Influence of different densities of the mayfly grazer Heptagenia criddlei on lotic diatom communities

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Abstract. Localized high densities of the mayfly nymph *Heptagenia criddlei* McD. occur in Oak Creek, Arizona during the summer. We examined the effects of different grazer densities of *H. criddlei* on diatom cell density and community structure in a laboratory stream over selected time periods ranging from 1 d to 4 wk. Insect densities at 800–1000 nymphs/m², 2800–4100 nymphs/m², and 7100–7700 nymphs/m² of periphyton cover were compared with ungrazed control channels. Our observations show that localized differential grazer densities are important in determining the abundance, composition, and physiognomy of lotic diatom communities. At grazer densities of 800 nymphs/m² there were no notable differences in diatom abundance and diatom assemblages between grazed and ungrazed systems throughout a 4-wk period. However, major differences were noted after 10 d at 2800 nymphs/m², 3 d at 4100 nymphs/m² and within 24 hr at grazing densities ≥7100 nymphs/m². At grazer densities ≥2800 nymphs/m² the overall density of diatoms declined and the relative proportions of larger upright diatom species to smaller adnate diatom species decreased through time with increased grazing pressure. Adnately attached diatom taxa like *Cocconeis placentula* var. *euglypta* (Ehr.) Cl. and *Epithemia adnata* (Kütz.) Breb. showed greatest resistance to grazing, while diatoms with smaller cell dimensions like *Achnanthes minutissima* Kütz. were next most resistant to grazing by *Heptagenia*.

Key words: grazer, *Heptagenia criddlei*, diatoms, streams, periphyton, mayflies, *Epithemia*, laboratory stream.

Invertebrate grazers can cause significant changes in the abundance and composition of periphyton in lotic systems (Lamberti et al. 1987, Lamberti and Moore 1984, Steinman et al. 1987). However, many previous studies investigating periphyton community structure show that fluctuations in abundance, diversity, and distribution of periphyton communities are largely due to changes in light conditions, current velocity, temperature, available nutrients and substratum (Blinn et al. 1980, Horner and Welch 1981, Keithan and Lowe 1985, Sand-Jensen 1983, Stevenson 1983, Tuchman and Blinn 1979, Whitton 1975).

Recently, investigators have begun to examine the importance of grazer-periphyton interactions in stream ecosystems (Gregory 1983, Lamberti et al. 1987, Lamberti and Moore 1984, Steinman et al. 1987), and several have documented marked reductions in periphyton standing crop due to grazing by snails (Hunter 1980), caddisfly larvae (Lamberti and Resh 1983, McAuliffe 1984), and isopods and amphipods

(Murphy 1984). Some studies have shown that low grazer densities of fish (Stewart 1987), crayfish (Flint and Goldman 1975) and insects (Lamberti and Resh 1983) can also accelerate turnover rates of periphyton and increase chlorophyll *a* concentrations per unit dry weight.

In addition to decreasing standing crop, stream herbivores may selectively alter the species composition of a periphyton assemblage (Hunter 1980, Jacoby 1985, Lamberti and Resh 1983, Steinman et al. 1987, Sumner and McIntire 1982). However, most aquatic macroinvertebrates appear to be generalists in their feeding (Cummins 1973) and for the most part, algal consumption is dependent upon the relative availability of food in the environment (Gregory 1983).

In view of the limited information on the importance of insect grazing on the standing crop and community structure of stream periphyton (Lamberti and Moore 1984), we examined the effects of different grazer densities of the mayfly nymph, *Heptagenia criddlei* McD., on diatoms in a laboratory stream. Grazer densities were calculated on the basis of both periphyton cover and area of stream bottom. *Hep-*
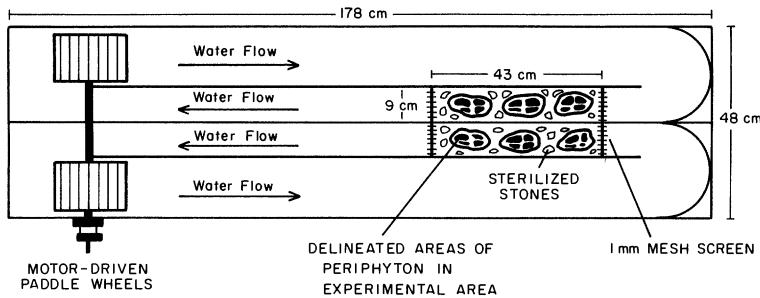
FIG. 1. Plan view of laboratory stream tank. The smaller return channel for each adjoining stream tank was divided into a 9 cm × 43 cm experimental area. One experimental area contained mayfly grazers, while the other experimental area was free of grazers. Sterilized stones covered the bottom of each experimental area. Larger stones with delineated areas of periphyton were placed in each experimental area. Unidirectional flow (see arrows) was maintained in each adjoining channel by a paddlewheel at one end.

tagenia criddlei is found in the western United States and Canada (Bednarik and Edmunds 1980, Ward 1986) and is a common insect scraper during the summer and early fall ($\bar{x}$ = 576 nymphs/ m²) in Oak Creek, Arizona (Colletti 1984). Densities of *H. criddlei* were estimated to be as high as 0.38 nymphs/cm² (3800 nymphs/m²) on certain individual stones in Oak Creek. We propose that localized high densities of *H. criddlei* during certain times of the year may be instrumental in regulating the composition and abundance of stream periphyton.

Methods

A closed and recirculating plexiglass laboratory stream (178 cm long, 48 cm wide, 24 cm high) was divided into separate grazing and control channels (Fig. 1). Each channel was partitioned into one smaller experimental area (43 cm long by 9 cm wide) by 1 mm-mesh screens. Small sterilized stones (1–4 cm) collected from Oak Creek, Arizona were placed within each partitioned channel to simulate natural channel substrata, and 38 L of water from Oak Creek, Arizona, were added to each channel; the water depth was maintained at ca. 7 cm during all feeding trials. The mean ambient nutrient concentrations for water collected from Oak Creek were 0.09 mg/L for O-PO₄, 0.06 mg/L for NO₃-N and 10.2 mg/L for SiO₂. Two adjoining motor-drive paddlewheels, located at one end of the tank, maintained the current within the partitioned experimental channels at approximately 22 cm/s. Current velocity was measured with a Pygmy meter above the substratum in

the stream tank. Gro-lux lamps positioned above the control and experimental channels provided 145–160 μE/m²/s light energy during the experiments. These light values are comparable to the average values in the canopy covered streambed of Oak Creek during the spring and fall (Duncan 1984). The photoperiod consisted of alternating periods of 12 hr light/12 hr darkness. The range of water temperature in the control and grazed channels was 11–14°C for the spring experimental period and 16–21°C for the fall period, approximating seasonal water temperatures in the 1st order section of the mountain stream of Oak Creek at the time of the experiments. Water was replaced every 3–5 d in the laboratory stream with grazer-free water from Oak Creek; algal cells remained in the replacement water.

Stones with epilithon and *H. criddlei* nymphs were collected from Oak Creek. Known areas (6–12 cm²) of periphyton were delineated on each stone (Fig. 1), and all remaining periphyton was removed with razor blades and brushes; i.e., grazer densities for Figures 2–7 and those presented throughout the text, unless otherwise indicated, were calculated on the basis of stone area covered by periphyton. This method of measure simulated the patchy nature of periphyton in Oak Creek (Duncan 1984, Korte and Blinn 1983) and provided a measurement for comparing mayfly grazer densities with available periphyton "food".

The delineated periphyton on the stones covered 30% of the 387 cm² area of the partitioned channel bottom for all trials. Therefore grazer density may also be computed on the basis of

total area of partitioned stream bottom; i.e., the lowest and highest grazer densities based on total surface area of stream bottom in the partitioned channels are 240 nymphs/m² (30% of 800 nymphs/m² periphyton cover) and 2310 nymphs/m² (38% of 7700 nymphs/m² periphyton cover), respectively. All grazers were removed from the stones with periphyton before the stones were placed into the experimental and control channels. *Heptagenia* nymphs, 4–9 mm in length, were introduced into the experimental grazer channel for each feeding trial.

Experiments were conducted with low (800 and 1000 nymphs/m² periphyton), intermediate (2800 and 4100 nymphs/m² periphyton) and high (7100 and 7700 nymphs/m² periphyton) densities of *Heptagenia*. Experiments for high grazer densities (i.e., ≥7100 nymphs/m²) were short term (3–4 d), because animals died after 4–5 d under these higher grazer density regimes, perhaps as a result of starvation; studies with ≤1000 nymphs/m² were conducted for 12–28 d. Intermediate-density experiments lasted about 7 d.

Three stones were randomly removed on selected days from the grazer and control channels, and periphyton was removed with brushes from 0.25 cm² areas. A proportionate number of mayfly nymphs was removed, when appropriate, to maintain the initial grazer density throughout the experiment. Diatoms were oxidized with peroxide dichromate and permanently mounted on glass slides with Hyrax. A minimum of 500 diatom frustules was counted from each replicate slide from the experimental and control channels. Since diatoms typically constituted between 80 and 90% of the periphyton assemblage in Oak Creek (Blinn et al. 1980, Duncan 1984, Korte and Blinn 1983) other algal components were not quantified. Ash-free dry weights (AFDW) were determined for trails employing 800 and 2800 nymphs/m² (APHA 1976).

The comparison of diatom community structure between grazed and ungrazed rocks was determined by means of the Shannon-Weiner diversity equation (Pielou 1969) and a similarity index (SIMI) as employed by Tuchman and Blinn (1979). Chi square was employed to determine significant differences between species composition on the initial day and subsequent days for grazed diatom assemblages.

Seven Surber collections were taken in Oak Creek during June to estimate summer densities of *H. criddlei*. Localized densities of *H. criddlei* were also estimated by randomly selecting submerged stones (4 cm² to 100 cm²; $n = 53$) within the streambed of Oak Creek. A net was placed immediately downstream from each stone while removing the stone from the stream bottom and insects were brushed into the net (Behmer and Hawkins 1986). Total surface area was determined by wrapping each stone in aluminum foil and estimating the area from known areal weights of foil. Some part of the surface area (5–30%) of the stones was embedded and perhaps inaccessible to invertebrates.

Results

Estimates taken from individual stones suggested that the distribution of *H. criddlei* in Oak Creek was patchy. Values ranged from 0.38 nymphs/cm² (3800 nymphs/m²) to no animals associated with individual stones; 14% of the stones examined had values of >0.28 nymphs/cm² (>2800 nymphs/m²). The mean density of *H. criddlei* estimated from individual stones was 740 nymphs/m² (±1 SE 138.6; $n = 53$). The average density of *Heptagenia criddlei* in Oak Creek estimated from Surber collections taken during June was 521 nymphs/m² (±1 SE 77.9; $n = 7$).

The cell numbers, biomass, and species composition of lotic diatom communities were differentially influenced by various grazer densities of *H. criddlei* in laboratory streams. There was a notable reduction in diatom cell densities at *Heptagenia* densities of ≥2800 nymphs/m², but not at ≤1000 nymphs/m² (Fig. 2). In fact, there was a minor increase in cell number after 21 d at 800 nymphs/m² (Fig. 2). Within a 10-d period, cell numbers of diatoms were reduced by nearly 80% when subjected to a grazing density of 2800 nymphs/m² (Fig. 2; Table 1). Similar reductions in cell densities were achieved by Day 3 at grazer densities of 4100 nymphs/m². Grazer pressure was so intense at densities ≥7100 nymphs/m² that the impact of high grazing pressure occurred within 24 hr and remained important throughout the 3-d experiment (Fig. 2, Table 1). A strong inverse relationship ($r = -0.83$) between mayfly grazer density and transformed ($\log_{nx}$) data for diatom cell density was observed after a 3-d grazing period (Fig. 3).

Ash-free dry weight (AFDW) measurements of periphyton showed a similar pattern to cell

DIATOM CELLS/cm^2

12,000,000
10,000,000
8,000,000
6,000,000
4,000,000
2,000,000
0
scale

800

1000

GRAZER DENSITY
(nymphs/m^2 periphyton)

2800

4100

7700

days
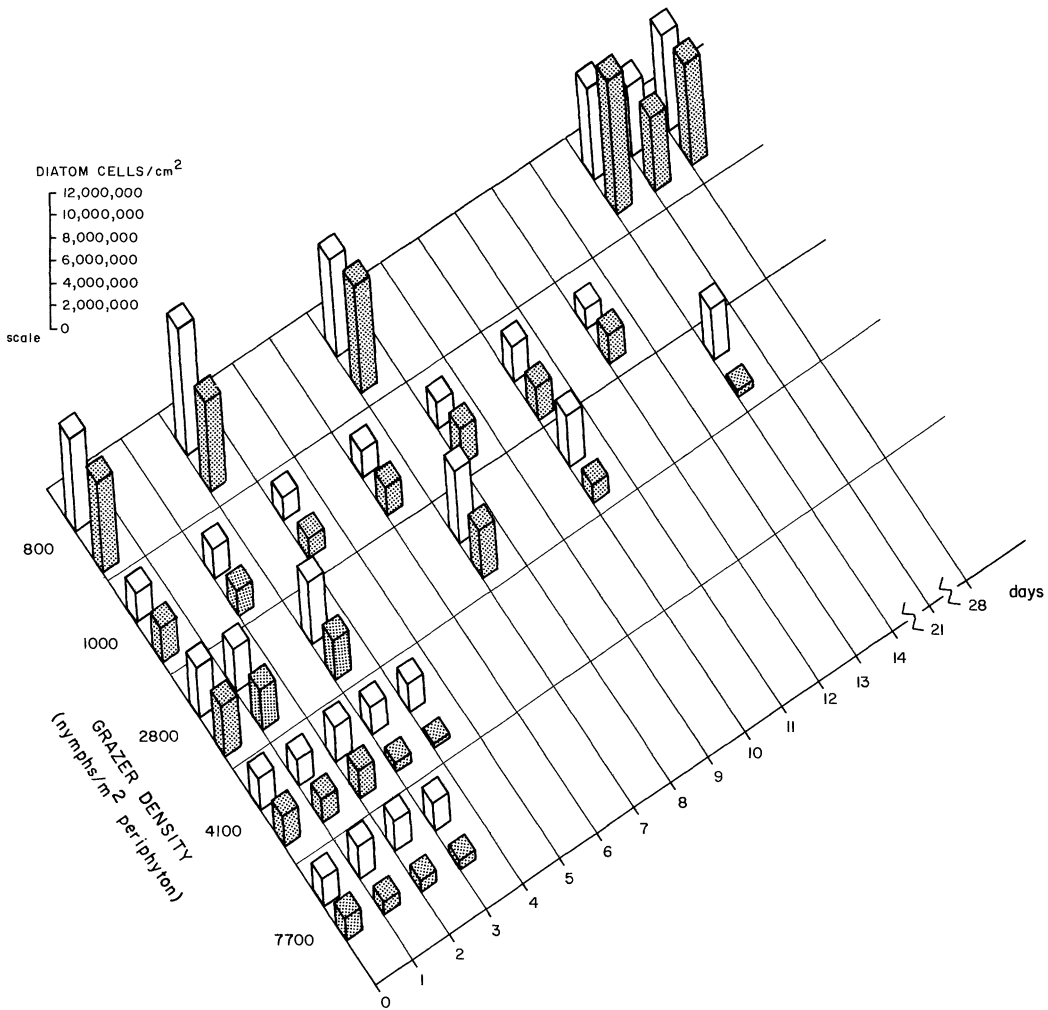28
21
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0

FIG. 2. Influence of different grazing densities of *Heptagenia criddlei* on diatom cell density. Stippled bars represent grazed treatments and open bars represent control ungrazed systems.

density under selected grazing regimes. There was a 4.5-fold reduction in biomass after 10 d in the grazed channels with 2800 nymphs/m^2, whereas channels at grazer densities of 800 nymphs/m^2 showed a slight increase in biomass after 21 d.

The epilithon assemblage collected from Oak Creek consisted of 32–38 diatom species for all experiments; 10 of these typically constituted over 90% of the entire diatom assemblage. The larger upright diatom species (>30 μm in length) that are important in the three-dimensional overstory of the Oak Creek assemblage included *Nitzschia dissipata* (Kütz.) Grun., *Cymbella affinis* Kütz., *Gomphonema clevei* Fricke, and *Syn-*edra ulna (Nitz.) Ehr., while *Achnanthes minutissima* Kütz., *Nitzschia frustulum* var. *perpusilla* (Rabh.) Grun., *Cymbella sinuata* Greg., and *Cocconeis placentula* var. *euglypta* (Ehr.) Cl. were important small and/or adnately attached taxa.

The relative proportions of the larger upright and smaller adnate assemblages showed little change from the initial day for ungrazed and 800 nymphs/m^2 treatments throughout a 28-d period (Fig. 4), whereas dramatic changes were noted at grazer densities ≥2800 nymphs/m^2 (Figs. 5, 6). After one week at 2800 nymphs/m^2, the proportions of the overstory assemblage and the smaller adnate assemblage did not change significantly, but by Day 10 a significant dif-
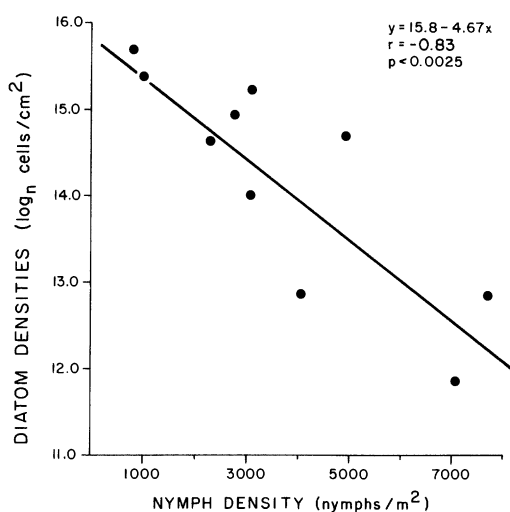
$y = 15.8 - 4.67x$
$r = -0.83$
$p < 0.0025$

FIG. 3. Relationship between density of *Heptagenia criddlei* and diatom cell numbers (cells/cm²) (log$_{nx}$ transformation) after three days of grazing. Each point represents a mean of three replicates.

ference ($\chi^2 = 31.7$, $p < 0.01$) from the initial day was noted and it remained significant ($\chi^2 = 36.9$, $p < 0.01$) at Day 14. The general pattern was an increase in the relative abundance of smaller adnate taxa and a decrease in the larger upright taxa through time with increased grazing pressure. A significant ($\chi^2 = 6.34$, $p < 0.01$) difference in total cell densities between these two assemblages from the initial day was noted by Day 2 at 4100 nymphs/m² and within 24 hr ($\chi^2 = 12.11$, $p < 0.01$) at 7100 nymphs/m². The change in abundance between these two assemblages is illustrated in Figures 5 and 6 for 2800 nymphs/

m² and 7100 nymphs/m², respectively, by the dramatic increase in the hatched portion of the diagrams (representing the smaller adnate taxa) through time. No significant differences in species composition were noted between the initial day and subsequent days in ungrazed channels.

Species that were attached adnately, like *C. placentula* var. *euglypta*, appeared to be most tolerant of heavy grazing pressures. The relative abundance of *C. placentula* var. *euglypta* increased dramatically over a 3-d period at grazer densities of 7100 nymphs/m² (Fig. 6). At somewhat lower grazer densities (2800 nymphs/m²), taxa with the smallest cell diameters (i.e., *N. frustulum perpusilla*, and *A. minutissima*) increased in relative abundance through time, while *C. placentula* var. *euglypta* showed little change in relative importance (Fig. 5).

Two species of *Epithemia* showed different responses to mayfly grazing based on mode of attachment. At the beginning of experiments with grazer densities of 7100 nymphs/m², the more loosely attached *Epithemia sorex* Kütz. was the more abundant of the two taxa (Fig. 7). However, after 3 d the proportion of the more adnately attached *Epithemia adnata* (Kütz.) Breb. increased by nearly 90% on grazed substrata; *E. sorex* remained dominant in the ungrazed channels (Fig. 7). Similar patterns occurred at lower grazer densities (2800 nymphs/m²) after a 10-d grazing period.

The species diversity (H') and structural similarity (SIMI) indices comparing grazed and ungrazed diatom communities were sensitive to changes caused by increased mayfly grazing. In

TABLE 1. Average diatom density (1×10^3 cells/cm²) for three grazer densities (nymphs/m² periphyton) of *Heptagenia criddlei* for selected days. Values in parentheses are ±1 SD.

	Grazer Densities					
	800		2800		7100	
Day	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Initial	7691 (569)	7691 (569)	3946 (1100)	3946 (1100)	3083 (528)	3083 (528)
1			3623 (715)	3098 (450)	4668 (1699)	591 (541)
2					4582 (996)	146 (21)
3	10,292 (2421)	7268 (518)	5349 (447)	3107 (1016)	3602 (1109)	142 (50)
7	7671 (1097)	8537 (4763)	5539 (282)	3383 (547)		
10			3310 (648)	710 (731)		
14	8168 (687)	11,437 (1647)	4134 (350)	283 (106)		
21	6236 (1885)	6179 (1682)				
28	7937 (1676)	8371 (1091)				

UNGRAZED   GRAZED
(800 NYMPHS/m²)

UNGRAZED   GRAZED
(2800 NYMPHS/m²)

INITIAL

3 DAY

7 DAY

14 DAY

21 DAY

28 DAY

INITIAL
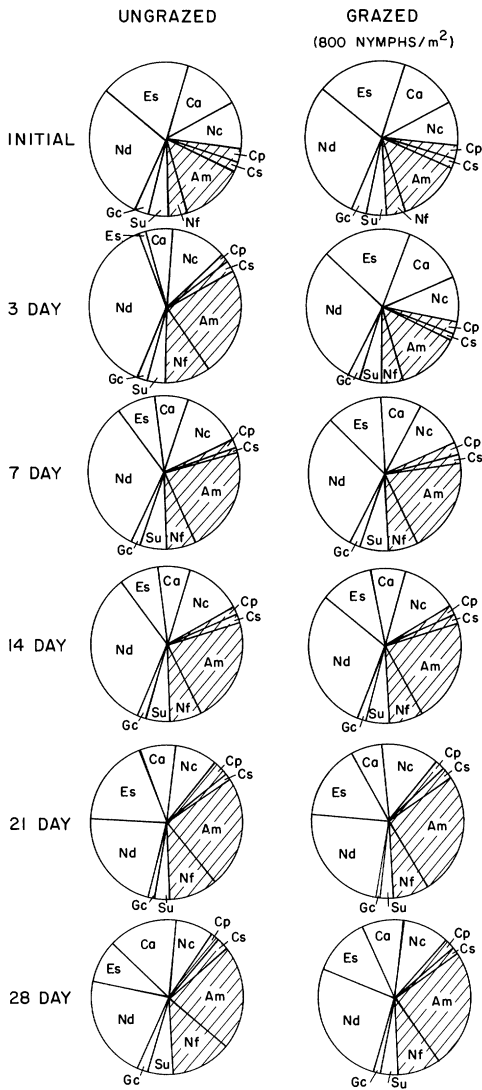
1 DAY

3 DAY

7 DAY

10 DAY

14 DAY

FIG. 4. Pie diagrams illustrating relative proportions of selected diatom species for grazed (800 nymphs/m² periphyton cover) and ungrazed trials over a 28-d period. Hatched sections represent diatom taxa that are small or adnately attached. Species size dimensions increase in the following order. Nf = *Nitzschia frustulum* var. *perpusilla*, Am = *Achnanthes minutissima*, Cs = *Cymbella sinuata*, Cp = *Cocconeis placentula* var. *euglypta*, Nc = *Navicula cryptocephala*, Ca = *Cymbella affinis*, Es = *Epithemia sorex*, Nd = *Nitzschia dissipata*, Gc = *Gomphonema clevei*, and Su = *Synedra ulna*.

high grazer density experiments (≥7100 nymphs/m²), diversity decreased from 2.79 to 1.94 within 24 hr. Similar reductions in diversity occurred after 10 d at 2800 nymphs/m². No
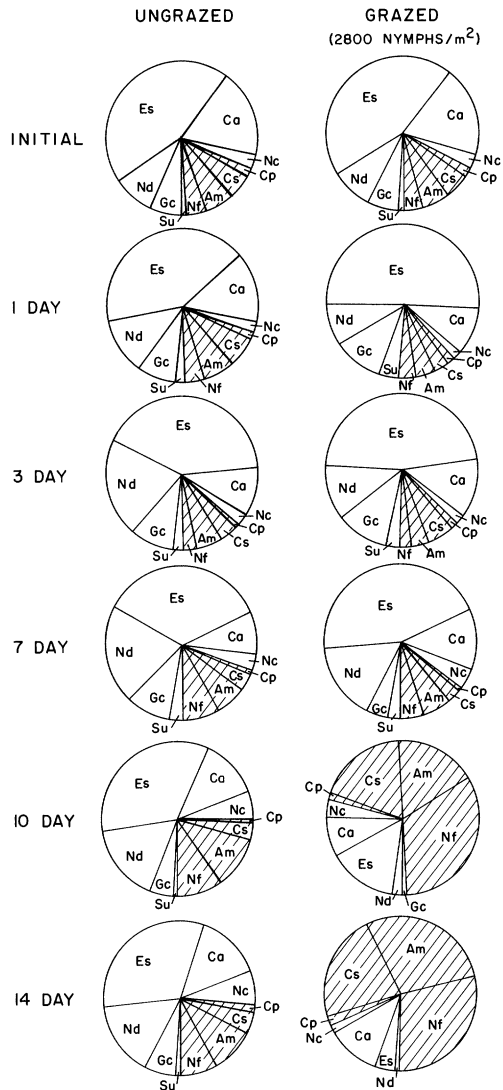
FIG. 5. Pie diagrams illustrating relative proportions of selected diatom species for grazed (2800 nymphs/m² periphyton cover) and control ungrazed trials over a 14-d period. Hatched sections represent diatom taxa that are small or adnately attached. See Figure 4 for species legend.

change in diversity (2.7–2.8) was evident in either channel at 800 nymphs/m² throughout the 28-d experiment; all values displayed <1% variation.

SIMI values for substrata at grazer densities of 800 nymphs/m² also indicated no apparent difference between grazed and control diatom assemblages (Table 2). SIMI values remained above 0.800 during the first 7 d at grazer den-
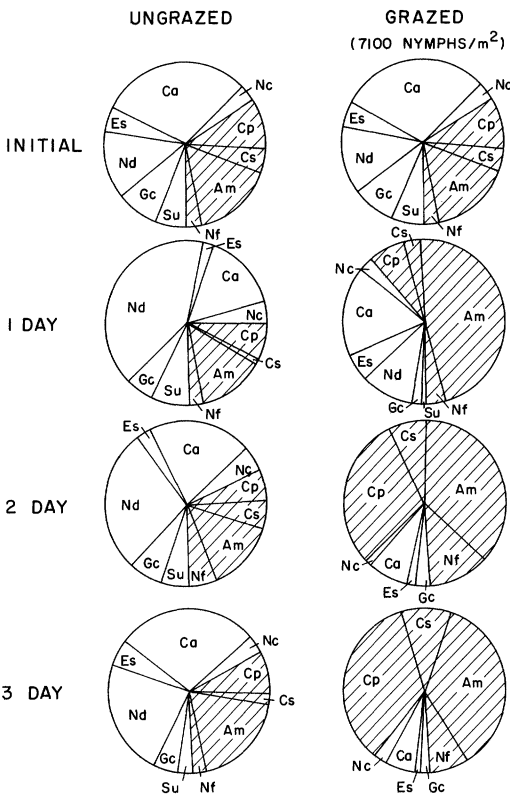
UNGRAZED   GRAZED   UNGRAZED   GRAZED
                    (7100 NYMPHS/m²)   (7100 NYMPHS/m²)

FIG. 6. Pie diagrams illustrating relative propor-
tions of selected diatom species for grazed (7100
nymphs/m² periphyton cover) and control ungrazed
trials over a 3-d period. Hatched sections represent
diatom taxa that are small or adnately attached. See
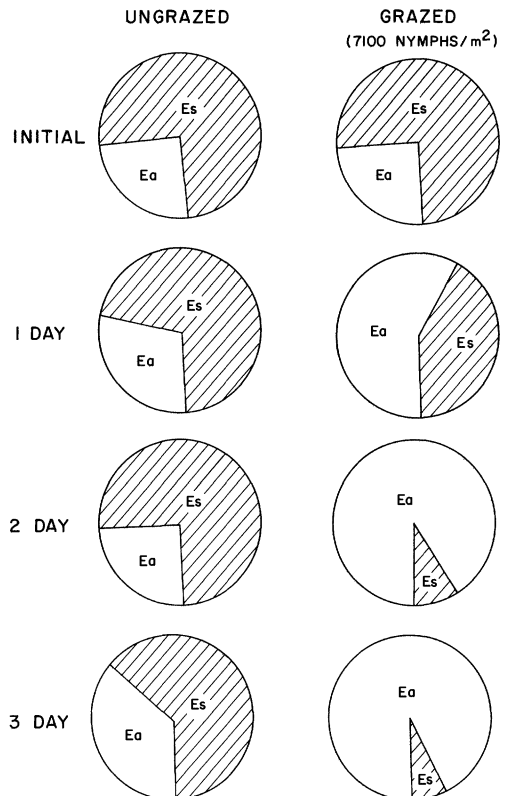Figure 4 for species legend.

FIG. 7. Pie diagrams illustrating relative propor-
tions of *Epithemia sorex* (Es, hatched) and *Epithemia
adnata* (Ea, open) between grazed (7100 nymphs/m²
periphyton cover) and ungrazed channels over a 3-d
period.

sities of 2800 nymphs/m²; however, after 7–10
d, SIMI values between grazed and control
channels decreased. Diatom community struc-
ture was notably different between paired
grazed and ungrazed channels by the first day
at grazer densities of 7100 nymphs/m² and SIMI
values remained relatively low throughout the
3-d experiment.

Discussion

Our observations suggest that a threshold
grazer density may exist between 1000 and 2800
nymphs/m² periphyton (300–840 nymphs/m²
area of stream bottom), at which point *Hepta-
genia criddlei* plays an important role in struc-
turing the lotic periphyton community. At
grazer densities ≥2800 nymphs/m², *Heptagenia*

dramatically reduced diatom cell density and
changed the diatom community from a three-
dimensional structure into a more two-dimen-
sional structure of smaller adnate taxa, charac-
teristic of an early successional seral stage
(Hoaglund et al. 1982, Korte and Blinn 1983).
At high grazing densities (≥7100 nymphs/m²),
the proportions of small and closely attached
diatoms such as *Cocconeis placentula*, *Achnanthes
minutissima*, and *Nitzschia frustulum* var. *perpu-
silla* increased dramatically within 24 hr.
Changes in diatom cell number and species
composition took longer at 2800 nymphs/m²,
whereas no changes were noted at ≤1000
nymphs/m². This pattern suggests that, in ad-
dition to physico-chemical factors, localized
grazing by stream invertebrates is very impor-
tant in determining the composition of stream
diatoms and may play a significant role in the
patchy nature of epilithon in lotic systems.

TABLE 2. Community similarity values (SIMI) of stream diatom periphyton comparing various grazing densities of *Heptagenia criddlei* with ungrazed treatments.

Grazer Density (nymphs/m² periphyton)	Days							
	1	2	3	7	10	14	21	28
800			0.931	0.970			0.968	0.959
2800	0.942		0.968	0.830	0.647	0.622		
7100	0.562	0.623	0.440					

Although Surber sample estimates of *H. criddlei* nymphs in Oak Creek (mean density = 521 nymphs/m²) were lower than the experimentally defined threshold grazer density determined in the laboratory (>1000 nymphs/m²; based on periphyton cover), we found that 14% of the individual stones examined in Oak Creek exceeded the proposed laboratory threshold grazer density for *Heptagenia*. The actual effective grazer densities in Oak Creek may have been even higher since 5–30% of the surface area of the stones examined was embedded and perhaps inaccessible to invertebrates. Furthermore, threshold grazer densities computed on the basis of area of laboratory stream bottom (300–840 nymphs/m²) instead of area of periphyton (1000-2800 nymphs/m²) are well within the range of Surber estimates for *Heptagenia* in Oak Creek. Therefore, we propose that the mayfly grazer densities employed in this laboratory study are achieved in certain localized areas of Oak Creek during the summer and may be very influential on at least 14% of the stones in determining the abundance and composition of the periphyton community, especially when other mayfly grazers are included. Colletti (1984) reported an average of 190 nymphs/m² for species of *Baetis* and *Epeorus* in Oak Creek during the summer.

One factor that seems to be important in determining the spatial variability of insect grazers is the patchy nature of algae that frequently occurs in lotic systems (Jones 1978, Patrick 1970, Pryfogle and Lowe 1979). A patchy distribution of periphyton has also been reported for Oak Creek (Duncan 1984, Korte and Blinn 1983). There is now good evidence that insect grazers actively search for and feed on dense localized patches of algae (Hart 1981, 1985, Kohler 1984, McAuliffe 1984). This can result in high densities of grazers in localized areas of the stream channel. It has also been determined that algal composition can significantly influence the composition of lotic insect species (Dudley et al. 1986). When food supply is limiting, insect grazers may enter stream drift (Bohle 1978). Perhaps this may explain why the upper range of localized insect densities (4100-7700 nymphs/m²) was never observed in Oak Creek; i.e., grazing rates greatly exceeded recruitment rates of periphyton. Alternatively, interference competition with *Baetis* and/or *Epeorus*, or exploitation competition within the *Heptagenia* population, might also explain why the upper range of densities was not observed in Oak Creek.

We propose that mayfly scrapers are responsible, through different localized grazing densities, for the heterogeneous matrix of periphyton composition and abundance in streams, perhaps equal to or greater than physico-chemical factors. Abiotic factors may influence the periphyton community indirectly by placing physical constraints on potential invertebrate grazers (e.g., inability of the insect herbivore to withstand high current velocity). Recently, Steinman and co-workers (1987) demonstrated that high densities of the snail *Juga silicula* (Gould) and relatively low densities of the caddisfly *Dicosmoecus gilvipes* (Hagen) were also able to change the physiognomy of lotic periphyton assemblages.

Heptagenia may have ingested the diatoms on the basis of accessibility resulting from the position of cells, size of cells or mode of cell attachment. Large, overstory species were probably more accessible than smaller, prostrate forms and thus more frequently removed. Based on observations of removal rates for various diatom species, the adnately attached species are most resistant to mayfly grazing, while diatoms

with smaller cell diameters are next most resistant and larger upright species are least resistant. Studies on insect grazers other than mayflies also have shown that small, adnate species are more resistant to grazing than the more upright species (Hall and Pritchard 1975, Lamberti et al. 1987, Pringle 1985).

Differential division rates between diatom species (Williams 1964) may also contribute to the greater proportions of smaller forms under high grazing pressure. The faster division rates of the small diatom species may help to maintain their populations, whereas larger diatom species may be unable to divide at the same rate at which they are being ingested. The removal of the canopy of larger upright species also may have enhanced the division rates of the smaller understory species by reducing competition for light and nutrients.

Two congeneric species of diatoms with different modes of attachment responded differently to grazing by *Heptagenia*. Although the larger *Epithemia adnata* (mean dimensions = 34.0 μm $\times$ 10.0 μm, n = 32) was consistently represented by fewer cells than *Epithemia sorex* (mean dimensions = 26.5 μm $\times$ 8.0 μm, n = 40) at the start of each experiment, the former species increased in relative abundance in response to grazing. *Epithemia sorex* remained the dominant in the absence of grazing in control channels (Fig. 7). This shift in abundance between these two congeneric species was most pronounced in channels with the highest grazing density (Fig. 7). Because the physico-chemical conditions in our experimental stream channels were similar, we propose that grazing, rather than physico-chemical factors, caused the changes in the relative abundances of these congeneric diatom species.

Species diversity did not increase at any of the experimental grazer densities, but did decrease dramatically after the first day at the highest grazer density. Similar changes in species diversity occurred after a longer time interval in the intermediate grazing pressure experiments (i.e., 2800 nymphs/m²). A decrease in species diversity has been observed in other grazer studies. Hunter (1980) found that certain freshwater pulmonate snails reduced periphyton diversity on artificial substrates placed in a shallow pond, and Dickman (1969) found that grazing tadpoles reduced periphyton diversity

in a shallow lake. Others (Kehde and Wilhm 1972, Sumner and McIntire 1982) have reported no change in algal diversity after grazing.

Acknowledgements

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