TROPHIC RELATIONS AND FUNCTIONAL GROUP COMPOSITION OF BENTHIC INSECTS IN THREE COLD DESERT STREAMS

WILLIAM L. GAINES, COLBERT E. CUSHING, AND STAMFORD D. SMITH

ABSTRACT—The food habits of the aquatic insects from three cold desert streams were determined. Detritivores were the dominant organisms in all streams, amounting to 55, 65, and 63% of the insect taxa in Douglas Creek, Snively Springs, and Rattlesnake Springs, respectively. Collecting (gathering and filtering) was the major feeding strategy employed, and we inferred that detritus in the form of fine particulate organic matter is the major food source in small, headwater cold desert streams.

The only known studies of the trophic relations of aquatic insects in cold desert streams are those of Koslucher and Minshall (1973) who determined the food habits of several benthic invertebrates in Deep Creek, Idaho, and Cushing and Rader (1982) who analyzed the food of Callibaetis sp. (Baetidae: Ephemeroptera) in Rattlesnake Springs, Washington. Indeed, little is known concerning the higher trophic levels of these small spring-streams, although some information is available concerning the amount of allochthonous detritus available to organisms in them (Cushing and Wolf, 1982; Cushing, 1988).

Dietary data were obtained for the dominant taxa of the benthic communities of three lotic systems in eastern Washington as part of a comprehensive study of secondary production of cold desert spring-streams (Gaines, 1987). Similar information for the less abundant taxa was obtained from the literature (Merritt and Cummins, 1984). Subsequently, functional groups and trophic classifications were identified to assess the trophic organization of these streams. This paper presents the food habits of the benthic insects.

MATERIALS AND METHODS—Douglas Creek, Snively Springs, and Rattlesnake Springs were within the cold desert physiographic province in eastern Washington. Detailed descriptions are provided in Gaines (1987), Cushing (1988), and Cushing and Wolf (1984), respectively.

Douglas Creek was a spring fed stream draining an area of 530 km². Average discharge during the study period was 0.6 m³/s. The average width was 4.0 m and average depth was 31 cm during base flow. Riparian vegetation was dominated by water birch (Betula occidentalis) and peachleaf willow (Salix amygdaloides).

Snively Springs was a small spring-stream located on the U.S. Department of Energy's Hanford Site. It drained an area of approximately 40 km². Average discharge during the study period was 0.04 m³/s. The average width and depth of Snively Springs during base flow were 1.3 m and 10 cm, respectively. Riparian vegetation was dominated by cattails (Typha latifolia) along the upper and lower reaches, and willow (Salix sp.) and wild rose (Rosa sp.) along the midreaches. Watercress (Nasturtium officinale = Rorippa nasturtium-aquaticum) grew extensively within the spring-stream.

Rattlesnake Springs was a small spring-stream also located on the Hanford Site. It drained an area of 350 km² (Cushing et al., 1980). Average discharge during the study period was 0.05 m³/s. The average depth and width during base flow was 1.7 m and 5 cm, respectively. Riparian vegetation was
dominated by peachleaf willow. Watercress was the main in-stream autotroph, although primary productivity was dominated by periphyton from 1969 to 1970 (Cushing and Wolf, 1984).

Quantitative macroinvertebrate samples were taken monthly from each stream from July 1985 to June 1986 with Surber samplers (0.09 m², mesh size 350 μm) in Snively Springs and Rattlesnake Springs, and a Portable Invertebrate Box Sampler (0.1 m², mesh size 350 μm) in Douglas Creek. Insects were separated by sugar flotation (Anderson, 1959), sorted, and identified to the lowest possible taxon. Monthly samples of each taxon were removed for qualitative gut content analysis. The number of individuals in the subsamples varied depending upon their abundance in the monthly quantitative samples. The entire digestive tract was removed by microdissection (Cummins, 1973), and gut contents were mounted on slides and examined under a light microscope. Three food categories were identified: detritus, algae, animal tissue. Detritus was differentiated from algae by the presence or lack of chlorophyll; this was facilitated by performing the gut analyses on fresh specimens.

RESULTS AND DISCUSSION—The results of our qualitative dietary analysis provide data about the kinds of foods consumed by the benthic insects but does not provide data on the quantity or quality of the foods. We applied this analysis to the entire macrobenthic insect fauna in these three cold desert spring-streams to provide insights into functional group organization and to compare with predictions of the river continuum concept (Vannote et al., 1980). Our functional group designations agreed with those of Merritt and Cummins (1984).

Our data represent a single year span of time, and we made no attempt at determining monthly or seasonal variations because sample sizes were often too small. We did not observe any changes in the seasonal diets of these organisms.

Fifty-five percent of the 22 taxa in Douglas Creek were detritivores, 23% carnivores, and 23% herbivores (Table 1). Herbivores (49.8%) and detritivores (48.4%) were dominant in numbers, and detritivores were dominant in terms of biomass (57.1%; Table 2). However, the dominant organisms in terms of numbers and biomass was an herbivore, _Optioservus_ sp. (Coleoptera). _Baetis_ sp., a mayfly, was the second most abundant in number, and _Hydropsyche_ sp., a caddisfly, had the second highest biomass; both are detritivores.

In Snively Springs, 65% of the 14 taxa were detritivores, 29% carnivores, and 7% herbivores (Table 1). Detritivores were dominant in numbers (93.4%) and biomass (94.1%; Table 2). _Baetis_ sp. was the dominant individual in numbers, and Tipulidae had the greatest biomass; both are detritivores.

Sixty-three percent of the 19 taxa found in Rattlesnake Springs were detritivores, with 32% being carnivores and only 5% being herbivores (Table 1). As in Snively Springs, detritivores were dominant both in numbers (94.2%) and biomass (79.6%) in Rattlesnake Springs (Table 2). _Simulium_ sp. (Diptera), a detritivore, was the dominant taxon in both numbers and biomass at this site.

The river continuum concept provides a physical template for comparison of biological communities. Two important factors affecting the stream biota are the amount of sunlight reaching the substrate for primary production and the nature of the substrate. The heavy shading by riparian vegetation and watercress, and the unstable sand and silt substrate in Snively Springs and Rattlesnake Springs (Gaines, 1987), inhibit the production of a significant periphyton standing crop. Thus, according to the river continuum concept, few, if any, grazer-scrapers that rely on algae and periphyton for food would be expected; this was the case at both of these sites where grazer-scrapers were absent (Table 3).

Douglas Creek, however, was larger and shading from riparian vegetation
**TABLE 1**—Qualitative gut content analysis and functional group and trophic level classification.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Site¹</th>
<th>Gut content</th>
<th>Functional group</th>
<th>Trophic level</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Diptera</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Simulium</em> sp.</td>
<td>D(14), S(43), R(47)</td>
<td>Detritus</td>
<td>Collector-filterer</td>
<td>Detritivore</td>
</tr>
<tr>
<td><em>Brilla</em> flavifrons²</td>
<td>D</td>
<td>Detritus, some algae</td>
<td>Shredder</td>
<td>Detritivore</td>
</tr>
<tr>
<td><em>Chironomus</em> sp.</td>
<td>D(21), S(14), R(14)</td>
<td>Detritus, some algae</td>
<td>Collector-gatherer</td>
<td>Detritivore</td>
</tr>
<tr>
<td><em>Parametriocnemus</em> sp.</td>
<td>D(14)</td>
<td>Detritus, some algae</td>
<td>Collector-gatherer</td>
<td>Detritivore</td>
</tr>
<tr>
<td><em>Thienemannimyia</em> sp.²</td>
<td>D, S, R</td>
<td></td>
<td>Predator</td>
<td>Carnivore</td>
</tr>
<tr>
<td><em>Chaetocladius</em> sp.</td>
<td>D(10), S(7)</td>
<td>Detritus, some algae</td>
<td>Collector-gatherer</td>
<td>Detritivore</td>
</tr>
<tr>
<td><em>Polyphemus</em> sp.²</td>
<td>D, S, R</td>
<td>Detritus, some algae</td>
<td>Shredder</td>
<td>Herbivore</td>
</tr>
<tr>
<td><em>Heleniella</em> sp.</td>
<td>D(10), S(14), R(13)</td>
<td>Detritus, some algae</td>
<td>Collector-gatherer</td>
<td>Detritivore</td>
</tr>
<tr>
<td><em>Phaenospectra</em> sp.²</td>
<td>D</td>
<td></td>
<td>Scraping</td>
<td>Herbivore</td>
</tr>
<tr>
<td><em>Tabanidae</em>²</td>
<td>D, S, R</td>
<td></td>
<td>Predator</td>
<td>Carnivore</td>
</tr>
<tr>
<td><em>Tipulidae</em>²</td>
<td>D, S, R</td>
<td></td>
<td>Shredder</td>
<td>Detritivore</td>
</tr>
<tr>
<td><em>Empididae</em>²</td>
<td>D, S, R</td>
<td></td>
<td>Predator</td>
<td>Carnivore</td>
</tr>
<tr>
<td><em>Dixidae</em>²</td>
<td>S, R</td>
<td></td>
<td>Collector-gatherer</td>
<td>Detritivore</td>
</tr>
<tr>
<td>Misc. Chironomidae²</td>
<td>R</td>
<td></td>
<td>Collector-gatherer</td>
<td>Detritivore</td>
</tr>
<tr>
<td><strong>Trichoptera</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Leuctrotrichia</em> pictipes</td>
<td>D(17)</td>
<td>Algae, some detritus</td>
<td>Scraping</td>
<td>Herbivore</td>
</tr>
<tr>
<td><em>Hydropsyche</em> sp.</td>
<td>D(45)</td>
<td>Detritus</td>
<td>Collector-filterer</td>
<td>Detritivore</td>
</tr>
<tr>
<td><em>Cheumatopsyche</em> sp.</td>
<td>D(16), S(41), R(37)</td>
<td>Detritus</td>
<td>Collector-filterer</td>
<td>Detritivore</td>
</tr>
<tr>
<td><em>Limnephilus</em> sp.</td>
<td>R(8)</td>
<td>Detritus</td>
<td>Shredder</td>
<td>Detritivore</td>
</tr>
<tr>
<td><em>Parapsyche</em> sp.</td>
<td>R(7)</td>
<td>Detritus, animal tissue</td>
<td>Collector-filterer</td>
<td>Detritivore</td>
</tr>
<tr>
<td><strong>Coleoptera</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Optioservus</em> sp.</td>
<td>D(50)</td>
<td>Algae, some detritus</td>
<td>Scraping</td>
<td>Herbivore</td>
</tr>
<tr>
<td><em>Hydaticus</em> sp.²</td>
<td>R</td>
<td></td>
<td>Predator</td>
<td>Carnivore</td>
</tr>
<tr>
<td><em>Hydrophilidae</em>²</td>
<td>R</td>
<td></td>
<td>Predator</td>
<td>Carnivore</td>
</tr>
<tr>
<td><strong>Ephemeroptera</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Leuctrothoe</em> sp.</td>
<td>D(44)</td>
<td>Algae, some detritus</td>
<td>Scraping</td>
<td>Herbivore</td>
</tr>
<tr>
<td><em>Baeotis</em> sp.</td>
<td>D(51), S(36), R(36)</td>
<td>Detritus, some algae</td>
<td>Collector-gatherer</td>
<td>Detritivore</td>
</tr>
<tr>
<td><em>Paraleptophlebia</em> sp.</td>
<td>D(44), S(10)</td>
<td>Detritus, some algae</td>
<td>Collector-gatherer</td>
<td>Detritivore</td>
</tr>
<tr>
<td><em>Tricorythodes</em> sp.</td>
<td>D(7), R</td>
<td>Detritus, some algae</td>
<td>Collector-gatherer</td>
<td>Detritivore</td>
</tr>
<tr>
<td><strong>Odonata</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Argia</em> tibialis</td>
<td>D, S(11), R(42)</td>
<td>Animal tissue</td>
<td>Predator</td>
<td>Carnivore</td>
</tr>
<tr>
<td><strong>Plecoptera</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Isoperla</em> sp.</td>
<td>D(26)</td>
<td>Animal tissue</td>
<td>Predator</td>
<td>Carnivore</td>
</tr>
</tbody>
</table>

¹ D = Douglas Creek; S = Snively Springs; R = Rattlesnake Springs. Number of guts examined is given in parentheses.

² Classification based on Merritt and Cummins (1984).
TABLE 2—Annual mean density (no./m²) and biomass (mg dry weight/m²) of insects by trophic level. Percent composition is given in parentheses.

<table>
<thead>
<tr>
<th>Site</th>
<th>Trophic level</th>
<th>Density (no./m²)</th>
<th>Biomass (mg dry weight/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Douglas Creek</td>
<td>Herbivore</td>
<td>4,670 (49.8)</td>
<td>672.9 (38.3)</td>
</tr>
<tr>
<td></td>
<td>Detritivore</td>
<td>4,543 (48.4)</td>
<td>1,004.4 (57.1)</td>
</tr>
<tr>
<td></td>
<td>Carnivore</td>
<td>170 (1.8)</td>
<td>80.5 (4.6)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>9,383 (100.0)</td>
<td>1,757.8 (100.0)</td>
</tr>
<tr>
<td>Snively Springs</td>
<td>Herbivore</td>
<td>123 (3.7)</td>
<td>3.2 (0.4)</td>
</tr>
<tr>
<td></td>
<td>Detritivore</td>
<td>3,082 (93.4)</td>
<td>685.6 (94.1)</td>
</tr>
<tr>
<td></td>
<td>Carnivore</td>
<td>96 (2.9)</td>
<td>40.0 (5.5)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>3,301 (100.0)</td>
<td>728.8 (100.0)</td>
</tr>
<tr>
<td>Rattlesnake Springs</td>
<td>Herbivore</td>
<td>13 (0.3)</td>
<td>0.6 (0.1)</td>
</tr>
<tr>
<td></td>
<td>Detritivore</td>
<td>3,942 (94.2)</td>
<td>373.9 (79.6)</td>
</tr>
<tr>
<td></td>
<td>Carnivore</td>
<td>228 (5.5)</td>
<td>95.4 (20.3)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>4,183 (100.0)</td>
<td>469.9 (100.0)</td>
</tr>
</tbody>
</table>

and watercress affected a smaller portion of the stream cross-section. The substrate was rocky (Gaines, 1987) and provided habitat for algae and grazerscrapers that were an important functional group in Douglas Creek (Table 3).

The river continuum concept suggests that a significant proportion of shredders will be present when the riparian vegetation covers the stream and contributes large amounts of allochthonous detritus. However, shredders were scarce in any of the three streams studied (Table 3). Cushing and Wolf (1982) and Cushing (1988) found that the amount of allochthonous detritus entering Rat-

TABLE 3—Annual mean density (no./m²) and biomass (mg dry weight/m²) of insects by functional group. Percent composition is given in parentheses.

<table>
<thead>
<tr>
<th>Site</th>
<th>Functional group</th>
<th>Density (no./m²)</th>
<th>Biomass (mg dry weight/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Douglas Creek</td>
<td>Grazer-scraper</td>
<td>4,637 (49.4)</td>
<td>670.7 (38.2)</td>
</tr>
<tr>
<td></td>
<td>Collector (total)</td>
<td>4,494 (47.9)</td>
<td>917.9 (52.2)</td>
</tr>
<tr>
<td></td>
<td>Gatherer</td>
<td>3,852 (41.1)</td>
<td>389.1 (22.1)</td>
</tr>
<tr>
<td></td>
<td>Filterer</td>
<td>642 (6.8)</td>
<td>528.8 (30.1)</td>
</tr>
<tr>
<td></td>
<td>Shredder</td>
<td>82 (0.9)</td>
<td>86.1 (4.9)</td>
</tr>
<tr>
<td></td>
<td>Predator</td>
<td>170 (1.8)</td>
<td>83.1 (4.7)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>9,383 (100.0)</td>
<td>1,757.8 (100.0)</td>
</tr>
<tr>
<td>Snively Springs</td>
<td>Collector (total)</td>
<td>3,057 (92.6)</td>
<td>466.4 (64.0)</td>
</tr>
<tr>
<td></td>
<td>Gatherer</td>
<td>2,348 (71.1)</td>
<td>231.2 (31.7)</td>
</tr>
<tr>
<td></td>
<td>Filterer</td>
<td>709 (21.5)</td>
<td>235.2 (32.3)</td>
</tr>
<tr>
<td></td>
<td>Shredder</td>
<td>148 (4.5)</td>
<td>222.4 (30.5)</td>
</tr>
<tr>
<td></td>
<td>Predator</td>
<td>96 (2.9)</td>
<td>40.0 (5.5)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>3,301 (100.0)</td>
<td>728.8 (100.0)</td>
</tr>
<tr>
<td>Rattlesnake Springs</td>
<td>Collector (total)</td>
<td>3,887 (92.9)</td>
<td>349.0 (74.3)</td>
</tr>
<tr>
<td></td>
<td>Gatherer</td>
<td>1,960 (46.9)</td>
<td>61.3 (13.1)</td>
</tr>
<tr>
<td></td>
<td>Filterer</td>
<td>1,927 (46.1)</td>
<td>287.7 (61.2)</td>
</tr>
<tr>
<td></td>
<td>Shredder</td>
<td>68 (1.6)</td>
<td>25.5 (5.4)</td>
</tr>
<tr>
<td></td>
<td>Predator</td>
<td>228 (5.5)</td>
<td>95.4 (20.3)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>4,183 (100.0)</td>
<td>469.9 (100.0)</td>
</tr>
</tbody>
</table>
tlesnake and Snively springs to be relatively low and that the watercress is not used extensively as food, at least not until it becomes part of the detritus pool. These factors indicate a lack of food for shredders. Fisher and Gray (1983) found that shredders were virtually absent from Sycamore Creek, a Sonoran desert stream, as was their food source of coarse particulate organic matter. Koslucher and Minshall (1973) observed that allochthonous food sources were absent in the diets of the benthic insects in Deep Creek. There may be a relationship between the absence of shredder organisms and the fact that these desert streams are subjected to severe spates that affect both the standing crop of coarse particulate organic matter and the diversity of the biota.

Detritivores were dominant in all streams studied. This indicates the presence of a large source of fine detritus as a food source, most likely from decomposition of filamentous algae and watercress. Collecting (filtering and gathering) was the major feeding strategy used to obtain detritus, and collectors generally consume fine particulate organic matter (Merritt and Cummins, 1984). From these results, we infer that detritus in the form of fine particulate organic matter is the major food source of insects in small cold desert spring-streams.

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**LITERATURE CITED**


