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The importance of algae to stream invertebrates

RANDALL L. FULLER, JEFFERY L. ROELOFS, AND TERRY J. FRY

Department of Biology, Colgate University,
Hamilton, New York 13346 USA

Abstract. A 20-m section of stream riffle was covered with black plastic to decrease light intensities and reduce algal standing crops. After four weeks, chlorophyll *a* concentrations were near zero and *Baetis tricaudatus* nymphs were far fewer in the experimental riffle than in control riffles above and below the shaded area. Also, *Baetis* adults, reared from pre-emergent nymphs collected in the experimental riffle, were significantly smaller than reared adults from the control riffles. After three months, we removed one half of the black plastic from the experimental riffle. The algae and *B. tricaudatus* nymphs recolonized the open section of the experimental riffle within 11 days. These results suggest that algae are an extremely important resource for *B. tricaudatus*, a collector-gatherer.

Reduction of epilithic algae did not greatly influence *Simulium*, a filter feeder. Other macroinvertebrates that apparently were not influenced by the algal reduction included *Asellus, Gammarus, Hyallela, Dugesia* and Chironomidae.

Key words: resource use, spatial distribution, algae, periphyton, stream invertebrates, Baetis tricaudatus, Simulium.

The importance of algae, particularly diatoms, to aquatic insects has been demonstrated in a number of laboratory growth studies (Bird and Kaushik 1984, Fuller and Mackay 1981, Richardson 1984, Sweeney and Vannote 1984). This evidence was obtained by measuring the growth of test insects whose diets were restricted to a single food type. Bird and Kaushik (1984) showed that periphyton produced a higher growth rate for *Ephemerella subvaria* than diets of decaying leaves or macroinvertebrate fecal material. Field studies have also shown that algae were responsible for increasing secondary production of different stream insects (Benke and Wallace 1980, Huryn and Wallace 1985).

Because algae appear to be an important food resource, the local distribution and abundance of at least some macroinvertebrates should be influenced by algal densities. Higher densities of filter feeders below lake outflows appear to be supported by the higher algal component in seston flowing from the lake (e.g., Wallace and Merritt 1980). Studies of scrapers have also shown a positive correlation between algal densities or algal primary production and macroinvertebrate abundance (Hart 1981, Lamberti and Resh 1983). Little research has dealt with the importance of algae to collector-gatherers. Shepard and Minshall (1984) showed in a laboratory study that gathering mayflies do not discriminate between algae and various forms of detritus (including insect feces) over a six-hour test period. Similarly, Williams and Moore (1985) showed that different epilithic coatings (algae, cyanobacteria and sterile gravel) did not significantly affect the initial colonization (5-day experiments) of substrata by different macroinvertebrates including many collector-gatherers (with the possible exception of some Chironomidae). Although these studies of gatherers suggest that epilithic material may have little influence on macroinvertebrate distribution, the studies were designed to test for short-term effects only. Wallace and Gurtz (1986) showed that when the stream canopy was removed by logging, *Baetis* mayflies had higher densities and secondary production, as a result of a higher consumption of diatoms, than *Baetis* in a shaded stream.

A long-term, experimental manipulation of the habitat appears to be necessary to identify which resources are most important to stream macroinvertebrates. In this paper, we describe an experiment in which we reduced algal biomass in a riffle by covering a section of the stream with black plastic; the lower light intensities resulted in lower algal standing crops. We hypothesized that any macroinvertebrates relying on algae as a major source of energy would emigrate from the shaded riffle or, if they remained, would have a smaller body size.

Study Site

The study site was located on Kingsley Creek approximately 1 km below Lebanon Reservoir, Madison County, New York. The stream is second order with a maximum width of 3 m and maximum depth of 40 cm. The substratum consists of cobbles and pebbles with lesser amounts of coarse-to-fine gravel and sand. The stream gradient is high (16 m/km) resulting in few pools and many riffles. Stream discharge remains constant throughout the summer because of a hypolimnion drain in the reservoir. From the reservoir to our study site, the stream flows through an open pasture of various grasses plus alfalfa and clover. High light intensities produce high algal standing crops consisting largely of diatoms and patches of *Cladophora*. Water temperatures measured with a maximum-minimum thermometer were 6–20°C in June and 10–18°C in September.

Methods

We selected three consecutive riffles, each approximately 20 m long and separated by a 20-m run. On 15 April 1985, we placed 30 clay tiles (8×8×0.5 cm) in each of the three riffles to allow natural colonization of algae. On 6 June, we collected three Surber samples (250 μm mesh) and scrapings from three tiles (for chlorophyll *a* analysis) in each of the three riffles; we then covered the middle riffle with black plastic (0.55 mm thick). Water samples were taken at the downstream end of each control riffle and the experimental riffle for chlorophyll *a* analysis. This sampling program was continued every two weeks through August.

Tile scrapings and water samples were filtered onto separate Gelman glass fiber filters (0.2 μm pore size), ground in a tissue grinder, and the chlorophyll extracted for 24 hr in 90% acetone. After centrifuging, chlorophyll *a* was measured using a Bausch and Lomb Spectronic 2000 spectrophotometer; these values were corrected for phaeophytin (APHA 1980).

Each Surber sample was dispersed in a basin and all the *Simulium* spp. and *Baetis tricaudatus* Dodds were removed and counted. These two taxa were the most abundant macroinvertebrates with which to test our hypothesis. A subsample (¼) of the remaining sample was used to measure densities of the other macroinvertebrates.

From 23 to 29 July, we collected *Simulium* pupae from each of the three riffles. Pupae were placed in separate petri dishes on moist paper towels and all adults were collected at least twice a day. The adults were dried at 50°C for 24 hr and weighed on a Cahn Model 29 Electrobalance (±1.0 μg). On these dates we also collected pre-emergent *B. tricaudatus* nymphs (those individuals with black wing pads) from each riffle. These nymphs were placed in separate, recirculating plexiglas chambers (Mackay 1981) and kept covered; all adults (mostly subimagos) from each chamber were collected at least twice daily. The *B. tricaudatus* adults were dried and weighed following the same procedure described for adult *Simulium*.

Ten *B. tricaudatus* nymphs were collected from each riffle on 7 August. Their foregut contents were spread on microscope slides and examined at 100× magnification.

On 5 September, we removed one half (a 10-m length) of the black plastic from the experimental riffle to allow algae to colonize this area. On 16 and 25 September, we sampled the undisturbed and still shaded section of the experimental riffle (EM), the control riffles, and the opened section of the experimental riffle (OEM). Collections included water samples, clay tile scrapings and macroinvertebrate samples. Besides quantifying different macroinvertebrates from these collections, we also measured total body length of *B. tricaudatus* nymphs at 20× magnification.

Chlorophyll *a* data were analyzed using a one-way analysis of variance for each sample date for water samples and rock scrapings. *Simulium* and *B. tricaudatus* densities on each sample date in the experimental riffle were compared with those in control riffles using a one-way ANOVA with log n+1 transformation. Adult dry weights of *Simulium* were compared using a one-way ANOVA testing for differences between control and experimental riffles. *Baetis tricaudatus* adults were divided into two groups for testing: adults that emerged during the first three days after collection and

TABLE 1. Chlorophyll *a* values (mean ±1 SE, µg/cm^2) of epilithic material in Kingsley Creek. Values with the same superscript letter did not differ significantly ($p>0.05$, ANOVA).

	Riffles		
Sample Date	Experimental	Lower Control	Upper Control
6 June 1985	2.64±0.91^{a}	4.85±2.18^{a}	2.68±0.97^{a}
18 June 1985	2.01±0.74^{b}	5.33±1.33^{b}	6.21±1.32^{b}
2 July 1985	0.40±0.21	4.97±1.79	7.95*
23 July 1985	0.07±0.02	1.08±0.25^{c}	2.70±0.94^{c}
7 Aug 1985	0.08±0.04	3.70±1.50^{d}	2.43±0.61^{d}
16 Aug 1985	0.03±0.01	3.90±2.33^{e}	2.43±0.74^{e}

* Only one of the three samples survived centrifugation.

those that took 4–6 days to emerge. This distinction was made because of the marked difference between body sizes of early and late emerging adults from all riffles. Adult weights were compared among different riffles, each group (early versus late emergers) being analyzed separately using a one-way ANOVA. Comparisons of the body lengths of *B. tricaudatus* in the September samples were done using a one-way ANOVA for each sample date. Differences between groups for all ANOVAs were tested using a Student-Newman-Keuls multiple range test. Our study, like many field manipulations, involved pseudoreplication (Hurlbert 1984). Therefore, differences between riffles cannot be attributed strictly to treatment effects; the reader should use discretion in making such attributions.

Results

Chlorophyll *a* concentrations in water samples showed no significant differences between riffles on any sample date; the chlorophyll *a* concentrations were low (ca. 0.20 µg/L) and did not change appreciably between sample dates. Chlorophyll *a* concentrations of tile scrapings did not differ significantly between the three riffles on 6 June (before we shaded the experimental riffle) and 18 June; but thereafter, the control riffles were significantly ($p<0.01$) higher in chlorophyll *a* than the experimental riffle (Table 1). The control riffles were similar in chlorophyll *a* concentrations on all sample dates (Table 1).

Simulium and *B. tricaudatus* showed different responses to the manipulation. *Simulium* larvae were present from the beginning of the experiment and showed a slight tendency toward increased densities in the experimental riffle before emergence in late July (Table 2). However, this increase was statistically significant only on 2 July. During the remaining experimental period, *Simulium* did not appear to be affected by the reduction of algae in the experimental riffle (Table 2). Other macroinvertebrates whose densities did not appear to be affected by the algal reduction included *Asellus, Gammarus, Hyallela, Dugesia,* and the Chironomidae. *Baetis tricaudatus* nymphs did not appear in our samples until mid-June and their abundance did not differ among riffles until early July (Table 3). The lower numbers of *B. tricaudatus* in the experimental riffle continued from July through August (Table 3) when we terminated this part of the experiment. Moreover, gut contents of *B. tricaudatus* from the control riffles on 7 August included significant amounts of diatoms (>20% by area). In contrast, nymphs from the experimental riffle rarely contained diatoms in their guts; when present, diatoms never composed more than 5% of the gut contents.

In late July, both *Simulium* and *B. tricaudatus* were entering their emergence periods. Comparisons of adult dry weights of *Simulium* showed no differences among control and experimental riffles ($p>0.80$) (Table 4). However, *B. tricaudatus* adults from the control riffle were significantly larger than adults from the experimental riffle ($p<0.05$) (Table 4). Adult *B. tricaudatus* from the two control riffles did not differ significantly in size ($p>0.10$) (Table 4).

On 16 September, 11 days after we had removed half of the black plastic from the experimental riffle, chlorophyll *a* concentrations from the tile scrapings in the OEM were similar to chlorophyll *a* concentrations in the control rif-

TABLE 2. Mean number (and range) of *Simulium* in Surber samples from Kingsley Creek. Three 0.09-m^2 samples per riffle were taken on each date.

	Riffles			
Sample Date	Experimental	Opened Experimental	Lower Control	Upper Control
6 June 1985	116 (16–308)		29 (0–87)	134 (3–290)
18 June 1985	216 (74–495)		43 (10–73)	95 (74–118)
2 July 1985	200 (113–299)		55 (2–142)	41 (4–107)
23 July 1985	31 (0–53)		21 (14–26)	16 (6–37)
7 Aug 1985	13 (0–28)		45 (0–134)	64 (12–91)
16 Aug 1985	66 (34–128)		211 (70–467)	181 (71–315)
5 Sept 1985	29 (4–48)		33 (7–65)	138 (47–312)
16 Sept 1985	16 (0–45)	2 (0–4)	92 (20–138)	26 (5–67)
25 Sept 1985	32 (25–40)	13 (2–22)	28 (3–54)	37 (29–49)

fles (Table 5); chlorophyll *a* concentrations in the undisturbed shaded portion of the experimental riffle (EM) remained significantly lower than the other riffles. At this time, *B. tricaudatus* densities were significantly higher in the OEM than in the EM (Table 3) but body lengths of the nymphs were similar (Table 6). *Baetis tricaudatus* nymphs from the OEM and EM were significantly smaller ($p<0.01$) than those found in the control riffles.

Nine days later, on 25 September, the nymphs in the OEM were similar in size and density to those in the control riffles, and chlorophyll *a* concentrations were similar among the OEM and the two control riffles (Table 5). In the EM, the chlorophyll *a* concentrations and *B. tricaudatus* densities were significantly lower than in the OEM and control riffles ($p<0.05$) (Tables 3, 5). Also, *B. tricaudatus* body lengths were significantly smaller in the EM than in the other sections (Table 6).

Discussion

Several possible responses by macroinvertebrates could have resulted from the algal reduction in the experimental riffle. A species could increase, decrease or remain at the same population density in the experimental riffle. Also, changes in secondary production or the size of individuals could have occurred.

Simulium population densities in the different riffles did not appear to be strongly influenced by changes in the epilithic material. *Simulium* larvae probably rely primarily on loosely deposited or suspended materials (Chance and Craig 1986). Therefore reductions in epilithic algae in the experimental riffle should not affect *Simulium*.

Other macroinvertebrates that showed no response to the manipulation included *Asellus, Gammarus, Hyallela, Dugesia* and the Chironomidae. At least three different subfamilies of chironomids were represented but the numbers of each were insufficient to allow us to draw conclusions regarding individual reliance on algae. Although the other four genera could feed on fine particulate organic matter (FPOM), no study has determined their nutritional need for algae versus detritus. Most studies have shown that the amphipods and isopods feed on decaying leaves (usually by

TABLE 3. Mean number (and range) of *Baetis tricaudatus* in Surber samples from Kingsley Creek. Three 0.09-m^2 samples per riffle were taken on each date.

	Riffles			
Sample Date	Experimental	Opened Experimental	Lower Control	Upper Control
6 June 1985	0		0	0
18 June 1985	5 (4-6)		4 (3-6)	8 (6-11)
2 July 1985	26 (15-37)		108 (49-251)	161 (140-190)
23 July 1985	24 (3-45)		173 (136-224)	104 (45-201)
7 Aug 1985	5 (2-9)		36 (15-60)	150 (75-204)
16 Aug 1985	3 (1-7)		70 (42-94)	61 (35-94)
5 Sept 1985	1 (0-4)		25 (18-32)	29 (15-43)
16 Sept 1985	1 (0-3)	11 (2-18)	44 (19-69)	18 (11-22)
25 Sept 1985	2 (0-3)	35 (9-79)	65 (52-77)	24 (19-29)

scraping, not shredding) and shift to FPOM when leaves are not available (Anderson and Sedell 1979). Findlay et al. (1984) suggested that *Lirceus* (an isopod) could use bacteria associated with coarse particulate organic matter (CPOM) and FPOM but its ability to use algae was not compared. There is some question as to how efficiently amphipods can digest bacteria but their gut passage times are short (ca. 2 hr) suggesting that they may be "stripping" bacteria from the particulates (Anderson and Sedell 1979, Bärlocher 1985, Willoughby and Earnshaw 1982). If any of the above macroinvertebrates relied on living algae as a major source of energy, then our results should have demonstrated a change in population density or individual size differences corresponding with changes in the algal standing crop in the experimental section. Neither of these changes were evident within the confines of our experiment.

The only macroinvertebrate to show a decrease in population density within the shaded riffle was *B. tricaudatus*. This suggests that *B.*

TABLE 4. Dry weights (mean ±1 SE, mg) of adult *Simulium* and *B. tricaudatus* from Kingsley Creek, 23–30 July 1985; *n* shown in parentheses.

	Riffles		
	Experimental	Lower Control	Upper Control
Simulium	1.10±0.049 (44)	1.08±0.048 (44)	1.14±0.064 (25)
Baetis			
(Early in emergence period)	0.77±0.068 (23)	0.93±0.044 (21)	1.05±0.040 (35)
(Late in emergence period)	0.42±0.042 (16)	0.68±0.027 (20)	0.86±0.074 (23)

TABLE 5. Chlorophyll *a* values (mean ±1 SE, μg/cm^2) of epilithic material in Kingsley Creek, after half of the experimental riffle was opened on 5 September. Values with the same superscript letter did not differ significantly ($p>0.05$, ANOVA).

	Riffles			
Sample Date	Experimental	Opened Experimental	Lower Control	Upper Control
5 Sept 1985	0.19±0.11^{a}	0.15±0.06^{a}	2.49±0.92^{b}	1.89±0.73^{b}
16 Sept 1985	0.04±0.02	2.60±0.70^{c}	1.49±0.15^{c}	2.41±0.45^{c}
25 Sept 1985	0.07±0.03	2.21±0.82^{d}	2.31±0.46^{d}	2.89±1.04^{d}

tricaudatus must rely on algae as a major source of energy. Kohler (1984) demonstrated that *B. tricaudatus* spent more time in periphyton patches than in areas without periphyton, and the movement pattern within patches was highly systematic. This pattern ensured maximum energy gains from this food source. Wallace and Gurtz (1986) showed that *Baetis* densities and secondary production in a stream in a clear-cut drainage basin were 17.6 to 26.7 times the annual production in a reference stream in an undisturbed area; this higher production was attributed largely to a higher consumption of diatoms. In contrast, Shepard and Minshall (1984) tested the selection of fine-particulate foods by *B. tricaudatus* (by observing the location of nymphs offered different food types in the laboratory) and found no preference for detritus versus diatoms over a six-hour trial period; however, this period may not have been long enough to elicit a normal response. In our study, the movement of *B. tricaudatus* into the OEM within 11 days strongly suggests that algae are an important resource for this macroinvertebrate.

Besides causing changes in density, decreases in algal biomass could also cause changes in production or differences in body size. We did not attempt to measure production but we did compare adult body sizes of *Simulium* and *B. tricaudatus. Simulium* did not differ in size between riffles. Therefore, locating in the experimental riffle did not cost *Similium* anything in adult body size (e.g., fecundity).

Adult body sizes of *B. tricaudatus* were significantly smaller in the experimental riffle further demonstrating the importance of algae to this stream insect. Moreover, during the second part of this study, we observed an increase in the size of nymphs within the OEM over a three-week period that was significantly greater than any increase seen in the EM. Either smaller *B. tricaudatus* in the OEM grew to a size comparable to nymphs in the control riffles or larger nymphs moved into the OEM and excluded the smaller nymphs. We did not test for intraspecific competition between different size classes of *B. tricaudatus* and therefore we can not conclude which of the possibilities was operating.

TABLE 6. Body lengths (mean ±1 SE, mm) of *Baetis* nymphs from Kingsley Creek, after half of the experimental riffle was opened on 5 September; *n* shown in parentheses. Values with the same superscript letter did not differ significantly ($p>0.05$, ANOVA).

	Riffles			
Sample Date	Experimental	Opened Experimental	Lower Control	Upper Control
5 Sept 1985	3.5±0.32 (4)	—	4.4±0.82^{a} (52)	4.9±0.41^{a} (57)
16 Sept 1985	3.8±1.21^{b} (3)	4.1±0.17^{b} (29)	5.1±0.16^{c} (38)	4.8±0.20^{c} (29)
25 Sept 1985	4.0±0.25 (9)	5.3±0.14^{d} (63)	5.3±0.11^{d} (63)	5.3±0.13^{d} (63)

In conclusion, we have demonstrated that *B. tricaudatus* distributions and body size are sensitive to algal standing crop. Other macroinvertebrates (e.g., *Asellus, Gammarus, Hyallela, Dugesia* and at least some of the Chironomidae) do not appear to depend on algae to the same extent as *B. tricaudatus* and therefore were not affected by the reduction of epilithic algae. As a filter feeder, *Simulium* may not have been influenced by changes in epilithic algae (assuming no change in the composition of the stream seston).

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