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Differential Response of Algae on Small Streambed Substrates to Floods

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ABSTRACT.—The effect of floods and base flow on temporal variation in algal biomass on small smooth streambed stones and creviced sand-cases of the caddisfly (Insecta: Trichoptera) *Gumaga nigricula* was examined in Big Sulphur Creek in coastal Northern California. Replicates of stones and cases were sampled 34 times over a 14 mo period that included nine floods. Stones had ~2× the algal biomass of cases, based on chlorophyll *a* concentration. The lower algal biomass on caddisfly cases is consistent with this species' burrowing behavior, which reduces algal biomass by abrasion and light limitation. Algal biomass on stones was reduced by floods and generally increased in the absence of floods. In contrast, neither floods nor extended base flow affected the pattern of algal biomass on caddisfly cases, and biomass on caddisfly cases often exceeded that on stones following floods. Streambed substrates with different textures may provide different degrees of disturbance-protection for benthic microalgae, and rougher substrates in streams may have more relict algae following floods than smoother substrates.

INTRODUCTION

The beds of most streams contain several different types of inorganic substrates that vary in size, shape and parent rock. Even in streams with apparently homogeneous parent rock types, there can be variation in crystal size, the distribution of intrusions and the amount of weathering.

Small-sized (<2 mm in diameter) inorganic particles of sand and silt are a major compositional component of the substrate in the majority of benthic habitats. They are also an essential component of the cases made by many species of caddisfly (Trichoptera) larvae. Most caddisfly cases, if examined at fine scales, are far from smooth (*e.g., see* case illustrations in Wiggins, 1996). Their surface roughness is an example of the type of small-scale spatial heterogeneity of benthic substrates that has been implicated in the colonization, establishment and protection of algae from some disturbances (*e.g.,* Dudley and D'Antonio, 1991; Bergey and Resh, 1994).

Surface roughness on stream beds consists of low areas or crevices and raised exposed areas (Johnson, 1994). Many algae settle in crevices (Dudley and D'Antonio, 1991; Downes *et al.,* 1998) and their survival may be enhanced by surface roughness because of the protection offered within crevices (Dudley and D'Antonio, 1991). Consequently, more algae are often found on rough than smooth substrates (Hardin and Lindbergh, 1977; Clifford *et al.,* 1992).

Crevices and other refuges can protect organisms when the sizes of the organism(s) and the refuge, and the scale of the disturbance are appropriate (Bergey, 1999; Bergey and Weaver, 2004). That is, to be protected, organisms must be able to fit within the space of the refuge and also be sheltered from the effects of disturbance. Crevices have been implicated in protection from disturbances such as grazers and predators (Lubchenco, 1983; Dudley

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and D'Antonio, 1991), abrasion (Bergey and Resh, 1994; Bergey, 1999), water flow (Holomuzki and Biggs, 1999) and desiccation (Gosselin and Chia, 1995).

In streams, floods are a major disturbance. Floods reduce algal biomass on streambed substrates (Power and Stewart, 1987; Grimm and Fisher, 1989), influence algal richness (Biggs and Smith, 2002) and patchiness (Matthaei *et al.,* 2003) and affect the temporal pattern of algal biomass in many streams (directly: Biggs and Close, 1989; indirectly through altering grazer density: Power, 1992; Marks *et al.,* 2000).

The protection of benthic algae in crevices can affect the recovery trajectories of algal assemblages following scouring floods. Algae remaining in crevices following floods include both microalgae, such as diatoms that may fit entirely within crevices, and holdfasts of attached filamentous algae, such as *Cladophora glomerata* (L.) Kützing. (Dudley and D'Antonio, 1991; Bergey, 1999). Algae remaining in crevices after disturbance are relict algae that can contribute to the rapid recovery of algal assemblages by direct growth, and by supplementing algal drift and subsequent settlement.

The objective of this study was to assess the interaction of crevice protection and disturbance in regulating algal biomass. We examined temporal variation in algal assemblages on stream substrates that differed in crevice refuges (smooth: small graywacke stones; and creviced: caddisfly cases) over a 14 mo period that included several floods and examined the relative influence of floods and base flow on patterns of algal biomass.

METHODS

Big Sulphur Creek is a perennial stream located in the Mayacmas Mountains (Sonoma County) of the Northern California Coast Range. The area's Mediterranean climate, along with its seasonal rainfall and the steep watershed, typically produce summers with continuous base flow and winters with numerous sizable floods.

Larger substrates in the stream range from boulder-cobble in the riffles to mostly gravels in the pools. Gravels are primarily graywacke, with some serpentine and schist. Graywacke, or lithic sandstone, is a gray stone that becomes quite smooth in streams (Bergey, 2005); serpentine and schist are both layered metamorphic rocks.

Fine substrates in this stream include sand particles derived from the parent greywacke, serpentine, schist and other rocks. Sand particles of 0.2 to 0.6 mm in diameter are incorporated in the larval and pupal cases of the caddisfly *Gumaga nigricula* (McL.) (Trichoptera: Sericostomatidae). The portable larval case of *G. nigricula* is constructed of sand and silk, and is in the form of a tapered curved tube (Fig. 1). Under magnification with a scanning electron microscope, the case, which may be 3 cm long, consists of emergent sand grains with deep crevices between the grains (Bergey and Resh, 1994; Fig. 1). *Gumaga nigricula* larvae are algal grazers that often burrow into the streambed sediments during the day (Bergey and Resh, 1994). The species typically has one generation per year, but larvae are present in Big Sulphur Creek throughout the year because of cohort splitting. Additional details on the life history and ecology of this species are found in Resh *et al.* (1997).

Algal biomass on *Gumaga nigricula* cases and on small similarly sized greywacke stones was sampled over a 14 mo period, beginning on 4 Sept. 1989 and ending on 11 Nov. 1990. Ten caddisfly cases and 10 streambed stones were collected on each of 34 sampling dates, at approximately 2 wk intervals. All collections were made in a large shallow pool, with a gravel and pebble bed and partial shade. Caddisflies were removed from cases; the insides of the cases were rinsed to remove sand and blotted dry. Cases and stones were then labeled, wrapped with foil, iced in the field and frozen upon return to the lab. In May and June, only small caddisflies were present and sets of three or four cases were combined into single

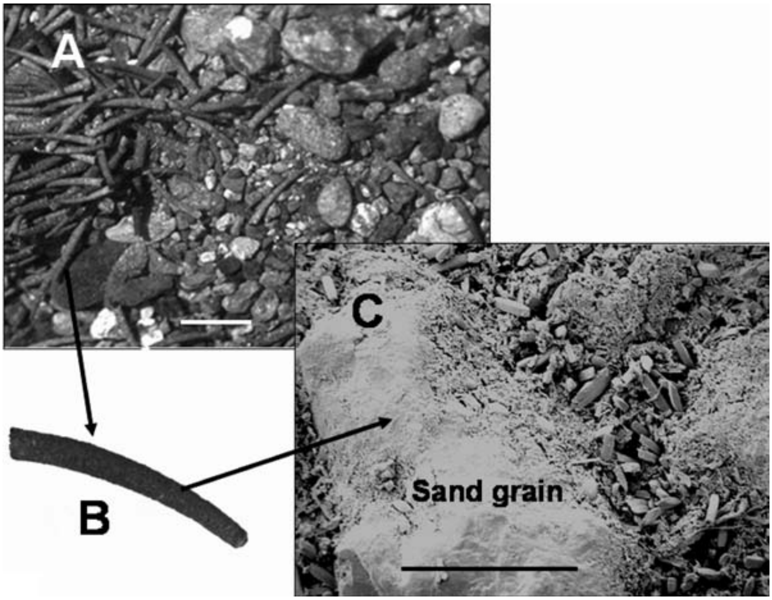

FIG. 1.—(A) *G. nigricula* in a pool of Big Sulphur Creek, showing part of a large natural aggregation, (B) a close-up of a sand-grain case and (C) a scanning electron photograph of a portion of the case, showing emergent sand grains with intervening diatom filled crevices. White scale bar is 2 cm; black scale bar is 100 μm

replicates. The collected stream stones were similar in length to late instar caddisfly cases (*e.g.,* 2 to 3 cm in length) and averaged ~5× the surface area of the cases.

Within 1 wk of collection, chlorophyll was extracted from cases and stones by complete immersion in methanol and chlorophyll *a* concentration was measured with a spectrophotometer using procedures in Tett *et al.* (1975). Surface area of *Gumaga nigricula* cases was determined by measuring cases with a calibrated ocular micrometer in a dissecting microscope and fitting the measurements into a formula for a truncated cone. Surface area of stones involved weighing aluminum foil that was wrapped over the stone and trimmed to cover the part of the stone with algae; weights were converted to surface area using the density of the foil.

Data on stream flow were obtained from the US Geological Survey, which has a gauging station on Big Sulphur Creek below the study site (Station 11463170; latitude 38°47′52″, longitude 122°48′5″).

Temporal patterns of algal biomass and floods were analyzed using chi-square tests. Change in chlorophyll *a* concentration over the intervals between consecutive samplings was scored as increasing, no change, or decreasing. Differences of ± 3 mg/m^2 or less were scored as 'no change'. This value was derived from the error in the chlorophyll analysis (Tett *et al.,* 1975) (95% confidence interval is $\pm 5\%$ for chlorophyll *a* and the mean chlorophyll value was 56.6 mg/m^2; 5% of 56.6 = 2.8). Sampling intervals with floods (defined as at least a 150% increase in discharge during the interval) were noted. The presence/absence of floods and scores of chlorophyll *a* change produced a 2×3 array of six cells. Expected values were derived from the null hypothesis that floods do not affect benthic chlorophyll *a* concentration (there is equal chance of increasing, no change, and decreasing chlorophyll

TABLE 1.—Chi-square analysis of the pattern of chlorophyll *a* change in sampling intervals with and without floods. Expected values were based on an equal number of occurrences among the patterns of chlorophyll *a* change (decrease, no change and increase) during intervals with floods (total $N = 9$ intervals, or $N = 3$ per pattern) and without floods (total $N = 24$ intervals, or $N = 8$ per pattern)

With a flood?	Chlorophyll *a* change	Expected	Observed-stones	Observed-cases
yes	decrease	3	7	2
yes	no change	3	0	5
yes	increase	3	2	2
no	decrease	8	5	7
no	no change	8	2	7
no	increase	8	17	10
chi-square value			24.4	2.8
$X^2_{0.05,5}$			11.07	11.07
P			<0.001	>0.05

a concentration over intervals) during the nine intervals with floods and the 24 intervals without floods. Expected values were 3 or 8 (Table 1). Although the expected value of 3 is below the generally accepted minimum cell count of 5, expected values of 3 are acceptable in these tests because they meet the criteria of Koehler and Larntz (1980); which are: $k \geq 3$; $n \geq 10$; and $n^2/k \geq 10$ (respective values for the dataset were: $k = 6$; $n = 33$; $n^2/k = 181.5$). Data for stones and caddisfly cases were tested separately.

RESULTS

Algal biomass, measured as chlorophyll *a* concentration, was higher on stream stones than on caddisfly cases (paired *t*-test: $t_{33} = 4.275$; $P = 0.0002$; Fig. 2). Stones averaged about twice the chlorophyll *a* concentration of caddisfly cases [respective means (SE): 78.7 (11.5) and 34.5 (4.3) mg/m^2]. Although the standard error among sampling dates was greater for stones than caddisfly cases, the difference was relative to the respective means and the coefficients of variation were similar (0.72 and 0.75, respectively).

The temporal pattern of stone chlorophyll *a* concentration followed discharge (Fig. 2). Chlorophyll concentrations on stones were reduced in most intervals with floods [mean change (SE): –12.8 (19.5) mg/m^2], whereas intervals without floods typically had increases in chlorophyll concentration [mean change (SE): +15.3 (6.3) mg/m^2]. This effect of floods on stone chlorophyll *a* concentration was significant (chi-square test: $P < 0.001$; Table 1). Algal recovery on stream stones after floods was rapid and chlorophyll *a* concentrations had largely rebounded within three weeks of floods.

In contrast to stones, the temporal chlorophyll pattern of *Gumaga nigricula* caddisfly cases was not significantly affected by floods (chi-square test: $P > 0.05$; Table 1). The patterns of chlorophyll change (*i.e.,* increase, level and decrease) were similar to those expected by chance, with no effect from the presence or absence of floods. This result is also apparent in Figure 2. Because algae on caddisfly cases were little affected by floods, post-flood chlorophyll *a* concentrations were often higher on caddisfly cases than on stones (Fig. 2).

The last 5 mo of the survey were virtually flood-free, as is typical of Mediterranean-climate streams; the single flood that qualified as such did so only because of the very low base flow associated with an extended drought. During this period, chlorophyll *a* concentrations increased greatly on stones. This high chlorophyll *a* concentration resulted from

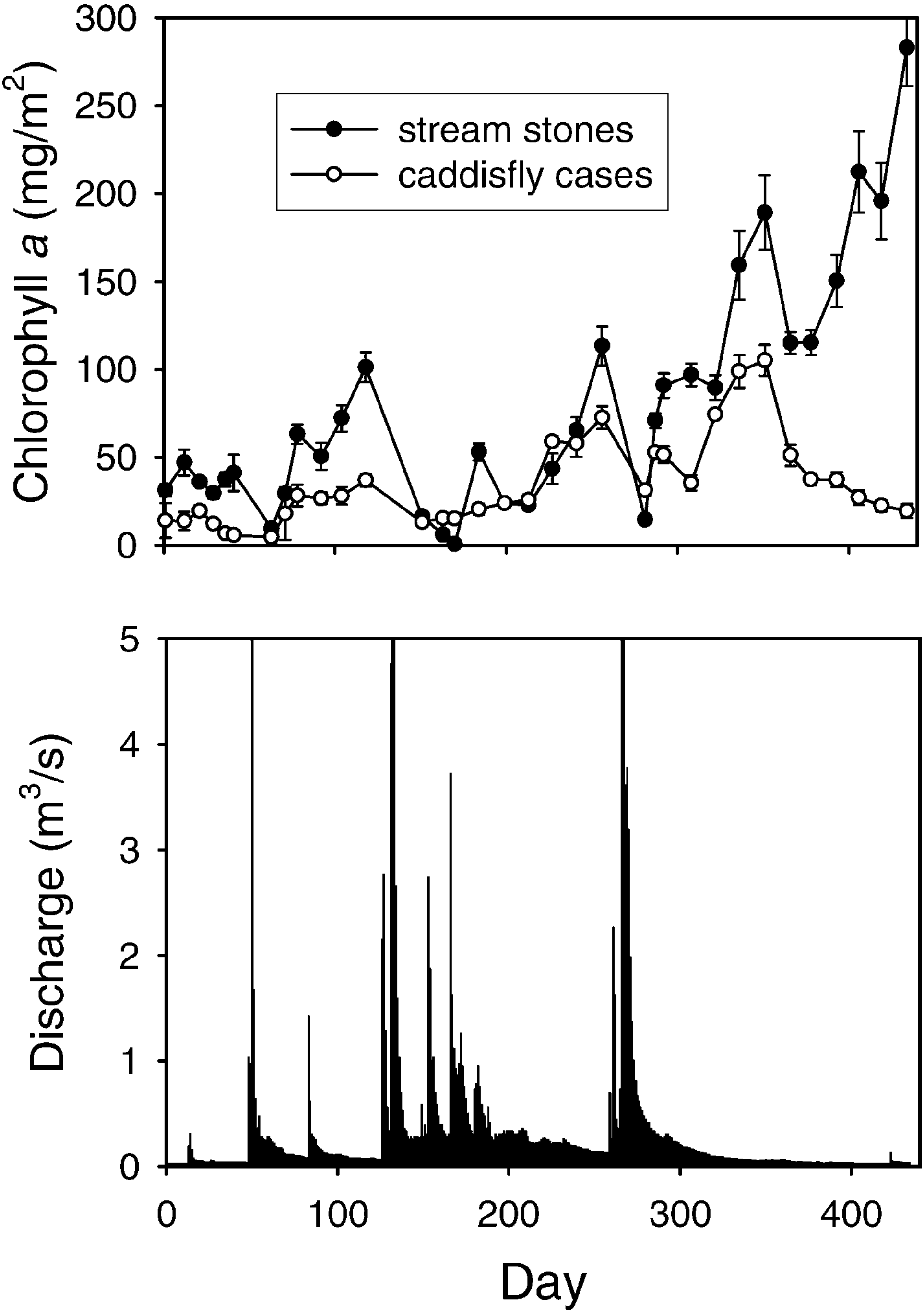

FIG. 2.—Benthic chlorophyll *a* concentrations and stream discharge in Big Sulphur Creek over a 14 mo period beginning in 4 Sept. (=Day 1). Error bars are ± 1 SE

the growth of the branched filamentous green alga *Cladophora glomerata.* This alga did not establish on caddisfly cases and case chlorophyll *a* concentrations did not show a similar increase.

DISCUSSION

Lamberti and Resh (1985) compared colonization of algae and invertebrates on clay quarry tiles (a commonly used artificial substrate) and cobbles in this same stream. They found similar algal assemblages on the two substrates. In contrast, we found a large difference in algal biomass between co- occurring streambed stones and caddisfly cases, with stones averaging twice the biomass of cases.

The biomass difference that we observed is consistent with differences in 'behavior' of the two substrates. The small stones were from the surface of the streambed, as were the introduced clay tiles and cobble used in the study of Lamberti and Resh (1985). Caddisfly cases were also collected at the surface, but *Gumaga nigricula* regularly burrow into the streambed (Bergey and Resh, 1994), and this burrowing abrades the cases and reduces algal biomass. Because burrowing occurs during the day, burrowing also reduces exposure of case-associated algae to light, and the growth of these algal assemblages is reduced.

Caddisfly burrowing affects not only the quantity of algae on *Gumaga nigricula* cases, but also largely restricts the diatom-dominated assemblages to the crevices between sand grains (Bergey and Resh, 1994; Bergey, 2004; Fig. 1). Their occurrence in crevices evidently also confers protection for the algae from floods, perhaps because both burrowing and exposure to floods are abrasive disturbances involving scraping by shifting substrate particles. Similarly, diatoms are found primarily in the crevices of other substrates, including sand grains (Meadows and Anderson, 1966; Miller *et al.,* 1987).

Algal biomass was greater on *Gumaga nigricula* cases than on stream stones after some floods, in part because algal biomass was very low on stream stones. Algae associated with *G. nigricula* cases after floods are relict algae and can be a source of colonists for the general streambed. In a laboratory experiment, algae from *G. nigricula* cases colonized cleaned streambed stones with exposures as short as 4 h (Bergey, 2004). This transfer of algae in combination with *G. nigricula*'s high densities (Resh *et al.*, 1997) and mobility in the streambed (Jackson *et al.*, 1999) may enhance post-flood algal recovery in Big Sulphur Creek, where *G. nigricula* cases add about 8% additional surface area to the streambed (Bergey and Resh, 1994). Because caddisflies are seldom this abundant and crevice diatom density varies among caddisfly species (Bergey and Resh, 1994), case-dwelling algae probably have a negligible effect on algal recovery in most other streams.

The comparison of crevice-poor and crevice-rich substrates in this survey may have wider application to streambeds with stones of differing textures. Stones of different textures vary in the protection of algae in crevices (Bergey, 2005) because the size and density of crevices affects algal protection (Bergey, 1999; Bergey and Weaver, 2004). Consequently, algal biomass varies among different rock types; especially during early colonization (Blinn *et al.*, 1980). A mosaic of rock types in a streambed may produce spatial heterogeneity in algal susceptibility to disturbance-loss and in the amount of relict algae following floods. The role of relict algae in recovery has been little studied because most colonization studies use clean substrates (Peterson, 1996), but relict algae are likely an important component in algal resilience.

Stream ecologists are cognizant of the effects of substrate particle size on the susceptibility of benthic algae and invertebrates to disturbance and of the positive relationship between particle size and biodiversity. The influence of surface roughness in algal protection also needs to be recognized and both the types and sizes of stones in the streambed should be reported.

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