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## Effects of burrowing by a stream caddisfly on case-associated algae

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**Abstract.** Diel burrowing behavior of *Gumaga nigricula* (McL.) (Trichoptera:Sericostratidae) was investigated in Big Sulphur Creek (Sonoma Co., California). Most of the population burrows during the day and surfaces at night, a behavior that facilitates feeding on periphyton while retaining many of the advantages of burrowing (e.g., protection from predators). Because of daytime burrowing, case algae (primarily diatoms) are potentially light-limited by overlying substrate and, indeed, chlorophyll *a* concentrations on stream-collected cases and diatom colonization on cleaned cases increased dramatically when daytime burrowing was prevented. Cases and case-associated algae are normally abraded during burrowing; therefore experimental abrasion had little effect. However, after cases were cultured to accrue algae, experimental abrasion drastically reduced the accrued algae. Blue-green algal filaments and diatoms were removed from exposed surfaces but were protected in crevices between sand grains. Comparison of cases of different caddisfly genera showed a trend between abrasion level and case-associated algae. Under low abrasion, grazer-resistant diatoms occurred on exposed surfaces and upright diatoms occurred in crevices (e.g., *Glossosoma* and *Discosmoecus* cases). As abrasion increased, diatoms were lost from exposed surfaces, although they remained in crevices (e.g., *Gumaga* cases); with continuous burrowing, cases were nearly devoid of algae (e.g., *Agarodes* cases).

**Key words:** diatoms, burrowing, diel periodicity, caddisfly cases, refugia, Trichoptera, *Gumaga*, streams.

The relatively large size, surface-dwelling behavior, and portable cases of many caddisfly larvae make them highly visible in freshwater habitats. Some case-making caddisflies also burrow into the streambed, a behavior that varies from living continuously within the hyporheic zone to retreating beneath rocks during the day but being active on the surface at night. Burrowing provides protection from surface predators, spates, and desiccation when water level drops (Rennerich and Schuhmacher 1983).

Cases associated with caddisfly larvae and other aquatic invertebrates (e.g., some Chironomidae) provide favorable habitats for the growth of algae and other organisms. For example, algal densities on the attached tube cases of chironomid (Diptera) larvae were higher than on stream substrates (Pringle 1985, Hershey et al. 1988). Likewise, bacterial concentrations were higher on the portable leaf cases of a non-burrowing limnephilid (Trichoptera) larva than on

similar leaves that were not incorporated into cases (Leff and McArthur 1989).

Algae on the cases of burrowing caddisflies are subjected to abrasion during burrowing and to shading if burrowing occurs during the day. Shading and abrasion occur commonly in streams and contribute to temporal and spatial patchiness in benthic algal assemblages. Shading can occur as a result of overlying sediment (Hill and Harvey 1990), an overstory of algae (Jørgensen and Des Marais 1988), and overhanging aquatic or riparian vegetation (Feminella et al. 1989). Abrasion includes grazing (i.e., scraping movements produced by the mouthparts of stream herbivores), non-consumptive algal dislodgment by organisms (Scrimgeour et al. 1991), and abrasion by flow during high discharge (Power and Stewart 1987).

Shading and abrasion can decrease algal abundances in streams but affect algae by different mechanisms. Shade produces physiological changes resulting primarily in altered concentrations of photosynthetic pigments (Darley 1982) and reduced primary production (Hill and Harvey 1990, DeNicola and McIntire 1991). Certain algae avoid shade through emigration

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(Bothwell et al. 1989). In contrast, abrasion is a physical force that removes (Power and Stewart 1987) or physically damages (Delgado et al. 1991) algae. Algae may be protected from abrasion by their size and growth habit (Peterson and Stevenson 1992) or by their location in crevices.

Our study had two objectives: (1) to assess the prevalence and timing of burrowing in a population of the caddisfly *Gumaga nigricula* (McL.) and (2) to determine possible effects of burrowing on algae associated with the caddisfly larva's case. For this second objective, we concentrated on the effects of shading by overlying substrate and of abrasion by substrate particles as cases are pulled through the streambed.

## Methods

### *Study sites and organism*

Field portions of this study were conducted in two streams. Big Sulphur Creek, a 2nd-order gravel-cobble stream in the Coast Range of northern California (Sonoma Co.; 38°47'N, 122°47'W), was the source of *Gumaga* larvae and the location of the shade experiment. Detailed descriptions of the site are given by Jackson and Resh (1989) and McElravy et al. (1989). Studies were conducted in two adjacent pools: a shallow upstream pool (with sand-gravel substrate) was sampled to assess the extent of burrowing and a deeper downstream pool (with sand-cobble substrate) was used for the shade experiment.

The second site was the South Fork of the Eel River (Mendocino Co.; 39°14'N, 123°38'W), also in the Coast Range mountains of northern California. The stream is 3rd order and has a cobble-dominated substrate at the study location; a more detailed description is given by Power (1990). A 50-m run was used for the experiment that simultaneously examined the effects of shade and abrasion on algal colonization.

*Gumaga nigricula* (McL.) (Trichoptera:Serico-stomatidae) is a stream-dwelling caddisfly that can be locally very abundant in western states (Resh et al. 1981). *Gumaga* makes a case of fine sand grains and silk. The silk cements the sand grains together and lines the case. This species of *Gumaga* is typically univoltine, and in Big Sulphur Creek, eggs hatch in early summer, larvae grow rapidly and overwinter as late instars, and pupation and emergence occur in late spring.

### *Burrowing*

Burrowing by *Gumaga* was surveyed in Big Sulphur Creek on three dates over a 6-wk period (16 September–28 October 1990). A total of 13 samples, each consisting of eight replicates, was collected at various times over the day-night cycle. We removed all live caddisflies from the substrate surface ("surface larvae") within a randomly located 270-cm<sup>2</sup> wire circle. The same location was immediately resampled with a cylindrical Hess sampler (area = 270 cm<sup>2</sup>) to the depth of the loose sand-gravel substrate (about 4 cm), thereby collecting the "burrowing larvae". Numbers of surface larvae and burrowing larvae were compared within each sample using the Wilcoxon paired-sample test ( $p \leq 0.05$ ,  $n = 8$ ).

### *Shade experiment*

Effects of shade by overlying substrate were examined in a field experiment. Empty *Gumaga* cases were added to 12 floating tubs made from 0.5-L plastic freezer containers with 1-mm plastic mesh on the upstream and downstream ends. Individual tubs were fitted with styrofoam collars that were, in turn, held in floating racks. Each tub contained a 1-cm-deep layer of sand collected from an exposed sandbar. Three treatments were used: (1) empty *Gumaga* cases resting on top of the sand (a control with full light); (2) empty cases resting 0.5–0.8 cm below the sand surface; and (3) empty cases on top of the sand but under black plastic (a shaded control). Using cases from which the caddisflies were removed before the experiment eliminated interference effects from the larvae, such as grazing or nutrient addition through excretion. Treatments were replicated four times and each replicate contained 16 cases. Replicates were sampled at the beginning of the experiment (13 October 1990) and then weekly until its conclusion (16 November 1990). On each sampling date, four cases were randomly collected from each replicate and rinsed, blotted dry, wrapped in aluminum foil, and frozen in preparation for chlorophyll *a* extraction. Chlorophyll *a* concentration, corrected for pheophytin *a*, was used as one measure of the quantity of algae on individual caddisfly cases. Chlorophyll was extracted from cases within a week of collection and freezing, using a methanol technique (Tett et

al. 1975). Chlorophyll *a* concentrations were calculated as mg/m<sup>2</sup>, after determining the surface areas of the extracted caddisfly cases (by fitting case measurements into the formula for a truncated cone). Data on chlorophyll *a* concentrations were analyzed using 1-way ANOVA (3 treatments,  $p \leq 0.05$ ) for the initial and final samples of the experiment followed by Tukey's multiple comparison test ( $p \leq 0.05$ ).

Light penetration was measured in the laboratory using a SPECTRA photometer, Model FC-200. Light penetration was measured through water, water plus 0.5 cm of sand from the study site, and water plus a black plastic cover.

#### *Abrasion experiment*

Effects of abrasion were examined by subjecting cases to varying levels of abrasion by sand and comparing changes in algal quantity and taxonomic composition. Because newly collected cases had already experienced abrasion, a second set of cases was prepared for this experiment by placing empty cases into floating tubs (described earlier) and allowing algae to accrue. After 3 wks, cases became green tinted; we refer to these cases as "algal-enriched" cases to distinguish them from "newly collected" cases. Algal-enriched cases develop an ungrazed and unabraded algal assemblage dominated by both diatoms and filamentous algae (newly collected cases have mostly diatoms). Although the algal assemblages differ, experimental abrasion of algal-enriched cases can be used to identify abraded and unabraded areas on cases. Because diatoms dominated on newly collected cases, diatoms but not filamentous algae were counted.

Both newly collected and algal-enriched cases were brought from the field site and held in aquaria overnight. Anterior openings of individual cases were plugged with paper and the cases were pulled through sand and water in a basin by a thread extending from the front of the case. Abrasion level was varied by changing the number of 20-cm long passes through the sand. Six levels of abrasion were used: 0, 1, 5, 10, 25, and 50 one-way passes. Ten algal-enriched and 10 newly collected cases were abraded at each level. Chlorophyll *a* concentration was determined for each case. Linear regression was used to compare chlorophyll *a* concentra-

tion with the number of passes through the basin (after log [ $x + 1$ ] transformation). Four additional algal-enriched and newly collected cases were abraded at the 0, 10, and 50 pass levels; half of these were preserved in 6% formalin for algal identification and enumeration and the remainder was preserved in cacodylate-buffered 2.5% glutaraldehyde for scanning electron microscopy (SEM).

The location of algae on abraded cases was viewed with scanning electron microscopy. Cases preserved in buffered glutaraldehyde or in 6% formalin were dehydrated by passage through a graded ethanol series (25%, 50%, 75%, 95%, and 100%). Cases were then transferred to freon before air drying. Individual cases were glued to aluminum stubs with a carbon-based glue, sputter-coated with platinum, and viewed using an ISI DS-130 scanning electron microscope.

Algae for counting and identification were removed from abraded caddisfly cases by 15 min of sonication (Koh-i-noor Rapidograph Ultrasonic Cleaner, Model 25K42; the time was based on previous SEM assessment of sonicated cases). Removed algae were centrifuged into a pellet, and water was added to a volume of 3.0 mL. Pellets were then dispersed, and a 1.0 mL subsample was removed for cell counts; the remainder was used for algal identification. Total numbers of diatom cells (living and dead) were estimated using a Whipple micrometer and a Sedgewick-Rafter counting cell. Counts were converted to number per cm<sup>2</sup> of case.

Diatoms in the remaining subsample were oxidized for one day in 30% hydrogen peroxide and mounted in Hyrax mounting medium. Using random-strip counts, at least 500 diatoms per sample were identified. These counts provided estimates of the relative proportions of diatom species, which, when combined with the total number of diatoms per cm<sup>2</sup> of case, gave estimates of density for individual diatom species.

The distribution of case algae of caddisfly species with different degrees of burrowing was assessed through SEM comparison of their cases. *Glossosoma oregonense* Ling (Glossosomatidae) and *Dicosmoecus gilvipes* (Hagen) (Limnephilidae) are two non-burrowing species that co-occur with *Gumaga*. Specimens were collected from Big Sulphur Creek on 21 May (*Gumaga*), 11 June (*Dicosmoecus*), and 22 July (*Glossosoma*)

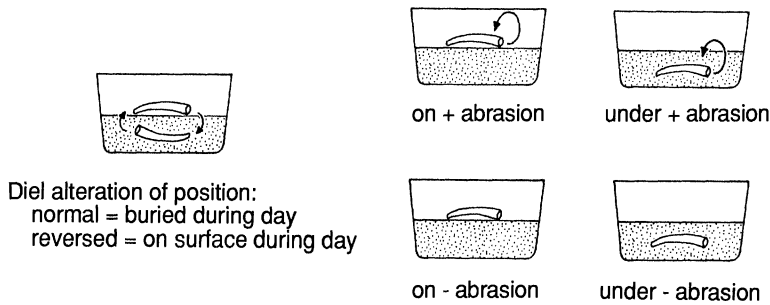


FIG. 1. Shade and abrasion experiment treatments, showing the position of *Gumaga* cases relative to the sand substrate (dotted area) within floating tubs. Arrows indicate the position of cases after abrasion at dawn and dusk. See text for further explanation of the experiment.

1990. Big Sulphur Creek lacks continuously burrowing caddisflies and so *Agarodes griseus* Banks (a continuously burrowing caddisfly in the same family as *Gumaga*, Sericostomatidae) were obtained from Pennsylvania (Walton Springs, 12 March 1991). Because species' cases varied in collection site and date, comparison of relative diatom density and location are more appropriate than comparison of diatom species composition.

#### Shade and abrasion experiment

In this experiment, cleaned *Gumaga* cases in floating tubs (described above) were colonized under different regimes of shade and abrasion. Stored cases were cleaned with 30% hydrogen peroxide, a treatment that removes both algae and detritus. To manipulate cases, monofilament fishing line was attached to the anterior opening of cases using a hot glue, a procedure that also sealed the front of the case.

The six treatments are shown graphically in Figure 1. The first treatment mimicked the **normal** burrowing behavior of *Gumaga*. At dawn, cases were pulled through approximately 8 cm of sand and left under the sand surface during the day. They were abraded again at dusk and left on the sand surface overnight. The second treatment **reversed** the day-night schedule of burrowing, but otherwise was identical to the normal treatment. In two more treatments, cases were kept on the surface and were abraded (**on + abrasion**) or not abraded (**on - abrasion**). The final two treatments consisted of cases that were under the surface (buried) and were abraded (**under + abrasion**) or not abraded (**un-**

**der - abrasion**). Treatments were randomly assigned to tubs and were replicated six times, with each replicate consisting of two *Gumaga* cases. The experiment ran for 2.5 weeks (5 to 22 June 1991), after which cases were preserved in 6% formaldehyde.

One case from each replicate was used for diatom counts. These cases were oxidized with hydrogen peroxide and potassium dichromate in a hot water bath. After rinsing, 1 mL of glass bead solution (bead diameter = 5–20  $\mu\text{m}$ ) was added to each sample and the resulting diatom-bead mixture was mounted in Hyrax medium. Random strip counts of diatoms and glass beads gave percent composition and density of diatoms (Battarbee and Kneen 1982). At least 350 diatoms were counted from each sample. Diatom densities and percent composition were analyzed by 2-way ANOVAs (sunlit or shaded during the day; abraded or unabraded). Values for  $p$  were 0.05 for density data and 0.0045 (=0.05/11 ANOVAs) for percent compositions of the 11 common diatom taxa. Percent composition data were arcsin square-root transformed before analysis.

The second caddisfly case from each replicate was viewed with SEM (described above). Each case ( $n = 36$ ) was observed and notes were taken on the abundance and location (sand grains faces or crevice areas) of algae and detritus. Cases were numbered by the location of their tubs in the field and not by treatment, a procedure that reduced observer bias. Six characters, each with two to four character states, were identified from the notes (Table 1). The most common character state among the six replicates was used to represent the character in each treatment. The re-

TABLE 1. Characters and character states used for cluster analysis in shade and abrasion experiment.

| Character              | Character states                                  |
|------------------------|---|
| Crevice area           | 1 = empty, 2 = detritus-filled, 3 = diatom-filled |
| Sand faces             | 1 = clean, 2 = obscured                           |
| Small diatoms          | 0 = absent, 1 to 3 = less to more abundant        |
| Large diatoms          | 0 = absent, 1 to 3 = less to more abundant        |
| Algal filaments        | 0 = absent, 1 to 3 = less to more abundant        |
| Unidentified filaments | 0 = absent, 1 to 3 = less to more abundant        |

sulting data were analyzed by cluster analysis (SYSTAT; Eucladian distance and average linkage).

## Results

### Burrowing

On average, 588 ( $\pm 35$  SE) *Gumaga* larvae were collected per m<sup>2</sup> of stream bottom. Most of the population burrowed during the day and occurred on the substrate surface during the night (Fig. 2; 3rd order polynomial curve,  $r^2 = 0.62$ ). During the daytime, only 26% of individuals were on the surface and the number burrowing was significantly larger in five of seven samples (Wilcoxon signed rank test,  $p \leq 0.05$ ). At night, 79% of total individuals collected were on the surface, and three of six surface samples had significantly larger numbers.

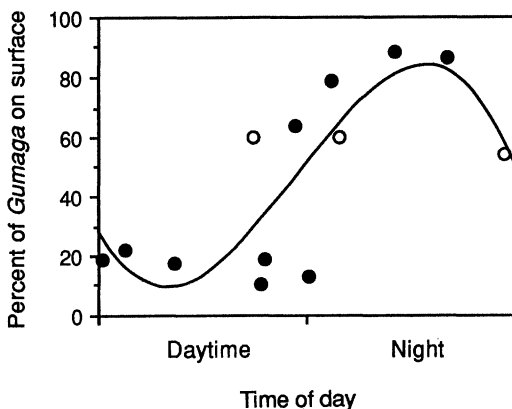


FIG. 2. Burrowing in *Gumaga nigricula* as the percent of total larvae on the substrate surface over the diel cycle (the remaining larvae are burrowing). ● =  $p \leq 0.05$  (Wilcoxon paired-sample test,  $n = 8$ ); ○ =  $p > 0.05$ .

### Shade experiment

Empty cases placed on the sand surface showed a rapid build-up of chlorophyll *a* to a concentration that was approximately four times the initial level, while burial under 0.5 to 0.8 cm of sand or shading by black plastic resulted in little change in chlorophyll *a* concentration (Fig. 3). No significant difference in chlorophyll *a* concentration was found among treatments at the beginning of the experiment (1-way ANOVA,  $p = 0.22$ ). However, significant differences were found at the end of the experiment (1-way ANOVA,  $p = 0.0002$ ). Tukey's multiple comparison tests showed significant ( $p \leq 0.05$ ) differences between cases on sand (=unshaded cases), and cases shaded by either sand or black plastic at the end of the experiment. Percent light transmission through these shade treat-

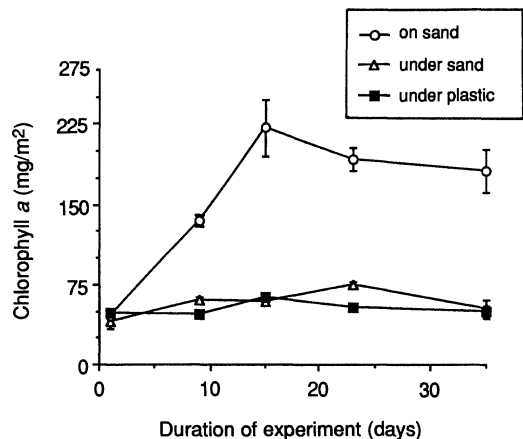


FIG. 3. Changes in mean ( $\pm 1$  SE) chlorophyll *a* concentrations over a 4-wk field incubation period for empty *Gumaga* cases exposed to three different shade treatments: (1) cases on top of sand; (2) cases buried 0.5–0.8 cm in sand; and (3) cases on top of sand, but under black plastic.

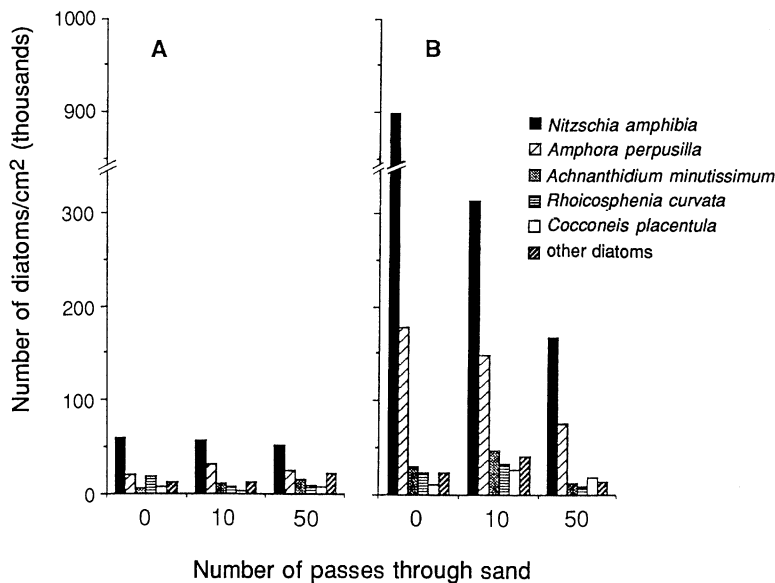


FIG. 4. Density of common diatoms on cases abraded by sand. A = newly collected cases, B = algal enriched; 0, 10, and 50 are the number of passes through the sand-filled basin.

ments was low (0.5 cm sand: 0.29%; black plastic: 0.13%).

#### Abrasion experiment

Pulling empty newly collected cases through sand substrate had little effect on chlorophyll *a* concentration of the cases. Regression of chlorophyll *a* concentration on number of passes through the sand basin produced a line with a negative slope that was not significantly different from zero ( $p = 0.079$ ,  $r^2 = 0.055$ ). In contrast, abrasion of algal-enriched cases affected chlorophyll *a* concentration. Regression of chlorophyll *a* concentration on number of passes produced a line with a negative slope that was significantly different from zero ( $p < 0.005$ ,  $r^2 = 0.407$ ).

The pattern of diatom densities among abrasion levels was similar to the pattern obtained with chlorophyll *a* concentration. Added abrasion did not affect diatom density on newly collected cases; conversely, diatom numbers were reduced by abrasion on the algal-enriched cases (Fig. 4). The rate of diatom loss in algal-enriched cases was greater at the onset of abrasion (4.8% loss per pass in the first 10 passes) than after cases had already been subjected to moderate abrasion (1.3% loss per pass in the

final 40 passes). These same patterns held for the dominant diatom, *Nitzschia amphibia* Grun. The less dominant diatoms *Achnanthydium minutissimum* (Kütz.), *Rhoicosphenia curvata* [Kütz.] Grun. ex Rabh., and *Cocconeis placentula* (Ehrenb.) Cl. were unaffected by abrasion on both newly collected and algal-enriched cases.

Algae on newly collected *Gumaga* cases were concentrated in the crevices between individual sand grains. Diatoms dominated in crevices and consisted of attached forms (primarily *Rhoicosphenia curvata*) and motile forms (primarily *Nitzschia amphibia*). Sand grain faces were covered with a film in which the prostrate diatoms *Cocconeis placentula* and *Achnanthydium minutissimum* were present. One other species, *Amphora perpusilla* (Grun.) Grun. was numerically abundant but not apparent with SEM (it was probably hidden by overlying *R. curvata* and *N. amphibia*).

Abrasion produced changes in the distribution of algal assemblages on cases. On newly collected *Gumaga* cases, experimental abrasion cleared most of the attached film from sand grain faces (Fig. 5, A-C). On algal-enriched cases, the algal flora that completely obscured the sand grain case (Fig. 5D) was reduced through abrasion. After 10 passes, sand grains were becoming visible on the cases (Fig. 5E), and after 50

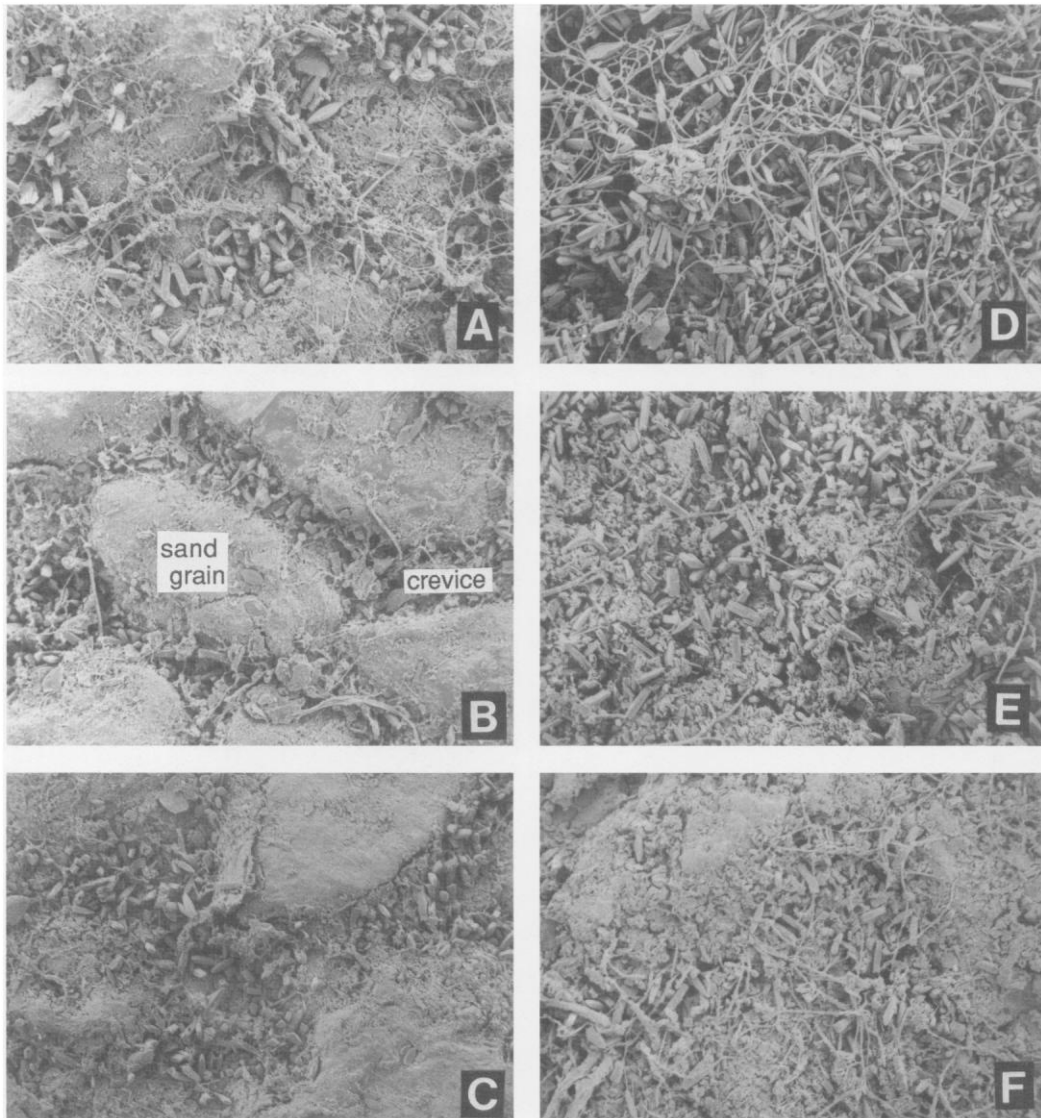


FIG. 5. SEM photographs of the surface of *G. nigricula* cases after three levels of abrasion: (A–C) newly collected cases, after 0 (A), 10 (B), or 50 (C) passes; (D–F) algal-enriched cases, after 0 (D), 10 (E), or 50 (F) passes. Magnification ranges from 290 $\times$  to 335 $\times$ .

passes, the cases resembled newly collected ones (i.e., the sand grain faces were cleared of algae, and diatoms predominated mainly in crevices; compare Figs. 5A and 5F). The abraded algal-enriched cases differed, however, in that the diatoms within crevices lacked the upright orientation found in the crevices of newly collected cases. In both newly collected and algal-enriched cases, abrasion removed algae from

the surface of the sand grains but had little effect on algae within the crevices between sand grains. The mineral cases themselves appeared unaffected by the abrasion treatments.

The pattern of diatom distribution on cases of the continuously burrowing *Agarodes griseus*, and the non-burrowing *Dicosmoecus gilvipes* and *Glossosoma oregonense* differed from the distribution on *Gumaga* cases (Fig. 6A, cf. B–D). Cases



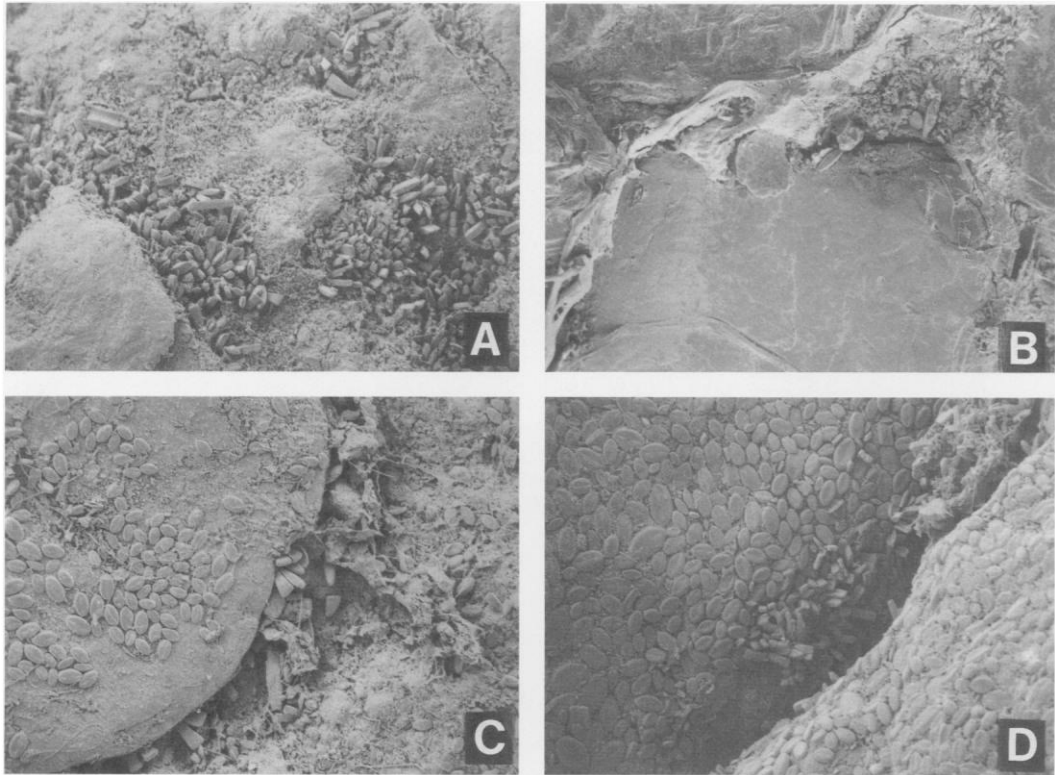


FIG. 6. SEM photographs of the outer surface of caddisfly cases, showing the location of algal assemblages with respect to the microtopography of the case: (A) *Gumaga nigricula* (308 $\times$ ) (daytime burrowing); (B) *Agarodes griseus* (341 $\times$ ) (continuously burrowing); (C) *Dicosmoecus gilvipes* (289 $\times$ ) and (D) *Glossosoma oregonense* (345 $\times$ ) (non-burrowing).

of *A. griseus* were clean, lacking the film visible on *Gumaga* cases, and diatoms were rare both on exposed sand grain faces and in crevices. Cases of *D. gilvipes* and *G. oregonense* had high densities of diatoms on the exposed stone surfaces (prostrate forms) and in crevices between stones (primarily upright forms).

#### Shade and abrasion experiment

Daytime light level (sunlit or shaded by substrate) significantly affected diatom density (2-way ANOVA,  $p = 0.0003$ ). Shading by substrate during the day reduced diatom density three-fold relative to the sunlit treatment. In contrast, the presence or absence of abrasion had no significant effect on diatom density ( $p = 0.33$ ). The interaction between light level and abrasion was also non-significant ( $p = 0.16$ ). For 10 of 11 common diatom taxa, percent composition differed

with daytime light level (2-way ANOVA using  $p \leq 0.0045$ ) but not with abrasion level, or the interaction between light and abrasion (Table 2). Four taxa were significantly more abundant in sunlit than shaded treatments and six taxa were significantly more abundant in shaded treatments.

Cases that were sunlit during the day (reversed, on + abrasion, and on - abrasion treatments) and cases that were shaded during the day (normal, under + abrasion, and under - abrasion treatments) grouped separately in the cluster analysis (Fig. 7). Sunlit cases had an abundance of diatoms (primarily *Epithemia sorex* Kütz. and *Epithemia turgida* [Ehrenb.] Kütz.) and filamentous algae (usually *Cladophora glomerata* [L.] Kütz.). Shaded cases had few diatoms and no filamentous algae. Within both sunlit and shaded treatment groups, the two treatments with abrasion clustered closer than the treat-

TABLE 2. Summary of 2-way ANOVAs comparing transformed (arcsin square-root) percent compositions of 11 diatom taxa between light treatments (sunlit or shaded during the day) and abrasion treatments (abraded or not abraded). Statistics designated by \* =  $p \leq 0.0045$  (=0.05/11 ANOVAs). Mean ( $\pm 1$  SE) percent compositions are given for significant  $p$  values and are untransformed.

|                                    | ANOVA $p$ value |          |             | Percent composition |                |
|------------------------------------|-----------------|----------|-------------|---------------------|----------------|
|                                    | Light           | Abrasion | Interaction | Sunlit              | Shaded         |
| <i>Achnanthes lanceolata</i>       | 0.0001*         | 0.07     | 0.66        | 1.6 $\pm$ 0.4       | 3.9 $\pm$ 0.4  |
| <i>Achnantheidium minutissimum</i> | 0.0001*         | 0.97     | 0.77        | 10.9 $\pm$ 1.5      | 24.8 $\pm$ 2.3 |
| <i>Amphora perpusilla</i>          | 0.0001*         | 0.31     | 0.79        | 2.5 $\pm$ 0.8       | 8.8 $\pm$ 1.0  |
| <i>Cocconeis placentula</i>        | 0.0003*         | 0.82     | 0.30        | 2.9 $\pm$ 1.0       | 9.7 $\pm$ 1.3  |
| <i>Epithemia sorex</i>             | 0.0002*         | 0.27     | 0.94        | 6.7 $\pm$ 0.8       | 1.7 $\pm$ 0.7  |
| <i>Epithemia turgida</i>           | 0.0002*         | 0.03     | 0.22        | 2.3 $\pm$ 0.4       | 0.7 $\pm$ 0.2  |
| <i>Navicula menisculus</i>         | 0.16            | 0.15     | 0.82        |                     |                |
| <i>Nitzschia amphibia</i>          | 0.0001*         | 0.32     | 0.68        | 2.9 $\pm$ 0.7       | 12.2 $\pm$ 1.5 |
| <i>Nitzschia dissipata</i>         | 0.0001*         | 0.77     | 0.75        | 15.2 $\pm$ 1.5      | 2.0 $\pm$ 0.7  |
| <i>Nitzschia</i> spp.              | 0.0001*         | 0.99     | 0.78        | 27.8 $\pm$ 3.1      | 6.9 $\pm$ 1.2  |

ment without abrasion. Unabraded cases in the sunlit group (on - abrasion treatment) had higher densities of large diatoms (e.g., *Epithemia turgida*) and fewer *Cladophora* filaments than abraded cases. Unabraded cases in the shaded group had less detritus than abraded cases.

## Discussion

### Burrowing

In the population of *Gumaga* studied, larvae burrow in the streambed during the day and move onto the surface at night. However during the day, 26% of individuals were found on the substrate surface, suggesting plasticity in burrowing behavior. Larvae that remain on the surface during the day have longer access to periphyton but might also have greater exposure to predators and spates (Rennerich and Schuhmacher 1983).

Although burrowing is common among spe-

cies in the caddisfly family Sericostomatidae (e.g., Wiggins 1977), the diel pattern of daytime burrowing and nighttime surfacing is known in only two species, *Gumaga nigricula* and *Sericostoma personatum* (results of this study and Elliott 1969, respectively). Both of these species graze algae (*Gumaga*: Feminella and Resh 1991 and *Sericostoma*: Elliott 1969), whereas most sericostomatids are detritivores (e.g., Thorup and Iverson 1974, Shapas and Hilsenhoff 1976, Wiggins 1977, McEwan 1980, Merritt and Cummins 1984), suggesting that nighttime surfacing is associated with grazing. Indeed, Elliott (1969) found that feeding occurred at night when *Sericostoma* larvae were on the surface.

### Effects of burrowing on case algae

Results from the shade experiment and light penetration data suggest that the daytime burrowing behavior of *Gumaga* causes light limi-

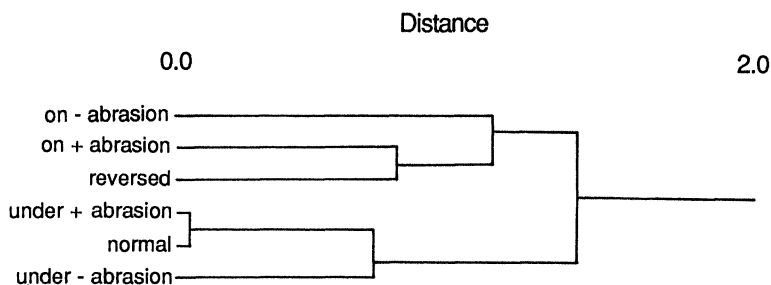


FIG. 7. Cluster analysis of shade and abrasion treatments based on SEM observation of algae and detritus on *Gumaga* cases. Character and character states are listed in Table 1.

tation of the algae on its case. Limitation was demonstrated by the dramatic increase in chlorophyll *a* concentration of unshaded cases when compared with the consistency of the chlorophyll *a* concentrations of cases shaded by overlying sand and black plastic. Light penetration through 0.5 cm of sand and through black plastic was less than 1%, a level considered as an approximate compensation point for benthic algae (Darley 1982). The low penetration of light accounts for the similarity in chlorophyll values of the two shaded treatments.

Exposure to light enhanced algal colonization, and shading caused by daytime burial prevented or retarded the establishment of the diatom community normally found on *Gumaga* cases. Once a community was established, however, continuous burial (in the shade experiment) did not change chlorophyll *a* content. Hence, colonization rate is slow on cases that are buried during the day (i.e., cases of daytime-burrowing caddisflies) and the diatoms that colonize are tolerant of low light levels.

Experimental abrasion reduced algal levels on colonized cases (abrasion experiment) but had no apparent effect on algal colonization of cleaned cases (shade and abrasion experiment). The discrepancy in abrasion effects was probably caused by a lower duration of abrasion (e.g., distance dragged) in the shade and abrasion experiment. Both experiments used unconsolidated sand, which is less abrasive than more consolidated streambed substrates. The following discussion is based primarily on the abrasion experiment and on the visual comparison between burrowing and non-burrowing caddisfly cases.

Abrasion on the sand grain faces of cases of *Gumaga* produced an extreme form of the two-dimensional architecture because diatom density was low, upright forms were entirely absent, and the assemblage was dominated by the prostrate diatom *Cocconeis placentula*. A two-dimensional growth form of benthic algae is associated with disturbance, whether in the form of invertebrate grazing (Pringle 1985, Steinman et al. 1987) or shear stresses resulting from either water movement (Luttenton and Rada 1986) or substrate movement (Robinson and Rushforth 1987, Stevenson and Hashim 1989). Abrasion from sand produces the same general changes in diatom architecture as other types of abrasion, including the biological effects of

grazing by invertebrates and physical effects associated with spates or substrate movement.

A three-dimensional community develops in the absence of disturbance (Patrick and Roberts 1979, Hudon and Bourget 1983, Luttenton and Rada 1986, Steinman et al. 1987). In crevices, the dense packing, dominance of upright forms, and abundance of *Nitzschia amphibia* (a motile species) suggest a distinct architecture that approaches the three-dimensional type, but whose overstory of stalked diatoms and filamentous algae cannot develop because of the restricted vertical space within crevices; algae extending upward beyond the refuge are removed by abrasion. Thus, the architectural variation of the diatom assemblage on *Gumaga* cases results from a combination of intense abrasion and spatial variation in the degree of exposure to this abrasion.

Whereas algae were plentiful on *Gumaga* cases, they were scarce on the cases of *Agarodes griseus*, a continuously burrowing species. Shade was likely more important than abrasion in reducing algal density on *A. griseus* cases because algae were extremely scarce within crevices (=refugia from abrasion). Therefore, as the level of burrowing increases, abrasion and shading first restrict algae to crevices (e.g., in *Gumaga*) and, eventually, algae are unable to maintain populations (e.g., in *A. griseus*).

*Gumaga* cases have lower chlorophyll *a* concentrations than stream stones (Bergey 1992). This lower chlorophyll content has consequences for both the caddisfly and the case algae. Lower algal density may improve caddisfly mobility by reducing drag and simultaneously enhancing the ballast function of the case by preventing changes in case density. Cases allowed to experimentally accrue algae for four weeks or longer became fuzzy with filamentous algae. When *Gumaga* larvae were reintroduced, they had difficulty moving and many of the cases floated to the water surface. A low algal standing crop leaves less algae available for grazers; hence, it is less likely that case-associated algae on *Gumaga* cases can be used as a food supply, as has been suggested for the non-burrowing caddisfly *Agapetus fuscipes* (Glossosomatidae) (Cox and Wagner 1989). Algae that are removed by abrasion disperse in the drift and contribute to downstream colonization.

*Gumaga* cases increased total surface area in Big Sulphur Creek by approximately 8% (825

cm<sup>2</sup>/m<sup>2</sup> of streambed). In the context of stream ecosystems, cases of *Gumaga* and other burrowing caddisflies can be viewed as patches of light-limited and abrasion-affected algal assemblages occurring within the mosaic of the benthic community. Such algal patches may be widespread because burrowing is common among cased caddisflies, and these patches increase total primary productivity and contribute to the spatial heterogeneity of stream benthic communities.

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