
17 Stream size and the distribution of selected Ephemeroptera

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Information on stream size and mayfly distribution has been largely anecdotal. We studied relationships of stream length (as distance of occurrence from headwaters) and distributions of 57 recently revised and well-documented species of North American Anthopotamus, Baetisca, Caenis, Isonychia, Pseudiron and Stenonema. Our data provide a numerical basis for predicting potential occurrences of these mayflies in different sized streams or regions of streams. Species are categorized as having high stream-size specificity (7 per cent), moderate (81 per cent) or low (12 per cent). Those inhabiting long streams show the least relative variability. Certain species, however, are apparently restricted to short streams. Our stream-length regions proved to be highly compatible with stream order concepts.

Introduction

Several studies of longitudinal zonation in streams have shown species abundance and diversity to change along a stream gradient (see reviews by Hynes 1970 and Hawkes 1975). Published reports of species of stream macroinvertebrates as being found in particular sized streams are often inexact or anecdotal, and surprisingly few attempts to quantify stream-size distributional limits of species have been made. Those ecological studies that have treated the relationship between stream size and species distributions are sparse and usually regionally restricted. Carpenter (1927), in one of the first such studies, demonstrated that short springbrooks contained many more species than lower reaches of long rivers in England. Ulfstrand (1968) related several insects, including Ephemeroptera, to stream size in northern Europe. Mussels were found to be strongly influenced by stream size in southeastern Michigan by Strayer (1990), and relationships between stream size and Trichoptera have been noted by Edington (1965), Mecom (1972) and Floyd and Schuster (1990) in other regions. Vinçon and Thomas (1987), by using factorial analysis, showed an association between stream order and clusters of mayfly

species in France. Like most studies that have included stream size data, the latter concentrated on other limiting ecological parameters.

Some studies have approached the relationship between stream size and occurrence of stream macroinvertebrates in the context of island biogeography theory. Sepkoski and Rex (1974) showed a correspondence between drainage area and numbers of mussel species; Brönmark et al. (1984) studied the role of stream size on macrobenthic community structure; and Minshall et al. (1985) considered species richness and diversity with respect to discharge and link number (Shreve 1966).

General accounts of typical habitats of mayfly species in terms of stream size are numerous, most commonly occurring in species reviews or revisions (e.g., Bednarik and McCafferty 1979), but also to a lesser extent in some biological studies (e.g., Soluk and Clifford 1984), and regional surveys (e.g., Burian and Gibbs 1991). The stream-size information provided in sources such as these is often based on limited or casual observations and is given in approximate or qualitative terms. Some ecological studies of mayfly distribution provide more quantitative data (e.g., Ward and Stanford 1990), but are generally restricted to one stream system and, therefore, lack the broader comparative basis found in revisions. We know of no studies that have quantified relationships between stream length and distributions of mayfly species across their entire ranges.

Our study was undertaken to quantify and analyze associations of well-documented species of Ephemeroptera with precise regions of streams in which they are known to occur. From this, we sought to determine to what degree the occurrence of these species in streams of different length or in different length regions of streams could be predicted.

Methods

Collection records listed in the "Material Examined" sections of recent North American systematic revisions of the mayfly genera *Anthopotamus* (Potamanthidae) (Bae and McCafferty 1991), *Baetisca* (Baetiscidae) (Pescador and Berner 1981), *Caenis* (Caenidae) (Provonsha 1990), *Isonychia* (Isonychiidae) (Kondratieff and Voshell 1984), *Pseudiron* (Pseudironidae) (Pescador 1985) and *Stenonema* (Heptageniidae) (Bednarik and McCafferty 1979) served as our primary raw data. Additional sources of collection records included regional surveys by Mingo, et al. (1979), McCafferty (1990a) and Burian and Gibbs (1991). Data for the only two new species (McCafferty 1981; 1990b) described for any of the above genera since their revisions were also incorporated. One species known as *Stenonema integrum* in Bednarik and McCafferty (1979) is now known as *S. mexicanum* (McCafferty 1984). No other name changes have occurred since the publication of these revisions.

Our study genera were selected because they constitute major groups in North America that recently have been well documented; their revisions contain extensive, accurately associated collection records of species over their entire ranges. Species found only in Mexico or Central America were not included in this study. We did, however, include species that are distributed in both North and Central America, but only the North American records were used in our database. *Baetisca callosa*, *B. columbiana* and *Isonychia notata* were excluded because of their dubious status, and species for which only adults are known had to be disregarded since their collection sites could differ from respective larval development sites. All species analyzed in this study are listed in Tables 1 and 2.

The over 2000 collection localities provided in the data sources listed above were reduced to some 1150 actually used, once lentic and imprecise records were discarded. These usable records were located on published topographic and drainage maps. For each locale record, we established the "size" of the stream at the locale by measuring the length of stream from the locale to the source of the most distant tributary of that stream, thus emphasizing the upstream component of the longitudinal stream dimension discussed by Ward (1989). All measurements were taken with a map wheel and included stream meanders. The map scales used varied depending upon the length of the system, but most measurements were taken from 1:250,000 and 1:100,000 scale maps. Streams were measured by the first author only, minimizing variation in any measurement error. Such quantification of the locales gave a comparative measure of upstream length and allowed us to characterize locales by different stream-length regions in which they occurred (see below).

Mean length location (locale position in terms of measured distance from stream source), geometric mean (of natural log transformed measurements), variance, and coefficient of variation were calculated for each species. The untransformed stream-length measurements were distributed among eight length classes whose limits were defined according to a natural log scale. As such, Class I included records up to 2.7 km in length, Class II from 2.8 to 7.4 km, Class III from 7.5 to 20.1 km, Class IV from 20.2 to 54.6 km, Class V from 54.7 to 148.4 km, Class VI from 148.5 to 403.4 km, Class VII from 403.5 to 1097 km and Class VIII more than 1097 km in length. Using this scheme, the number of records in the length classes approximated a normal distribution. This classification system allowed us to determine frequency distributions based on the number of records in a particular length class for each species. A resulting 57 X 8 table was partitioned into six groups of species based on mean stream length as described below.

Although the eight classes of stream lengths were useful for distributional analysis, a more general classification system was needed for descriptive purposes. We use a gradient of comparative size terms to describe six ranges or regions of stream length. According to our classification, a headwater region is up to eight km from the source (Classes I-III); a very short stream region is 8.1 to 20.0 km from the source (Class III); a short stream region is 20.1 to 40.0 km from the source (Class

IV); a medium length stream region is 40.1 to 100.0 km from the source (Classes IV and V); a long stream region is 100.1 to 200.0 km from the source (Classes V and VI); and a very long stream region is greater than 200 km from the source (Classes VI-VIII). Each species was assigned to a stream region based upon its geometric mean.

Stream order (according to Strahler 1957) at locale positions was also determined for approximately 90 per cent of the records. Stream order data were corrected for minor differences in map scales to match the 1:100,000 scale data (see Leopold et al. 1964). The remaining 10 per cent of the records were from very long rivers and as such were measured from maps with insufficient detail to accurately determine order.

An ANOVA was conducted to compare the mean (log transformed) stream length locations among species. Only species for which five or more reasonably precise collection records could be obtained (51 of the 57 species) were included in the ANOVA, and the analysis employed SAS procedures that were appropriate for unbalanced data (SAS 1989). This statistical technique was chosen because of its simplicity and unambiguous results.

Results and Discussions

The most apparent trend in the untransformed data was the correlation between the mean length locations and their respective variances. Species with means of low magnitude exhibited low variance, whereas species with larger means tended to have proportionally greater variance. For this reason, the data were transformed on a natural log scale and coefficients of variation were used to compare species based on their relative variability. Descriptive statistics for all species are given in Tables 1 and 2.

Results of the ANOVA conducted to compare mean log transformed stream-length locations across species indicated that the means are not equal ($P < 0.001$). Considering the large size of our data set and observed differences in the distribution of location data between species, these results are not surprising. However, the integrity of this statistical analysis is limited by several assumptions (see Sokal and Rohlf 1981). A non-statistical technique (described below) was used to identify trends for individual species.

A method of determining degree of stream-size specificity for species was derived from coefficients of variation (V) and provided a numerical basis for predicting potential occurrences of species in streams based on stream length. The limits of one standard deviation from the mean on an approximately normal curve of coefficients of variation were used to group species according to specificity. A low coefficient of variation calculated for a species indicates high specificity (i.e., relative variation is low enough that the mean is a reliable predictor of the typical

Table 1. Data summary for species associated with relatively short (≤ 40 km) stream regions. Species are assigned to regions based on their geometric means. Means and ranges for regions are in terms of distance from stream source. \bar{x}^* = geometric mean, Range = asymmetric lower-upper limits of one standard deviation of the mean, V = coefficient of variation, H = high, M = moderate, L = low.

	\bar{x}^*	Range	V	Specificity
Headwater Region (0-8 km)				
<i>Isonychia similis</i>	4.7	2.3 - 9.4	45.4	M
<i>Isonychia tusculanensis</i>	5.2	1.6 - 16.3	69.8	L
<i>Stenonema sinclairi</i>	5.6	3.3 - 9.4	30.4	M
<i>Stenonema meririvulatum</i>	6.4	2.4 - 17.1	52.8	L
Very Short Stream Region (8.1-20 km)				
<i>Stenonema luteum</i>	8.1	0.6 - 104.2	121.5	L
<i>Stenonema pudicum</i>	8.7	2.4 - 31.5	59.2	L
<i>Isonychia serrata</i>	10.0	4.3 - 23.5	36.9	M
<i>Isonychia neneri</i>	12.5	2.8 - 56.5	59.8	L
<i>Baetisca berneri</i>	12.9	7.2 - 23.1	22.7	M
<i>Stenonema smithae</i>	13.6	3.7 - 49.1	49.3	M
<i>Stenonema carlsoni</i>	14.0	7.4 - 26.6	24.2	M
<i>Caenis bajaensis</i>	15.8	4.3 - 58.6	47.3	M
<i>Stenonema ithaca</i>	17.9	6.6 - 48.5	34.6	M
<i>Baetisca carolina</i>	18.7	5.7 - 61.1	40.4	M
<i>Caenis macafferti</i>	18.7	5.8 - 60.4	40.0	M
<i>Stenonema modestum</i>	18.7	3.3 - 106.1	59.3	L
Short Stream Region (20.1-40 km)				
<i>Anthopotamus distinctus</i>	21.4	5.7 - 80.4	43.2	M
<i>Stenonema femoratum</i>	21.4	7.6 - 60.3	33.8	M
<i>Stenonema bednariki</i>	21.6	9.4 - 49.5	26.9	M
<i>Stenonema vicarium</i>	23.5	5.8 - 95.4	44.4	M
<i>Baetisca rogersi</i>	23.9	10.2 - 56.2	26.9	M
<i>Isonychia georgiae</i>	24.4	11.1 - 53.8	24.8	M
<i>Caenis diminuta</i>	26.4	9.4 - 73.7	31.4	M
<i>Caenis youngi</i>	26.8	12.7 - 56.7	22.7	M
<i>Isonychia obscura</i>	29.7	7.8 - 112.5	39.3	M
<i>Baetisca becki</i>	33.1	16.1 - 67.9	20.5	M
<i>Baetisca rubescens</i>	33.7	5.3 - 213.7	52.5	L
<i>Isonychia bicolor</i>	37.9	7.7 - 185.8	43.7	M
<i>Stenonema pulchellum</i>	38.3	13.2 - 110.7	29.1	M
<i>Stenonema mediopunctatum</i>	39.1	14.9 - 102.7	26.4	M

Table 2. Data summary for species associated with relatively long (>40 km) stream regions. Species are assigned to regions based on their geometric means. Means and ranges for regions are in terms of distance from stream source. \bar{x}^* = geometric mean, Range = asymmetric lower-upper limits of one standard deviation of the mean, V = coefficient of variation, H = high, M = moderate, L = low.

	\bar{x}^*	Range	V	Specificity
Medium Length Stream Region (40.1-100 km)				
<i>Isonychia hoffmani</i>	40.6	18.5 - 89.1	21.2	M
<i>Caenis amica</i>	49.6	11.3 - 217.2	37.8	M
<i>Baetisca obesa</i>	51.0	11.3 - 230.1	38.3	M
<i>Caenis latipennis</i>	52.2	12.0 - 227.8	37.3	M
<i>Baetisca gibbera</i>	58.5	29.6 - 115.9	16.8	M
<i>Isonychia velma</i>	61.5	24.3 - 156.0	22.6	M
<i>Caenis punctata</i>	64.6	17.3 - 241.3	31.6	M
<i>Baetisca laurentina</i>	68.0	21.5 - 214.6	27.2	M
<i>Stenonema exiguum</i>	76.8	21.0 - 280.7	29.9	M
<i>Isonychia arida</i>	77.3	21.5 - 278.4	29.5	M
<i>Baetisca escambiensis</i>	79.8	48.2 - 132.0	11.5	H
<i>Caenis anceps</i>	85.9	22.9 - 321.9	29.7	M
<i>Isonychia rufa</i>	88.1	18.1 - 428.4	35.3	M
<i>Anthopotamus myops</i>	91.2	38.3 - 217.1	19.2	M
Long Stream Region (100.1-200 km)				
<i>Stenonema lenati</i>	100.1	87.1 - 115.0	3.0	H
<i>Anthopotamus neglectus</i>	107.5	51.7 - 223.4	15.6	H
<i>Isonychia intermedia</i>	114.2	37.8 - 345.2	23.3	M
<i>Stenonema terminatum</i>	114.4	30.9 - 423.8	27.6	M
<i>Isonychia sayi</i>	142.0	39.1 - 515.6	26.0	M
<i>Caenis hilaris</i>	148.1	39.1 - 561.0	26.6	M
<i>Baetisca lacustris</i>	164.1	36.3 - 741.2	29.6	M
<i>Pseudiron centralis</i>	176.1	47.9 - 647.3	25.2	M
<i>Stenonema mexicanum</i>	179.5	42.9 - 750.6	27.6	M
Very Long Stream Region (>200 km)				
<i>Anthopotamus verticis</i>	213.2	84.7 - 536.9	17.2	H
<i>Isonychia sicca</i>	235.6	66.1 - 840.4	23.3	M
<i>Caenis tardata</i>	242.0	63.9 - 916.0	24.3	M
<i>Isonychia campestris</i>	408.3	181.3 - 919.6	13.5	M

habitat for a species). We consider all species with $V < 16.2$ ($< \bar{x} - 1$ SD) to have high stream-size specificity, species with V between 16.3 and 51.5 ($\bar{x} \pm 1$ SD) to have moderate stream-size specificity and species with $V > 51.5$ ($> \bar{x} + 1$ SD) to have low stream-size specificity. Based on these divisions, 7 per cent of species have high stream-size specificity, 81 per cent moderate and 12 per cent low specificity.

Some species typically occurring >40 km downstream from the stream source have high specificity (Table 2), whereas those species occurring in our headwater, very short and short stream regions tend to show moderate or low specificity (Table 1). There are individual exceptions to both of these tendencies. The ranges of untransformed data for each species showed that most species associated with long stream regions also occur in short stream regions. These species are apparently not limited in distribution by stream length. It should not be inferred that the means for more variable stream species are inaccurate representations of their typical stream-length locations. Nonetheless, predictions based upon those means would be unreliable because of the extreme variation.

At the very minimum, our collation of available data (Tables 1 and 2) provide quantitative ecological distributions for each of the study species, and we view these data as valuable additions to the ecological profiles characterizing mayflies at the species level. Stream size is obviously only one of several ecological factors potentially related to mayfly distributions. Many other factors may act independently, exclusive of stream size, or in concert with stream size to limit mayfly distributions, depending on the species. With regard to the genera treated herein, we offer the following summaries of stream-size distribution.

The typical habitat of *Anthopotamus* has been described by McCafferty (1975) and Bae and McCafferty (1991) as medium sized streams to large rivers. Our results for all four currently recognized species of *Anthopotamus* tend to support their observations. Based on our stream-size specificity criteria (Tables 1 and 2), most species are generally restricted to our longer stream regions. Extensive sampling data from the North Carolina Department of Natural Resources corroborate our conclusions (D. Lenat, personal communication).

With regard to *Baetisca*, Pescador and Berner (1981) gave stream-size information only for *B. escambiensis*, stating that it typically inhabits small to medium sized rivers. Our data show that *B. escambiensis* occurs near the margin of our medium and long stream regions. Berner and Pescador (1980) described the typical nymphal habitat of *B. laurentina* as medium to large rivers. The mean of our measurements indicates that their description is accurate.

Our data strongly agree with descriptions of typical lotic habitats of species of *Caenis* by Provonsha (1990). However, no species in this genus exhibited high stream-size specificity. The fact that several species of caenids can be found in both

lotic and lentic habitats may be related to their general lack of stream-size specificity.

The data that we have accumulated for the North American species of *Isonychia* agree with most of the stream-size information provided by Kondratieff and Voshell (1984). They describe *I. rufa* and *I. serrata* as typically occurring in third to fifth order streams. We found these two species to be near the outer limits of that range. Our data showed *I. rufa* to be primarily distributed in our medium length stream region, and *I. serrata* proved to be fairly specific for our very short stream region. Of all genera studied, *Isonychia* showed the broadest distribution of collection records among the eight stream length classes used for distributional analysis (i.e., species of *Isonychia*, together, occur in a wider range of stream-length locales than species of other genera studied).

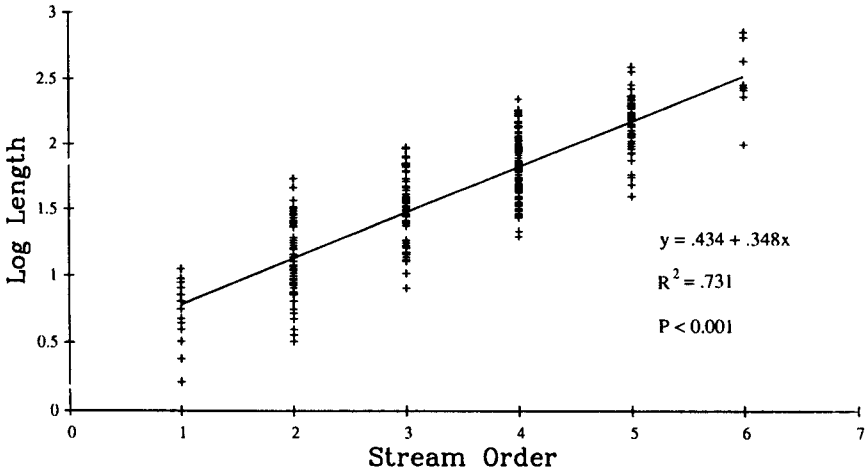
The habitat description by Pescador (1985) for the only presently recognized North American species of *Pseudiron*, *P. centralis*, does not refer to stream size. The mean of measurements taken from that work indicates that it is mainly a long stream region species. Publications treating the biology (Soluk and Clifford 1984) and distribution (McCafferty 1991) of this species described its typical habitat as medium sized or large streams.

Stream-size information was provided for many species of *Stenonema* by Bednarik and McCafferty (1979). Our stream-length location data strongly support their descriptions in all cases. *Stenonema*, compared to other genera, showed the narrowest distribution of collection records among the eight length classes, yet 24 per cent of the species had low stream-size specificity.

This study additionally allowed us to make some observations regarding stream order. Horton (1945), Strahler (1957), Leopold et al. (1964) and others have shown that a log-normal relationship exists between stream length and stream order. A plot of our stream order and downstream length data (Fig. 1) also indicated this relationship ($P < 0.001$). The entire length of a stream segment of a given order was not measured in this study, and this could explain much of the scatter among data points on the plot. Calculating from the regression equation, collection locales on first order streams are predictably ca. six km downstream from the source; second order, 13.5 km downstream; third order, 30 km downstream; fourth order, 67 km downstream; fifth order, 150 km downstream; and sixth order, 333 km downstream. Based upon these results, a collection record from a first order stream would typically occur in our headwater region, a record from a second order stream in our very short stream region, a record from a third order stream in our short stream region, and so on.

Despite the above correlation, we would caution that stream order alone may not be a totally reliable comparative ecological parameter when applied across a number of geological provinces, especially when porous land surfaces, karstlands and glaciated regions are included (Hughes and Omernik 1981). Leopold et al. (1964) showed that streams of different geologic provinces having similar

Figure 1. Simple linear regression of log transformed stream length (distance from stream source, km) against stream order at collection locales. Note that many data points are hidden by overlap.



morphometric properties (e.g., drainage area) may be of different order. The scatter of the data around our regression line (Fig. 1) may also be partially attributed to regional differences in stream morphology.

Finally, further examination of Fig. 1 revealed a relationship that was not anticipated. The relatively large number of data points around third and fourth order streams implies that the species studied herein (and perhaps mayflies in general) most frequently occur in mid-order streams or in the middle reaches of long streams. Although it is tempting to associate this information with the differences in species diversity predicted along a river continuum by Vannote et al. (1980), such a comparison is not entirely appropriate with the type of data used in this study. The distributional trend of the data plotted in Fig. 1 may be biased by the efforts and interests of collectors, however, it is noteworthy regardless of its validity.

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