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All the best,
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Use of alternative classifications in studying broad-scale distributional patterns of lotic invertebrates

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Abstract. Multivariate analyses were used to examine relationships between each of three biological classifications of mayfly (Ephemeroptera) larvae and environmental variables recorded at 95 river sites encompassing 18 degrees of latitude in northwestern North America. Biological samples, collected by kick net, were classified by family and superfamily, by size, and by morphological/behavioural group. Environmental variables included measures obtained from topographical maps and hydrological features recorded at each site.

Results of canonical correlation analyses showed that all three biotic indicators were significantly associated with environmental variables. Morphological/behavioural classification yielded stronger correlations with environmental data than did taxonomic or size classifications. Multivariate curvilinear regression analyses gave equivalent results and showed that, although several relationships were curvilinear, all were monotonic. Environmental variables independently and significantly associated with mayfly relative abundance included river size, velocity, slope, latitude, and conductivity. Use of alternative classification variables can potentially reveal patterns not evident when standard taxonomic units are applied.

Key words: rivers, Ephemeroptera, taxonomy, morphology, behaviour, size, multivariate analysis.

Empirical relationships between benthic invertebrates and environmental variables at river sites have been examined extensively to identify zones of invertebrate assemblages arranged from headwaters to river mouth (Hawkes 1975). Taxonomic and/or functional feeding classifications of benthic invertebrates have been used as the biotic indicator in most such lotic studies (Hawkins and Sedell 1981, Minshall et al. 1982, Ward and Berner 1980). Relationships derived from taxonomic categorization reflect broad environmental requirements and the biogeography of constituent groups. Trophic classifications, which combine animals possessing similar feeding behaviour, can reveal patterns of energy availability and use that may not be apparent when taxonomically related but ecologically distinctive organisms are grouped together. Our study investigated whether two alternative classifications of invertebrates (body size and morpho-behavioural design) also might reveal biotic/abiotic associations of ecological significance.

Sprules (1984) showed that certain size classes of zooplankton corresponded strongly with particular limnological features of lakes in large-scale comparative studies. In lotic systems as in other habitats, size of animals at maturity may reflect prevailing environmental characteris-

tics. Additionally, biotic selective forces such as predation can be related to relative size of predators and prey; size-selective feeding in streams has been documented for both invertebrates (Allan 1982, Sjöström 1983) and vertebrates (e.g., Newman and Waters 1984).

Locomotory behaviour (usually constrained by morphological form) also may be associated with both biotic and abiotic habitat features. Convergence in body form is such that morphologically similar but distantly related animals occupy equivalent lotic habitats on a global basis (Hynes 1970). This similarity in form presumably induces characteristic behavioural responses to environmental conditions (Ciborowski and Corkum 1980, Otto and Sjöström 1986). Furthermore, modes of foraging and predator avoidance are entirely locomotory behavioural attributes (Corkum and Clifford 1981, Molles and Pietruszka 1983, Peckarsky 1987).

In this study, we assess the potential utility of three different classification systems in revealing distributional patterns of lotic invertebrates over broad geographical regions. We examined the associations of classifications of taxonomy, morphology/behaviour, and size of mayfly (Ephemeroptera) larvae with environmental variables recorded at river sites throughout northwestern North America by us-

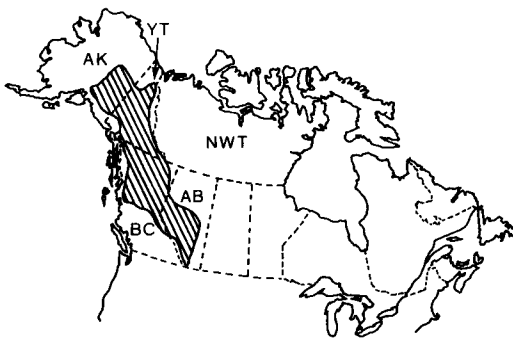


FIG. 1. Study area. Locales indicated are AB, Alberta; AK, Alaska; BC, British Columbia; NWT, Northwest Territories; YT, Yukon Territory.

ing multivariate analytical techniques. Mayflies occur throughout the study area and all larval stages can be identified to family level; the same is not always true for other taxa. Additionally, these larvae display diverse morphology/behaviour and vary markedly in size at maturity. Because most lotic mayfly larvae are similar in feeding habit and exhibit stereotyped feeding behaviour (usually collecting or scraping; Britain 1982, Edmunds 1978), trophic categories were not included in our study.

Methods

Study area

The study area included 101 river sites in northwestern North America (Alberta, northern British Columbia, the Yukon Territory, and Alaska) (Fig. 1). Considerable variation in river characteristics (Table 1) was recorded within this extensive geographical area (latitude 49°23'N to 66°59'N, longitude 112°07'W to 150°15'W). To ensure that a sufficient number of sites would be sampled equitably among the various regions of the study area, sites were preselected from overlays of maps showing continental drainage basins, physiographic regions, geological types, and vegetative zones. Sample sites were restricted to locales free from municipal and industrial effluents. However, some rivers draining agricultural regions were sampled. Riffles, if present at a site, were sampled in preference to pools. River names, sample site locations, and other data are presented

TABLE 1. River characteristics at sites where mayflies occurred ($n = 95$).

| Variables (Units) | Minimum | Median | Maximum |
|-----------------------------------|---------|--------|---------|
| Elevation (m) | 56 | 838 | 1219 |
| Slope (m/km) | 0.3 | 6.0 | 303.4 |
| Distance to Pacific Ocean (km) | 35 | 557 | 994 |
| Site distance to source (km) | 1 | 19.5 | 501 |
| Stream width (m) | 1.8 | 9.0 | 230.0 |
| Mean current velocity (m/s) | 0.01 | 0.62 | 4.50 |
| Mean depth (cm) | 6 | 30 | >70 |
| Conductivity ($\mu\text{S/cm}$) | 9 | 188 | 1380 |
| pH | 4.4 | 8.0 | 8.9 |

by Corkum and Currie (1987) and Corkum (1988).

Sampling procedure

River sites were visited once in summer: forty-two Alberta sites were sampled in 1979 (11–21 June); the remaining northwestern sites were sampled in 1980 (22 July–26 August). Although repeated collections encompassing all seasons are preferable to single visits, we attempted to minimize possible problems of seasonal community progression by sampling from south to north.

Environmental variables examined ($n = 10$) included some measures obtained from topographical maps and others recorded at each river site. Values of latitude, elevation, slope, river distance from site to source, and straight line distance from site to Pacific Ocean (to incorporate possible maritime climatic effects) were determined from maps. Hydrological variables recorded at each site included river width, mean current velocity (Price Gurley meter), mean depth (average of three to five measurements equidistant along a transect), conductivity (Yellow Springs Instrument Co., model 33), and pH (Fisher digital meter, model 109).

The objective of the benthic sampling procedure was to obtain the greatest invertebrate diversity possible within a limited time. Three-minute kick net samples have been used extensively in Britain to evaluate relationships between lotic invertebrates and environmental

factors (Armitage et al. 1983, Wright et al. 1984). In our study, benthic fauna was collected by taking three, 1-min kick net samples (mesh opening: 180 μm) at $\frac{1}{4}$, $\frac{1}{2}$, and $\frac{3}{4}$ of the distance across the stream channel. The samples were pooled and preserved in Kahle's fluid. Sorting was done in the laboratory using a dissecting microscope. Insects composed 33.4% of all aquatic invertebrates ($n = 480,935$) collected at 101 sites; mayflies were found at 95 sites and represented 32.6% of all insects collected.

Following sorting, mayflies at each site were enumerated according to each of three forms of classification. Larvae were initially tabulated by family, producing a classification consisting of eight groups. Representatives of a ninth family, Baetiscidae, occurred in small numbers at two sites; they were not considered in this particular enumeration. Because our other two classification schemes (below) each contained only five classes, we also analysed a coarser taxonomic grouping, wherein mayflies were assigned to one of five superfamilies (McCafferty and Edmunds 1979): Baetoidea (Siphonuridae, Baetidae, Heptageniidae), Leptophlebioidea (Leptophlebiidae), Ephemerelloidea (Ephemerellidae, Tricorythidae), Caenoidea (Caenidae), and Ephemerioidea (Ephemeridae).

A second, morpho-behavioural classification entailed grouping together mayflies of similar body form and locomotory behaviour (Corkum 1978, Edmunds 1978, Needham et al. 1935). Mayflies were assigned among five groups. These groupings may be related to mayfly taxonomic designations (Swimmer: Siphonuridae, Baetidae; Clinger: Ephemerellidae; Crawler: Heptageniidae, Leptophlebiidae; Sprawler: Tricorythidae, Caenidae, Baetiscidae; Burrower: Ephemeridae).

Lastly, size (total body length, excluding cerci) of mature mayfly larvae was considered. All mature animals (those with mesothoracic wing-pad lengths greater than the distance between them: Clifford's (1970) stage III and IV) from every fourth river site were measured to produce a pooled size frequency distribution for each family of mayflies. Total length of all mature mayflies ranged from 1.76 to 13.00 mm. Accordingly, five 2.24-mm size classes were created (1.76-4.00 mm, 4.01-6.25 mm . . . 10.76-13.00 mm). The members of a family at each site were then assigned to size classes in proportion

determined by the appropriate size frequency distribution.

Data analysis

We used two approaches to evaluate the biotic/abiotic relationships in rivers. Initially, canonical correlation and redundancy analyses were performed to determine the degree of association between the relative abundance of groups in each of the three biological classifications (taxonomy, morpho-behaviour, size) and environmental variables for the 95 river sites. Several authors (Green 1972, Miles and Ricklefs 1984, Miles et al. 1987, Quinn and Hower 1986, Sheldon and Haick 1981, Sprules 1984) have applied this approach to resolve similar sorts of ecological problems. However, this form of analysis has shortcomings in that the statistical model assumes that there is no intercorrelation within groups of variables (i.e., all environmental variables are independent of one another and all biological groups are independent of one another). Lack of independence does not affect the value of correlation coefficients, but makes estimates of statistical significance taken from standard tables unreliable. A second assumption of the analysis is that any relationship between groups of variables (i.e., between biological and environmental measurements) will be linear (Pimentel 1979, Sheldon and Haick 1981). The analysis will not detect cases in which maximum abundance might occur at some intermediate value within the measured range of an environmental variable.

To make the assumption of linearity more tenable, we transformed the data. Relative abundance data for the biological variables were transformed into octaves (Gauch 1982). The environmental variables were normalized through logarithmic transformations (with the exception of pH, which is already in logarithmic form); degrees of latitude were transformed into radians.

To further address the problems of linearity and independence, we used a second statistical approach incorporating principal component and multiple regression analyses. Principal component analysis was applied to the (potentially intercorrelated) environmental variables to express these data as a smaller number of statistically independent variables. Multiple

regressions were then performed to relate relative abundance of biological groups to linear and quadratic values of the principal component scores. Nonlinear relationships between biological and environmental variables, if present, would then be described by quadratic regression coefficients significantly different from zero.

Canonical correlation analysis

Canonical correlation analysis (CCA) (Cooley and Lohnes 1985) was used to examine the degree to which components of each biological data set were correlated with the environmental variables. This analysis determines the linear combination of variables (known as canonical variates) from each of the data sets such that the correlation between the canonical variates from each set is maximized. An additional pair of canonical variates, uncorrelated with the first, may be extracted (as are subsequent pairs) and the statistical significance of the association may be assessed for each pair. Redundancy coefficients quantify the percentage of total variance of one data set that is explained by the linear combination derived for the second set of variables. Separate analyses were performed to relate each of the three mayfly classifications to the environmental data set using the SAS procedure, CANCECORR (SAS 1985).

In comparing the relative strengths of association between the biological and environmental data sets for the three different mayfly classifications, it is important to select a similar number of variable classes within each biological category. The fewer the number of variables, the greater will be the total variance extracted by the first canonical variate. Accordingly, we performed three analyses to compare five taxonomic (superfamily), five behavioural, and five size designations with the environmental data set. To determine the effect of increasing taxonomic resolution, we also examined the association between eight mayfly families and the environmental data set.

Principal component and multiple regression analyses

We used principal component analysis (PCA) to reduce the environmental data set to a few independent components (Dixon and Brown

1979). Variables were transformed (see above) before analysis. The first principal component accounts for the greatest proportion of total variation among sites; successive components contribute progressively smaller portions of the total variation explained by the analysis. We interpreted the ecological meaning of the principal components by calculating the Spearman rank correlation (Sokal and Rohlf 1981) between the principal component scores and each of the original environmental variables for the 95 river sites. Subsequently, we examined relationships (linear and quadratic) between the relative abundance of the biological groups and the environmental variables represented by the independent principal components. Multiple regression analysis was used to test for the best fit between the biotic and abiotic data sets using the SAS procedure, GLM (SAS 1985).

Results

Canonical correlation analyses

Taxonomic classification.—Results from the canonical correlation analysis of the five taxonomic (superfamily) and environmental data sets showed that only the first canonical variate (CV) differed significantly from zero ($p < 0.0001$) (Appendix 1). The abundance of Caenoidea (and to a lesser extent, Ephemerelloidea) varied with conductivity, latitude, mean current velocity, and mean depth (Appendix 1). These larvae were more abundant in deep, slow-flowing waters with high conductivity levels at low latitudinal river sites.

Comparison of eight mayfly families with the environmental variables also produced only one canonical variate significantly different from zero ($p < 0.0001$) (Appendix 2). Abundances of Caenidae, Ephemerellidae, and Heptageniidae were correlated with latitude, conductivity, and mean current velocity. Caenids (and to a much lesser extent, ephemerellids) tended to occur at low latitudinal river sites with high conductivity levels and low mean current velocities. In contrast, heptageniid larvae were relatively more abundant at river sites at high latitudes with faster currents and lower conductivity levels.

Morpho-behavioural classification.—In comparisons between morpho-behavioural and environmental data sets, CV-I ($p < 0.0001$) and CV-

TABLE 2. Redundancies of biological and environmental data sets for all significant canonical factors for the three biological classifications. SF = superfamilies, F = families.

| Classification | Canonical Factor | Biological | | Environmental | | Canonical R^2 |
|----------------|------------------|--------------------|-----------------------|--------------------|-----------------------|-----------------|
| | | Variance Extracted | Cumulative Redundancy | Variance Extracted | Cumulative Redundancy | |
| Taxonomy | | | | | | |
| 5 SF | 1 | 0.251 | 0.145 | 0.316 | 0.182 | 0.577 |
| 8 F | 1 | 0.196 | 0.131 | 0.303 | 0.203 | 0.670 |
| Behaviour | 1 | 0.296 | 0.204 | 0.332 | 0.229 | 0.690 |
| | 2 | 0.500 | 0.270 | 0.465 | 0.272 | 0.325 |
| Size | 1 | 0.316 | 0.140 | 0.157 | 0.070 | 0.443 |

II ($p < 0.03$) were both significantly greater than zero; the third CV ($p = 0.703$) was not (Appendix 3). Results of correlations with CV-I revealed that sprawlers were most abundant in rivers at low latitudes and with high conductivity levels. A similar, but weaker association was observed for swimmers and clingers. Values of CV-II suggested that the relative abundances of crawling, clinging, swimming, and sprawling larvae were correlated positively with river width, slope, and mean current velocity, but negatively with distance from site to ocean. The clingers and crawlers were most abundant in large, steep-gradient, swift rivers of British Columbia, the Yukon, and Alaska.

Size classification.—When size categories and environmental data sets were compared, CV-I ($p < 0.0001$) was significantly different from zero, but CV-II ($p = 0.088$) was not (Appendix 4). Mid- to large-sized larvae (size class III: 6.26–8.50 mm and size class IV: 8.51–10.75 mm) were most abundant in wide, fast-flowing rivers.

The degree to which variation in biological and environmental space is related to the canonical variates is shown by canonical redundancy analysis (Table 2). The squares of the correlation coefficients (R^2), which represent the variance shared by the linear composites of each biological grouping and environmental data set, were higher for morpho-behavioural type than either taxonomic (5-group) or size designations.

The first two significant morpho-behavioural variates extracted 50.0% of the variance in the behavioural variables among sites; the first two significant environmental variates extracted 46.5% of the variation in the environmental variables (Table 2). The cumulative redundancies between morpho-behavioural and environmental data sets were 0.270 and 0.272, respec-

tively. Thus, 27.0% of the variance in the original morpho-behavioural data was accounted for by the environmental data and 27.2% of the variance in the environmental data was accounted for by the morpho-behavioural data set. Lower proportions of the variance were explained for superfamilial/environmental (0.145 and 0.182, respectively), familial/environmental (0.131 and 0.203, respectively), and size/environmental (0.140 and 0.070, respectively) data sets. We are unaware of a method to determine whether or not these differences among classifications are statistically significant.

Principal component and multiple regression analyses

Principal component analysis.—Three principal components accounted for a total of 72.2% of the variability in the environmental data from the 95 river sites (Table 3). Six of ten variables had strong correlations ($p < 0.01$) with PC-I. The first principal component accounted for 43.4% of variability in the data set. Variables most highly correlated with PC-I ($p < 0.001$) were measures of river size and geographical location. Thus, sites possessing high PC-I scores were characteristically on large (deep, wide) rivers with gentle slopes, well downstream from headwaters, away from maritime effects, and at lower latitudes in the study area.

An additional 17.2% of total variability in the data was summarized by PC-II. Values of PC-II were negatively correlated with current velocity ($p < 0.001$) and positively correlated with distance to ocean, conductivity, and altitude ($p < 0.001$). Typical river sites having high PC-II scores would be located at high elevations away from the ocean, and would be described by re-

TABLE 3. Eigenvectors and correlations of environmental variables with the first three principal components (PC-I, PC-II, PC-III) for the 95 river sites. Probability (p) of obtaining observed product-moment correlation if true value is zero (2-tailed test). * $p < 0.01$, ** $p < 0.001$.

| Variable | PC-I | | PC-II | | PC-III | |
|--------------------|-------------|-------------|-------------|-------------|-------------|-------------|
| | Eigenvector | Correlation | Eigenvector | Correlation | Eigenvector | Correlation |
| Width | 0.914 | 0.89** | -0.139 | -0.18 | 0.031 | -0.08 |
| Distance to source | 0.901 | 0.88** | 0.155 | 0.16 | 0.192 | 0.12 |
| Depth | 0.846 | 0.87** | 0.124 | 0.11 | -0.056 | -0.19 |
| Slope | -0.721 | -0.74** | -0.425 | -0.39* | -0.023 | 0.01 |
| Latitude | -0.617 | -0.65** | -0.260 | -0.33* | -0.250 | -0.21 |
| Distance to ocean | 0.491 | 0.62** | 0.697 | 0.63** | -0.035 | -0.10 |
| Conductivity | 0.220 | 0.23 | 0.553 | 0.46** | 0.714 | 0.73** |
| Altitude | 0.169 | 0.21 | 0.584 | 0.42** | 0.169 | 0.24 |
| Mean velocity | 0.082 | 0.07 | -0.774 | -0.76** | -0.041 | 0.04 |
| pH | 0.023 | -0.06 | -0.010 | -0.02 | 0.976 | 0.96** |
| % Total variance | 43.34 | | 17.22 | | 11.65 | |
| Cumulative % | 43.34 | | 60.56 | | 72.21 | |

duced current velocities and relatively high conductivity levels.

The third PC, which accounted for an additional 11.6% of the variability in the data, separated river sites on the basis of water chemistry. River sites with high PC-III values exhibited elevated levels of pH and conductivity ($p < 0.001$).

Multiple regression.—Multiple regressions were performed to relate each set of biotic classifications (taxonomy, morpho-behaviour, size) with independent abiotic (principal components) variables using the model:

$$Y = B_0 + B_1(\text{PC-I}) + B_2(\text{PC-I})^2 + B_3(\text{PC-II}) + B_4(\text{PC-II})^2 + B_5(\text{PC-III}) + B_6(\text{PC-III})^2$$

To simplify descriptions of these results, we will use the following terms to represent each of the three principal components: PC-I, river size; PC-II, current velocity; PC-III, water chemistry.

Results of the multiple regressions closely matched results of CCA in that the same groups within each classification were related to equivalent environmental variables in both analyses. Although regression coefficients of some quadratic terms were significantly different from zero, these coefficients were always of the same sign as the coefficient of the linear term of a variable (Table 4). This shows that nonlinear relationships between biological groups and

environmental variables were exponential, not parabolic.

Taxonomic relationships.—The strongest taxonomic/abiotic association ($R^2 = 0.54$, $F = 17.35$) was described for Caenoidea (Table 4). Relative abundances of both Caenoidea and Ephemeroidea were related linearly to river size (PC-I) and curvilinearly to current velocity (PC-II). However, whereas abundance of Caenoidea was greatest at slow velocity sites, that of Ephemeroidea was greatest at rapid velocity locations. No significant associations were observed between larvae of Baetoidea, Leptophleboidea, or Ephemeroidea and any of the principal components (Table 4).

Because Caenoidea was represented by one family, Caenidae, results of the regression analyses between larval abundance and principal components for superfamily and family were identical (Tables 4, 5). Larval abundance of both families within the Ephemeroidea (Ephemeroidea and Tricorythidae) increased linearly with river size (PC-I). Relative abundance of ephemeroellids, which decreased curvilinearly with decreasing flow, accounted for the same trend observed within the superfamily. Although no significant associations were observed between larval abundance of Baetoidea and principal components, significant relationships were noted between data sets for representative families, Heptageniidae ($R^2 = 0.34$) and Baetidae ($R^2 = 0.16$). Relative abundance of heptageniids decreased in curvilinear fashion

TABLE 4. Summary of multiple regression analyses to test for the relationship between relative abundance of biotic (taxonomy, morpho-behaviour, size) and abiotic (three principal components) variables "Relationship" column describes whether a term is linear or quadratic. Values of *t* are presented only for those regression coefficients significantly different from zero. Sign of *t*-value indicates whether relationship is positive or negative. *F*-values indicate significance of overall regression. Probability: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| Biotic Variables | Abiotic Variables | Relationship | <i>t</i> -value | Regression <i>F</i> -value | <i>R</i> ² |
|--------------------|-------------------|--------------|-----------------|----------------------------|-----------------------|
| Taxonomy: | | | | | |
| Baetoidea | — | — | — | 1.89 | 0.11 |
| Leptophlebioidea | — | — | — | 0.89 | 0.06 |
| Ephemeroidea | PC-I | linear | 3.08** | 4.44*** | 0.23 |
| | PC-II | linear | -2.93** | | |
| | PC-II | quadratic | -2.40* | | |
| Caenoidea | PC-I | linear | 3.55*** | 17.35*** | 0.54 |
| | PC-II | linear | 7.95*** | | |
| | PC-II | quadratic | 5.09*** | | |
| Ephemeroidea | — | — | — | 2.06 | 0.12 |
| Morpho-behaviour: | | | | | |
| Swimmer | PC-III | quadratic | -2.72** | 4.06** | 0.22 |
| Clinger | PC-I | linear | 2.59* | 3.78** | 0.20 |
| | PC-II | linear | -2.96** | | |
| | PC-II | quadratic | -2.18* | | |
| Crawler | PC-II | linear | -5.37** | 7.66*** | 0.34 |
| | PC-II | quadratic | -3.31** | | |
| Sprawler | PC-I | linear | 5.69*** | 17.00*** | 0.54 |
| | PC-II | linear | 6.87*** | | |
| | PC-II | quadratic | 4.03*** | | |
| | PC-III | linear | 2.59* | | |
| Burrower | — | — | — | 2.06 | 0.12 |
| Size: | | | | | |
| I (1.76-4.00 mm) | PC-I | linear | 3.12** | 2.47* | 0.14 |
| II (4.01-6.25 mm) | — | — | — | 1.52 | 0.09 |
| III (6.26-8.25 mm) | PC-I | linear | -2.32* | 4.42*** | 0.23 |
| | PC-II | linear | -3.79*** | | |
| | PC-II | quadratic | -2.52* | | |
| IV (8.51-10.75 mm) | PC-I | linear | 2.03* | 6.09*** | 0.29 |
| | PC-II | linear | -4.59*** | | |
| | PC-II | quadratic | -3.42*** | | |
| V (10.76-13.00 mm) | PC-II | linear | -3.42*** | 3.84** | 0.21 |
| | PC-II | quadratic | -2.07* | | |

with decreasing current velocity (PC-II). A weak, but significant relationship showed that larval abundance of baetids increased curvilinearly with elevated levels of pH and conductivity (PC-III). No significant relationships were found between larvae of Siphonuridae or Ephemeridae and any of the principal components (Table 5).

Morpho-behavioural relationships.—Significant

associations were observed between four of the five morpho-behavioural groups and abiotic variables (Table 4). The most highly significant relationship was described for sprawlers ($R^2 = 0.54$, $F = 17.0$). Relative abundance of sprawlers increased linearly with river size (PC-I) and water chemistry values (PC-III), but was curvilinearly reduced at high velocity sites (PC-II). In contrast, abundance of both crawlers and

TABLE 5. Summary of multiple regression analyses to test for the relationship between relative abundance of mayfly larvae for each family and abiotic (three principal components) variables. "Relationship" column describes whether a term is linear or quadratic. Values of *t* are presented only for those regression coefficients significantly different from zero. Sign of *t*-value indicates whether relationship is positive or negative. *F*-values indicate significance of overall regression. Probability: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| Mayfly Family | Abiotic Variables | Relationship | <i>t</i> -value | Regression <i>F</i> -value | <i>R</i> ² |
|-----------------|-------------------|--------------|-----------------|----------------------------|-----------------------|
| Siphonuridae | — | — | — | 1.01 | 0.06 |
| Baetidae | PC-III | quadratic | -2.63* | 2.74* | 0.16 |
| Heptageniidae | PC-II | linear | -5.52*** | 7.43*** | 0.34 |
| | PC-II | quadratic | -3.12** | | |
| Leptophlebiidae | — | — | — | 0.89 | 0.06 |
| Ephemerellidae | PC-I | linear | 2.59* | 3.78** | 0.20 |
| | PC-II | linear | -2.96** | | |
| | PC-II | quadratic | -2.18* | | |
| Tricorythidae | PC-I | linear | 3.12** | 2.47* | 0.14 |
| Caenidae | PC-I | linear | 3.55*** | 17.35*** | 0.54 |
| | PC-II | linear | 7.95*** | | |
| | PC-II | quadratic | 5.09*** | | |
| Ephemeridae | — | — | — | 2.01 | 0.12 |

clingers was positively curvilinearly related with water velocity. A positive linear relationship also was noted between clinger abundance and river size. Abundance of swimmers was curvilinearly reduced at sites of increased levels of pH and conductivity (PC-III).

Size relationships.—Significant relationships were observed between four of five size classes of mayflies and environmental variables represented by the first and second principal components. The abundance of the largest size classes (III, IV, V) decreased curvilinearly with increasing levels of PC-II. Thus, larger mayfly larvae were more prevalent in faster waters. There were positive linear relationships between larval abundance of size classes I and IV and river size. In contrast, a negative linear relationship was noted between size class III mayflies and river size.

Discussion

In large geographical areas, organisms that are identified to family, genus, or species are seldom pandemic. If faunal predictions are to be applicable across extensive regions, "life forms" should be more useful than taxonomic designations when developing empirical relationships (Thorup 1966). Hawkes (1975) showed that when attempts were made to apply the taxonomic designations derived from single-

river zonation studies to other drainage basins, the predictive power of such schemes declined dramatically. Yet, equivalent morpho-behavioural groups of organisms may occur in similar riverine environments on different continents. Hynes (1970) related morphological adaptations (e.g., flattening of body, streamlining) of benthic invertebrates to changes in current flow and substrate type using examples from riverine studies conducted throughout the world. Larval size at maturity, which may reflect growth period, fecundity (Sweeney and Vannote 1978), or possible outcomes of competitive interactions, is another potentially useful biological component in synoptic studies.

Our study showed that three different classification groupings of mayflies (taxonomy, morphology/behavior, and size) could each be related to environmental variables at river sites throughout northwestern North America. In addition to the traditionally used taxonomic variables, both morpho-behavioural and size classifications were useful in developing empirical relationships. Results of canonical correlation analysis showed that morpho-behavioural grouping was better than coarse taxonomic or size classifications in terms of the strength of the statistical association between mayfly larval abundance and environmental data sets at river sites within the study area.

We detected a positive association between relative abundance of Caenoidea and deep, slow-flowing rivers with high conductivity levels at low latitudes within the study area. Canonical correlation analysis also showed weak, but significant relationships between larvae of Ephemerelloidea and these same environmental features. The regression analysis verified that Ephemerelloidea were more dominant in larger rivers but, in contrast to Caenoidea, larvae prevailed in fast-flowing waters. Larvae within the mayfly family Heptageniidae were abundant in higher latitude, fast-flowing waters with low conductivity. Such river sites are located in hilly or mountainous regions of the study area. No consistent associations were discerned for other families within Baetoidea or for other superfamilies.

The most highly significant relationship of all morpho-behavioural groups was between the relative abundance of sprawlers (Baetiscidae, Caenidae, Tricorythidae) and abiotic variables. Although morpho-behavioural types were identified by family for convenience, no taxonomic knowledge is required to describe the activity traits of mayfly larvae. Direct observation of living specimens or the morphological description of preserved specimens would result in the same or similar groupings.

Sprawling mayfly larvae were positively associated with low latitudinal rivers high in conductivity. These river sites were within the Interior Plains of Alberta that drained eastward into Hudson Bay or northward into the Arctic Ocean. Despite the apparent relationship with latitude, other workers have collected sprawling mayflies in northern rivers of the Interior Plains (Wiens et al. 1975). Thus, the significance of latitude may reflect merely the influence of the physiographic region, Interior Plains, in the southern portion of the study area rather than climatic features (e.g., temperature). Rivers of the Plains flow over sedimentary rock and characteristically have high conductivity. River sites sampled in the north and west were located within the Cordillera. Here, clingers and crawlers were most abundant; these larvae occurred in large, steep-gradient, fast-flowing rivers.

Significant associations also were noted between size class groupings and environmental variables. We found mature individuals of both small and large mayfly larvae to be most abundant in wide, deep, fast-flowing waters. Mid-

sized larvae predominated in narrow, shallow rivers. Thus, size of larvae at maturity reflected the prevailing physical characteristics of rivers.

The patterns that we have discerned represent correlations between variables and do not of themselves explain the relationships. Several of the trends that we detected are perhaps those that could be anticipated by a naturalist familiar with mayflies within a particular region of North America. Other trends may be less obvious. Many reasonable a posteriori arguments could be developed to account for the patterns that we observed, but none would be conclusive. We prefer not to speculate on explanations for specific findings. Yet, the fact that trends are evident in the data affirms that alternative classifications can provide variables suitable for testing predefined hypotheses.

The selection of appropriate variables in a study should be a function of both research objective and scale. For example, the river continuum concept of Vannote et al. (1980) synthesized a complex description of biological mechanisms operating in a drainage basin. Since their analysis dealt with energy transport and transfer among trophic levels, it was logical for them to predict qualitative changes in the benthic fauna in terms of functional feeding groups (a trophic classification) rather than on the basis of taxa. Theoretically, the working hypotheses of the continuum concept could be translated into predictions relating energy flow in streams of different sizes, flow rates, or water chemistry (simply measured variables such as we used in our study) and relative abundance of invertebrates (e.g., Minshall et al. 1983) that would permit quantitative testing. Alternatively, size class distributions of invertebrates could be used to test continuum concept predictions that are independent of functional feeding groups. The goodness-of-fit of such predictions could then be directly contrasted with predictions of other energy-based models of ecosystem structure. Dickie et al. (1987) showed that by using two-fold scaling factors of physiological and ecological size relationships, energy flow within a community could be determined from the distribution of body sizes without specifying the trophic levels of the organisms involved.

Other hypotheses have been proposed to explain the community structure of rivers whose significance may best be tested using size classifications. Vannote and Sweeney (1980) pro-

posed a "thermal equilibrium hypothesis" to explain the size variation, geographic distribution, and community structure of aquatic insects in rivers. They showed that fecundity and adult body size of aquatic insects depended on thermal conditions during larval growth. Small adults and reduced fecundity occurred when water temperatures deviated from species-specific thermal optima (Sweeney and Vannote 1978). Since magnitude of diel variation in water temperature varies markedly with river size (Vannote and Sweeney 1980) as well as with other hydrological (depth, velocity) and landscape (riparian shading) features, the correlation of environmental attributes with size class distributions may provide suitable tests of temperature-community hypotheses.

If groups of herbivorous organisms (e.g., mayflies) are associated with particular environmental variables, then it may also be possible to predict the distribution of their predators. Predacious stoneflies ingest a diversity of prey items (Molles and Pietruszka 1983) suggesting that biological cues other than taxon (size or shape) may be important to the foraging behaviour of predators. Indeed, Sjöström (1983) demonstrated that prey size was more important than prey species to the diet of a perlid, *Dinocras cephalotes* (Curtis). Accordingly, one might speculate that mayfly larvae having different body sizes at maturity invoke different predator avoidance mechanisms.

Hypotheses that address patterns of community development by considering colonization and foraging dynamics of invertebrates (Ciborowski 1987, Hart 1985, McAuliffe 1984) might become more broadly applicable through consideration of strategies of morphological types in addition to taxonomic relationships. Although species and genera may be habitat-specific, highly vagile foragers may contrast strongly in appearance and size with those that occupy single localized, stable microhabitats. Relative abundance of such groups will vary with physical stability of the stream (McAuliffe 1984).

Taxonomy will continue to serve as a basis for classifications in benthological investigations and as a starting point for trophic assignments of aquatic insects (Merritt and Cummins 1978). Our results suggest that morpho-behavioural and/or size classifications may be equally appropriate and useful in macrodistributional

studies. Appropriate a priori selection of biological as well as environmental variables may improve the likelihood of revealing patterns of greatest ecological significance (cf. Sprules 1984).

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APPENDIX 1. Canonical correlation analysis for five mayfly superfamilies and 10 environmental variables. Wilk's lambda is used to test the null hypothesis that the canonical correlation coefficients are zero. The vectors are standardized and normalized. Data are evaluated by determining which variables contributed most to the paired canonical variates. Coefficients $> \pm 0.3$ (in bold face) were arbitrarily selected as revealing associations between the biological and environmental variables. For example, relative abundance of Caenoidea (0.976) is positively associated with conductivity (0.458) and mean depth (0.330), but negatively associated with latitude (-0.377) and mean velocity (-0.342). Variables are listed in order of the strength of their coefficients.

| Canonical Variate | I | II |
|----------------------------------|---------------|-------|
| Canonical correlation | 0.760 | 0.512 |
| Degrees of freedom | 50 | 36 |
| Wilk's lambda <i>F</i> statistic | 2.372 | 0.990 |
| Probability | 0.0001 | 0.491 |
| Taxonomic variables: | | |
| Caenoidea | 0.976 | |
| Ephemerelloidea | 0.314 | |
| Ephemeroidea | 0.273 | |
| Leptophlebioidea | 0.079 | |
| Baetoidea | 0.050 | |
| Environmental variables: | | |
| Conductivity | 0.458 | |
| Latitude | -0.377 | |
| Mean velocity | -0.342 | |
| Mean depth | 0.330 | |
| Width | -0.276 | |
| Distance to source | 0.178 | |
| pH | -0.150 | |
| Distance to ocean | -0.086 | |
| Slope | -0.055 | |
| Elevation | -0.018 | |

APPENDIX 2. Canonical correlation analysis for eight mayfly families and 10 environmental variables. See Appendix 1 for explanation of results.

| Canonical Variate | I | II |
|----------------------------------|---------------|--------|
| Canonical correlation | 0.818 | 0.599 |
| Degrees of freedom | 80 | 63 |
| Wilk's lambda <i>F</i> statistic | 2.263 | 1.169 |
| Probability | 0.0001 | 0.1883 |
| Taxonomic variables: | | |
| Caenidae | 0.711 | |
| Heptageniidae | -0.310 | |
| Ephemerellidae | 0.305 | |
| Ephemeridae | 0.272 | |
| Baetidae | 0.212 | |
| Siphonuridae | 0.116 | |
| Tricorythidae | 0.116 | |
| Leptophlebiidae | -0.038 | |
| Environmental variables: | | |
| Latitude | -0.424 | |
| Conductivity | 0.408 | |
| Mean velocity | -0.350 | |
| Width | -0.256 | |
| Mean depth | 0.251 | |
| Distance to source | 0.132 | |
| Elevation | -0.108 | |
| Slope | -0.104 | |
| Distance to ocean | -0.066 | |
| pH | -0.009 | |

APPENDIX 3. Canonical correlation analysis for five behavioural groups of mayfly larvae and 10 environmental variables. See Appendix 1 for explanation of results.

| Canonical Variate | I | II | III |
|-------------------------------|---------------|---------------|--------|
| Canonical correlation | 0.830 | 0.570 | 0.378 |
| Degrees of freedom | 50 | 36 | 24 |
| Wilk's lambda | | | |
| F statistic | 3.551 | 1.538 | 0.825 |
| Probability | 0.0001 | 0.0295 | 0.7033 |
| Morpho-behavioural variables: | | | |
| Sprawler | 0.743 | 0.433 | |
| Swimmer | 0.333 | 0.457 | |
| Clinger | 0.310 | 0.730 | |
| Crawler | -0.238 | 0.748 | |
| Burrower | 0.186 | -0.147 | |
| Environmental variables: | | | |
| Latitude | -0.523 | -0.201 | |
| Conductivity | 0.386 | 0.210 | |
| Mean velocity | -0.235 | 0.487 | |
| Mean depth | 0.145 | 0.056 | |
| Slope | -0.129 | 0.497 | |
| Distance to source | 0.103 | 0.269 | |
| Width | -0.103 | 0.634 | |
| Elevation | -0.099 | 0.284 | |
| Distance to ocean | 0.073 | -0.435 | |
| pH | 0.044 | -0.077 | |

APPENDIX 4. Canonical correlation analysis for five size classes of mayfly larvae and 10 environmental variables. See Appendix 1 for explanation of results.

| Canonical Variate | I | II |
|--------------------------|--------------|-------|
| Canonical correlation | 0.660 | 0.549 |
| Degrees of freedom | 50 | 36 |
| Wilk's lambda | | |
| F statistic | 2.100 | 1.362 |
| Probability | 0.0001 | 0.088 |
| Size variables: | | |
| Size IV (8.51-10.75 mm) | 0.832 | |
| Size III (6.26-8.50 mm) | 0.547 | |
| Size I (1.76-4.00 mm) | 0.279 | |
| Size II (4.01-6.25 mm) | 0.252 | |
| Size V (10.76-13.00 mm) | 0.216 | |
| Environmental variables: | | |
| Mean velocity | 0.608 | |
| Width | 0.472 | |
| Slope | 0.298 | |
| Conductivity | -0.249 | |
| Elevation | 0.218 | |
| Mean depth | -0.182 | |
| Distance to source | 0.175 | |
| pH | -0.138 | |
| Latitude | 0.132 | |
| Distance to ocean | -0.056 | |