than unaggregated detritus. Increased food quality may offset the energy expenditure of mucus production when the food source is refractory.

5) Bacterial ^{14}C-glucose respiration was significantly less in grazed cultures despite higher bacterial biomass estimates with grazing. Higher respiration rates in control cultures may reflect more efficient utilization of substrate by ungrazed bacterial assemblages in response to relatively lower nutrient concentrations. Undigestable bacterial types, which would be exposed to high substrate concentrations in the gut and the feces, may dominate grazed culures.

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APPENDICES

Appendix 1. Statistical Results Of Early Summer Assemblage

	Variable			
	Grazing	Duncans	Time	Interaction
Biomass Measurements				
Protein	.48	AA	.0097(I)	.0573
Carbohydrate	.014(C)	AB	.0059(I)	.0357
Prot/Carbo	.02 (G)	AB	.0003(I)	.823
Chlorophyll a	.32	AA	.0001(I)	.0010
Algal Composition				
Nitzchia	.0056(C)	AB	.0713	.0019
Synedra	.3598	AA	.0091(I)	.9972
Gomphonema	.0057(C)	AB	.0343(D)	.0323
Fragilaria	.9017	AA	.0984	.0386
Mucilaginous Green Coccoid	.0341(G)	AB	.0243(I)	.1198
Green Coccoid	.3516	AA	.0001(D)	.8993
Cocconeis	.61	AA	.35	.014
Naviculoid	.0789	AA	.252	.0015
Rhopalodia	.0054(G)	AA	.0001	.1475
Diversity				
Simpson's D	.52	AA	.0033(D)	.97

Numbers represent p values for ANOVA analysis. Letters in parentheses refer to treatment which had significantly higher values (C=control, G=grazed), and if numbers increased (I) or decreased (D) significantly with time. AB refers to significant Duncan's multiple range test.

Appendix 2. Structural Measurements for Early Summer Assemblage

	Days		
	2	5	10
Protein (ug protein/mg dry wt)			
Control		8.42 (1.59)	13.48 (2.53)
Grazed		11.18 (1.05) (p=.01)	12.13 (1.56)
Carbohydrate (ug CHO/mg dry wt)			
Control		14.43 (3.80)	36.92 (5.10)
Grazed		11.52 (3.39)	25.84 (1.42) (p=.01)
Prot/Carbo			
Control		.22 (.040)	.38 (.086)
Grazed		.30 (.037) (p=.02)	.47 (.050) (p=.10)
Chlorophyll a (10^{-4} ug chla/mg dry wt)			
Control	1.18 (.25)	1.92 (.67)	5.44 (0.70)
Grazed	1.65 (.29) (p=.05)	2.25 (.32)	3.98 (1.35) (p=.1)
Diversity (Simpson's D)			
Control	.33 (.04)	.25 (.03)	.27 (.02)
Grazed	.32 (.05)	.23 (.03)	.27 (.05)

Data reported as means of four replicates with standard deviation in parentheses. P values correspond to student's t tests.

Appendix 3. Diatom %Biovolumes for Early Summer Assemblage

	Days		
	2	5	10
Nitzchia			
Control	5.78 (3.05)	8.77 (2.67)	11.51 (3.01)
Grazed	5.34 (0.99)	8.21 (0.84)	2.22 (0.96) (p=.001)
Naviculoid			
Control	0.70 (0.28)	1.04 (0.38)	1.10 (0.21)
Grazed	0.84 (0.19)	0.63 (0.21)	0.21 (0.22) (p=.002)
Gomphonema			
Control	6.46 (1.17)	6.77 (1.56)	2.69 (1.76)
Grazed	3.11 (1.00) (p=.005)	2.94 (0.98) (p=.0046)	3.10 (1.42)
Synedra			
Control	21.10 (5.43)	25.50 (5.64)	14.82 (1.53)
Grazed	18.82 (4.45)	22.20 (4.43)	14.00 (5.22)
Fragilaria			
Control	20.44 (6.27)	28.25 (5.71)	35.56 (8.61)
Grazed	26.00 (8.25)	37.36 (4.71) (p=.045)	22.52 (8.92)
Rhopalodia			
Control	0.85 (0.87)	1.98 (1.81)	9.06 (3.26)
Grazed	2.94 (1.74)	1.29 (0.86)	22.84 (12.0) (p=.043)
Cocconeis			
Control	2.70 (0.63)	3.90 (0.47)	1.47 (0.67)
Grazed	2.98 (0.65)	2.23 (0.69) (p=.01)	3.49 (2.13)
Total Diatom			
Control	58.57 (7.30)	76.96 (5.81)	77.07 (9.11)
Grazed	60.94 (10.29)	75.34 (6.74)	69.09 (4.57)

Data reported as means of four replicates with standard deviations in parentheses. P values correspond to student's t tests.

Appendix 3 (continued).

Green Algal %Biovolumes for Early Summer Assemblage

	Days		
	2	5	10
Mucilaginous			
Green Coccoids			
Control	7.16 (0.96)	3.73 (1.34)	4.26 (1.52)
Grazed	8.34 (3.15)	4.64 (2.98)	10.54 (3.38) (p=.01)
Green Coccoids			
Control	26.28 (6.05)	13.61 (2.98)	10.13 (3.55)
Grazed	24.90 (7.25)	12.05 (3.02)	7.75 (5.35)
Large Mougeotia			
Control	0.94 (1.21)	1.00 (0.25)	2.49 (3.36)
Grazed	0.81 (0.83)	1.05 (1.37)	2.48 (2.26)
Cosmarium			
Control	2.54 (1.53)	1.03 (0.74)	1.19 (1.02)
Grazed	1.52 (1.04)	1.78 (0.93)	5.96 (7.62)
Pediastrum			
Control	2.32 (3.05)	2.19 (2.24)	1.19 (1.02)
Grazed	1.00 (1.73)	3.04 (1.28)	2.19 (1.62)
Total Coccoid			
Control	38.57 (7.68)	20.72 (5.69)	17.03 (6.17)
Grazed	35.96 (9.44)	21.67 (5.24)	26.48 (6.56)
Total Filamentous			
Control	1.43 (1.64)	1.73 (0.44)	3.80 (3.57)
Grazed	2.36 (0.94)	2.15 (1.47)	8.32 (3.09)

Data reported as means of four replicates with standard deviations in parentheses. P values correspond to student's t tests.

Appendix 4. Statistical Results of Late Summer Assemblage

	Variable			
	Grazing	Duncan's	Time	Interaction
Biomass Estimates				
Total Algal Biovolume Density	.75	AA	.73	.27
Functional Estimates				
C-14 Glucose Resp.	.0008(C)	AB	.0001(I)	.076
Algal Densities				
Cocconeis	.78	AA	.42	.38
Cymbella	.030(C)	AB	.42	.74
Gomphonema	.011(C)	AB	.11	.61
Fragilaria	.48	AA	.69	.48
Naviculoid	.32	AA	.69	.48
Synedra	.99	AA	.012(D)	.01
Large Mougeotia	.30	AA	.30	.79
Small Mougeotia	.032(G)	AB	.15	.64
Oedogonium	.70	AA	.66	.56
Green Coccoids	.18	AA	.33	.82
Pediastrum	.70	AA	.66	.56
Combined Densities				
Diatoms	.98	AA	.012(D)	.12
Filamentous Grn.	.63	AA	.07	.96
Coccoid Greens	.37	AA	.59	.82
Blue-greens	.65	AA	.0003(I)	.46
Diversity				
Simpson's D	.024(G)	AB	.83	.24

Numbers represent p values for ANOVA analysis. Numbers in parentheses refer to which treatment was significantly greater (C=control, G=grazed), and if numbers significantly increased (I) and decreased (D) with time. AB represents a significant Duncan's multiple range test.

Appendix 5. Structural and Functional Measurements for Late Summer Assemblage

	Days		
	0	6	12
Protein (ug protein/mg dry wt)			
Control			16.82 (2.37)
Grazed			21.34 (3.20) (p=.054)
Carbohydrate (ug CHO/mg dry wt)			
Control			44.87 (1.27)
Grazed			39.54 (8.12)
Prot/Carbo			
Control			0.37 (.045)
Grazed			0.57 (.175) (p=.0596)
Diversity			
Control	.084 (.015)	.081 (.002)	.077 (.007)
Grazed		.086 (.007)	.092 (.010) (p=.0386)
C-14 Glucose (ug glucose/hr/mg dry wt)			
Control	0.15 (.10)	0.27 (.11)	0.64 (.06)
Grazed		0.16 (.05)	0.35 (.07) (p=.001)
Total Algal Density (10_6 um_3/mm_2)			
Control	1.10 (.30)	0.97 (.14)	1.06 (.11)
Grazed		1.15 (.34)	0.96 (.18)

Data reported as means of four replicates with standard deviations in parentheses. P values correspond to student's t tests.

Appendix 6. Diatom Biovolume Densities for Late Summer Assemblage

	Days		
	0	6	12
Cymbella			
Control	29.0 (13.0)	26.8 (4.5)	23.8 (6.1)
Grazed		17.4 (10.8)	11.5 (5.8) (p=.02)
Gomphonema			
Control	23.1 (9.1)	19.3 (3.6)	15.8 (5.2)
Grazed		12.0 (5.9) (p=.08)	5.4 (5.2) (p=.02)
Cocconeis			
Control	10.2 (5.2)	12.8 (3.7)	13.2 (7.6)
Grazed		15.2 (9.4)	8.8 (2.1)
Fragilaria			
Control	112.6 (46.5)	73.0 (6.3)	79.2 (30.9)
Grazed		73.0 (43.6)	51.0 (40.5)
Naviculoid			
Control	22.2 (3.8)	27.3 (7.0)	29.1 (9.9)
Grazed		28.1 (5.6)	19.6 (5.1)
Synedra			
Control	367.7 (84.1)	370.2 (80.4)	290.7 (72.9)
Grazed		498.0 (207.0)	176.2 (24.4) (p=.012)

Data reported as means of four replicates with standard deviations in parentheses. P values correspond to student's t tests.

Appendix 7. Non-Diatom Biovolume Densities for Late Summer Assemblage

	Days		
	0	6	12
Large Mougeotia			
Control	236.0 (195.0)	169.2 (87.6)	244.2 (137.8)
Grazed		124.3 (74.0)	168.9 (71.2)
Small Mougeotia			
Control	78.4 (14.3)	71.4 (14.2)	112.0 (32.3)
Grazed		145.5 (23.4)	222.0 (124.6)
		(p=.001)	
Oedogonium			
Control	16.4 (23.5)	16.3 (11.4)	17.6 (15.7)
Grazed		18.1 (22.5)	8.6 (9.2)
Green Coccoids			
Control	10.4 (3.7)	12.6 (0.9)	19.0 (5.9)
Grazed		21.1 (3.0)	25.2 (16.6)
		(p=.001)	
Pediastrum			
Control	4.2 (7.3)	24.3 (24.3)	16.5 (12.4)
Grazed		24.4 (6.9)	34.3 (34.3)
Anabena			
Control	0.6 (0.6)	16.8 (14.4)	80.8 (21.9)
Grazed		18.6 (7.6)	67.5 (25.6)

Data reported as means of four replicates with standard deviations in parentheses. P values correspond to student's t tests.

Appendix 8. Estimations of Cell Biovolumes

Taxa	Shape	Early Summer Biovolume (um_3)	Late Summer Biovolume (um_3)
Anabaena	cylinder	np	2147
Achnanthes	rectangle	np	370
Cocconeis	ellipsoid	3500	3500
Cosmarium	cylinder	900	9000
Cymbella	1/2 cylinder	2700	2900
Diatoma	ellipsoid	4000	np
Fragilaria	rectangle	4700	3000
Gomphonema	2 circ. cones	4300	1600
Green Coccoids	sphere	610	610
Mucil. Grn. Coc.	sphere	610	610
Blue-green Coc.	sphere	np	100
Mougeotia (large)	cyl.	9100	38600
Mougeotia(small)	cyl.	7325	4740
Naviculoids	2 circular cones	870	925
Nitzchia	rectangle	465	856
Pediastrum	cylinder	28000	28000
Oedogonium	cyl.	2250	2000
Rhopalodia	ellipsoid	22000	np
Rhicosphenia	rectangle	900	np
Schizothrix	cylinder	12	100
Scenedesmus	ellipsoid	120	140
Synedra	rectangle	11700	12700

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