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Habitat characterization of the morphologically similar mayfly larvae, *Caenis* and *Tricorythodes* (Ephemeroptera)

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Abstract

The larvae of *Caenis* (Caenidae) and *Tricorythodes* (Tricorythidae), once considered to be confamilial, have notable morphological and behavioural similarities. Univariate and multivariate (discriminant analysis) techniques were used to determine which environmental variables best characterized the larval habitats of *Caenis* and *Tricorythodes* at 40 sample sites on 29 rivers within the Interior Plains of Alberta, Canada. River width, depth and substrate type distinguished riverine habitats of the two genera. Larvae of *Tricorythodes* occurred in wide rivers of varying depths that possessed coarse substrates. Although larvae of *Caenis* occurred in a variety of habitats, they were found more frequently on stable substrates in narrow, deep rivers.

Introduction

Although the genera of *Caenis* and *Tricorythodes* were once considered to be confamilial, within Caenidae, Edmunds *et al.* (1976) recognized the evolutionary convergence of these small mayflies and placed them in separate families, Caenidae and Tricorythidae. Caenidae are closely related to the Neoephemeridae, whereas Tricorythidae have affinities with the Ephemerellidae (Edmunds *et al.*, 1976). There are, however, notable similarities in morphological (operculate gills) and behavioural (sprawling) traits of the larvae.

Mayfiles originated in cool, fast-flowing waters (Edmunds *et al.*, 1976). Larvae of most mayfly species inhabit rivers; many dwell in both lakes and rivers; and a few are restricted to lakes (Edmunds *et al.*, 1976; Corkum, 1987). In the Nearctic region, larvae of Caenidae and Tricorythidae occur in rivers, yet caenid larvae also occur in lentic areas and are often more abundant in these habitats (Leonard & Leonard, 1962). Larvae of *Caenis* are found in puddles, ditches, marshes, lakes and rivers (Berner, 1950; Edmunds *et al.*, 1976; Corkum, 1984, 1985). In contrast, *Tricorythodes* larvae prevail in permanent running waters. Clemens (1915) collected *Tricorythus* (= *Tricorythodes*) *allectus* Needham from Georgian Bay in the Great Lakes of North America, but I know of no other records of *Tricorythodes* specimens from lake habitats.

Although mayfly workers can identify likely habitats in which *Caenis* and *Tricorythodes* larvae occur, it is difficult to attribute their presence or absence to any particular environmental feature. I attempted to quantify the lotic habitats of both genera in the Interior Plains of Alberta, Canada.

Methods

Study area

During an extensive sampling program of benthic invertebrates in rivers of Alberta conducted between 1979 and 1981, I collected larvae of *Caenis* and/or *Tricorythodes* at 30 sites. A review of the literature and information from colleagues provided data for an additional ten sites. Thus, my analysis was based on samples from 40 sites obtained throughout the open water season (but with an emphasis in June because of the prevalence of mature sprawling mayfly larvae then). A variety of collecting techniques was used including kick net, modified Hess sampler, corer, Ekman grab and hand-picking of organic and inorganic substrates at river margins and across channels. To ensure that each locale was thoroughly sampled, I considered only smaller rivers (i.e., channel width < 100 m).

Data collection

At each site that I sampled, values were obtained for pH (Fisher model 109), conductivity (YSI model 33), river width, mean current velocity (Price Gurley meter) and mean depth (obtained from measurements at five equal intervals across the channel). I also recorded land use (farming, rangeland and forested areas), substrate type of rivers (fine < 2 mm, coarse ≥ 2 mm and mixed substrates) and the presence/absence of aquatic macrophytes. Techniques used by other workers, whose data I incorporated, were similar and are outlined in references cited in Table 1.

I obtained values for latitude, elevation and distance of site from river source for all 40 sites, using 1:50000 NTS (National Topographic Series) maps. The rationale for the choice of these environmental variables was based on their correspondence with the presence of sprawling mayflies in other studies (cf. Berner, 1950; Hall *et al.*, 1975, 1980; Edmunds *et al.*, 1976; Newell & Minshall, 1978; Whiting & Clifford, 1983).

Statistical analysis

Canonical variate (multiple discriminate) analysis was used to differentiate pre-identified groups. All river sites were coded according to the occurrence of mayflies retrieved from the benthic samples (1., *Tricorythodes*; 2., *Caenis*; 3., *Caenis* and *Tricorythodes*). The discrimination was based on quantitative differences in environmental measures obtained from the river sites. Thus, the procedure identified those environmental variables that best distinguished river sites characterized by each of the mayfly groups. Logarithmic transformations were applied to continuous environmental variables (except pH, which is already in logarithmic form); degrees of latitude were transformed into radians. The analysis was performed using the SPSSX procedure for discriminant analysis (SPSS Inc., 1983; Norusis, 1985).

Since combining continuous and discrete variables for canonical variate analysis is not recommended (Norusis, 1985), I analysed the discrete variables separately, using a G-statistic, goodness-of-fit test for the multistate land use and substrate characters, and a binomial frequency test for the presence/absence of aquatic macrophytes (Sokal & Rohlf, 1981).

Results

The 40 benthic sample sites supporting larvae of either *Caenis, Tricorythodes* or both genera occurred in 29 rivers (Table 1). Seven of the rivers were sampled at two locations; two (Oldman & Calumet) were sampled at three locations; and single samples were obtained from the remaining 20 rivers (Table 1). *Caenis* and Tricorythodes were found alone at 21 and 10 sites, respectively. Larvae of both genera were found together at nine sites.

Canonical variate analysis was performed on the 40 samples using eight continuous environmental variables. The first discriminant function was highly significant ($X^2 = 49.2$, 16 d.f., $p < 0.0001$) accounting for 82.2% of the variation among the mayfly groups. The second discriminant function was not significant ($X^2 = 12.2$, 7 d.f., $p = 0.0950$). The overlap in discriminant scores (Fig. 1) indicates similarity in the environ-

Table 1. Collections of larvae (T, *Tricorythodes*; C, *Caenis*; TC, both genera) from Alberta. Source: site numbers (No.) 1 & 3, Davies *et al.*, 1977; 24, E. R. Whiting, personal communication; 26, 31 to 34, J. J. H. Ciborowski, personal communication; 29 & 30, Robertson, 1967; remaining sites, Author.

No.	River	Latitude (North)	Longitude (West)	Date (Month)	Code
1	Oldman	49 43 14	113 27 10	Ap, Jl, Oc	TC
2	Oldman	49 47 25	113 07 25	Ju	T
3	Oldman	49 51 50	112 50 54	Ap, Jl, Oc	T
4	Tributary of Willow	49 58 15	113 51 00	Ju	T
5	Willow	49 52 00	113 32 30	Ju	TC
6	Willow	50 06 45	113 46 40	Ju	T
7	Little Bow	50 07 24	113 08 00	Ju	C
8	Little Bow	50 20 38	113 32 36	Ju	T
9	Mosquito	50 20 38	113 46 15	Ju	C
10	Jct. Sheep & Highwood	50 46 54	113 49 03	Ju	T
11	Crowfoot	50 46 54	112 46 00	Ju	C
12	Rosebud	51 18 30	113 14 33	Ju	C
13	Rosebud	51 39 45	114 06 24	Ju	C
14	Lonepine	51 29 15	112 50 45	Ju	C
15	Kneehills	51 47 38	113 38 15	Ju	C
16	Little Red Deer	51 41 06	114 30 00	Ju	T
17	Little Red Deer	51 49 20	114 21 15	Ju	TC
18	Red Deer	51 56 24	114 30 00	Ju	T
19	Medicine	52 22 24	114 21 40	Ju	C
20	Tributary of Buffalo Lake	52 27 10	113 18 00	Ju	C
21	Rose	52 43 33	114 52 20	Ju	C
22	Battle	52 47 20	113 52 45	Ju	C
23	Battle	52 57 12	112 57 52	Ju	C
24	Whitemud	53 24 44	113 35 30	Ja to De	C
25	Bigoray	53 30 33	115 26 15	Ju	C
26	Sturgeon	53 43 36	114 10 47	Ju	TC
27	Pembina	53 07 52	115 29 00	Ju	C
28	Pembina	54 03 00	114 19 00	Ju	TC
29	La Biche	54 58 25	112 21 30	Ju, Jl	TC
30	Wandering	55 12 30	112 29 00	Ju, Jl	TC
31	Poplar	56 54 46	111 29 00	Ju	C
32	Upper Beaver	56 56 29	111 33 54	Ju, Jl, Se	C
33	Dover	57 10 12	111 47 38	Ju, Jl, Se	TC
34	MacKay	57 12 38	111 41 36	Ju, Se	TC
35	Calumet	57 24 17	111 40 52	Au	T
36	Calumet	57 22 52	111 46 03	Au, Se	C
37	Calumet	57 26 45	111 47 25	Ju	C
38	Pierre	57 27 35	111 38 27	Au	T
39	Pierre	57 28 40	111 40 30	Ju	C
40	Muskeg	57 22 50	111 10 12	Se	C

mental features of river sites where *Tricorythodes* larvae occurred alone and together with *Caenis* larvae.

The standardized canonical discriminant function coefficients identified river width (1.316) and mean depth (– 0.868) as important in characterizing the mayfly groupings (Table 2). Larvae of both genera occurred in rivers exhibiting a similar range of pH and conductivity. A total of 85.0% of the 40 sites was correctly assigned to the three groupings by discriminant functions (Table 3). Most misidentified cases were in the *Tricorythodes*

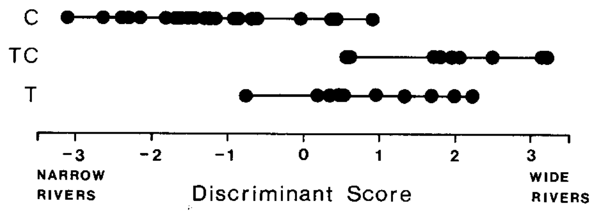

Fig. 1. Discriminant scores of river sites with *Caenis* (C), *Tricorythodes* (T) or both genera (TC). Circles represent scores of individual sites along the first discriminant axis.

group, where one site was assigned to the *Caenis* group and two were assigned to the group where the taxa co-occurred.

Tricorythodes larvae occurred alone at larger (i.e., wider) river sites ($\bar{X} \pm$ S.E. = 32.9 ± 9.99 m) than *Caenis* larvae (9.6 ± 1.31 m). At the nine sites where larvae of the two genera co-occurred, river width ranged from 10 to 78 m (37.4 ± 7.58 m). *Caenis* larvae were found alone at sites characterized by somewhat greater river depths (53 ± 3.8 cm) than sites inhabited by *Tricorythodes* larvae (48 ± 8.0 cm) or by both taxa (47 ± 6.0 cm). Overlap occurred among groups.

Table 2. Canonical variate (discriminant) analysis of 40 river sites with larvae of *Tricorythodes, Caenis* or both genera using continuous environmental variables. The discriminant function is standardized and normalized. N.S. = not significant.

Variable	Function 1	Function ·2
Latitude	0.143	2.705
Elevation	− 0.569	2.035
Distance (site to source)	− 0.188	0.248
pH	− 0.129	− 0.011
Conductivity	− 0.055	− 0.034
Width	1.316	0.716
Mean current velocity	0.421	− 0.658
Mean depth	− 0.868	− 0.773
Percent variability	82.16	17.84
Probability	0.0001	N.S.

Table 3. Prediction of the three mayfly groupings (T, *Tricorythodes*; C, *Caenis*; TC, both genera) for 40 sample sites using discriminant analysis.

Group	No. of sites	Predicted group membership			Sites correctly predicted
		(T)	(C)	(TC)	(%)
T	10	7	1	2	70.0
C	21	1	19	1	90.5
TC	9	1	0	8	88.9

Percentage of sites correctly classified: 85.0.

The distribution of the three mayfly groups (*Tricorythodes, Caenis* or both taxa) did not differ from random occurrence among agricultural, rangeland or forested land use areas ($p > 0.05$, G-test; Sokal & Rohlf, 1981) (Fig. 2). Aquatic macrophytes commonly occurred at river sites wherever sprawling mayflies were collected, and the presence of vegetation did not differ significantly among the groups ($p > 0.05$, binomial frequency test; Sokal & Rohlf, 1981). Whenever larvae of *Caenis* were found on coarse substrates, aquatic plants, grasses or periphyton were present.

Significant differences were noted between substrate and mayfly taxa (Fig. 2). *Caenis* larvae were collected more frequently than expected by chance at river sites with fine substrates ($p < 0.05$). *Tricorythodes* larvae, when found alone, were associated with coarse, rocky substrates. At river sites where larvae of *Caenis* and *Tricorythodes* co-occurred, the riverbed was characterized by coarse substrates or a mixture of coarse and fine particles.

Discussion

There are shortcomings in identifying habitat characteristics for genera rather than species in that habitat differences between genera may be less than for species within genera. Taxonomic difficulties in distinguishing larval forms of *Caenis* and *Tricorythodes* are well known (Edmunds *et al.*, 1976); and, without imagoes, I was unable to identify specimens to species. Four species of *Caenis* (*C. simulans* McDunnough, *C. forcipata* McDunnough, *C. tardata* McDunnough and *C. youngi* Roemhild) (Whiting & Clifford, 1983; A. Provonsha, personal communication) and three

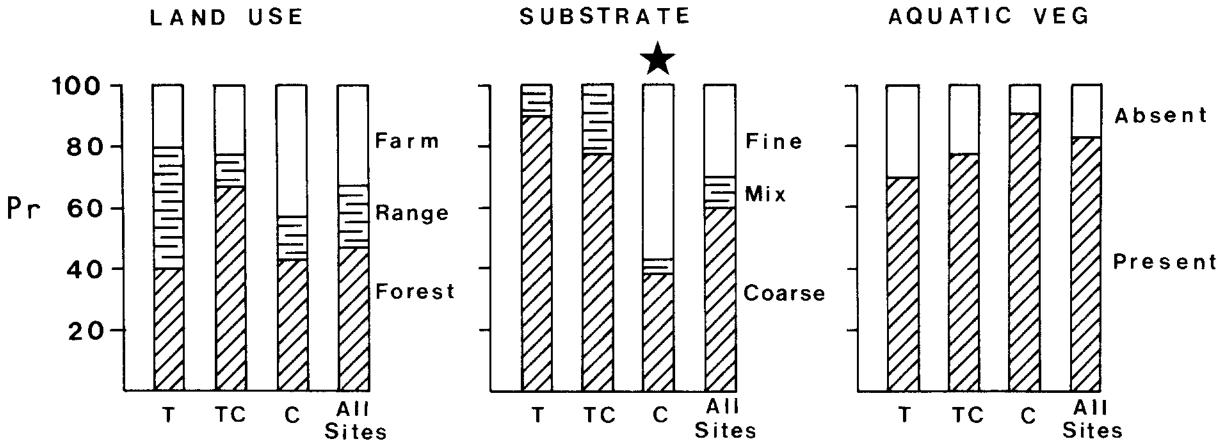

Fig. 2. Distribution of sites among land use areas, substrate type and the presence/absence of aquatic vegetation characterized by larvae of *Caenis* (C), *Tricorythodes* (T) and both genera (TC). A star indicates a significant difference from expected occurrence at the 0.05 level or less. Pr = proportion.

species of *Tricorythodes* (*T. atratus* McDunnough, *T. stygiatus* McDunnough and *T. minutus* Traver) are known to occur in the study area. As it is typical rather than exceptional for two or more conspecifics of *Caenis* (A. Provonsha, personal communication) and *Tricorythodes* to occur at any one river site, my descriptions of Alberta sample sites reflect the range of habitat requirements for each genus.

Study results showed that measures of river size (width and mean depth) and substrate type distinguished riverine habitats characterized by larvae of *Caenis* and *Tricorythodes*. *Tricorythodes* larvae typically occurred in wide rivers with varying depths and coarse substrates. In contrast, *Caenis* larvae occurred more often in narrow, deep rivers. Although *Caenis* larvae were prevalent on riverbeds with fine particle sizes, the larvae also were found on coarse substrates (Fig. 2).

Larvae of *Caenis* and *Tricorythodes* co-occur in large northern rivers. I have collected *Caenis* and *Tricorythodes* larvae at rock outcroppings along an 85 km stretch of the sand-bottomed Athabasca River (width = 450 m) in northeastern Alberta (Corkum unpublished). Wiens *et al.* (1975) also reported the presence of both taxa in large rivers, the Porcupine Drainage and channels of the Mackenzie Delta entering the Beaufort Sea. G. Pritchard (personal communication) found larvae of *Tricorythodes* and larvae and female subimagoes of *Caenis* in samples from the Donnelly River, Northwest Territories (65° 53′ N, 128° 11′ W). Despite the northern latitudes, these river sites are not representative of true arctic locales, but occur within the treed areas of the Interior Plains. To date, there are no records of sprawling mayflies from arctic areas (above tree line), suggesting the importance of climate and vegetation in the macrodistribution of sprawling mayflies (H. V. Danks, G. Pritchard, B. Stewart, N. Winchester, personal communications).

Clearly, larvae of *Caenis* and *Tricorythodes* can co-occur in permanent running waters. However, many of the life history studies on these larvae (Robertson, 1967; Kosluchér & Minshall, 1973; Hall *et al.*, 1975; Newell & Minshall, 1978) have been restricted to small rivers, where insects are more easily collected. Berner (1950) suggested that the link between river size (width) and the distribution of sprawling mayflies was related to a permanent water supply required for the maintenance of aquatic macrophytes with which the mayflies were associated.

In Alberta rivers, aquatic plants were present at most sites inhabited by larvae of *Caenis* and *Tricorythodes*. Aquatic vegetation was always present whenever *Caenis* larvae were found on coarse substrates. Thus, plants provided a sheltered habitat for *Caenis* larvae in areas of increased current flow (i.e., where larger substrate particle sizes occur). Although significant relationships were noted between substrate particle size and the distribution of *Caenis* larvae in this study, other moderating features of the habitat associated with the substrate may be more important than particle size in characterizing the microdistribution of larvae.

Bishop (1973) noted the association of *Caenis* larvae with roots of *Saraco thaipingensis* Cantley in the Sungai Gombak, a small Malayan river. He suggested that the microdistribution of *Caenis* larvae in this stream was a function of food availability and habitat stability rather than a particular substrate type. B. S. Svensson (personal communication) also suggested the importance of substrate stability rather than particle size to explain the occurrence in Europe of *Caenis rivulorum* Eton in stony streams with elevated flow. A dense layer of vegetation covers the stones and localizes food particles.

Those river sites where *Tricorythodes* larvae alone were found may be viewed as a subset of all habitats in which *Caenis* larvae occurred (Fig. 1). Although current velocity was unrelated to the presence or absence of either taxa, the indirect sorting effect of flow on substrate particle size probably determined taxonomic occurrence. The particular association between *Tricorythodes* larvae and clean, coarse substrates in large or permanent rivers suggests a potential for these larvae to invade wave-washed, rocky shores of lakes (cf. Clemens, 1915). Larvae of *Caenis* were found on both fine (silty) and coarse substrates in narrow deep rivers within the study area. The variety of stable substrate types with which *Caenis* larvae was associated accounts for the prevalence of the group in lentic and lotic systems.

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