

## Habitat selection by the stream mayfly *Paraleptophlebia guttata*

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**Abstract.** The causes and consequences of habitat distribution of larvae of the mayfly *Paraleptophlebia guttata* were analyzed in a 2nd-order stream in west-central Kentucky. Among macrohabitats, larvae were typically significantly more dense in runs and riffles than in pools. Densities were positively related to the percentage of coarse substrata in macrohabitats, but were not correlated with current velocity, predatory fish densities, or the quantity of fine particulate organic matter (food) in macrohabitats. This relationship between density and substratum coarseness was further evidenced in an in-situ colonization experiment in which larvae selected gravel and pebble substrata over sand. Among microhabitats, larvae were more abundant in leaf litter and in gravel/pebble than in silt/sand. Laboratory manipulations showed that predation rates by fish were significantly lower on mayflies in leaf litter and gravel than in fine substrata. The combined effects of substratum particle size and fish predation determine habitat distributions of larvae.

Larger larvae were more abundant in runs than in riffles, but larval growth rates in artificial stream channels were similar between current velocities simulating those in riffles and runs. These results, coupled with data from drift samples, suggest that larvae shifted macrohabitats with size. Size-related differences in macrohabitat use may reflect size-related changes in microhabitat use; larvae were significantly larger in leaf litter than in other microhabitats, and leaf litter amounts were greater in runs than in riffles.

**Key words:** *Paraleptophlebia guttata*, habitat distribution, larvae, substratum, fish predation, size.

Many environmental factors interact to affect the habitat distribution and abundance of lotic benthic macroinvertebrates. Often only a few factors, however, are primary determinants of distribution patterns, and the order of importance of these factors varies from species to species. These primary determinants include abiotic factors such as substratum type (e.g., Rabeni and Minshall 1977, Peckarsky 1991), substratum stability (e.g., Cobb and Flannagan 1990), current velocity (e.g., Edington 1968), pH (e.g., Willoughby and Mappin 1988), temperature (e.g., Vannote and Sweeney 1980), light (e.g., Hughes 1966), and food supply (e.g., Williams and Hynes 1973, Culp et al. 1983) as well as biotic factors such as predation (e.g., Hemphill and Cooper 1984, Schofield et al. 1988) and competition (e.g., Wiley 1981, Lancaster et al. 1988, Hemphill 1991). Spatial and/or temporal variation in these factors can create a mosaic of habitat patches (Pringle et al. 1988) of major consequence to the distribution of many organisms, and hence to stream community structure and dynamics. Because of this importance, dis-

tributional aspects of organisms are among the most intensively studied areas of benthic stream ecology (Minshall 1984).

Despite numerous studies documenting within-population interhabitat variation in benthic stream macroinvertebrates, few studies have addressed the consequences of such variation on growth and survival of larval stages (Feltmate et al. 1986, Holomuzki and Hoyle 1990). If growth rate and body size are affected through habitat use, then size distribution and life history aspects of the population, together with size-mediated biological interactions within the community, should also be affected. Thus, assessing individual size differences among habitats is important in developing an understanding of the population and community dynamics of macroinvertebrates.

In this paper, we document larval habitat and size distributions of the lotic mayfly *Paraleptophlebia guttata* (McDunnough) and examine substratum, current velocity, food supply, and fish predators as primary determinants of distribution. *Paraleptophlebia* nymphs are common benthic detritivores inhabiting small streams to large rivers (Pennak 1978, Edmunds 1984), but the habitat distributions of most species, including *P. guttata*, have not been detailed. We

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also present results from experiments that address the consequences of larval use of certain habitats. Because substratum and current greatly influence the microenvironmental conditions under which stream insects live (Minshall 1984), it follows that these factors may profoundly affect larval growth and survival. In accordance with the importance of these factors as fitness determinants, we assess the effects of current on growth and of substrate particle size on survival of *P. guttata* larvae.

### Study Site

We conducted the study during spring in 1989 and 1990 in Hart's Run, an ephemeral 2nd-order tributary of Wilson Creek in Bullitt County, Kentucky. The drainage basin of Hart's Run is primarily dolomitic limestone with a diverse hardwood forest and is within Bernheim Forest (37°50'N, 85°35'W), a nature preserve 50 km southeast of Louisville. Discharge in May during the study periods was about 0.07 m<sup>3</sup>/s but dropped to 0.02 m<sup>3</sup>/s by June. Dissolved oxygen remained at or above saturation levels ( $\geq 8$  ppm) during May and June. Springtime water temperatures ranged from 14 to 22°C. Flow generally ceases from early summer until late fall, and the stream becomes fragmented into a series of isolated pools of standing water.

Benthic algae are dominated by small *Synedra* spp. and *Achnanthes minutissima* in early spring (Stevenson et al. 1991), but *Cymbella* is predominant in early summer. Mayflies and chironomids are the most abundant macroinvertebrates, and *Paraleptophlebia guttata* is by far the most abundant mayfly in spring. Longear sunfish (*Lepomis megalotis*), green sunfish (*L. cyanellus*), and grass pickerel (*Esox americanus*) are the most abundant fish species, but overall fish densities are low ( $\sim 1$  per 10 m<sup>2</sup>) (Holomuzki and Stevenson 1992).

### Methods

#### Habitat distributions

Mayfly distributions were compared among macro- and microhabitats. Macrohabitats were pools, runs, and riffles and were differentiated by current regime and depositional features of the stream channel. Pools were sites with current velocities  $< 3$  cm/s and with considerable

silt accumulation, whereas riffles were sites with currents  $> 25$  cm/s and with stony bottoms. Sites with intermediate velocities were designated as runs. Microhabitats within macrohabitats were submerged clumps of leaf litter, and different substrate particle sizes (i.e., silt/sand, gravel, pebble, cobble; Cummins 1962).

We sampled mayflies on six dates during 31 May–23 June in 1989 and on four dates during 26 April–30 May in 1990. A box sampler, with open top and bottom (Holomuzki and Short 1988) and placed firmly on the stream bottom, was used to collect mayflies. All animals were removed with a dipnet (80  $\mu$ m mesh) from the enclosed substratum to a 3–6-cm depth and immediately preserved in 70% ethanol. We took 5–10 samples from each macrohabitat on each date, and attempted to sample a variety of microhabitats within each macrohabitat when feasible. Mayflies were separated from substrata by sugar flotation (Lind 1974) and hand sorting.

#### Determinants of habitat distributions

We compared current velocity, water temperature, fish density, substrate particle size, and food levels among macrohabitats to assess which factors were most influential in determining distributions of *P. guttata*. Current velocity, as measured by a Mead HP-302 meter, and water temperature were taken near the bottom (range 1–5 cm) in each macrohabitat. We seined and/or electroshocked macrohabitats to determine fish density and assemblage. The percentage composition of substrate particle sizes was visually estimated within 1-m wide belt transects and categorized as silt/sand, gravel (2–16 mm), pebble (16–64 mm), cobble (64–256 mm) and boulder ( $> 256$  mm).

To determine whether *P. guttata* showed a preference for a particular substratum, we conducted a colonization experiment and compared numbers of individuals among three substratum treatments. Twenty four aluminum trays, 30 cm  $\times$  22 cm and 3 cm deep, were filled with washed sand, or gravel, or pebbles ( $n = 8$  for each substratum treatment). Trays of different substratum were positioned randomly in a single run on 30 May and countersunk so that the tray contents were flush with the bottom substratum. By placing all trays in the same run, and hence under roughly the same flow velocity (15–20 cm/s), we attempted to separate the

individual effects of substratum, without the effects of current, on *P. guttata* distribution. Trays were removed from the stream after 6 d and all contents were preserved in 70% ethanol. Mayflies were separated from each substratum as described above.

*Paraleptophlebia* larvae are generally collector-gatherers, eating predominantly fine particulate organic matter (FPOM) <1 mm (Edmunds 1984). Thus, detritus comparisons were made to assess food levels between macrohabitats. We were interested not only in FPOM distribution among macrohabitats but also in the distribution of coarse particulate organic matter (CPOM), because the generation of FPOM from CPOM by shredding detritivores can apparently influence the distribution of collectors like *Paraleptophlebia* (Richardson and Neill 1991). Three substrate samples, each to a depth of 15 cm, were taken by a dredge within 1-m-wide belt transects in each macrohabitat on each sampling date in 1989. All animals and wood were removed from samples by sugar flotation in the laboratory. Samples were then wet sieved to sort detritus into CPOM (>2.0 mm) and FPOM (200  $\mu\text{m}$ –2 mm). The particulate organic matter was air-dried, then oven-dried (70°C), weighed, and expressed in g(dry mass)/m<sup>2</sup>.

#### *Size and survivorship*

We typically measured total length (TL), excluding caudal filaments, of 25 randomly selected individuals from each sample on all sample dates to compare size distributions among macro- and microhabitats. Because *Paraleptophlebia* larvae of some species are known to shift habitats with growth (Lehmkuhl and Anderson 1971), we also monitored the drift of *P. guttata* in runs and riffles to help explain any differential size distributions between habitats. Two to five drift traps (0.4-mm mesh) were placed at the downstream ends of both a run and an adjacent riffle for 24 h on each of the four sampling dates in 1990. Sizes of drifting and non-drifting individuals were compared within and between macrohabitats on each date.

To further explain any variation in sizes among macrohabitats and to assess the possible consequences of living in certain habitats, we tested the null hypothesis that current velocity had no effect on growth rates of larvae. Larvae were collected from a run on 20 May, and their

TL was measured to the nearest 0.1 mm in the laboratory. On 21 May, larvae were returned to the field and placed in enclosures in artificial stream channels. Water in the 30 vinyl gutters (each 3.05 m long, 0.1 m wide) used as channels was drawn from Hart's Run by a 1-hp pump through PVC pipe. Valves at the head of each channel regulated current velocity in the flow-through channels. Each channel contained one enclosure (each 15 cm long and 2.5 cm high) made from longitudinal sections of 5-cm-diameter PVC pipe. Nitex screening (0.4-mm mesh) was glued to the ends of enclosures, and water levels were kept just below the tops of enclosures to prevent escape by larvae. Each enclosure contained one larva and the same substratum and food level. The substratum was gravel (2 cm deep) and the food was 1 gm of naturally conditioned sycamore leaves (*Platanus occidentalis*) ground by a blender to 0.1–1 mm pieces ( $\sim 80\% < 0.5$  mm). Fifteen enclosures were placed in fast current and 15 in a slow current. Current velocities in the enclosures, as estimated by displacement of dyes, were 20 cm/s in fast treatments and 3 cm/s in slow treatments. These velocities corresponded to velocities of fast-flowing runs and slow-flowing pools, respectively, in Hart's Run. Shade screening, allowing 60% transmittance, was placed over all channels to simulate canopy conditions. After 10 d, larvae were removed from enclosures, preserved, and measured to the nearest 0.1 mm; growth was determined as the increase in TL during the experiment.

To further assess consequences of habitat use, we also tested the null hypothesis that survival of larvae from predatory sunfish attacks was independent of substrate particle size. We compared predation rates of sunfish on mayflies in the laboratory among three substratum treatments: leaf litter, sand, and gravel ( $\sim 10$  mm diameter). Thirty 38-L aquaria filled with dechlorinated tap water contained leaf litter, or sand, or gravel ( $n = 10$  for each treatment). Leaves were a mixture of sycamore and white oak (*Quercus alba*) collected from runs and pools in Hart's Run. The bottom of each aquarium was covered uniformly with a thin (1–2 cm) layer of substratum washed free of invertebrates. We stocked each aquarium with one green sunfish (6–12 cm standard length) collected from Hart's Run. Fish had been captured 2–3 wk earlier to allow acclimation to laboratory

TABLE 1. Comparison of mean ( $\pm 1$  SE) densities (numbers/m<sup>2</sup>) of *P. guttata* larvae in macrohabitats on sample dates in both years, and the ANOVA results, with *F*-values, using  $\log(x + 1)$  transformed densities. Numbers in parentheses are the number of samples collected from that macrohabitat; none were collected from pools in 1989.

Dates	Pool	Run	Riffle	<i>F</i>
1989				
31 May		327 $\pm$ 74 (9)	275 $\pm$ 34 (6)	0.09
1 June		199 $\pm$ 29 (8)	410 $\pm$ 69 (6)	10.56**
6 June		213 $\pm$ 50 (10)	405 $\pm$ 76 (6)	4.39*
8 June		171 $\pm$ 50 (9)	473 $\pm$ 141 (6)	3.30
17 June		9 $\pm$ 6 (9)	68 $\pm$ 15 (6)	22.56***
23 June		6 $\pm$ 6 (9)	36 $\pm$ 17 (6)	5.95*
1990				
26 April	68 $\pm$ 44 (6)	184 $\pm$ 69 (9)	174 $\pm$ 34 (5)	2.16
12 May	901 $\pm$ 276 (6)	1023 $\pm$ 116 (6)	742 $\pm$ 128 (6)	0.91
25 May	95 $\pm$ 47 (6)	326 $\pm$ 102 (7)	342 $\pm$ 98 (5)	5.61*
30 May	76 $\pm$ 47 (5)	319 $\pm$ 85 (8)	152 $\pm$ 67 (5)	3.02

\*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

conditions. We then placed 10 mature larvae in each aquarium. After 2 h, fish were removed from aquaria and surviving mayflies in each substratum treatment were counted. Aquaria were aerated and kept at  $20 \pm 1^\circ\text{C}$  in lighted conditions.

## Results

### Macro- and microhabitat distributions

Among macrohabitats, *P. guttata* was generally more dense in runs and riffles than in pools (Table 1). Densities in runs and riffles were similar until 1 June. Thereafter, densities were typically significantly greater in riffles than in runs, suggesting more larvae were emerging from runs than riffles. Most individuals emerged between 8 and 17 June, as indicated by the 85–95% reduction in densities over this period. Among microhabitats, larval densities were significantly greater in coarser substrates and leaf litter than in silt/sand in both years (ANOVA on  $\log(x + 1)$  transformed densities;  $p < 0.001$ , Fig. 1a).

### Determinants of habitat distributions

Differences in mayfly densities among macrohabitats were strongly associated with differences in substrate particle sizes. Particle sizes in pools, runs, and riffles were predominantly sand, gravel/pebble, and pebble/cobble, re-

spectively (Fig. 2a). Thus, higher densities of mayflies in runs and riffles were associated with a higher percentage of coarser substrata in these macrohabitats. This relationship was corroborated by the colonization experiment (Fig. 3a)

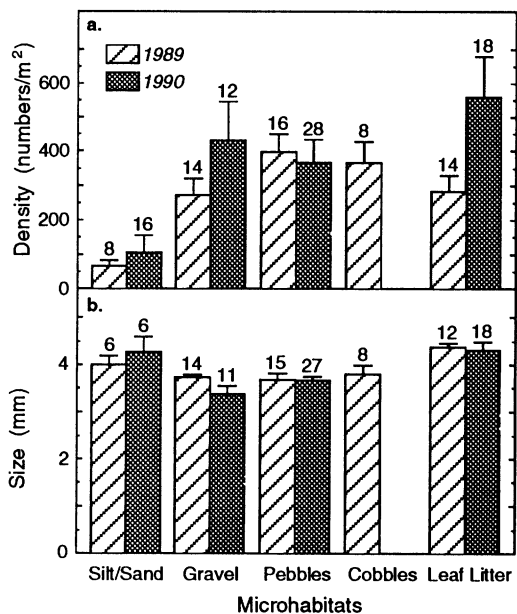


FIG. 1. Mean ( $\pm 1$  SE) densities (a) and sizes (TL) (b) of larvae in microhabitats in both years. Numbers over bars are the number of samples collected in microhabitats from which means were calculated; no samples were collected from cobbles in 1990.

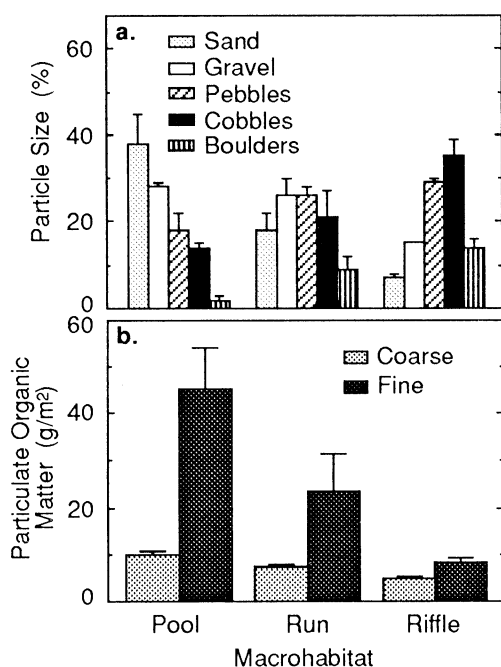


FIG. 2. Mean ( $\pm 1$  SE) percent composition of particle sizes (a) and amounts of coarse and fine POM (b) in macrohabitats. Replicates ( $n$ ) per macrohabitat were 4 for (a) and 7 for (b).

in which significantly more mayflies colonized trays with gravel and pebble substrata than trays with sand (ANOVA;  $p < 0.001$ ).

No other factors had an obvious effect on habitat distributions of larval *P. guttata*. Mayfly densities in macrohabitats were not significantly correlated with current velocity, fish densities, or FPOM (food) amounts (range  $r^2 = 0.004$ – $0.027$ ;  $p > 0.60$ ), despite differences in these factors among macrohabitats. Mean ( $\pm 1$  SE) current velocities were 2 (1) cm/s in pools, 13 (5) cm/s in runs, and 35 (6) cm/s in riffles. Fish densities were at least three times greater in pools ( $\sim 3$  per  $10 \text{ m}^2$ ) than in runs and riffles ( $\sim 1$  per  $10 \text{ m}^2$ ). Densities in pools were underestimated, however, because we could not seine or electroshock all fish from deeper areas. Further, food supply was unevenly distributed among macrohabitats (Fig. 2b) and unrelated to mayfly densities. Amounts of both FPOM and CPOM were significantly greater in pools than in riffles (ANOVA; FPOM:  $p < 0.01$ , CPOM:  $p < 0.001$ ). Lastly, temperature ( $\sim 20^\circ\text{C}$ ) and dissolved oxygen ( $\sim 8.5 \text{ mg/L}$ ) were uniform among macrohabitats on sampling dates.

#### Size and survivorship

Among macrohabitats, larvae were generally larger in runs and pools than in riffles (Table 2). When comparing the sizes of individuals within runs and riffles to the size distribution of individuals drifting from these macrohabitats, larger larvae were disproportionately represented in the drift, particularly in riffles (Fig. 4). Among microhabitats, larvae were significantly larger in leaf litter than in other microhabitats, except silt/sand (ANOVA on  $\log(x + 1)$  transformed densities; 1989:  $p < 0.01$ , 1990:  $p < 0.001$ ; Fig. 1b).

Current, as manipulated in artificial stream channels, did not affect larval growth (ANOVA on  $\log(x + 1)$  transformed data;  $p = 0.50$ ,  $n = 12$  for each treatment). Mean ( $\pm 1$  SE) increase in larval size (TL) was 0.95 (0.09) mm in the fast current and 0.86 (0.10) in the slow current. Substratum, however, as manipulated in aquaria, influenced risk of predation by sunfish (Fig. 3b). Percent survivorship of mayflies was significantly lower on sand than on leaf litter and gravel (ANOVA on arcsine transformed proportions,  $p < 0.001$ ). Survivorship was not significantly different in leaf and gravel substrata ( $p = 0.10$ ).

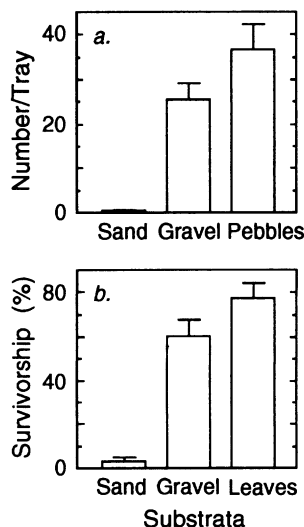


FIG. 3. Mean ( $\pm 1$  SE) number of colonizers of trays (a) and survivorship from green sunfish attacks in aquaria (b) containing different substrata (trays,  $n = 8$ ; aquaria,  $n = 10$ , for each substratum treatment).

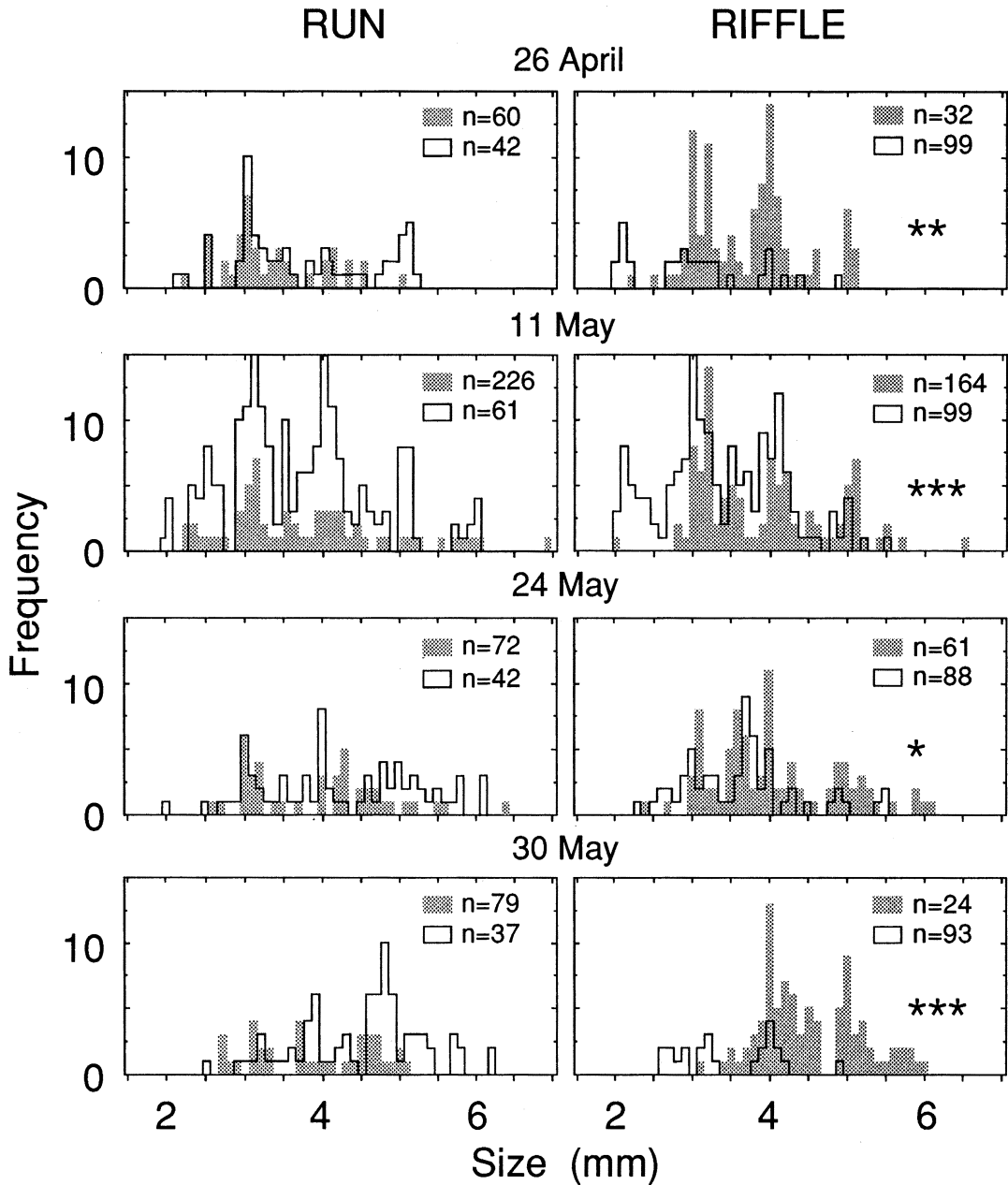


FIG. 4. Size (TL) frequencies (numbers) of drifting (stippled) and non-drifting larvae in runs and riffles on the four sample dates in 1990. Sample sizes are number of nymphs measured. Drifting and non-drifting size distributions within each macrohabitat on each sample date were statistically compared using Kolmogorov-Smirnov tests; significance at  $p = 0.05$ ,  $0.01$ , and  $0.001$  indicated by \*, \*\*, and \*\*\*, respectively. Drifting and non-drifting size distributions were not significantly different on all sample dates in runs.

TABLE 2. Comparison of grand means ( $\pm 1$  SE) of sizes (mm) of larvae in macrohabitats on sample dates in both years, and the ANOVA results, with  $F$ -values, using  $\log(x + 1)$  transformed sizes. Numbers in parentheses are the number of samples from which larval sizes were averaged. Usually 25 randomly selected individuals were measured per sample. No samples were taken from pools in 1989.

Dates	Pool	Run	Riffle	$F$
1989				
31 May		3.95 $\pm$ 0.08 (9)	3.47 $\pm$ 0.12 (5)	12.32**
1 June		4.09 $\pm$ 0.12 (8)	3.38 $\pm$ 0.12 (6)	16.33**
6 June		4.52 $\pm$ 0.09 (10)	3.52 $\pm$ 0.12 (6)	43.87***
8 June		4.14 $\pm$ 0.07 (6)	3.65 $\pm$ 0.14 (6)	4.91*
17 June		4.50 $\pm$ 0.50 (2)	3.90 $\pm$ 0.43 (6)	<sup>a</sup>
23 June		3.50 $\pm$ 0.00 (1)	4.78 $\pm$ 0.32 (4)	<sup>a</sup>
1990				
26 April	3.22 $\pm$ 0.34 (3)	3.56 $\pm$ 0.15 (7)	3.14 $\pm$ 0.20 (5)	1.42
12 May	4.70 $\pm$ 0.25 (6)	3.74 $\pm$ 0.10 (6)	3.36 $\pm$ 0.11 (6)	16.32*** <sup>b</sup>
25 May	4.48 $\pm$ 0.04 (3)	4.30 $\pm$ 0.24 (7)	3.60 $\pm$ 0.06 (5)	3.19
30 May	4.34 $\pm$ 0.00 (1)	4.57 $\pm$ 0.90 (7)	3.26 $\pm$ 0.20 (5)	<sup>a</sup>

\*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

<sup>a</sup> ANOVA not performed because of inadequate sample sizes.

<sup>b</sup> Tukey's hsd at  $p = 0.05$  is 0.63.

### Discussion

The distribution of *P. guttata* varied among macrohabitats and was determined largely by substratum type. Mayflies were generally more abundant in runs and riffles than in pools, and densities were positively related to the amount of coarser substrata in macrohabitats. This relationship between density and substratum coarseness was also evident in the colonization experiment. Few, if any, mayflies colonized trays with sand, in contrast to trays containing gravel or pebble.

The effects of substratum and current on distribution are frequently so closely intertwined in natural conditions that it is often difficult to separate the individual effects of the two on zoobenthos distribution (Minshall 1984). We could, to some extent, separate individual effects of these factors in the colonization experiment because all trays were at similar depths, in the same run, and thus roughly under the same current conditions. While different substrata are known to generate microzones with different hydraulic dynamics (Statzner et al. 1988), a preference for coarse versus fine substrata in this experiment, coupled with the non-significant correlation between distribution and current, suggest that substratum is more important than current velocity in determining distribution of *P. guttata* in Hart's Run.

Current seems to have some effect, however, on distribution as indicated by the drift of larger larvae from riffle to run macrohabitats. This ontogenetic shift in macrohabitat distribution may be a result of mature larvae requiring slower-flowing areas to successfully emerge. However, size-related changes in macrohabitat use may also reflect a divergence in uses of microhabitat or food as individuals increase in size. Indeed, larvae in Hart's Run tended to be larger in leaf packs than in other microhabitats, and there were more leaf packs in runs than in riffles. It is unclear, however, whether microhabitat preference changed with size or whether larvae grew faster in leaf litter than in other microhabitats. FPOM (food) may accumulate in leaf packs from CPOM breakdown as a result of shredder feeding activity and from FPOM transport (Short et al. 1980). Thus, leaf litter may provide *P. guttata* with a patch rich in food and favorable conditions for growth. Further research into the precise mechanisms causing size-related variation in macro- and microhabitat use is needed.

Substratum and current velocity are also important determinants of distribution for *P. heterona* in Mink Creek, Idaho (Minshall and Minshall 1977, Rabeni and Minshall 1977). Numbers of *P. heterona* increased in pools when coarse substrata were supplied (Minshall and Minshall 1977), and densities tended to be higher in sub-

strata ranging from 2.5–3.5 cm in diameter than in finer (sand) and larger (3.5–7.0 cm) substrata (Rabeni and Minshall 1977). Many benthic stream insects preferred particle sizes between 1.0–3.5 cm because detrital accumulation (food) tended to be higher in this size range than in smaller or larger particle size ranges, as reasoned by Rabeni and Minshall (1977). Indeed, detritus is a major determinant of distribution of many stream detritivores (Culp et al. 1983). However, we found that distribution of *P. guttata* among macrohabitats was not related to detrital distribution. Amounts of FPOM and CPOM were significantly higher in pools, which contained a high proportion of sand, than in other macrohabitats, and *P. guttata* distribution was not correlated with FPOM (food) distribution. These results suggest that food amount or quality is not limited in macrohabitats in Hart's Run and support Sweeney's (1984) notion that shortages of food seldom occur for detritivorous insects in streams.

If substratum and macrohabitat were not related to food distribution in Hart's Run, why did *P. guttata* apparently prefer coarser substrata? It seems that the coarser substrata provided mayflies with shelter from the current and refugia from predation. We predicted that mayflies in fast-flowing stream channels in the growth experiment would grow more slowly than those in slow-flowing conditions. Because *Paraleptophlebia* are generally rather poor swimmers (Edmunds 1984), we reasoned that fast current would decrease foraging efficiency, and hence growth rate. Instead, we found that growth rates of mayflies were similar in fast- and slow-flowing conditions. This result is likely because mayflies fed among the interstitial spaces of the gravel which provided shelter from the current. In nature, gravel and larger particle sizes likely also provide mayflies with shelter from mild scouring floods (Brown and Brussock 1991).

We also hypothesized that substratum particle size would influence mortality rates from predatory fish. We found that green sunfish ate significantly more mayflies on sand than in leaf litter and gravel. This result agrees with other studies that showed that larger substratum sizes were more effective than smaller ones at deterring predation and promoting coexistence of prey with fish predators in streams (Fraser and Cerri 1982, Gilliam et al. 1989, Holomuzki and

Hoyle 1990). Further, pools in Hart's Run contained more sand and silt than other macrohabitats, which suggests pools were more dangerous habitats than runs and riffles. Thus, lower densities in pools are probably from the combined effect of substratum and fish predation.

Our study illustrates how substratum, fish predation, and current interact to determine mayfly distribution and abundance. Considering that *Paraleptophlebia* are generally poor swimmers, it is interesting that *P. guttata* was usually more abundant in runs and riffles than in pools. Apparently, the cost of using pools with less protective substrata outweighs the benefits of lower current velocity and higher food density. The tendency to use leaf litter, particularly by larger larvae, may be a function of both protection from predators and presence of food (FPOM). Assessing actual costs and benefits incurred by macroinvertebrates using specific macro- and microhabitats will advance our understanding of the mechanisms that regulate benthic communities.

### Acknowledgements

We thank John Loring, Heather Sanders, Chris Grady, and Mont McQuinn for their assistance with field sampling and/or for sorting animals from substrata samples. Terry Short kindly did the particle size estimates in macrohabitats and helped with the sorting of particulate organic matter. Figures were prepared by Helen I'Anson. We thank Jan Stevenson for use of the artificial stream facilities at Bernheim Forest. We also appreciate the cooperation of the Isaac W. Bernheim Foundation for making the Bernheim Forest Nature Preserve available for study. This research was supported by a David and Betty Jones Faculty Development Grant and a Kentucky Research Enhancement Grant to JRH.

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*Received: 8 July 1992*

*Accepted: 7 February 1993*