Patterns of dispersion of aquatic insects colonizing artificial substrates in a southern Ontario stream

Jane E. Rutherford

Abstract: Modified artificial turf substrates were readily colonized by stream invertebrates, supporting 20 or more taxa after 10 or 22 days in the stream. Of the individuals present, 50–80% belonged to four taxa: Hydropsychidae, Hydroptila sp. (larvae and pupae), Rheotanytarsus sp., and Baetidae. All four taxa displayed significantly aggregated patterns of dispersion (as shown by Clark–Evans–Donnelly indices) on most of the 6 substrates. The hydropsychids and the Hydroptila sp. pupae appeared to have the highest degree of aggregation, especially at high densities; both taxa occupied about the same areas on the substrates, forming discrete bands of occupation at the upstream and downstream edges as well as along a narrow band near the middle of the substrates. Weakly positive (but generally nonsignificant) $\Phi_2$ values (intertaxon association indices based on presence–absence data) coupled with negative $I_a$ values (intertaxon association indices based on joint abundances) for the Hydropsychidae – Rheotanytarsus sp. and Hydroptila sp. – Rheotanytarsus sp. pairings indicate that Rheotanytarsus sp. occupies quite different areas of the substrates than either the hydropsychids or Hydroptila sp. pupae, suggesting that competition for space may be important amongst these sessile taxa.

Résumé : Des substrats de gazon artificiel modifiés installés dans un ruisseau ont été colonisés très rapidement par les invertébrés puisqu'on y a trouvé plus de 20 taxons après 10–22 jours. De 50 à 80% de la faune présente appartenait à quatre taxons: Hydropsychidae, Hydroptila sp. (larves et nymphes), Rheotanytarsus sp. et Baetidae. Les quatre taxons avaient une répartition significativement contagieuse (d'après les indices Clark–Evans–Donnelly) sur la plupart des six substrats. C'est chez les Hydropsychidae et chez les nymphes d'Hydroptila sp. que la contagion était le plus importante, particulièrement lorsque ces taxons avaient une forte densité; ces deux taxons occupaient à peu près la même surface sur les substrats et formaient des bandes discontinues le long de la bordure amont et de la bordure aval, de même que le long d'une bande étroite près du milieu des substrats. Des valeurs positives faibles (et généralement non significatives) de $\Phi_2$ (indices d'association entre les taxons, basés sur les données présence–absence) combinées à des valeurs négatives de $I_a$ (indices d'association entre les taxons, basés sur les abondances combinées) pour les Hydropsychidae – Rheotanytarsus sp. et Hydroptila sp. – Rheotanytarsus sp. indiquent que Rheotanytarsus sp. occupe sur les substrats des zones très différentes de celles occupées par les Hydropsychidae ou par les nymphes d'Hydroptila sp. et il peut donc y avoir une compétition importante pour l'espace entre ces deux taxons sessiles.

[Traduit par la Rédaction]

Introduction

Despite increasing urbanization and intensification of agriculture, many of the streams of southern Ontario continue to support communities of aquatic invertebrates. Riffle communities are often dominated by the net-spinning caddisflies (Trichoptera: Hydropsychidae and Philopotamidae) and many dipterans (especially the Chironomidae). Other important members of these communities include Baetidae, Ephemereellidae, and Heptageniidae (Ephemeroptera), riffle beetles (Coleoptera: Elmidae), and the amphipod Hyalella azteca (Saussure) (Talitridae). Hydropsychids are especially abundant in many of these streams, and several species of Hydropsyche Pictet and Cheumatopsyche Wallengren often coexist (Mackay 1978; Rutherford and Mackay 1986). Many of the taxa are sessile, constructing fixed retreats on the substrates. For example, hydropsychid, philopotamid, and Rheotanytarsus Bause (Chironomidae) larvae are filter feeders; larvae of each taxon build retreats incorporating filtering devices on the stream-bed substrates. Potentially, individuals of these taxa could compete with each other for the best locations for filtering. Other taxa are free-living throughout most of their larval life, but complete pupation within a fixed case. Larvae of the genus Hydroptila Dalman (Hydroptilidae: Trichoptera) are piercers (herbivores) and scrapers; the larvae are mobile but the pupae are sessile. Final-instar larvae attach their purselike cases firmly to the substrate and complete pupation inside. Individuals of all these taxa require a space on a stream-bed substrate for their own exclusive use, and consequently could potentially compete with one another for spatial resources.
In this study, I examined the microdistribution patterns of invertebrates on stream-bed substrates, with particular emphasis on the sessile taxa, to investigate their use of space. The irregularly shaped rocks and cobbles of the riffles of southern Ontario streams are often covered with filamentous algae and travertine deposits, making it difficult to accurately establish the original location of an individual after a rock is removed from the stream. In addition, the dark colour of the natural substrates makes the use of viewing boxes or buckets and photography difficult. Accordingly, I used flat artificial substrates intended to mimic as closely as possible the dimensions and texture of natural stream-bed substrates. Others have mapped the microdistribution of insects on tiles in laboratory streams (Eymann et al. 1987; Ciborowski and Craig 1989), on tiles or bedrock in streams (Lamberti and Resh 1983; Martin and Barton 1987), and on boulders and bedrock in western streams (McAuliffe 1984; Hemphill and Cooper 1983; Hemphill 1988). Elucidation of the microdistribution patterns of the co-occurring taxa on the substrates is a first step in studying the nature of the interactions between individuals and between taxa.

Methods and materials

Study site
Canagagigue Creek is a hard-water tributary of the Grand River, draining rich farmland in Waterloo County, southern Ontario; the study station is located about 1 km upstream of the confluence of the creek with the Grand River and has been described more fully previously (Rutherford and Hynes 1987). The stream at this station is third order, partly shaded by willows and other vegetation, and bordered on the northeastern side by semiwooded land, where a small (<20) herd of cattle is pastured. The cattle have free access to the stream. The stream width is about 5 m during the summer months; the range in maximum temperature is 20—24°C through July and August. Because of extensive clearing of the land in the headwaters of the drainage system, the creek is subject to intense spates following thunderstorms, and receives considerable enrichment via runoff from the bordering farms. Travertine deposits 0.2—1 cm thick accumulate on the riffle cobbles, and Cladophora Kuetzing (phylum Chlorophyta) grows profusely in early and late summer.

Sample collection
Six artificial substrates were placed in a riffle where current velocities (0.3—0.5 m/s at 0.6 of the depth), water depths (13—19 cm), and natural substrates varied little during normal summer-flow conditions. The substrates were 11 × 22 cm rectangular mats of artificial turf of the type typically used on patios and balconies. The relatively soft polypropylene fibres had been trimmed as close as possible to the synthetic rubber backing, leaving a stubble 1—2 mm high. The rough texture of the mats was intended to mimic the travertine and alga-covered surfaces of the natural substrates. The mats were clipped to chicken wire anchored flush to the syn-
dant taxa on each mat) of individuals in a single dimension was determined by drawing numbers from a container; the randomization procedure resulted in the mats in the grid being interspersed with respect to time. All mats were collected on August 22. This collection scheme avoided any confounding of the patterns of colonization due to differences in the timing of the life cycles of the biota involved (Shaw and Minshall 1980). Each mat was removed from the stream, placed in a dry basin, and treated immediately with Cytokool® (an aerosol topical anesthetic), freezing the invertebrates in place. Mats were labelled, bagged, and transported on ice to the laboratory where they were frozen at −10°C. Before examination, the mats were thawed and Kahle’s solution was applied liberally to the surface of each mat to preserve the individuals present.

To map the individuals, each mat was placed under an open colour-coded grid (6 × 16; approximate size of each opening 1.5 × 1.7 cm) and examined at low power under a Wild® M5 dissecting microscope. The location of each individual was marked on a map with the aid of the grid; each individual was preserved in 70% alcohol in its own numbered vial for later identification.

Aquatic insects were identified to genus whenever possible (using the keys of Merritt and Cummins 1984), although the poor condition of some of the specimens (attributable to the freezing and thawing involved in the preservation technique) hindered the identification of some of the smaller invertebrates. Generally, chironomids were not identified beyond tribe; however, the distinctive fixed case of Rheotanytarsus sp. aided identification of these specimens. No attempt was made to identify the water mites. Identification of hydropsychid species was made with aid of Mackay (1978) and Scheffer and Wiggins (1986). Other invertebrates were identified using Pennak (1989).

Dispersion maps of the four most abundant insect taxa (i.e., the sessile taxa Hydropsychidae, Hydropila sp. pupae, Rheotanytarsus sp. larvae, and the mobile Baetidae) were prepared using the original location map of each mat as a template; these maps were digitized using Thunderscan® (hardware and software) on a Macintosh Plus® computer. Distances (in millimetres) between conspecific nearest neighbours for all individuals of the four most abundant taxa were measured (using software).

Data analysis
Numbers of taxa and of individuals per taxon were tallied for each mat. Count data were transformed by Bartlett’s modified square-root transformation \( x' = \sqrt{x} + 0.5; \) Zar 1984). Thirteen comparisons of transformed counts were made between the 10-day and the 22-day mats; accordingly, the experimentwise Type I error rate was set at 5% \((a = 0.05)\), so the critical \( P \) value for each comparison was 0.004 \((P = 1 - 0.95^{13})\) where \( n \) is the number of comparisons; Sokal and Rohlf 1981).

The spatial distribution (for each of the four most abundant taxa on each mat) of individuals in a single dimension as defined by the direction of water flowing over the mats was assessed by dividing each mat into twenty-two 1-cm zones along the upstream—downstream axis. For each taxon, the individuals in each zone were tallied, and the data analyzed using a Kolmogorov—Smirnov goodness-of-fit test for
Fig. 1. Summary of preferred zones of occupation from the upstream to the downstream edges of mats (the arrow shows the direction of current flow). Bars represent the proportion of the mats that scored above the median number of individuals in each of 22 zones. (A) Hydropsychidae (5 mats). (B) Hydroptila sp. pupae (5 mats). (C) Rheotanytarsus sp. larvae (6 mats). (D) Baetidae (6 mats).

grouped and ordered data (Zar 1984). The null hypothesis is that individuals have an equal probability of occupying each of the 22 zones (i.e., expected frequencies per zone, f_i, are equal). Twenty-two such tests were performed; accordingly, the \( P \) value for rejection of the null hypothesis was set at 0.002 to preserve the experimentwise error rate of 5%. For each taxon on each mat, a zone occupied by more than the median number of individuals on that mat was scored as positive, other zones as negative. Positive scores for each zone were tallied over all mats for each taxon to indicate preferred areas of occupation; this information is presented in Fig. 1.

Examination of the 22 data sets of distance to conspecific nearest neighbours (i.e., where \( n > 5 \), very few hydropsychids or hydroptilids were found on mat 10-2) for each taxon and mat indicated that most (18 of 22) failed to conform to the assumptions of normality (Lilliefors test; Conover 1980). Accordingly, the data were transformed (\( \ln x \)); transformation improved conformation to the assumptions of normality for many of the data sets (16 of 22).

For each of the four most abundant taxa on the mats, the spatial pattern (in two-dimensional space) was assessed using the Clark–Evans Index of Dispersion as modified by Donnelly for edge effects and correlation arising from reflexive pairs (Clark and Evans 1954; Sinclair 1985). Because all individuals on a mat were used, problems associated with the random selection of individuals for measuring distance, or with the estimation of population densities from quadrats, were avoided (Clark and Evans 1979). The equations require the use of “observed” mean distances as well as the computation of “expected” mean distances, based on the density of individuals (of each taxon) on a mat. The observed mean nearest-neighbour distances were obtained by back-transforming the arithmetic mean of the transformed data (i.e., the antilog of the mean of the transformed data gives the geometric mean). Because 24 indices were calculated, the significance of each was tested at the \( P = 0.002 \) level to preserve an experimentwise Type I error rate of 5%. Indices of aggregation for the three sessile taxa on each mat were compared using a fixed-effects (duration of exposure, taxon) analysis of variance, treating mats as a nested variable of replication (Zar 1984; Wilkinson 1987).

The dispersion maps prepared for each of the four taxa on each mat were transferred to separate transparent sheets of acetate, using a pen of a different colour for each taxon. The colour-coded maps for each mat were then overlaid one upon the other (i.e., Hydropsychidae with Hydroptilidae, then Hydropsychidae with Rheotanytarsus sp., and so on). An additional acetate sheet ruled with a 11 \( \times \) 22 cm grid (each “block” measured 1 cm\(^2\), for a total of 242 blocks) was laid over each pairing of dispersion maps, taking care to align the outside borders of the maps and the grid. Each block was scored for the presence or absence of each taxon. These data were used in the following analyses.

First, the data were used to quantify the space occupied by each taxon on a mat. Because of the pairwise examination of each taxon with the other three co-occurring taxa on a mat, three separate counts of blocks occupied by at least one individual of that taxon were obtained for each mat. The small differences between counts arose because of slight discrepancies in aligning the colour-coded maps and the grid during each pairwise comparison. The average of the three counts (rounded up to the next integer) represents the space occupied by a taxon on a mat. The space occupied by a taxon was plotted against \( n \), the number of individuals of each taxon on each of the 6 mats. These plots were superimposed on a set of curves generated by calculating the number of blocks theoretically expected to be occupied by at least one individual (for a range of densities, 1–120, that is comparable to the actual densities on the mats) if individuals were dispersed randomly (represented by the Poisson distribution) or with increasing degree of aggregation (represented by negative binomial distributions where \( k \) was set to 2.0, 1.0, 0.5,
Table 1. Comparison of colonization patterns between 10- and 22-day mats: arithmetic means (\(\bar{x}\)) of raw data and means (\(\bar{x}'\)) and variances (\(s^2\)) of transformed data for counts of numbers of individuals per mat for the most abundant taxa.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>10-day mat</th>
<th>22-day mat</th>
<th>t test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(\bar{x})</td>
<td>(\bar{x}')</td>
<td>(s^2)</td>
</tr>
<tr>
<td>No. of taxa</td>
<td>19.0</td>
<td>4.41</td>
<td>0.087</td>
</tr>
<tr>
<td>No. of individuals</td>
<td>228.7</td>
<td>15.05</td>
<td>3.863</td>
</tr>
<tr>
<td>Hydropsychidae</td>
<td>32.0</td>
<td>5.17</td>
<td>8.650</td>
</tr>
<tr>
<td>Hydropsyche sp.</td>
<td>24.3</td>
<td>4.52</td>
<td>6.615</td>
</tr>
<tr>
<td>Cheumatopsyche sp.</td>
<td>7.7</td>
<td>2.61</td>
<td>2.015</td>
</tr>
<tr>
<td>Hydropsyche sp.*</td>
<td>27.0</td>
<td>5.03</td>
<td>3.345</td>
</tr>
<tr>
<td>Larvae</td>
<td>8.0</td>
<td>2.87</td>
<td>0.439</td>
</tr>
<tr>
<td>Pupae</td>
<td>19.0</td>
<td>4.17</td>
<td>3.153</td>
</tr>
<tr>
<td>Rheotanytarsus sp.</td>
<td>37.0</td>
<td>6.08</td>
<td>0.791</td>
</tr>
<tr>
<td>Baetidae</td>
<td>67.0</td>
<td>8.15</td>
<td>1.627</td>
</tr>
<tr>
<td>Hyallela azteca</td>
<td>6.3</td>
<td>2.58</td>
<td>0.232</td>
</tr>
<tr>
<td>Hydracarina</td>
<td>13.7</td>
<td>3.66</td>
<td>1.204</td>
</tr>
<tr>
<td>Physella sp.</td>
<td>16.3</td>
<td>4.10</td>
<td>0.034</td>
</tr>
</tbody>
</table>

*All individuals, i.e., includes larvae and pupae.*

\(t\) value used here are recommended by Zar (1974). Because 3 1 evaluations of association were made in total, each \(\chi^2\) value was tested at the \(P = 0.002\) level to preserve an experimentwise error rate of 5%.

and 0.1). (The parameter \(k\) can be used as an index of aggregation (Southwood 1978); the smaller its value, the more aggregated the dispersion pattern.) Comparing the plotted data with the theoretical curves is a way of indicating whether a taxon has a greater degree of aggregation at higher densities than at lower densities.

Secondly, the presence—absence data were used to evaluate intertaxon associations, using the \(\Phi_2\) index of association (Southwood 1978). Presence—absence data for each pair of taxa on each mat were arranged in two-way contingency tables so that the taxon heading the columns in the table was the most abundant taxon. The index, \(\Phi_2\), is defined as follows:

\[
\Phi_2 = \frac{f_{11}f_{22} - f_{12}f_{21}}{\sqrt{C_1C_2R_1R_2}}
\]

where \(f_{11}\) (cell frequency in row 1, column 1) represents the number of blocks in which both taxa were present, \(f_{12}\) is the number of blocks in which the first taxon (heading the rows of the table) was present, but the second taxon (heading the columns of the table) was absent, \(f_{21}\) is the number of blocks in which the first taxon is absent but the second taxon is present, and \(f_{22}\) is the number of blocks that lacked both taxa. \(C_1\) and \(C_2\) represent the column totals and \(R_1\) and \(R_2\) the row totals. The index ranges from +1 to −1, expressing both the strength and the direction of the association; the significance of the association can be assessed by the \(\chi^2\) value of the contingency table (Southwood 1978; Zar 1984). Debauche (1962) points out that the contingency table is the appropriate way to evaluate associations between taxa exhibiting nonrandom dispersion patterns. Both \(\Phi_2\) and the Cochrane-corrected \(\chi^2\) value used here are recommended by Zar (1974). Because 31 evaluations of association were made in total, each \(\chi^2\) value was tested at the \(P = 0.002\) level to preserve an experimentwise error rate of 5%.

A second index of association, \(I_{ai}\), was calculated. This index is based on Sorensen’s coefficient (Southwood 1978) and uses the overall abundances of the two taxa (\(A\) and \(B\)) of interest:

\[
I_{ai} = 2\left(\frac{J}{A + B} - 0.5\right)
\]

where \(J\) represents the total number of individuals of both taxa, \(A\) and \(B\), in samples (i.e., in this case, grid blocks) where they occur together, and \(A\) and \(B\) represent the number of individuals of the respective taxon in all samples (i.e., all 242 blocks). \(I_{ai}\) can range from +1 to −1. Calculating both indices is useful, since a contrast between a positive \(\Phi_2\) value and a negative \(I_{ai}\) value, for a particular taxon pair, would suggest competition between the taxa for the spatial resource.

Analyses were performed using a Macintosh Plus® computer, Microsoft Excel®, and SYSTAT® (Wilkinson 1987).

**Results**

**Colonization patterns**

The mats were readily colonized by aquatic invertebrates: 17–22 taxa and 177–368 individuals were present after a short time in the stream, and densities ranged from 0.73 to 1.52 individuals/cm². In total, 1704 individuals belonging to 31 distinct taxa were mapped and identified. Chironomidae (Diptera), Baetidae (Ephemeroptera), Hydropsychidae, and Hyroptilidae (Trichoptera) were the most abundant taxa, Coleoptera, other Ephemeroptera, and other Diptera were rare, and the stoneflies (Plecoptera) were completely absent. Together, the Hydropsychidae, *Hydropsyche* sp. (larvae and pupae), *Rheotanytarsus* sp. (Diptera: Chironomidae) and *Hydropsyche* sp., *Hydracarina* and *Physella* sp. constituted most of the remainder (79–92% of the totals). The Hydropsychidae included, in descending order of overall abundance, *Cheumatopsyche* sp., *Hydropsyche* sp., *Hydropsyche* sp. and *Hydropsyche* sp.
Fig. 2. Dispersion maps of the four most abundant taxa on the mats that supported the greatest number of individuals of the sessile taxa: among the 10-day mats, 10-3 (A), and among the 22-day mats, 22-1 (B). a, Hydropsychidae; b, Hydroptila sp. pupae; c, Rheotanytarsus sp. larvae; d, Baetidae.

Table 2. Patterns of occurrence of Hydropsychidae, Hydroptila sp. pupae, Rheotanytarsus sp., and Baetidae from the upstream to the downstream edge of a mat.

<table>
<thead>
<tr>
<th>Mat No.</th>
<th>Hydropsychidae</th>
<th>Hydroptila sp. pupae</th>
<th>Rheotanytarsus sp.</th>
<th>Baetidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>10-1</td>
<td>4.500</td>
<td>5.727</td>
<td>6.364</td>
<td>7.818</td>
</tr>
<tr>
<td>10-2</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>7.636</td>
</tr>
<tr>
<td>10-3</td>
<td>10.364</td>
<td>5.091</td>
<td>6.364</td>
<td>9.727</td>
</tr>
<tr>
<td>22-1</td>
<td>17.818*</td>
<td>21.500*</td>
<td>2.727</td>
<td>2.909</td>
</tr>
<tr>
<td>22-2</td>
<td>21.136*</td>
<td>4.318</td>
<td>3.182</td>
<td>2.727</td>
</tr>
</tbody>
</table>

Note: Based on a (Kolmogorov–Smirnov analysis for ordered and grouped data; *, maximum $d_i >$ critical $d_{max}$, $P < 0.002$. Note that mat 10-2 had only 3 Hydropsychidae and 4 Hydroptila sp. and the statistic was not calculated.

psche betteni Ross, H. sparna Ross, H. bronta Ross, H. morosa Hagen, and H. slossonae Banks. The Baetidae included species of both Baetis Leach and Pseudocloeon Klapalek. Only one of the comparisons of abundance (Table 1) between 10- and 22-day mats revealed a significant difference: there were more H. azteca on the 22-day mats. The other comparisons suggest the following trends: more individuals in total, more Cheumatopsyche sp. and Hydroptila sp. larvae and pupae, and fewer Rheotanytarsus sp. on the 22-day mats than on the 10-day mats (comparisons where $0.004 < P \leq 0.05$; Table 1).

Dispersion patterns

One-dimensional dispersion

Analysis of the distribution of the individuals of the four most abundant taxa from the upstream to the downstream edge of a mat showed that only the hydropsychid larvae and Hydroptila pupae had a non-uniform pattern of dispersion (Table 2). These two taxa had a strong tendency to be aggregated at the upstream and downstream edges as well as along a narrow band near the middle (Figs. 1A, 1B). Aggregation with respect to the direction of current flow was not
Fig. 3. The number of blocks on 6 mats occupied by at least one individual of the four most abundant taxa compared with expected values generated by assuming either a random dispersion pattern (Poisson distribution) or an increasing degree of aggregation (negative binomial distributions where \( k = 2, 0.5, \) and 0), for a range of densities (1–120 per mat). The lines represent the theoretical expectations and the symbols the observed values for the taxa studied.

Table 3. Clark–Evans–Donnelly indices of dispersion for Hydropsychidae (larvae), Hydroptila sp. (pupae), Rheotanytarsus sp. (larvae), and Baetidae colonizing mats.

<table>
<thead>
<tr>
<th>Mat No.</th>
<th>Hydropsychidae</th>
<th>Hydroptila pupae</th>
<th>Rheotanytarsus larvae</th>
<th>Baetidae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Index</td>
<td>P</td>
<td>n</td>
<td>Index</td>
</tr>
<tr>
<td>10-1</td>
<td>0.807</td>
<td>0.0410</td>
<td>37</td>
<td>0.502</td>
</tr>
<tr>
<td>10-2</td>
<td>1.384</td>
<td>0.2660</td>
<td>3</td>
<td>1.385</td>
</tr>
<tr>
<td>10-3</td>
<td>0.695</td>
<td>0.0002</td>
<td>56</td>
<td>0.892</td>
</tr>
<tr>
<td>22-1</td>
<td>0.554</td>
<td>0.0001</td>
<td>79</td>
<td>0.639</td>
</tr>
<tr>
<td>22-2</td>
<td>0.539</td>
<td>0.0001</td>
<td>43</td>
<td>0.745</td>
</tr>
<tr>
<td>22-3</td>
<td>0.572</td>
<td>0.0001</td>
<td>70</td>
<td>0.610</td>
</tr>
</tbody>
</table>

Note: Significant P values are in boldface type where P < 0.002; the experimentwise Type I error rate is 5%.

Table 4. Summary of comparisons of degree of aggregation amongst sessile taxa on the 10- and 22-day mats.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Sum of squares</th>
<th>df</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taxon</td>
<td>0.029</td>
<td>2</td>
<td>0.014</td>
<td>0.121</td>
<td>0.889</td>
</tr>
<tr>
<td>Duration (of exposure)</td>
<td>0.183</td>
<td>1</td>
<td>0.183</td>
<td>1.550</td>
<td>0.281</td>
</tr>
<tr>
<td>Mat</td>
<td>0.471</td>
<td>4</td>
<td>0.118</td>
<td>3.807</td>
<td>0.051</td>
</tr>
<tr>
<td>10-day mat</td>
<td>0.455</td>
<td>2</td>
<td>0.227</td>
<td>7.347</td>
<td>0.015*</td>
</tr>
<tr>
<td>22-day mat</td>
<td>0.017</td>
<td>2</td>
<td>0.008</td>
<td>0.268</td>
<td>0.772</td>
</tr>
<tr>
<td>Taxon \times duration</td>
<td>0.175</td>
<td>2</td>
<td>0.087</td>
<td>0.742</td>
<td>0.532</td>
</tr>
<tr>
<td>Error</td>
<td>0.248</td>
<td>8</td>
<td>0.031</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*P < 0.05.

Table 3. Clark–Evans–Donnelly indices of dispersion for Hydropsychidae (larvae), Hydroptila sp. (pupae), Rheotanytarsus sp. (larvae), and Baetidae colonizing mats.

Table 4. Summary of comparisons of degree of aggregation amongst sessile taxa on the 10- and 22-day mats.

Source of variation | Sum of squares | df | Mean square | F   | P     |
---------------------|----------------|----|-------------|-----|-------|
| Taxon               | 0.029          | 2  | 0.014       | 0.121 | 0.889 |
| Duration (of exposure) | 0.183       | 1  | 0.183       | 1.550 | 0.281 |
| Mat                 | 0.471          | 4  | 0.118       | 3.807 | 0.051 |
| 10-day mat          | 0.455          | 2  | 0.227       | 7.347 | 0.015* |
| 22-day mat          | 0.017          | 2  | 0.008       | 0.268 | 0.772 |
| Taxon \times duration | 0.175       | 2  | 0.087       | 0.742 | 0.532 |
| Error               | 0.248          | 8  | 0.031       |       |       |

*P < 0.05.
attributable to taxon ($F = 0.121, P = 0.889$) or duration of colonization period ($F = 1.550, P = 0.281$); however, there was significant variation amongst the 10-day mats ($F = 7.347, P = 0.015$), which contributed to the high (but not quite significant) level of variability seen in the nested variable (mats, $F = 3.807, P = 0.051$) (Table 4). On 4 of the mats (10-3, 22-1, 22-2, and 22-3), the index calculated for Hydropsychidae was less than those for the other sessile taxa (Table 3).

Plots of the space occupied by each taxon as it varied with number of individuals show that at densities <40/mat, the observed data and the theoretical curves generated by assuming either random dispersion (Poisson distribution) or aggregated dispersion (negative binomial distributions with $k > 0.5$) are indistinguishable (Fig. 3). However, at higher densities (>40/mat), 5 of the points for hydroptilids and hydropsychids plot lower than 4 of the theoretical curves, lying below the expected values generated by the Poisson distribution or by negative binomial distributions defined by $k$ values ranging from 0.5 to 2. The points for the hydropsychids are the lowest of those for the four taxa examined. Only the negative binomial curve generated by assuming $k = 0.1$ (extremely aggregated) lies below the observed values for all taxa.

### Intertaxon association

On 2 of the mats (10-1 and 22-1), significantly positive (i.e., $P < 0.002$) $I_s$ values (based on presence–absence data) were found for an association between Hydropsychidae and Hydroporia sp. pupae (Table 5), and on a third mat, a positive association was strongly suggested (mat 22-3, $I_s = +0.1948, P < 0.005$). On 1 of these mats (22-1), a significant positive association was also found between Hydroptila sp. pupae and Rheotanytarsus sp. larvae (Table 5, Fig. 2B). Baetids were positively associated with Rheotanytarsus sp. on mat 10-3, and a positive association with Hydropsychidae was strongly suggested for mat 22-3 ($I_s = +0.1919, P < 0.005$) (Table 5). There were no significant negative associations when presence–absence data were used.

By contrast, intertaxon association indices based on the abundances of the taxa in grid blocks where they occurred together were often negative, even for the Hydropsychidae — Hydroptila sp. pupae pairing (Table 5). Most of the very negative associations (i.e., $I_s < -0.6$) involved Hydropsychidae and Rheotanytarsus sp. (4 of 5 values), Hydroptila sp. pupae and Rheotanytarsus sp (3 of 5 values), and Hydroptila sp. pupae and Baetidae (4 of 5 values) (Table 5).

### Discussion

#### Colonization patterns

The taxa colonizing the mats in this study are typical inhabitants of streams in Waterloo County and Wellington County, Ontario, where agricultural practices have caused summer warming and moderate enrichment of the originally cool streams; similar assemblages of aquatic invertebrates have been found in nearby streams (Godbout 1979; Boyko 1991).
would not have been sampled by means of the mats used in this study. The colonization periods used here (10 and 22 days) may not have been long enough to achieve a stable macroinvertebrate community; other studies have demonstrated changes in both taxon number and numbers of individuals after much longer periods (Ulfsstrand et al. 1974; Williams and Hynes 1977; Shaw and Minshall 1980). However, others have found 8 to 21 days adequate for full colonization of either artificial substrates (Ulfsstrand 1968) or natural rock substrates (disturbed by brushing; Boulton et al. 1988). Generally, all have found the initial colonization to be rapid, with about one-half the final number of taxa present after 1 or 2 days, especially in summer. The increase in the total number of individuals present between the 10- and 22-day mats is not have been long enough to achieve a stable macroinvertebrate community; other studies have demonstrated changes in various taxa of aquatic insects: Baetis rhodani (Pictet) (Ephemeroptera: Baetidae) (Bohle 1978), Simuliidae (Diptera) (Ciborowski and Craig 1989), Helicopsyche borealis Hagen (Trichoptera: Helicopsychedae) (Lamberti and Resh 1983), Leucotrichia Mosely (Trichoptera: Hydropylidae) (McAluliffe 1984), Glossosoma nigroid Banks (Trichoptera: Glossosoma- tidae) (Hart 1985), Neophasys fuscus Banks (Trichoptera: Uenoiidae) (Martin and Barton 1987), and Cheumatopsyche sp. (Trichoptera: Hydropsychidae) (Glass and Bovbjerg 1969). These taxa include sessile filter feeders (black flies and net-spinning caddisflies) and slow-moving scrapers and shredders (other caddisflies), as well as more active forms (B. rhodani).

In this study, all three sessile taxa (hydropsychids, Hydroptila sp. pupae, and Rheotanytarsus sp. larvae) as well as the mobile Baetidae displayed aggregated dispersion patterns. Of the sessile taxa, the hydropsychids had the greatest degree of aggregation, as shown by the low values of the Clark–Evans–Donnelly indices (Table 3), and by the fewer than expected blocks occupied at high densities (Fig. 3). By these criteria, Hydroptila sp. pupae had the next highest degree of aggregation. Examination of the one-dimensional dispersion pattern indicated that only the hydropsychids and the Hydroptila sp. pupae had a detectable tendency to aggregate in particular zones of the mats. Moreover, the zones of occupation by hydropsychids and Hydroptila sp. pupae were approximately the same, the upstream and downstream edges and a narrow midsection zone being favoured (Figs. 1A, 1B).

The co-occurrence of hydropsychids and Hydroptila sp. pupae is confirmed by the results of the intertaxon association analysis. The positive \( \Phi_2 \) values (2 of 5 significant) indicate that hydropsychids and Hydroptila sp. pupae often occupied approximately the same areas on the mats. The \( I_{ai} \) index was negative for 4 of the 5 possible pairings of hydropsychids and Hydroptila sp., although only one of the pairings was strongly negative (i.e., \( < -0.6 \)) (Table 5). This suggests that there may be some competition for the spatial resource between these taxa. In contrast, the low \( \Phi_2 \) values (only 1 of 10 was significantly positive) and strongly negative \( I_{ai} \) indices (7 of 10 \( < -0.6 \)) for the Rheotanytarsus sp. – hydropsyched and Rheotanytarsus sp. – Hydroptila sp. pairings indicate that Rheotanytarsus sp. occupied quite different areas of the mats than the two caddisflies (Table 5, Figs. 1 and 2).

The location of the hydropsychids on the mats in this study may be related to microhabitat requirements for their filter-feeding mode of life. In general, numerous workers have shown that hydropsychids prefer moss-covered substrates in shallow (about 10 cm), fast-flowing water (e.g., Sprules 1947; Tanaka 1968; Williams and Hynes 1973). In a series of laboratory experiments to determine net-spinning activity at different temperatures and velocities, Fuller and Mackay (1980) used artificial turf substrates similar to those used in this study. At summer temperatures (20°C), net construction by fourth- and fifth-instar larvae was enhanced by faster currents. In addition, at the highest velocity tested (about 40 cm/s at a point 1 cm above the substrate), they
found that velocities were significantly faster at the upstream edges than at the downstream edges (by 1.5 cm/s) of the substrates. Nowell and Jumars (1984) demonstrated that boundary-layer effects change downstream from an edge. Fuller et al. (1983) found that nets of hydropsychids that were directly downstream of other nets had one-third to one-quarter of the particles. It appears that the hydropsychid larvae in this study sought the areas on the mats where current velocities and particle delivery would have been enhanced, producing the rather discrete bands or zones of occupation. Fuller et al. (1983) found that nets of hydropsychids that were directly downstream of other nets had one-third to one-quarter of the particles. Chance and Craig (1986) showed that the regular spacing of larvae in rows induced beneficial flow patterns between neighbours. The presence of the Hydropila sp. pupae in the same general areas of the mats as the hydropsychids perhaps reflects a need for the same sort of current regimes, not for feeding but to prevent silt deposition, which would decrease levels of oxygen for the developing adults.

This study indicates that the three sessile taxa used the spatial resource available to them in different ways. The two taxa that were actively feeding and may be supposed to have been competing for similar sites for retreat and net construction, i.e., the hydropsychids and Rheotanytarsus sp. larvae, did not in fact overlap spatially at the fine scale that I examined. Whether this separation in space represents competition (nonoverlapping realized niches) or simply different microhabitat requirements (nonoverlapping fundamental niches) can only be answered by a manipulative study. However, it is known that hydropsychid larvae will interact with one another using both stridulation and directed aggression (Glass and Bovbjerg 1969), and other studies have documented aggressive territorial behaviour in hydropsychids (Jansson and Vuoristo 1979; Hildrew and Edington 1979; Boon 1984). In a study of the relative abundances of two filter feeders in a small stream, Hemphill and Cooper (1983) concluded that the simulids were opportunistic, quickly occupying new space, but that the hydropsychids were superior competitors. Hemphill (1988) demonstrated that Hydropsyche oslari Banks (Trichoptera: Hydropsychidae) aggressively preempted space that would have been occupied by Simulium virgaum Coquillet (Diptera: Simuliidae) had the hydropsychids not been present. Similarly, in this study, Rheotanytarsus sp. larvae seemed to colonize the mats first, only to become relatively less abundant later. Direct interference by hydropsychid larvae as well as the development of Cladophora may have influenced the microdistribution of Rheotanytarsus sp. larvae.

The aggregated patterns of dispersion displayed by the Baetidae on the mats (3 of 6 were significant) probably result from quite different processes than those proposed for the sessile taxa. Baetids are generally collector–gatherers or scrapers (Merritt and Cummins 1984), have a demonstrated preference for the top surfaces of substrates (Kohler 1983), and are adapted for active swimming and drifting (Elliott 1968). Corkum (1978) found that Baetis vagans McDunnough (Ephemeroptera: Baetidae) nymphs never interacted with each other, and were continuously leaving the substrate to enter the water column. In this study, as the mats were being removed from the water, many of the foraging nymphs that had been present may well have been swept away. However, in Kohler’s (1983) study, where similar sorts of substrates were used to determine positioning of mayfly nymphs (largely Baetidae), loss of animals was less than 5% when the substrates were removed from the water. It is interesting to note that of the positive associations noted here for Baetidae, two were with the hydropsychids and two with Rheotanytarsus sp. No positive association was found between Baetidae and Hydropila sp. pupae. Bohle (1978) found that local aggregations of B. rhodani nymphs occurred where food concentrations were high. In a separate study, Bohle (1983) found that B. rhodani larvae fed on the upwuchs that developed on the fixed cases and upper body surfaces of the caddisfly Drusus discolor (Rambur) (Trichoptera: Limnephilidae); as a result, the baetids appeared to be aggregated near the caddisfly larvae. The aggregations of baetid larvae in this study, and their tendency to congregate near hydropsychids and Rheotanytarsus sp. larvae on the mats, may have been a response to the presence of food resources rather than the other organisms. The baetids may have simply been taking advantage of the material carried by microcurrents created by the retreats and filtering devices of Rheotanytarsus sp. and the hydropsychids.

The high densities of macroinvertebrates on the mats, coupled with the patterns of aggregation and intertaxon association noted for the dominant taxa in this study, suggest that competition for space may be an important factor governing the microdistribution of these insects, at least during certain phases of their life cycle. Manipulative experiments, in which potential competitors are removed from the substrates, are required to further elucidate the interactions between the major sessile taxa present in Canagagigue Creek.

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References


Boon, P.J. 1984. Habitat exploitation by larvae of


