

Spatial and temporal abundance, substrate partitioning and species co-occurrence in a guild of Neotropical blackflies (Diptera: Simuliidae)

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Abstract

Blackfly larvae were sampled monthly from two small Neotropical mountain streams 500 m apart from each other in northern Venezuela during a 15-month period, and ten habitat variables were measured at two altitudes (800 and 900 m) to determine local spatial and temporal variations in abundance, stream variables, species co-occurrence, and substrate preference within the blackfly guild. The blackfly species composition of each stream was the same, with five species (in order of abundance): *Simulium ochraceum* Walker s.l., *S. paynei* Vargas, *S. metallicum* Bellardi cytospecies E, *Simulium* sp., and *S. horacioi* Okazawa & Onishi. There were clear differences in community structure between streams (not among altitudes), although *S. ochraceum* s.l. was the most abundant species in both habitats. Principal component and correlation analyses revealed that structural (great depth, width, flow, and discharge) and chemical (low conductivity) factors were the stream variables best associated to the spatial distribution of most blackfly species. Blackfly abundance was greater in the larger stream. Larvae were most abundant on submerged rocks and fallen leaves, although the patterns of substrate use within the guild revealed substrate partitioning among most blackfly species. There was one general annual peak of abundance at the end of the rainy season. We suggest that blackfly community structure in these Neotropical headwaters streams, over the small spatial scale examined here, is largely influenced by interactions among stream size and velocity-related factors (width, streamflow, discharge and substrate availability-stability) and the rainfall regime.

Introduction

Blackflies (Diptera: Simuliidae) often are dominant members and important detritivores of lotic ecosystems (Cummins, 1987). Most studies on population dynamics and community structure in blackflies have been confined to the temperate regions (Adler & Kim, 1984; Shipp & Procnier, 1986; Corkum & Currie, 1987; Pistrang & Burger, 1988; Ciborowski & Adler, 1990; McCreadie & Colbo, 1991, 1992; McCreadie et al., 1995), and comparable studies on Neotropical blackflies are limited to a few studies in Guatemala (Okazawa & Takahashi, 1981), Brazil (Hamada, 1993), and Venezuela (Grillet et al., 1995).

The following variables are known to influence the population dynamics and community structure of

blackflies in the temperate regions (Ross & Merritt, 1987): physicochemical variables (e.g., Pistrang & Burger, 1988; McCreadie & Colbo, 1992), physical characteristics of streams (e.g., Ciborowski & Adler, 1990; McCreadie et al., 1995), land use and riparian vegetation (e.g., Corkum, 1990; Brewin et al., 1995), and biotic interactions (Hart, 1987). These studies show that variations in abundance and community structure of blackfly can occur over several scales (regional: among different water bodies; local: different altitudes or stream sections along one stream; and single-space: different microhabitats within a stream section; *sensu* Wiens 1989), and that different ecological factors can be important depending on the scale of the study. Therefore, an adequate understanding of the factors influencing blackfly assemblages should be

reached at each level in the scale (Boulton & Lake, 1992; Downes et al., 1993).

The intimate association between lotic organisms life history traits and spatial heterogeneity degree have recently conferred ecological importance at the small scale level (e.g., stream reach, Poff & Ward, 1990; Downes et al., 1993; Scarbrook & Townsend, 1993), since lotic ecosystems are highly variable and heterogeneous environments (e.g., Resh et al., 1988). As an example, significant differences producing changes in the species (morphospecies and/or cytospecies) composition, abundance and habitat use (particularly substrate), over distances within stream sections as short as 100 m have been observed in temperate blackfly communities (e.g., Colbo, 1985; Adler, 1987; McCreddie & Colbo, 1992; Timm, 1994). These patterns have been mainly related to local differences in habitat quality and structure. Consequently, habitat is partitioned along the stream sections where several blackfly species occur. Toward an understanding of the organization of Neotropical blackfly communities, we aimed to examine the existence of those patterns as well as their associated ecological factors within and between neighbouring streams that are located in the same biogeographical region, to minimize the influence of historical or chance events on the local composition of the communities. As Wiens (1989) suggested, finer-scale studies may reveal details about mechanisms underlying broader ecological patterns.

In this work, we study the immature blackfly assemblages of two neighbouring Neotropical streams at two different altitudes (800 and 900 m) with the following objectives: (i) to characterise ecologically the aquatic habitats (physicochemical factors, structural characteristics, and substrate) of the simuliid species encountered, (ii) to compare within (two altitudes) and between-stream variations in blackfly composition and community structure in relation to the observed variations in the aquatic habitats, (iii) to examine substrate preference and species co-occurrence within the blackfly guild, and (iv) to determine phenological changes in blackfly assemblages related to temporal changes in habitat factors.

Methods

Study area

The study was carried out in two permanent first-order mountain streams (Stream I and Stream II) in Altamira

(10° 00' N, 67° 47' W, 800–900 m altitude), Carabobo State, northern Venezuela as part of a larger project on the ecological characterisation of the main vector of onchocerciasis in that area (Grillet et al., 1995). The vegetation of the surrounding catchment is a combination of lowland wet forest, semi-deciduous forest and land cleared for agriculture. Mean annual temperature is 24 °C and total rainfall 1100 mm. There is a rainy season from May to October and a dry season from November to April (Ewel et al., 1976).

The two streams are approximately 500 m apart with moderate slopes along their routes, and their beds are composed predominantly of rock and gravel. Two sampling stations at altitudes 800 and 900 m were selected to provide comparable stations within each stream. Riparian vegetation along Stream I was relatively undisturbed, with a canopy dominated by native, deciduous trees, whereas in Stream II, the vegetation was dominated by cultivated fruit trees and coffee shrubs that formed a partial canopy. Stream II was closer to the village of Altamira than Stream I.

The general characteristics of the two streams were described previously by Grillet et al. (1995) and they can be summarised as follows. The streams consisted of alternating pools and riffles of clear, slightly alkaline water (pH rarely exceeding 8.0), with a mean conductivity about 300 $\mu\text{mhos cm}^{-1}$. The mean water temperature was 21 °C, and the concentration of dissolved oxygen was near saturation (8 mg l⁻¹). The average widths of Streams I and II were 67.4 and 42.3 cm, respectively, and the mean depth at normal flow conditions, 4.9 and 2.5 cm, respectively. Flow was low and highly variable, with an average discharge of $5.55 \times 10^3 \text{ cm}^3 \text{ s}^{-1}$ and $1.77 \times 10^3 \text{ cm}^3 \text{ s}^{-1}$ in Streams I and II, respectively. The rocky substrate predominated in both streams and elevations. Overall, Stream I was significantly wider, deeper, with larger discharge, denser tree canopy cover, greater annual streamflow permanency, and lower conductivity and temperature than Stream II.

Sampling

Blackfly larvae and pupae were sampled monthly with a 0.25 m² quadrat from the riffles of the streams from July 1990 to September 1991, to cover in excess a complete annual hydrological cycle. The sampling interval was similar to the duration of the life cycle of the species on which exist such information (*S. ochraceum* s.l.: 14–31 days, and *S. metallicum* s.l.: 28–31 days; Dalmat, 1955). Eight to ten monthly samples were tak-

en at each station, commencing downstream to minimise disturbance. Larvae of all instars were removed with forceps from the surface of natural substrates within the quadrat, blotted on paper, and preserved in 80% ethanol for future identification and counting. Mature pupae were collected and placed on moist paper to allow for the emergence of adults. Four substrate types predominated in these streams: rocks, fallen leaves and twigs, and roots. Rocky substrates were sampled *in situ* carefully, disturbing as little as possible, scraping, brushing and removing all attached blackfly larvae from this substrate. Vegetal substrates (leaf litter, twigs, roots) were placed in labelled plastic bags and kept on ice for transportation to the field laboratory, where the larvae and pupae were removed, counted and identified.

Environmental variables

Ten physical and chemical stream variables (width, depth, surface current velocity, discharge, temperature, pH, dissolved oxygen, conductivity, canopy cover and substrate type) were studied on the basis of previous reports in the literature about their significance in determining the distribution of immature stages of blackflies (Ross & Merritt, 1987). All these variables were measured (3 replicates) for each collection event at each sampling site. Stream width and depth measurements were made with a meter stick. Because the streams are shallow with irregular topography, the current velocity (cm s^{-1}) was estimated by recording the time required for a small piece of cork to travel 100 cm. Discharge was determined on the basis of depth, width and mean current velocity readings taken at three points across the stream (Newbury, 1984). Water temperature, conductivity, dissolved oxygen and pH were determined with portable apparatus. Percentages of both canopy and substrate cover (rocks, leaf litter, roots, and twigs) within each sampling quadrat were estimated by the same person to ensure consistency.

Data analyses

Blackfly abundance and environmental variables

The percentage of occurrence was calculated as the proportion of samples where a species was located. Blackfly density between two sampling stations or streams were compared by Mann-Whitney tests. A multivariate approach, Principal Component Analysis (PCA), helped elucidate spatial and temporal pat-

terns in the community and environmental data. This analysis is recommended when the community variation, mainly species-abundance changes, is within a narrow environmental range (Ter Braak & Prentice, 1988). Similarly, since many of the stream variables were correlated, the PCA was used to summarise them into a smaller number of statistically independent principal components. Following PCA, the relationships among stream variables, species occurrence (excepting the rarest species) and scores of derived environmental components (principal components) were determined by Pearson correlation analysis. Two-tailed *t*-tests were used to compare means of stream variables between two sampling stations or streams. Stream variables not showing symmetrical distributions were transformed using the \log_{10} transformation (width, depth, current velocity, discharge and conductivity) or the angular transformation (canopy cover) prior to the analysis.

Substrate partitioning

The degree of microhabitat or substrate partitioning among simuliid species was determined in several ways. First, we used X^2 to test the null hypothesis that each species used the substrate types in proportion to their occurrence in the habitat. Second, the overlap in substrate utilisation between any two species (*i* and *j*) was estimated by the proportional similarity index (Whittaker, 1975):

$$PS_{ij} = \sum_{k=1}^n \min(p_{ik}, p_{jk}),$$

where PS_{ij} is the proportional similarity in substrate use between species *i* and *j*, p_{ik} is the proportion of the species *i* on a particular substrate (*k*), p_{jk} is the proportion of the species *j* on a particular substrate (*k*) and *n* is the total number of substrate types. Thus, when $PS_{ij} = 1$, it indicates perfect overlap for two species, and, when $PS_{ij} = 0$, it indicates no overlap. Finally, an additional analysis on the original data matrix based on the standardized residual analysis of contingency tables (Bulla & Solano, unpublished; modified from Haberman, 1973; Legendre & Legendre, 1983) was used to explore in greater detail the patterns of substrate utilisation among blackfly species, producing: (i) a total niche overlap index among the set of blackfly species, (ii) an index of differential resource use for each species, and (iii) an index of resource differentiation. The index of total niche overlap for the guild of blackfly is the value of the X^2 statistics, calculated from a contingency table (species \times substrates)

measuring the departure from the null hypothesis of independence, and its transformation to Cramer's V index (Bulla & Solano, unpublished). The index of differential resource use of a species is the standardised departure of the observed frequency from its expected frequency for every resource, or residuals (Bulla & Solano, unpublished):

$$D_i = O_{ik} - E_{ik}/E_{ik},$$

where O_{ik} is the observed value and E_{ik} the expected value of abundance of species i on the substrate k . D_i is calculated for each resource type, and it is a relative measurement of the departure from the mean profile of resource use in the guild being analysed. A large positive value of D_i on a particular substrate is expected when species i is more frequent on this substrate than the average for the rest of the species. On the contrary, a large negative value of D_i occurs when species i is less abundant on a substrate that is commonly used by the rest of the species. This measurement has an approximately normal Z distribution provided that the sample size is large enough (Bulla & Solano, unpublished). The arithmetic mean of the absolute values of D per species, \bar{D}_i , is a global measurement of differential resource use by each species. The measure of resource differentiation is the mean value of the residuals (\bar{R}) per resource type (substrate) across species. Large values of the latter index show which substrate was differentially used by one or more species (Bulla & Solano, unpublished).

Co-occurrence of blackfly species

Species associations and co-occurrence among blackfly species were investigated with 2×2 contingency table analysis using presence-absence data, and X^2 tests for pairs of $(N(N-1)/2)$ species (Pielou, 1977), along with Fisher's exact tests and Cramer's values (V) of association. Non-parametric correlation analysis (Spearman) were also calculated.

Species identification

Blackfly larvae and pupae were identified following morphological descriptions (Ramírez-Pérez, 1983). We did cytological analyses only on *Simulium metallicum* cytospecies E (Grillet et al., 1995). One species could not be identified and is referred as *Simulium* sp. Voucher specimens were deposited in the British Museum of Natural History, and in the Entomological

Table 1. Results of Principal Component (PC) and Pearson Correlation analyses between stream variables and derived principal components (* $P < 0.01$; $n = 60$)

Variables	PC	
	PC1	PC2
Depth (cm)	0.86*	0.12
Width (cm)	0.85*	-0.27
Current velocity (cm s ⁻¹)	0.72*	-0.16
Discharge (cm ³ s ⁻¹)	0.96*	-0.13
pH	0.13	-0.14
Conductivity ($\mu\text{s cm}^{-1}$ at 21°C)	-0.70*	0.04
Dissolved oxygen (mg l ⁻¹)	0.02	0.82*
Temperature (°C)	-0.22	-0.83*
Canopy cover (%)	0.30	0.58*
% Variance explained	39.9	20.6
Proportion cumulative	39.9	60.5

Table 2. Results of Pearson Correlation analyses between species abundances and stream sites conditions. (* $P < 0.01$; $n = 60$)

Species	Principal components (PC)	
	PC1	PC2
<i>S. ochraceum</i>	0.70*	0.09
<i>S. paynei</i>	0.51*	-0.13
<i>S. metallicum</i>	0.26	-0.18
<i>Simulium</i> sp.	0.73*	-0.07

Museum at Universidad Central de Venezuela, Caracas, Venezuela.

Results

Blackfly species composition, habitat, abundance and spatial patterns

Both streams had the same composition of Simuliidae species or species complexes: *Simulium ochraceum* s.l. Walker, *S. paynei* Vargas, *S. metallicum* s.l. Bellardi (specifically *S. metallicum* cytospecies E), *Simulium* sp. and *S. horacioi* Okazawa & Onishi. The first two Principal Components (PC) calculated on the physicochemical and structural variables of the streams, explained 60.5% of the total variance (Table 1). The inclusion of substrate types did not improve the percentage of variance explained. The first PC was a linear combination with high loads on the structural variables describing the streams (depth, width, current, and dis-

charge), and water conductivity. Samples with high PC 1 scores corresponded to the larger Stream I with the lowest water conductivity level. Samples also resulted ordered seasonally along PC1, with the rainy season samples of each stream getting the highest scores. PC2 was a linear combination with high loads on low water temperature, high dissolved oxygen, and canopy cover (Table 1), corresponding to sites within Stream I. Therefore, PC2 seems to be related to stream exposition. Together, PC1 and PC2 helped to separate most samples from Stream I and II, stressing the environmental and structural differences between them.

Pearson correlation analyses between PC1 and the density of each blackfly species were positively significant, with the exception of *S. metallicum* cytospecies E (Table 2). Most blackfly larvae were associated with widest, deepest, fastest and with lowest conductivity reaches in the streams. Blackfly density was not significantly correlated with PC2.

Blackfly density was greater in Stream I than in Stream II (Mann-Whitney test, $U = 17\,444$; $Z = -4.8$; $P < 0.05$), and although it seems to be a larger density at higher altitudes within streams (Table 3), there were no significant differences between them ($U = 22\,707$; $Z = -0.8$; $P > 0.05$). We evaluated the interaction stream \times altitude graphically (not shown), concluding that the response in blackfly density did not differentially change (data in Table 3). *Simulium ochraceum* s.l. was the most abundant and widely distributed taxon, occurring at every sampling station, with the largest density in Stream I ($U = 285.5$; $Z = -2.4$; $P < 0.05$). *Simulium paynei* was the second most abundant species, occurring at both streams and altitudes, and although seems reach a slightly larger density in Stream I, this was not significant ($U = 322$; $Z = -1.9$; $P > 0.05$). *Simulium metallicum* cytospecies E follows in abundance, occurring mostly in Stream II ($U = 274.5$; $Z = -2.6$; $P < 0.05$; Table 3). *Simulium* sp. occurred mainly in Stream I ($U = 187.5$; $Z = -3.9$; $P < 0.05$), whereas *S. horacioi* was relatively rare in both streams.

Previous analyses on the differences in habitat variables between these streams revealed that Stream I is structurally larger, with a lower water conductivity than Stream II (Grillet et al., 1995). Within-stream comparisons reveal that the 900 m altitude station in Stream I was deeper (Student's $t = -2.9$; $P < 0.05$), with a larger canopy cover ($t = -8.5$; $P < 0.05$), and lower water conductivity ($t = 10.4$; $P < 0.05$) than the station at 800 m altitude. For Stream II, the station at 900 m altitude had a sparser canopy cover ($t = -4.5$; $P < 0.05$), with

higher water temperature ($t = -3.8$; $P < 0.05$), and less dissolved oxygen ($t = 2.7$; $P < 0.05$) than at 800 m altitude. The composition of submerged substrates (rocks, leaves, roots, and twigs) within and between streams was essentially the same, with a dominance of rocks, followed by leaves, roots, and twigs (Table 4).

Substrate partitioning and species co-occurrence

The null hypothesis stating that blackfly species were distributed in proportion to substrate availability (Table 4), was rejected for every species (*S. ochraceum* s.l., $X^2 = 193.2$; *S. paynei*, $X^2 = 11.29$; *S. metallicum* cytospecies E, $X^2 = 88.5$; *Simulium* sp., $X^2 = 171.1$; and *S. horacioi*, $X^2 = 125.4$; $df = 3$, $P < 0.05$). Immatures were collected mainly from the two most abundant and similarly distributed substrates between both streams and altitudes (submerged rocks and fallen leaves, Table 4). Total niche overlap among species (79%; $X^2 = 3616.94$, $df = 12$, $P < 0.05$) and proportional similarity between most species pairs (Table 5) were high. *Simulium ochraceum* s.l. was found on every substrate, but used comparatively more submerged roots than most species (Table 6). *Simulium paynei* showed a positive, significant D value on rocks indicating that larvae of this species were collected on this substrate more frequently than expected in relation to the occupancy of all species on the same substrate (Table 6). Larvae of *S. metallicum* cytospecies E and *Simulium* sp. used leaves and twigs, and roots and leaves, respectively, in a larger proportion than expected for the guild. *Simulium horacioi* showed small residuals across all substrate types, except for leaves. The analysis of resource differentiation (\bar{R}) showed that submerged roots (*S. ochraceum* s.l., *Simulium* sp.) and leaves (*S. metallicum* cytospecies E, *Simulium* sp., and *S. horacioi*) were the substrates most differentially used by the species within this guild. Rocks were mainly discriminated by *S. paynei*, but otherwise were utilised by most species (Table 6). Thus, despite the relatively high overlap observed in substrate occupancy, there were niche differences among species, which agrees well with the values of overlap in substrate use (Table 5). The highest overlap was observed between species using preferentially roots (*S. ochraceum* s.l. and *Simulium* sp.) and leaves (*S. metallicum* cytospecies E, *S. horacioi*, and *Simulium* sp.), whereas the lowest overlap occurred between *S. paynei* and each of the other species.

Every analysis of co-occurrence between pairs of species resulted in the rejection of the null hypothesis

Table 3. Mean density (larvae per m²; $\bar{X} \pm$ SE) and relative abundance (%) of blackflies in two streams in Altamira, Venezuela.

Species	Stream				Relative abundance (%)
	I		II		
	Altitude: 800	900	800	900	
<i>S. ochraceum</i>	80.8 + 12.0	71.1 + 4.9	38.3 + 3.9	53.1 + 6.4	62.6
<i>S. paynei</i>	9.4 + 2.9	25.8 + 4.5	13.1 + 4.5	12.0 + 3.2	15.6
<i>S. metallicum</i>	3.0 + 0.6	2.8 + 0.7	17.5 + 2.5	24.6 + 5.8	12.2
<i>Simulium</i> sp.	10.3 + 1.4	20.5 + 1.7	0.6 + 0.1	2.6 + 0.3	8.8
<i>S. horacioi</i>	0.3 + 0.0	2.5 + 0.4	0.8 + 0.2	1.3 + 0.5	1.2
TOTAL	103.8 + 2.6	123.1 + 7.6	69.5 + 7.2	93.6 + 10.2	100

Table 4. Relative and overall percentage of each substrate type, and relative larval abundance (%) of five blackfly species per substrate type in the two streams and altitudes of Altamira, Venezuela.

Stream/altitude	Substrate types			
	Rocks	Leaves	Roots	Twigs
I/800 m	79	16	3	2
I/900 m	82	14	3	2
II/800 m	86	12	0	1
II/900 m	82	14	2	2
Total substrate	82	14	2	2
Species				
<i>S. ochraceum</i>	50.3	28.4	20.9	3.0
<i>S. paynei</i>	93.2	3.6	3.1	1.0
<i>S. metallicum</i>	48.9	47.1	2.3	1.7
<i>Simulium</i> sp.	40.9	42.2	16.4	0.0
<i>S. horacioi</i>	43.2	53.0	3.4	0.0

Table 5. Proportional similarity (PS_{ij}) of substrate usage between pairs of blackfly species in two streams of Altamira, Venezuela.

Species	Species number				
	1	2	3	4	5
1. <i>S. ochraceum</i>	–				
2. <i>S. paynei</i>	0.56*	–			
3. <i>S. metallicum</i>	0.78*	0.53*	–		
4. <i>Simulium</i> sp.	0.99*	0.47	0.90*	–	
5. <i>S. horacioi</i>	0.74*	0.49	0.92*	0.86*	–

* $p < 0.05$

of independence ($P < 0.05$, Table 7). The association values (Cramer's V) between species pairs were all positive, although relatively low. *Simulium ochraceum*

s.l. and *Simulium* sp. showed the greatest positive association ($r_s = 0.63$; $n = 109$; $P < 0.05$).

Temporal variation

The most important temporal change in these two streams was observed in water discharge, which was closely associated with the seasonal distribution of rain (Figure 1). Depth, width and current varied from periods of steady flow (August–November) to low, intermittent streamflow (March–May) with the drying out of some sections of Stream II by the end of the dry season (April–May). Blackfly species also showed seasonal changes, with two peaks in density, the main one at the end of the rainy season (September–November), and a smaller one in the dry season (January–February), alternating with few or no immatures by the end of the dry season (March–June), excepting *S. ochraceum* s.l. (Figure 2). Also, there was site-specific seasonal dynamics for every species. For example, *S. ochraceum* s.l. showed the most uniform temporal distribution, occurring in both streams for a longer period of time than the other species (72% occurrence), with peaks of immature density (Figure 2) in the dry season and in the rainy season. On the contrary, larvae of *S. paynei* and *S. horacioi* showed the most restricted distribution and occurrence in time (19%). *Simulium paynei* occurred only in the rainy season at Stream II (Figures 2c, d), with just one peak of abundance at the end of the rainy season, whereas in Stream I, this species exhibited 2 peaks of abundance (Figures 2a, b), one at the end of the rainy season and the other one in the dry season (January at 900 m altitude). *Simulium horacioi* showed its highest density in February in Stream I at 900 m altitude

Table 6. The total number of blackfly larvae on each substrate type, the total number per row and column, n_{i+} , n_{j+} , the index of differential resource use of each species on each substrate, (D_i), the index of resource discrimination, \bar{R}_j , and the mean of the absolute values of the standardized residuals, \bar{D} , by species in two streams of Altamira, Venezuela. For further explanation see text.

Species	Substrates types				n_{i+}	\bar{D}
	Rocks	Leaves	Roots	Twigs		
<i>S. ochraceum</i>	6666 (-7.3)*	3767 (-12.8)*	2776 (45.8)*	46 (-2.5)	13255	17.1*
<i>S. paynei</i>	3074 (29.6)*	118 (-30.5)*	103 (-1.2)*	2 (-3.6)*	3297	18.7*
<i>S. metallicum</i>	1263 (-4.2)*	1215 (10.3)*	60 (-1.3)*	44 (8.7)*	2582	8.6*
<i>Simulium</i> sp.	761 (0.0)	784 (5.3)*	305 (10.7)*	7 (0.7)	1857	4.2*
<i>S. horacioi</i>	114 (-2.6)	140 (5.0)*	9 (0.4)	0 (-1.2)	263	2.3
Total n_{i+}	11878	6024	3253	199	21254	
\bar{R}	8.7*	12.8*	15.9*	3.3		

(*) $P < 0.05$, $D_i > Z = 3.33$

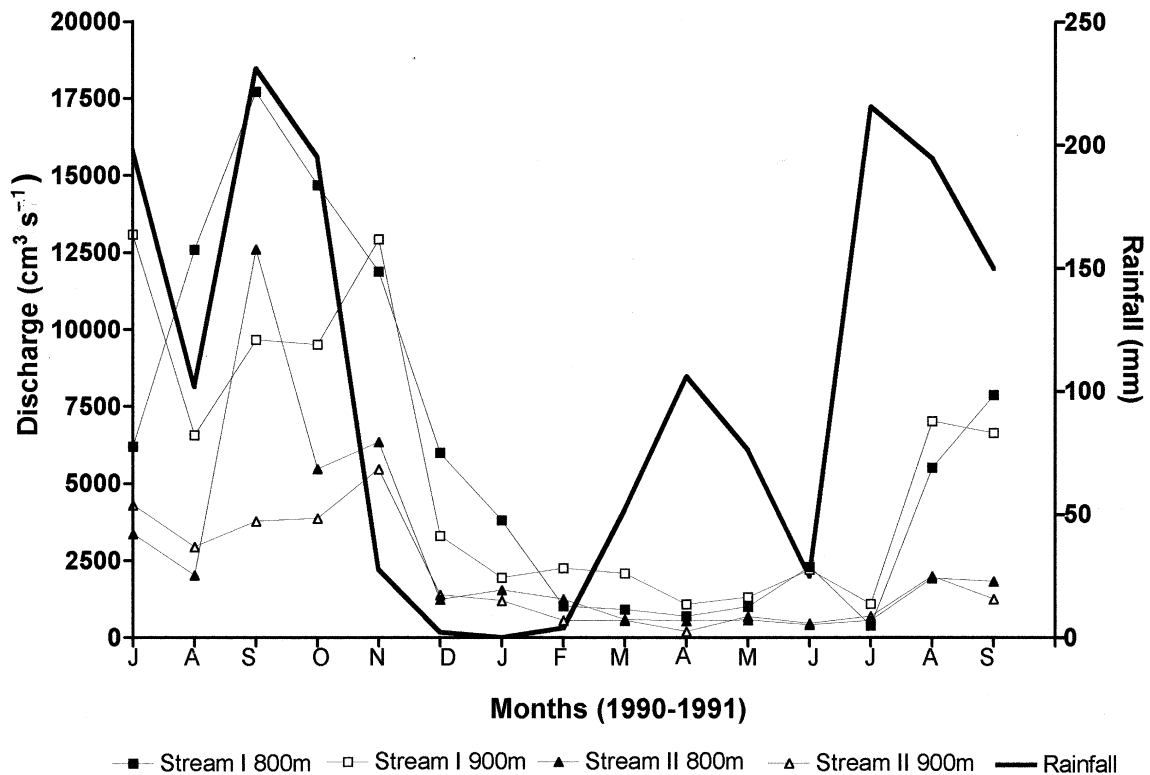


Figure 1. Discharge in Stream I and II, and rainfall at Altamira, July 1990 to September 1991.

(Figures 2a, b). *Simulium* sp. was the second species in order of occurrence (39%), showing the highest densities from August to November at Stream I (Figures 2a, b). *S. metallicum* cytospecies E (29% occurrence) was more abundant in Stream II with 3 peaks of abundance (Figures 2c, d), one in the dry season (February 1990), at the beginning of the rainy season (July 1991) and the main peak at the end of the rainy season (September–October 1990).

Discussion

The importance of studying local spatial variations in the distribution, abundance and community structure of freshwater invertebrates (Downes, et al., 1993; Scarsbrook & Townsend, 1993) was revealed in this study when two nearby streams were compared, showing differences in the associated blackfly community that may have been obscured at broader scales. Both streams had the same blackfly species composition, were numerically dominated by *S. ochraceum* s.l., and did not show significant differences in blackfly distribution and abundance between the two altitudes (800 and 900 m). Nonetheless, there were more immatures in the larger Stream I, and the guild structure in the smaller Stream II was characterised by numerical reduction of two species (*S. paynei* and *Simulium* sp.) and a significant increase of *S. metallicum* cytospecies E. A similar morphospecies richness would be expected over the small spatial scale examined (two nearby streams and altitudes); however, the blackfly species richness could increase if additional cytological studies would eventually reveal the presence of mixed cytospecies populations of the *S. ochraceum* s.l. complex coexisting in these streams. *S. ochraceum* s.l. was the most abundant and widely distributed species in the two streams, and as Adler (1987) have pointed out, sibling speciation may be suspected wherever a blackfly species occupies a wide range of microhabitats in a stream section as well as a wide temporal (annual) occurrence. The first component of the Principal Component Analysis of stream variables was mainly a summary of structural variables (depth, width, discharge) separating the larger Stream I from the smaller Stream II. The positive correlation between this component and the density of most species, and the larger total density of larvae in Stream I reveal the importance of the structural factors of the two streams at this finer scale more than the physicochemical variables on the distribution of the blackfly community, which agrees with studies from

Table 7. Values of chi-square (χ^2) and Cramer's values (V) of association between pairs of blackfly species in two streams of Altamira, Venezuela.

Species	$\chi^2, (V)$				
	1	2	3	4	5
1. <i>S. ochraceum</i>	–	277* (0.25)	31.7* (0.26)	92.0* (0.46)	25.4* (0.24)
2. <i>S. paynei</i>	–	–	36.8* (0.29)	54.9* (0.35)	38.3* (0.29)
3. <i>S. metallicum</i>	–	–	–	18.8* (0.21)	21.4* (0.22)
4. <i>Simulium</i> sp.	–	–	–	–	36.4* (0.29)
5. <i>S. horacioi</i>	–	–	–	–	–

(*) $P < 0.05$, df. = 1.

the temperate regions (e.g., Colbo, 1985; Adler, 1987; McCreadie & Colbo, 1992; Timm, 1994). Indeed, the stream variables which did not appreciably changed within stream (between altitudes) were structural variables (composition of the submerged substrate, stream width, current velocity, and discharge). The abundance of blackflies and other aquatic insects in temperate, lotic ecosystems increase with stream size factors, such as flow and discharge, and chemical factors (e.g., low conductivity) (Corkum & Currie, 1987; Richards & Minshall, 1992; McCreadie & Colbo, 1992; McCreadie et al., 1995). The association of blackfly immatures with high flow and discharge, and low conductivity appears to be related to the type of food and turbulence, which are important for larval filter-feeding organisms (Orth & Maughan, 1983; Corkum & Currie, 1987).

At an even smaller scale, within stream differences in substrate occupancy were observed in the guild of blackfly species. Despite the high and positive values of co-occurrence between species on the limited variety of submerged substrata (rocks, fallen leaves, twigs, and roots), the analysis employed (Bulla & Solano, unpublished) allowed us to account for subtle differences in substrate use. *Simulium paynei* seemed to be a submerged-rock specialist, whereas *S. ochraceum* s.l. and *Simulium* sp. seemed to be substrate generalists, with a disproportionate occurrence of the first species on submerged-roots. *Simulium metallicum* cytospecies E and *S. horacioi* were found on rocks and leaves, with a larger occurrence on leaves than otherwise expected for the guild. The relative segregation of blackfly species among attachment substrates agrees with studies from the temperate regions (Ciborowski & Adler,

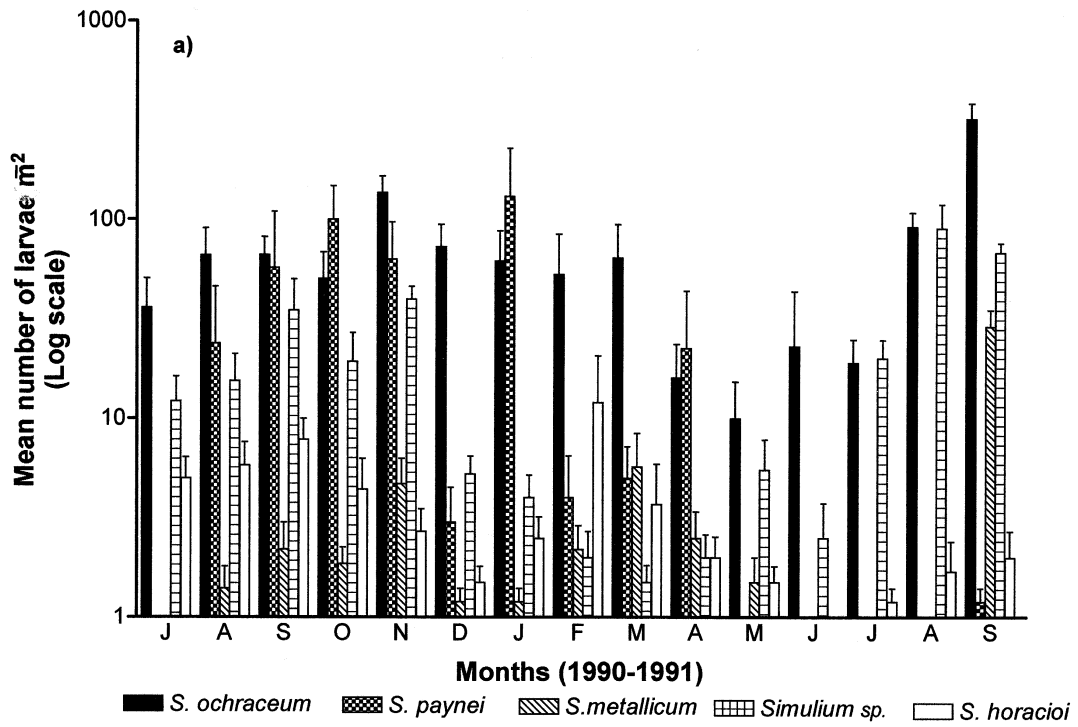


Figure 2A. See p. 206.

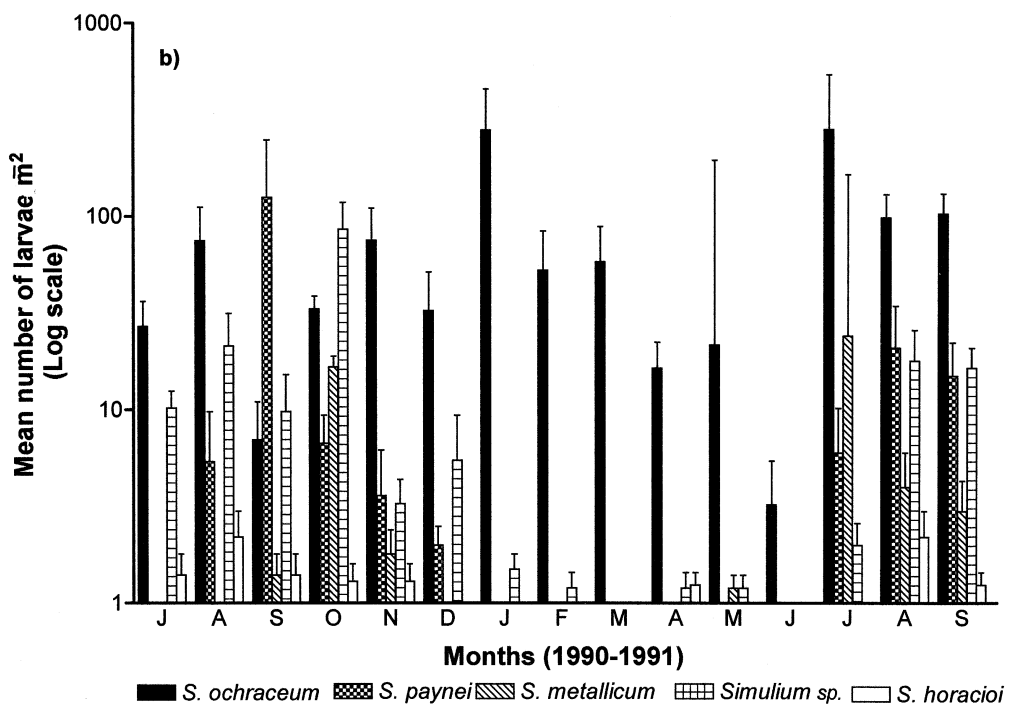


Figure 2B. See p. 206.

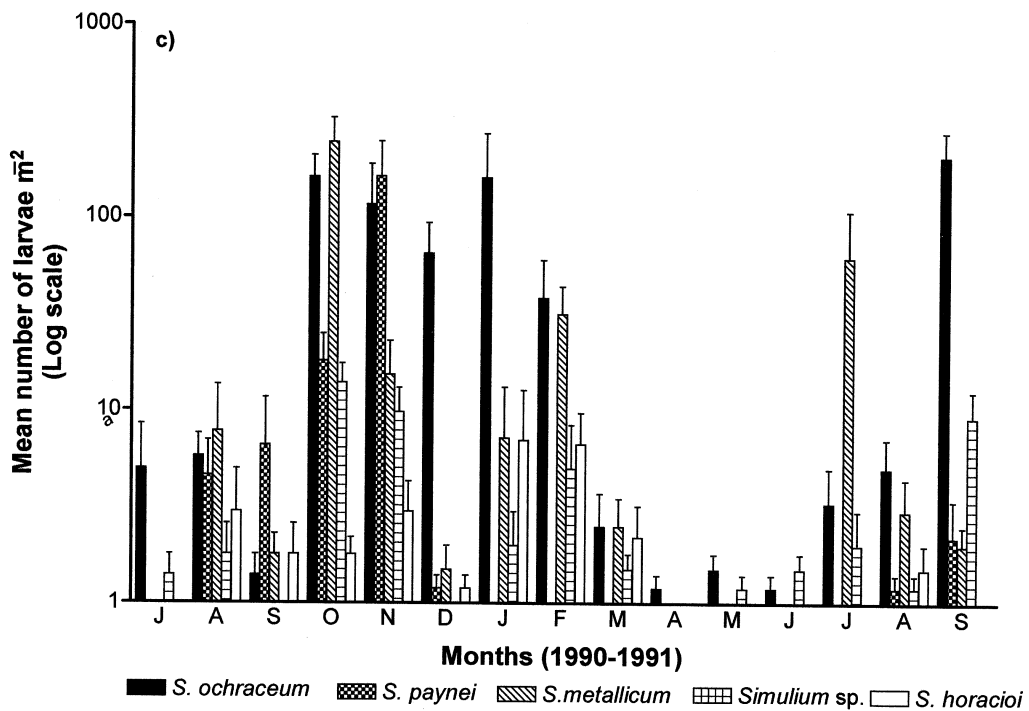


Figure 2C.

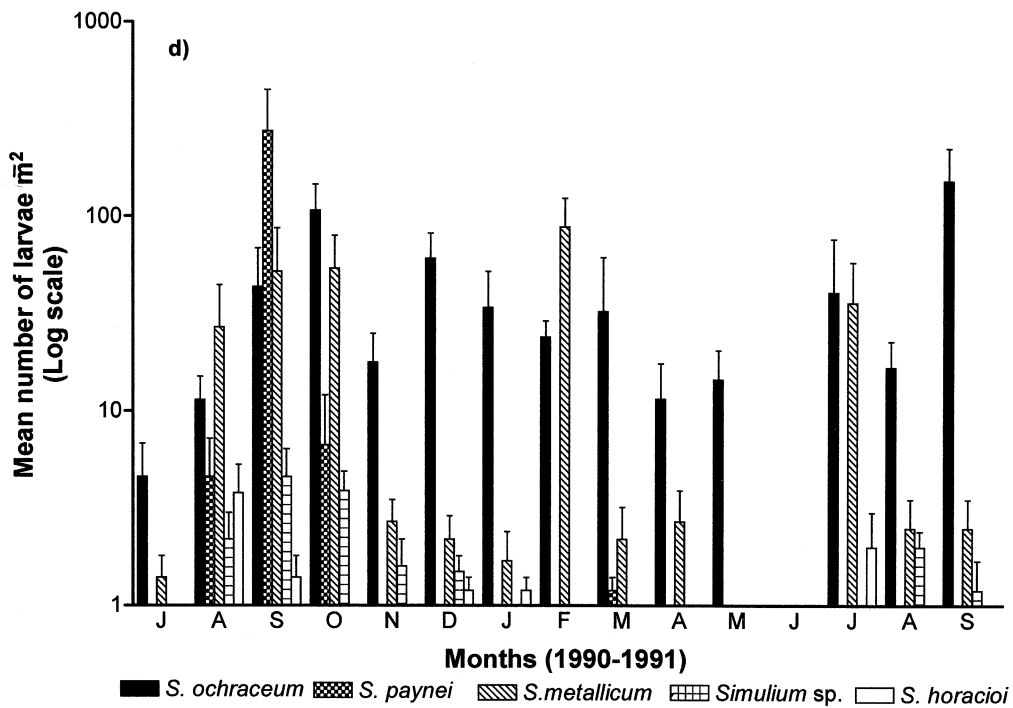


Figure 2D. Larval density (per m²) of blackfly species in Stream I, altitude of 900 m (a) and 800 m (b), and Stream II, altitude of 900 m (c) and 800 m (d) at Altamira, July 1990 to September 1991. Vertical bars show standard errors (± 1SE).

1990; McCreddie & Colbo, 1991). Future studies could be designed to indicate whether the observed distribution of blackflies across different substrata in these streams is a result of specific attachment preferences or the action of ecological factors, such as predation, competition or food availability, which may vary according to substrate type. Strong seasonal variations in blackfly abundance were observed over the fifteen months of study. Larval density reached maximum levels during the rainy season with secondary peaks of population density early in the dry season. Although most aquatic variables showed different degrees of temporal variations in both streams (data not shown), seasonal fluctuations in precipitation along with the associated changes in the size and velocity of the streams could be a primary cause for these temporal population dynamics of blackfly species in the study area. Seasonal change in discharge, which is an important variable for blackflies (Shipp & Procnier, 1986; Cobb, et al., 1992), can act as a multifactor variable influencing the feeding and respiration rates, as well as substrate availability, stability and persistence (Orth & Maughan, 1983; Bunn, 1986). Previous studies done in Australia at the same small local scale of the present work have demonstrated a strong association between changes in the benthic community structure and the seasonal variation of streamflow (Boulton & Lake, 1992). Seasonal fluctuations in discharge affect the volume of available habitat, with contractions during periods of low rain, catastrophic events at peak discharge events, and increases in habitat availability during the rainy season. Thus, changes in substrate availability and stability may be a function of the seasonal distribution of rainfall, and could be determining the seasonal dynamics of the blackfly community in these two small Neotropical mountain streams.

The presence of positive associations among species observed in this study could reflect: (i) the usual spatial aggregative behaviour of blackfly larvae, (ii) the low diversity of substrate types, and/or (iii) that the structure of this community is mainly dominated by the abiotic vagaries of the environment. Indeed, the small Neotropical mountain streams can be highly variable and unstable habitats (Covich, 1988), where resource states, abiotic factors or biotic interactions could be changing frequently. Biotic interactions may play a role during periods of habitat contraction, during the dry season, when the surface of available substrate attachment is minimal. Resource partitioning could promote coexistence in these particular instances of resource limitation. For example, the most abundant

species in this study, *S. ochraceum* and *S. paynei*, showed temporal and spatial separation (among substrates, among altitudes).

This study has demonstrated that blackfly abundance, community structure and abiotic variables can vary considerably between adjacent streams of the same order. Although many factors must influence the structure of the blackfly guild in these two headwater streams, variables related to the size of the streams play a significant role over the narrow physicochemical and local range encompassed by the present work.

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