Community Structure of Larval Black Flies (Diptera: Simuliidae) from the Avalon Peninsula, Newfoundland

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ABSTRACT This study, the last in a series, examines empirical relationships between the community structure of larval black flies from Newfoundland's Avalon Peninsula (Canada) and stream conditions. The primary emphasis is on spring and summer *Simulium* species. Principal component and correlation analyses were used to assess correlative relationships between species distribution and stream site variables. Fifty-five stream sites were sampled between May and August of 1987, 1988, and 1989. The spatial distribution of species examined was nonrandom and correlated with stream size (*Simulium caledonense* Adler & Currie, *S. craigi* Adler & Currie, *S. tuberosum* Lundström cytospecies AB, *Prosimulium mixtum* Syme & Davies) and proximity to lake outlets (*S. tuberosum* Lundström cytospecies FGH, *S. vittatum* complex Zetterstedt, *S. decorum* Walker). *S. craigi*, *S. tuberosum* AB, *S. tuberosum* FGH, and *S. aureum* Fries cytospecies C are reported from Newfoundland for the first time. Because this is the first cytotaxonomic investigation of the *S. tuberosum* complex from Newfoundland, notes on the cytology of the two sibling species are presented.

KEY WORDS Simuliidae, community, cytospecies

MOST BLACK FLY MORPHOSPECIES are complexes of reproductively isolated, often morphologically isomorphic, ecologically unique, sibling species (e.g., Adler 1987, Rothfels 1987). This phenomenon has precipitated the necessity for a comprehensive reevaluation of existing behavioral, physiological, taxonomic, and ecological data. This situation is exemplified on the Avalon Peninsula (Newfoundland, Canada), which has one of the most intensively studied black fly faunas in the world. Although more than a hundred publications exist on the local species, these data are of limited value, i.e., because most of the studies identified specimens (immature and adults) only to the complex level. In addition, several new species of *Simulium* have recently been described (e.g., Adler & Currie 1986), some of which could occur in Newfoundland.

With a reexamination of the Newfoundland fauna clearly warranted, our initial research focused on the aquatic stages of *Simulium truncatum* Lundström, *S. venustum* complex (three sibling species), *S. rostratum* Lundström, and *S. verecundum* Stone & Jamnback cytospecies AA (McCreadie & Colbo 1991, 1992, 1993). These studies showed that sibling species composition and abundance were strongly correlated with stream size and proximity to lake outlets.

The current study continues the analysis of black fly community structure by examining other species from the Avalon Peninsula, with the primary emphasis on spring and summer *Simulium* species. The winter-developing simuliids, *Prosimulium mixtum* Syme & Davies, *Cnephia ornithophilia* Davies, Peterson, & Wood, and *Stegopterna mutata* (Malloch) (triploid), have been examined in detail by Colbo (1979). The objective of this study was to examine the relationship between species occurrence (presence/absence) and stream variables. Because this was the first detailed report of the *Simulium tuberosum* complex from the Avalon Peninsula, notes on the cytology of its sibling species are included.

Materials and Methods

Sampling. The study area included streams on Newfoundland's Avalon Peninsula (9,000 km^2), which lies between 46° 35′–48° 11′N and 54° 13′–52° 38′W. Details about Newfoundland streams can be found in Jamieson (1974), Larson & Colbo (1983), and McCreadie & Colbo (1991). Each site was sampled by walking a swath from bank to bank while hand collecting larvae from all available natural substrates. Sites within 50 m of a lake or pond outlet were classified as outlet sites; those >500 m were classed as downstream sites. Rationale for our sampling protocol and details of collection methodology is given in McCreadie & Colbo (1991). As

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in similar studies (e.g., Corkum & Currie 1987, McCreadie & Colbo 1991), we assumed that species found in the swath sample from each site were representative of local occurrences.

Fifty-five sites were sampled in the months of May to August from 1987 to 1989 (87% of the samples taken in 1988 and 1989). Twelve sites were at pond outlets and 43 sites were located in downstream reaches. Of the 55 stream sites sampled, 20 sites were sampled in the spring only (May and June), 8 sites in the summer only (July and August), and 27 sites sampled in both the spring and summer. A total of 86 collections was made. No two stream sites were farther than 120 km apart. To our knowledge, all streams sampled are permanent.

Stream width, depth (mean of 3–5 equidistant measurements along the collection swath), conductivity (Yellow Springs Instrument, model 5890), pH (Lamotte Instruments), dissolved oxygen (Cole-Palmer DO meter, model 5513-60 or Hach chemical kit, model CA-10), and water temperature (hand-held thermometer) were measured at the time of each collection. During the spring and summer months on the Avalon Peninsula, stream temperature at the time of collection is strongly correlated with mean temperature during the previous week (see McCreadie & Colbo 1991). Collection date, size of streambed particles, riparian vegetation, and the extent of canopy cover were also noted at each site. Classification of streambed (mud, sand, small stones, rubble, or boulders), riparian vegetation (open, brush, or forest), and canopy (open, partial, or complete) followed the system of McCreadie & Colbo (1991).

Cytotaxonomic Identification. In the laboratory, larvae were fixed in acetic ethanol (1:3). Three to five changes of fixative were used, depending on the amount of debris present in each sample. Larvae were stored in acetic ethanol at 4°C until needed. Polytene salivary gland chromosomes of last or penultimate instars were stained following Rothfels & Dunbar (1953). Identifications of larvae of the *S. tuberosum* complex were based on IIS arm inversions and followed the chromosome maps and descriptions of Landau (1962). The IIS arm of larvae from a subsample of sites was analyzed in detail. Voucher specimens are deposited in the Clemson University Arthropod Collection (Clemson, SC) as is the complete list of site locations, stream conditions, and species identifications.

Data Analysis. Spring and summer collections were analyzed separately. To calculate meaningful correlation coefficients, statistical analysis was restricted to those species that occurred in ≥10% of the spring or summer collections. Because many of the measured stream variables were intercorrelated, principal component analysis (PCA) was used to collapse stream variables into a smaller number of statistically independent variables or principal components (e.g., Ciborowski & Adler 1990). Variables not normally distributed were subjected to a $\log_{10}$ (stream depth, width) or square (streambed) transformation before analysis. Because a suitable transformation could not be found for conductivity, this variable was excluded from the PCA. Following PCA, relationships among stream variables and derived principal components were determined by correlation analysis (Pearson's coefficient) (e.g., McCreadie & Colbo 1992). To identify rigorous and conclusive interpretations of the principal components, the significance level for these correlations was set at $P < 0.01$. Correlation analysis was also used to examine the association of species occurrence with principal components, site classification, and conductivity. Because species occurrence (present, absent) and site classification (outlet, nonoutlet) are nominal variables, special cases of the Pearson product moment correlation coefficient and tests of significance were used (Wherry 1984). For purposes of computation, variables were coded as 1 (species present, outlet site) or 0 (species absent, nonoutlet site). Correlations between occurrence and stream variables were considered significant at $P < 0.05$.

Results

The following account excludes results for six species: *S. truncatum*, *S. venustum* complex (three species), *S. rostratum*, and *S. verecundum* AA. Results for these taxa are given in McCreadie & Colbo (1991). Of the additional thirteen species of simuliids (n = 2,197) we found on the Avalon Peninsula, *S. craigi* Adler & Currie, *S. tuberosum* Lundström cytospecies AB, *S. tuberosum* Lundström cytospecies FGH, and *S. aureum* Fries cytospecies C are reported from insular Newfoundland for the first time. The most frequently collected species included *S. tuberosum* FGH, *S. tuberosum* AB, *S. vittatum* complex[2] *Zetterstedt, and S. caledonense* Adler & Currie (Fig. 1).

Principal Component Analysis. Four principal components (PC) accounted for 79.6% of the variability in spring stream conditions (Table 1). Variables correlated with PC-1 were measures of stream size, with increasing values of PC-1 corresponding to streams with increasing canopy, and decreasing depth, width, streambed particle size, and streamside vegetation. PC-2, accounting for an additional 22.0% of site variability, was related to stream cover, dissolved oxygen and temperature; higher PC-2 values indicated cool, well-canopied, highly oxygenated streams. PC-3 accounted for another 16.8% of site variability and reflected cover and water chemistry. Sites with high PC-3 scores were more acidic, and had lower dissolved oxygen content and greater vegetation cover than those with lower scores. PC-4, which accounted for an-

[2] The single collection of the *S. vittatum* complex that has been examined cytologically from Newfoundland is of uncertain affinity (Rothfels & Featherson 1981).

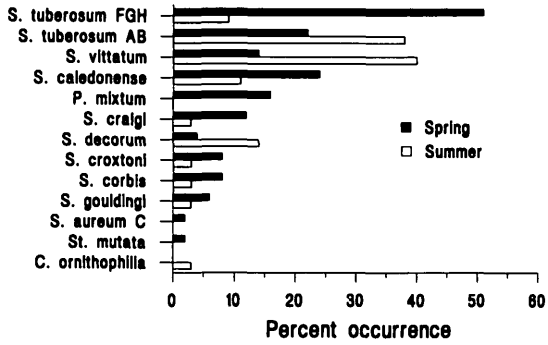

Fig. 1. Frequency of species occurrence. Percentage of occurrence was calculated as the number of sites from which a species was taken divided by the total number of sites sampled. Percentages were calculated separately for spring (n = 51) and summer (n = 35) collections.

other 11.0% of variability, was negatively correlated with pH; thus, higher PC-4 values would indicate increased acidity.

For the summer data set, four principal components accounted for 80.6% of the variability in stream conditions among collections. Variables correlated with PC-1 were measures of stream size and temperature. Increasing values of PC-1 corresponded to cooler streams and smaller size as shown by decreasing depth and width. The increase in canopy cover and decreases in streambed particle size and dissolved oxygen content with increasing PC-1 scores (Table 1) are also consistent with smaller Newfoundland streams (McCreadie & Colbo 1991). PC-2, accounting for an additional 17.0% of site variability, was related to stream cover. Higher PC-2 values indicated decreased riparian vegetation and canopy. PC-3 accounted for another 15.3% of site variability and reflected differences in physicochemical aspects of the water column. Sites with high PC-3 scores were cooler, more acidic, and had higher dissolved oxygen content than streams with lower scores. An increasing PC-4 score reflected increasing pH and decreasing streambed particle size. This component accounted for another 12.6% of variability.

Community Structure. Results of the correlation analysis suggest a strong association between community structure and stream size (Table 2). In the spring, the occurrence of *P. mixtum, S. craigi,* and *S. caledonense* was positively correlated with PC-1; i.e., these species were most frequently collected in smaller shaded streams. Correlation analysis also showed *P. mixtum* and *S. craigi* were most commonly found in cool, well-covered streams with high oxygen (PC-2). Although *S. gouldingi* Stone (n = 4) and *S. croxtoni* Nicholson & Mickel (n = 5) were collected too infrequently for statistical analysis, both simuliids were taken from streams no wider than 4 m, suggesting these species may be largely restricted to small streams. *S. tuberosum* AB was taken from streams varying in width from <1 to 35 m, although it was most frequently taken from larger streams, as shown by the

Table 1. Results of principal component (PC) and correlation analyses between stream variables and derived principal components

Variables	Variables		PCA			
	Min.	Max	PC-1	PC-2	PC-3	PC-4
			Spring (n = 51)			
Depth, m	0.04	0.41	−0.716**	−0.231	0.103	0.036
Temp, °C	8.5	22.0	−0.086	−0.896**	0.189	0.119
pH	5.2	6.9	−0.161	−0.280	−0.450**	−0.831**
Dissolved oxygen, mg/L	7.6	12.4	−0.292	0.776**	−0.457**	0.088
Riparian vegetation	1.0	3.0	−0.582**	0.239	0.610**	−0.205
Canopy cover	1.0	3.0	0.358*	0.368*	0.715**	−0.317
Streambed particle size	1.0	5.5	−0.774**	0.161	0.061	−0.049
Stream width, m	0.20	30.0	−0.826**	−0.086	−0.038	0.141
% variance explained						
Proportion			29.7	22.0	16.8	11.0
Cumulative			29.7	51.7	68.6	79.6
			Summer (n = 35)			
Depth, m	0.06	0.53	−0.618**	−0.427	0.260	0.236
Temp, °C	9.0	26.0	−0.636**	0.348	−0.575**	−0.146
pH	5.2	7.0	−0.193	0.081	−0.599**	0.742**
Dissolved oxygen, mg/L	6.4	11.4	−0.488*	0.364	0.587**	0.258
Riparian vegetation	1.0	3.0	−0.348	−0.774**	−0.127	−0.039
Canopy cover	1.0	3.0	0.734**	−0.509*	−0.098	0.150
Streambed particle size	1.0	5.5	−0.705**	−0.157	−0.230	−0.505*
Stream width, m	0.20	35.0	−0.795**	−0.181	0.211	0.198
% variance explained						
Proportion			35.6	17.0	15.3	12.6
Cumulative			35.6	52.6	67.9	80.6

*, $P < 0.01$; **, $P < 0.001$.

Table 2. Results of correlation analysis between species occurrence and stream site conditions

Species	Principle components				Outlet, +/−	Conductivity
	PC-1	PC-2	PC-3	PC-4		
			Spring (n = 51)			
P. mixtum	0.303*	0.406**	0.259	−0.178	−0.186	0.041
S. craigi	0.320*	0.304*	0.186	−0.287	−0.157	0.161
S. caledonense	0.324*	0.118	0.125	0.005	0.015	−0.089
S. tuberosum AB	−0.329*	−0.078	−0.044	−0.069	0.027	−0.224
S. tuberosum FGH	0.154	0.016	0.160	0.074	−0.451**	0.196
S. vittatum complex	−0.128	0.007	−0.314*	−0.028	0.768***	−0.280
			Summer (n = 35)			
S. caledonense	0.448**	−0.347*	−0.215	0.040	−0.028	0.463**
S. decorum	−0.149	0.178	0.112	0.020	0.645***	−0.089
S. tuberosum AB	−0.317	0.001	0.176	−0.098	0.156	−0.028
S. vittatum complex	0.092	0.191	0.111	0.122	0.645***	−0.072

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

negative correlation with PC-1 (Table 2). *S. tuberosum* FGH occurred rather uniformly across a wide range of stream sizes (nonsignificant correlation with PC-1).

In the summer, the occurrence of *S. caledonense* was positively correlated with PC-1 and negatively correlated with PC-2, indicating that it was most frequently found in small, cool, well-covered streams (Table 2).

Of the 86 samples taken, 50 harbored members of the *S. tuberosum* complex. Within spring collections of this latter subset, the occurrence of *S. tuberosum* AB showed a negative correlation with occurrence of *S. tuberosum* FGH (r = -0.660; df = 29; $P < 0.001$) i.e., the two siblings of the *S. tuberosum* complex occupy different lotic habitats. *S. tuberosum* FGH was collected too infrequently for a similar summer correlation.

The relationship between species occurrence and lake outlets is also apparent (Table 2). Highly significant ($P < 0.001$) correlations between outlets and the occurrence of *S. vittatum* complex (spring and summer) and *S. decorum* Walker (summer) suggest these flies are sublacustrine species, although both could be found on occasion at sites farther (>500 m) downstream (*S. decorum* 1 out 7 of collections; *S. vittatum* complex 6 out of 21 collections). During the spring, the occurrence of *S. vittatum* complex also showed a negative correlation with well-covered, lower oxygenated, more acidic streams (PC-3). In contrast to *S. decorum* and *S. vittatum* complex, all 28 collections of *S. tuberosum* FGH were at downstream sites, which accounts for the negative correlation with outlets (Table 2). Although this species selects a wide range of stream sizes, it appears only to colonize reaches removed from outlets.

Cytology of the S. tuberosum Complex. Two cytospecies were found on the Avalon Peninsula: *S. tuberosum* AB and *S. tuberosum* FGH. *Simulium tuberosum* AB larvae had the classical sex-chromosome system originally described by Landau (1962): X chromosome = AB, Y chromosome = the standard. *S. tuberosum* FGH typically displayed a diagnostic FGH sequence on the IIS arm and undifferentiated sex chromosomes. However, populations on the Avalon Peninsula were polymorphic for the Y chromosome, whereas all females but one (heterozygous for FGH-6, see Landau 1962) carried no polymorphisms on the IIS arm and, thus, were homozygous for the FGH sequence (Table 3). Males were either homozygous for FGH (n = 9) or were heterozygous for one of three predominant sequences: FGH-7 (n = 16), FGH-8 (n = 28), or FGH-8 + 9 (n = 22). Each of these sequences predominated at a different site (Table 3). An additional male was heterozygous for FGH-6 and two others were FGH-6 + 10 heterozygotes. Inversions 7, 8, 9, and 10 (Fig. 2) have not been recorded previously, although they occur in the area distal to the Ring of Balbiani where inversions 1 through 6 of Landau (1962) and Mason (1982) are found. A small sample of larvae (n = 11 male, 4 female) from Labrador City (28 June 1989), the nearest collection of this cytospecies on the mainland, had undifferentiated sex chromosomes.

Discussion

To date, 25 species of simuliids have been reported from the Avalon Peninsula (Table 4). However, the presence of *S. excisum* Davies, Peterson, & Wood, *S. furculatum* (Shewell), *S. rugglesi* Nicholson and Mickel, and *S. quebecense* Twinn needs to be confirmed (Table 4). This is particularly true for *S. excisum* because the single collection record of this species was given two locations (cf., Lewis 1973, Lewis & Bennett 1973). Our collection (15 May 1994) from the site at which Lewis (1973) recorded *S. quebecense* produced *S. euryadminiculum* Davies, which, like *S. quebecense,* has a four-filamented pupa that might have been confused with that of *S. quebecense.*

Our results demonstrated a strong association between stream size and species distribution. For instance, *S. craigi* was found in small streams (0.6–3.5 m), which is consistent with observations of

Table 3. Summary of inversions identified on the IIS arm of *S. tuberosum* FGH from the Avalon Peninsula, with breakpoints given in Fig. 2

Site[a]	FGH/FGH[b]		FGH/FGH-6		FGH/FGH-7		FGH/FGH-8		FGH/FGH-8+9		FGH/FGH-6+10	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Bauline River 47° 42′ 45″ N 52° 47′ 00″ W							1					
Piccos River 47° 12′ 15″ N 52° 44′ 00″ W	3	10		1	2		25					
Piccos tributary 1 47° 30′ 15″ N 52° 43′ 15″ W	3	8			14							
Piccos tributary 2 47° 41′ 45″ N 52° 44′ 15″ W		1										
Back River 47° 12′ 15″ N 53° 22′ 15″ W	3	7	1				2		22		2	

[a] Collection dates are as follows: Bauline River (10 June 1987), Piccos (20, 28 May 1987; 5 June 1988) Piccos tributary 1 and 2 (10 June 1887), and Back River (9 June 1987).
[b] Slash separates sequences of the two homologues.

Adler & Currie (1986) in Alberta. In constrast, *S. tuberosum* AB tended to inhabit larger streams. A similar tendency has been described for this species in western Canada (Adler 1986, Ciborowski & Adler 1990). More than half of the collections of this species (31 May–24 July) were taken in July, suggesting a multivoltine life history. It has been collected as late as 13 September from Newfoundland streams (J.W.M. & P.H.A, unpublished data).

In contrast, the presence of *S. tuberosum* FGH was independent of stream size. Pistrang & Burger (1988) also noted that this species occurs in a variety of stream types and sizes in New Hampshire. However, in contrast to our finding, FGH in New Hampshire frequents lake outlets. The existence of several Y chromosomes in *S. tuberosum* FGH is, so far, unique to the Avalon Peninsula and suggests that there is either a Y-chromosome polymorphism within a single species or that two or more siblings are involved. In either case, our limited analysis suggests that the various Y chromosomes are related to habitat, each tending to predominate in a different stream. Perhaps these various Y chromosomes provide an extra measure of variability, allowing *S. tuberosum* FGH to colonize a range of habitats on the Avalon Peninsula. Although *S. tuberosum* FGH was found from 31 May to 24 July, only four collections were in July (also see Fig. 1), suggesting a univoltine life history or a limited second generation. This species is univoltine throughout the rest of its known range (Adler 1986, Adler & Kim 1986, Pistrang & Burger 1988). The negative correlation between *S. tuberosum* AB and *S. tuberosum* FGH showed that these siblings segregate themselves along an ecological continuum. Similar findings have been reported elsewhere (Adler 1986, Pistrang & Burger 1988, Ciborowski & Adler 1990).

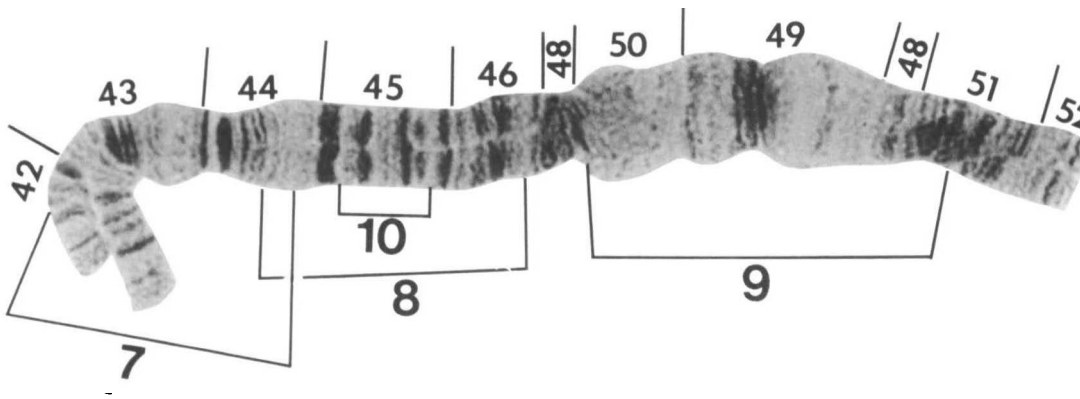

Fig. 2. End of the IIS arm of *S. tuberosum* FGH, showing breakpoints of novel inversions (plotted on the FGH sequence) from larvae on the Avalon Peninsula. Sections are numbered relative to the *S. tuberosum* standard of Landau (1962). Inversion numbers correspond to those in the text and in Table 1. Chromosomal preparation is that of a male larva collected in Waterville Valley, Grafton County, New Hampshire, 26 May 1987.

Table 4. Inventory of the black fly species reported from the Avalon Peninsula, Newfoundland, Canada

Species	References[a]
C. ornithophilia Davies, Peterson & Wood	1, 2
P. mixtum Syme & Davies	1–5
P. mysticum Peterson	1, 5
S. mutata (Malloch) triploid cytospecies	1–4
S. aureum Fries cytospecies C	2
S. caledonense Adler & Currie	2, 6
Similium corbis Twinn	2, 4
S. craigi Adler & Currie	4
S. croxtoni Nicholson & Mickel	2, 4
S. decorum Walker	2, 4
S. excisum Davies, Peterson & Wood	4
S. euryadminiculum Davies[b]	2, 4
S. furculatum Shewell	4
S. gouldingi Stone	2, 4
S. quebecense Twinn	3, 4
S. rostratum (Lundström)	7, 8
S. rugglesi Nicholson & Mickel	3
S. tuberosum (Lundström) cytospecies AB	2
S. tuberosum (Lundström) cytospecies FGH	2
S. verecundum Stone & Jamnback cytospecies AA	7, 8
S. truncatum (Lundström)	7, 8
S. venustum Say cytospecies CC2	7, 8
S. venustum Say cytospecies CC3	8
S. venustum Say cytospecies AC(gB)	7, 8
S. vittatum complex Zetterstedt	1–4

[a] 1, Colbo (1979); 2, current study; 3, Pickavance et al. 1970; 4, Lewis 1973 or Lewis & Bennett 1973; 5, Rothfels & Freeman 1977; 6, Brockhouse 1985; 7, Rothfels et al. 1978; 8, McCreadie & Colbo 1991.

[b] Collected on 15 May 1994, Manuels River, Avalon Peninsula, Newfoundland (47° 28′ N, 52° 55′ W) by M.H.C.

Few studies have examined the species-specific structure of black fly communities and even fewer have attempted to correlate these assemblages with riparian characteristics over a number of sites (e.g., Ciborowski & Adler 1990). Although many factors, both biotic and abiotic, have been associated with larval distributions (e.g., Ross & Merritt 1987), the few studies which have focused on species-specific larval identification clearly demonstrate the importance of stream size and outlets on species assemblages. For example, Ciborowski & Adler (1990) found the assemblage patterns of 20 cytotaxonomically defined species in northern Saskatchewan were determined by proximity to outlets, as well as stream size. McCreadie & Colbo (1991, 1992, 1993) showed that species distribution, composition, and abundance of S. truncatum, members of the *S. venustum* complex, *S. rostratum*, and *S. verecundum* AA were strongly correlated with stream size and distance downstream. Corkum & Currie (1987) were able to group simuliid assemblages throughout northwestern North America into five distinct clusters and predict occurrence of these groups (error, 29%) based on a few stream variables, one of which included stream width. Bass & Armitage (1987) showed that the presence of reservoir outlets reduced black fly community diversity. However, because larvae were only identified to the morphotaxonomic level in these last two studies, conclusions must be viewed with extreme caution. The results of our study clearly illustrate the relationships among stream size, outlets, and community structure. The spatial distribution patterns of species examined was nonrandom and partially predictable on the basis of stream size and occurrence of outlets.

Our study and those of Ciborowski & Adler (1990) and McCreadie & Colbo (1991, 1992, 1993) were each conducted within relatively small geographic areas in northern Canada. Accordingly, each study area was relatively homogenous, thus minimizing the effects of biogeographic factors. Although this has the advantage of simplifying the analysis by removing confounding effects between biogeographic variables and stream conditions, it does limit extrapolation of results to other ecoregions. Currently, it is not clear if stream size has the same influence on community structure across different ecoregions. In addition, many lakes and ponds in the southern United States are artificial. It is not known if these artificial sublacustrine habitats have as much effect on community structure as their naturally occurring counterparts in northern areas. Corkum (1989) demonstrated a strong association between the distribution patterns of benthic macroinvertebrates and the land through which streams flow. It has also been suggested that habitat selection in some sibling species may vary with geographic location (Pistrang & Burger 1988, McCreadie & Colbo 1991). Given these findings, the proximal factors controlling simuliid community structure might be ecoregion specific. The question of whether the empirical relationships between community structure and stream conditions are universal or region specific warrants further investigation.

Although current studies have begun to elucidate the proximal relationships between simuliid species assemblages and stream conditions, the ultimate factors regulating community structure can only be addressed after the costs and benefits of habitat selection, measured in terms of fitness, are assessed for each member of the community. For example, in Newfoundland *S. vittatum* complex is most frequently found at lake outlets (Table 2; Colbo 1979), but occasionally populations are found farther downstream. Knowledge of differences in growth rate, larval survival, and adult fecundity, all of which affect fitness, among these habitat types is crucial for understanding why this species colonizes these two apparently distinctive environments. By applying such inquiry to each species within a community, a lucid relationship between structure and lotic conditions should emerge.

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