

Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States

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Abstract. Estimation of invertebrate biomass is a critical step in addressing many ecological questions in aquatic environments. Length–dry mass regressions are the most widely used approach for estimating benthic invertebrate biomass because they are faster and more precise than other methods. A compilation and analysis of length–mass regressions using the power model, M (mass) = $a L$ (length) b , are presented from 30 y of data collected by the authors, primarily from the southeastern USA, along with published regressions from the rest of North America. A total of 442 new and published regressions are presented, mostly for genus or species, based on total body length or other linear measurements. The regressions include 64 families of aquatic insects and 12 families of other invertebrate groups (mostly molluscs and crustaceans). Regressions were obtained for 134 insect genera (155 species) and 153 total invertebrate genera (184 species). Regressions are provided for both body length and head width for some taxa. In some cases, regressions are provided from multiple localities for single taxa. When using body length in the equations, there were no significant differences in the mean value of the exponent b among 8 insect orders or Amphipoda. The mean value of b for insects was 2.79, ranging from only 2.69 to 2.91 among orders. The mean value of b for Decapoda (3.63), however, was significantly higher than all insects orders and amphipods. Mean values of a were not significantly different among the 8 insect orders and Amphipoda, reflecting considerable variability within orders. Reasons for potential differences in b among taxa are explained with hypothetical examples showing how b responds to changes in linear dimensions and specific gravity. When using head width as the linear dimension in the power model, the mean value of b was higher (3.11) than for body length and more variable among orders (2.8–3.3). Values of b for Ephemeroptera (3.3) were significantly higher than those for Odonata, Megaloptera, and Diptera. For those equations in which ash-free dry mass was used, % ash varied considerably among functional feeding groups (3.3–12.4%). Percent ash varied from 4.0% to 8.5% among major insect orders, but was 18.9% for snails (without shells). Family-level regressions also are presented so that they can be used when generic equations are unavailable or when organisms are only identified to the family level. It is our intention that these regressions be used by others in estimating mass from linear dimensions, but potential errors must be recognized.

Key words: freshwater invertebrates, aquatic insects, length–mass regression, biomass, secondary production, allometry, dry mass.

Estimation of invertebrate biomass is a critical step in addressing many ecological questions at organism, population, community, and ecosystem levels of organization, regardless of whether one is dealing with freshwater, marine, or terrestrial environments. There are 3 basic approaches to biomass determination: 1) direct weighing of fresh, frozen, or preserved animals, 2) biovolume determination, and 3) length–dry

mass conversion (Burgherr and Meyer 1997). Length–mass conversions usually are considered superior to other approaches, primarily because they are faster and more precise (e.g., Burgherr and Meyer 1997). Furthermore, direct weighing of preserved organisms is often a problem because of the loss of dry mass upon preservation (e.g., Howmiller 1972, Leuven et al. 1985). Given its many advantages, determination of biomass from linear dimensions (e.g., total length or head width) using regression analysis has been widely used for terrestrial (e.g.,

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Rogers et al. 1976, Schoener 1980, Sample et al. 1993, Hódar 1996), benthic (e.g., Smock 1980, Meyer 1989, Towers et al. 1994, Burgherr and Meyer 1997), and planktonic (e.g., McCauley 1984, Kawabata and Urabe 1998) invertebrates.

Length-mass regressions can be used for many purposes in ecological studies where measuring length (or some other linear dimension) is easier than obtaining mass: 1) they are useful for estimating biomass in the laboratory where growth rates or other bioenergetic variables are measured, 2) they allow estimation of prey biomass in a predator gut (particularly equations for head width) even when the prey may be torn apart or partially digested, 3) they enable estimation of population or community biomass, given quantitative length-frequency data from the field, 4) they are useful in establishing size-specific mass for most secondary production methods, 5) they allow for more comprehensive comparisons of invertebrate populations within and between habitats and ecosystems, and 6) they provide more energetically based response variables for asking questions about interspecific relationships (Benke 1993).

The most common approach in developing length-mass equations for freshwater macroinvertebrates is to describe mass as a power function of a linear dimension. The power function usually provides a better fit to the data than most other mathematical formulations (e.g., Wenzel et al. 1990). Unfortunately, equations predicting mass from linear dimensions are widely scattered in the literature. Many investigators report the development of such relationships, particularly in studies of secondary production, but often the equations are not actually presented in the publications. It is becoming widely recognized that there is a need to make such regressions available for others to use. For example, recent compilations of such information have been presented for Europe (Meyer 1989, Wenzel et al. 1990, Burgherr and Meyer 1997) and New Zealand (Towers et al. 1994). The only compilation of such regressions for North American macroinvertebrates was completed by Smock (1980), which contained specific equations for 43 species/genera from 31 insect families, and 8 order-level equations for insects. Given the paucity of specific regressions for North America, a more comprehensive update

and inventory of length-mass regressions is needed.

Thus, the purpose of this paper is to present a compilation of length-mass relationships for North American macroinvertebrates, to evaluate some of these relationships, and to make the equations available to others. Much of this compilation is possible because, in the course of conducting studies on secondary production, we have accumulated many such equations over the past 30 y. We present many unpublished equations that primarily focus on species found in the southeastern USA. We also include as many published length-mass relationships as we could find in the literature to make our presentation for North America more complete. We have exercised some discretion in our selection of regressions from the literature.

Basic length-mass model

Length-mass equations in the context of this paper will refer only to those that predict mass as a power function of a linear dimension (particularly body length and head width):

$$M = aL^b \quad [1]$$

where M is organism mass (mg), L is any linear dimension (mm), and a and b are constants. Equation 1 often is converted to a linear form by using a logarithmic transformation:

$$\log_{10} M = \log a + b \log L \quad [2]$$

or

$$\log_e M = \ln M = \ln a + b \ln L \quad [3]$$

For equations 2 and 3, the exponent b of the power model becomes the slope of a linear regression, and $\log_{10} a$ and $\ln a$ are Y intercepts (i.e., the value of $\log_{10} M$ or $\ln M$ when $\log_{10} L$ or $\ln L = 0$, which occurs when $L = 1$). In this paper, values for a are not logarithmically transformed.

Both the power curve and the \log_{10} -transformed linear regression are illustrated for the aquatic megalopteran *Corydalus cornutus* (Fig. 1). The statistics for this large predaceous insect are interesting for 2 reasons. First, the range in mass from 1st to final instar may be the highest of any aquatic insect (ca $\times 10,000$). Second, the exponent b (or slope of the linear regression) = 3.0, which represents a perfect cubic relationship between length and mass (see below).

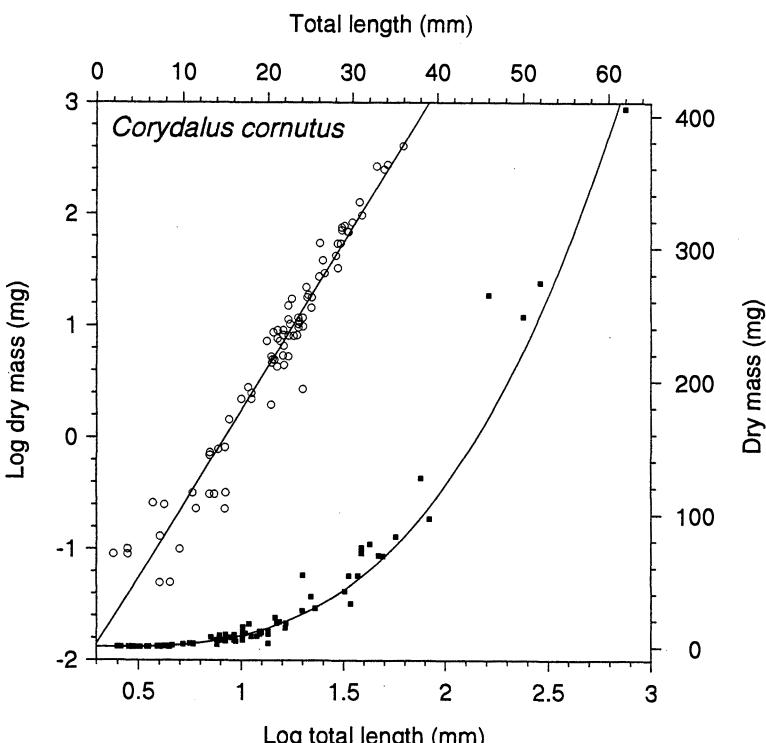


FIG. 1. Length-mass curves for the aquatic megalopteran *Corydalus cornutus* from Coastal Plain rivers in Georgia, using both linear (filled squares) and logarithmic (\log_{10} , open circles) scales. The power equation is $DM = 0.0018 L^{2.997}$, where DM = dry mass and L = body length ($r^2 = 0.95$, $n = 82$, and lengths ranged from 2.4 to 62.0 mm).

For any length-mass equation, mass is predicted by taking a known length (L) to the power b and multiplying by a . For example, the dry mass (DM) of *C. cornutus* having a length of 30 mm would be estimated as $DM = 0.0018 \times 30^{2.997} = 48.1$ mg.

Methods

New equations from the eastern USA

Invertebrates for regression analysis were collected from 1968 through 1998 from ponds, streams, rivers, and wetlands in Alabama, Georgia, Maine, North Carolina, South Carolina, and Virginia. For each population, ≥ 1 linear measurements were made of total length, head width, or some other taxon-specific dimension such as carapace length of crayfish. Most invertebrates (i.e., those < 30 mm long) were measured using a stereoscopic microscope with an ocular micrometer, accurate to 0.01 mm. Cali-

pers were used to measure larger animals such as crayfish and molluscs. All animals used by A. C. Benke and L. A. Smock to measure DM were either fresh or frozen (without chemical preservation). Animals used by A. D. Huryn and J. B. Wallace were either fresh, frozen, or formalin-preserved (10% formalin). We assumed that formalin-preserved animals provided DM estimates very close to those using fresh animals (e.g., Ross 1982, Leuven et al. 1985), unlike estimates from ethanol-preserved animals, which lose a substantial portion of their DM through leaching (e.g., Howmiller 1972, Dermott and Paterson 1974, Leuven et al. 1985). Dry mass was obtained by drying animals at 60°C to 105°C for up to 24 h, and then cooling in a desiccator. It was sometimes necessary to clean animals by sonication before drying, particularly if debris particles were entrapped by setae. Animals were weighed on balances accurate to either 10 µg or 0.1 µg, depending on their size.

Ash-free dry mass (AFDM) was used in regressions estimated by A. D. Huryn and J. B. Wallace. After DM was measured, invertebrates were ashed in a muffle furnace at 500°C. Ash mass was then subtracted from DM to obtain AFDM.

We provide the following statistics for most of the regressions presented from our original data: $a \pm 1$ SE, $b \pm 1$ SE, coefficient of determination (r^2), range of the linear measurement, number of data points in the regression (n), and collection location (i.e., state). For most of the equations estimated by A. D. Huryn and J. B. Wallace, the % ash also is provided so that one can estimate DM as well as AFDM (see Huryn et al. 1994 for details) as follows:

$$DM = AFDM \cdot \frac{100}{100 - \% \text{ ash}}. \quad [4]$$

A. D. Huryn's regressions for snails (*Elimia* spp.) are revisions of those found in Huryn et al. (1994). Percent ash for snails is presented both with and without shells.

The ability to convert DM to AFDM and vice versa would be very useful to investigators who may wish to use any of these equations. Furthermore, it is of biological interest to determine whether there are differences in ash content among invertebrates with different feeding modes and among major taxonomic groups. We therefore separated those organisms with AFDM equations into functional groups (filtering collectors, scrapers, shredders, gathering collectors, and predators; Merritt and Cummins 1996), and calculated mean values of % ash. We also calculated mean % ash for major taxonomic groups.

Published equations and selection criteria

We established several restrictive criteria in the selection of published regressions: 1) Equations must have been based on the power model described above. 2) Mass must have been expressed as either DM or AFDM. Regressions based on live (= wet) mass were not included. 3) Dry mass must have been determined from either fresh animals or animals preserved in formalin. 4) There was sufficient information about the units of the linear dimension and mass, and whether standard procedures were followed (e.g., type of preservative used). 5) Equations obtained from the literature made biological

sense. Published equations that generated unrealistic numbers and that could not be corrected were excluded.

We attempted to present the same statistics for the literature values as for our original equations. However, although many published regressions included n and r^2 , most did not include standard errors of a and b . All equations are presented using mg for DM and mm for length; other units (e.g., g, cm, μm) were converted to these standard units to obtain the final form of the equation. We used a one-way analysis of variance (ANOVA) and, if significant, a Tukey-Kramer test to compare the mean values of b among major insect and crustacean orders. Homogeneity of variances was tested with Bartlett's test. For those orders in which b was not significantly different, the same statistical test was followed for the a value (prior to analysis, all a values in AFDM regressions 1st were converted to DM). Tests of the a value were restricted to orders with no differences in b values because of the likelihood that a is not independent of b . ANOVA and Tukey-Kramer tests also were used to compare mean values of b for head width among insect orders, and to compare differences in % ash content among different functional feeding groups and among major taxonomic groups.

Although we focus on the need for genus- and species-level regressions, some investigators may require the use of family-level regressions. Such regressions might be useful when genus-level regressions are unavailable, or when individuals are identified only to the family level. To provide such equations, we estimated mean values of a and b for equations based on total body length for each insect family, and other major groups. All a values based on AFDM first were converted to DM.

Results

Regression equations

We present a total of 442 new and published regressions based on either total body length or a shorter dimension (e.g., head width) in Appendices 1, 2, and 3. Sixty-four families of aquatic insects and 12 families of other invertebrates are represented by at least 1 regression, with all but Empididae and Sciaridae (Diptera) having at least 1 genus-level equation per family (Table

TABLE 1. Numbers of families, genera, and species of invertebrates for which length-mass regressions are presented in Appendices 1, 2, and 3. For the insect taxa, the total number of families from North America within each order is also presented in parentheses (based on Merritt and Cummins 1996).

Taxonomic group	No. of families	No. of genera	No. of species
Insecta			
Ephemeroptera	12 (21)	29	34
Odonata	7 (9)	17	18
Plecoptera	9 (9)	24	29
Hemiptera	3 (18)	4	4
Megaloptera	2 (2)	3	3
Trichoptera	14 (22)	24	29
Lepidoptera	1 (5)	1	1
Coleoptera	7 (25)	12	12
Diptera	9 (27)	23	25
Total Insecta	64 (139)	134	155
Mollusca	4	7	12
Crustacea	7	9	15
Turbellaria	1	2	2
Total Invertebrates	76	153	184

1). Most of the families of Ephemeroptera, Odonata, Plecoptera, Megaloptera, and Trichoptera found in North America (Merritt and Cummins 1996) are represented, even though our own analyses focused only on 6 eastern states. Thus, orders found primarily in lake, stream,

and river benthos are well represented. However, the Hemiptera, Lepidoptera, Coleoptera, and Diptera, containing several families with semi-aquatic taxa, had a poor family-level representation. Regressions were found for 134 insect genera and 155 species. Considering total invertebrates, 76 families, 153 genera and 184 species are represented.

The number of equations reported in the Appendices exceeded the total number of represented taxa because there were often several equations per taxon for a given genus (e.g., *Baetis* spp.) or species (e.g., *Corydalus cornutus*). In some cases, taxa had regressions for both length and head width; in others taxa had regressions from >1 state and >1 stream, river, or lake within a state (e.g., Appendix 2, several *Elmia* spp.); and in still others there were regressions from >1 site within the same stream, river, or lake (e.g., Appendix 2, Hornbach et al. 1996).

Variability in length-mass constants among macroinvertebrates

There were no significant differences in mean *b* values for body length among all insect orders and the Amphipoda (Table 2, Fig. 2; ANOVA and Tukey-Kramer test; variances homogeneous). However, the mean *b* for Decapoda (3.626 ± 0.084) using carapace length was significantly higher than mean *b* values for all other

TABLE 2. Mean values of *b* and *a* from length-mass regressions for the major insect and crustacean orders using total length (Appendix 1). Equations using a dimension other than total length (e.g., thorax length) were not used in calculating means, except for Decapoda (carapace length; included only in ANOVA for *b*). If letters under signif. (c and d) are the same for any 2 taxa, then means were *not* significantly different between taxa (ANOVA and Tukey-Kramer test, $p > 0.05$). Min. and max. indicate the minimum and maximum values of *b* and *a* from all regressions for that order. *n* = number of equations used for each order. *Galerucella nymphaea* was excluded from the Coleoptera estimates because it is primarily terrestrial and has *a* and *b* values that deviate substantially from most other taxa.

Order	<i>n</i>	<i>b</i> \pm 1 SE	Signif.	Min.	Max.	<i>a</i> \pm 1 SE	Signif.	Min.	Max.
Decapoda	9	3.626 ± 0.084	c	3.357	4.066	0.0147 ± 0.0030		0.0041	0.0307
Amphipoda	7	3.015 ± 0.087	d	2.740	3.404	0.0058 ± 0.0014	c	0.0010	0.0120
Coleoptera	9	2.910 ± 0.117	d	2.311	3.521	0.0077 ± 0.0021	c	0.0011	0.0181
Trichoptera	34	2.839 ± 0.060	d	2.389	4.179	0.0056 ± 0.0006	c	0.0005	0.0180
Megaloptera	7	2.838 ± 0.053	d	2.691	3.001	0.0037 ± 0.0006	c	0.0018	0.0062
Ephemeroptera	54	2.832 ± 0.046	d	2.252	4.140	0.0071 ± 0.0007	c	0.0001	0.0257
Odonata	18	2.792 ± 0.052	d	2.239	3.124	0.0078 ± 0.0009	c	0.0015	0.0180
Plecoptera	36	2.754 ± 0.041	d	1.950	3.232	0.0094 ± 0.0017	c	0.0019	0.0538
Hemiptera	4	2.734 ± 0.068	d	2.596	2.904	0.0108 ± 0.0032	c	0.0031	0.0169
Diptera	43	2.692 ± 0.052	d	2.091	3.830	0.0025 ± 0.0003	c	0.0002	0.0066
All Insects	205	2.788 ± 0.022		1.95	4.179	0.0064 ± 0.0004		0.0001	0.0538

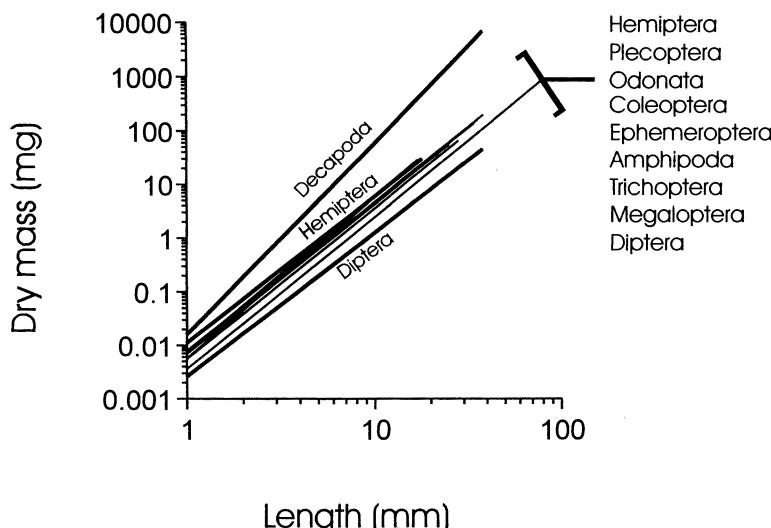


FIG. 2. Comparison of composite length-mass relationships for the major orders of aquatic insects and crustaceans. All equations are of the form $DM = a L^b$, where DM = dry mass and L = body length. Neither of the fitted coefficients (a and b) were significantly different among the 8 insect orders and the Amphipoda. The slope (b) for the Decapoda was significantly different from all other orders. Because the decapod equation was based on carapace length, not total body length, comparison of the a value for decapods with other a values was irrelevant. Length of each line indicates the maximum value for each order.

orders. Mean b for all insect orders was 2.788 ± 0.022 ($n = 205$), with a range in means of b from only 2.69 to 2.91 among orders.

Because there were no differences in mean b among insect orders and amphipods, we conducted the same multiple-comparison test to determine whether there were differences in a . All a values based on AFDM 1st were converted to DM. Although the highest mean values of a (Hemiptera and Plecoptera) were several times higher than the lowest value (Diptera), the variability within orders was too large to detect any significant differences among orders (Table 2, Fig. 2). Variances were heterogeneous for this ANOVA, even after data transformation. Therefore, data were reanalyzed using the Games-Howell method designed for cases when variances are heterogeneous (Sokal and Rohlf 1995). The results were the same as the original ANOVA, with no differences among the mean a values. The variability of a within orders can be seen from examination of their coefficients of variation (CV), which ranged from 43 to 108%. In contrast, CV for b values ranged from only 5 to 13%.

The mean b for head-width equations using all insect orders was 3.111 ± 0.037 ($n = 147$,

Table 3). However, b for head width differed more among orders than b for body length. Mean values of b for head width ranged from 2.8 (Diptera) to 3.3 (Ephemeroptera), and differences were highly significant (ANOVA, variances homogeneous, $p < 0.001$). Ephemeroptera b was significantly higher than values for Odonata, Megaloptera, and Diptera (Tukey-Kramer test). Trichoptera b was significantly higher than the value for Diptera.

No attempt was made to conduct statistical analyses on the equations for molluscs (Appendix 2) because the total number of species listed was relatively low, and the length dimension represented 3 different and therefore incomparable measures: maximum shell length, maximum shell width (gastropod only), or maximum shell width at aperture (gastropods only).

Sixty-one family-level regressions for insect larvae were estimated (Table 4) using mean a and b values based on total body length (Appendix 1). Regressions included 12 families of Ephemeroptera, 7 Odonata, 9 Plecoptera, 2 Megaloptera, 14 Trichoptera, 1 Lepidoptera, 4 Coleoptera, and 9 Diptera. Only 9 of these families had mean b values >3 . Regressions were also estimated for 3 major crustacean orders and

TABLE 3. Mean values of b for length-mass regressions for the major insect orders using head width (Appendix 3). If letters under signif. (c, d, e) are the same for any 2 taxa, then means are *not* significantly different between taxa (ANOVA and Tukey-Kramer test, $p > 0.05$). Min. and max. indicate the minimum and maximum values of b from all regressions. *Galerucella nymphaeae* was excluded from the Coleoptera estimates because it is primarily terrestrial and has a and b values that deviate substantially from most other taxa.

	<i>n</i>	$b \pm 1 \text{ SE}$	Signif.	Min.	Max.
Ephemeroptera	32	3.319 ± 0.053	c	2.764	4.111
Trichoptera	30	3.252 ± 0.088	cd	2.284	4.580
Coleoptera	8	3.140 ± 0.154	cde	2.645	3.794
Plecoptera	39	3.094 ± 0.073	cde	2.000	4.000
Odonata	17	2.871 ± 0.092	de	2.401	3.592
Megaloptera	9	2.838 ± 0.089	de	2.474	3.256
Diptera	12	2.791 ± 0.160	e	2.311	4.347

Turbellaria. Two of 3 b values were >3 for crustaceans.

Variability of mass for a given linear dimension

To illustrate the variability associated with individual length-mass regressions, we have chosen a holometabolous insect, the caddisfly *Hydropsyche elissoma* (Fig. 3). It is apparent that the last 4 instars fall within a narrow range of head-width values when plotting head width vs mass (Fig. 3A). With each molt, dimensions of sclerotized body parts (e.g., head width) rapidly increased by $\sim 50\%$. The average caddisfly volume would therefore be expected to triple at molting (i.e., $1.5^3 \sim 3$), even though dry mass will decline slightly (from loss of exuviae). This prediction is consistent with the observation that variation of DM within an instar is ~ 3 -fold (Fig. 3A). In spite of this clumping of head-width values and relatively large differences in mass within an instar, there was still a highly significant regression with narrow 95% confidence limits (CL) and a high r^2 . In contrast, the body length plot for the same species showed no clumping of instars (Fig. 3B), probably because growth of the un sclerotized abdomen was more continuous than growth of the head. Nonetheless, r^2 and 95% CL were similar for both regressions.

Percent ash

Percent ash was estimated for 80 of the regressions in Appendices 1, 2, and 3, and mean % ash was calculated for functional feeding groups and taxonomic groups. Mean values of

% ash varied considerably among functional feeding groups (Fig. 4A). Filtering collectors and scrapers had mean values ca 11–12%, shredders and gathering collectors ca 5–6%, and predators ca 3%, possibly indicating differences in the material ingested by species of different functional feeding groups. Although mean values of % ash were significantly different among functional groups (ANOVA, $p < 0.05$), the Tukey-Kramer test only found that the predator value was significantly lower than either scrapers or filtering collectors, and the other functional groups were not significantly different from one another (square root arcsin transformation of percentages, variances homogeneous).

Mean values of % ash varied from only 4.0% to 8.5% among major insect orders (Fig. 4B). Gastropoda, Decapoda, and Lepidoptera were noticeably higher ($>17\%$), but the latter 2 only had a single measurement and could not be used in statistical analyses. Mean values of % ash were significantly different among those groups represented by >1 equation (ANOVA, $p < 0.05$, square root arcsin transformation of percentages, variances homogeneous). The mean % ash content for Plecoptera and Diptera was significantly lower than ash content for Trichoptera and Gastropoda (Tukey-Kramer test). The mean ash contents for Ephemeroptera, Coleoptera, and Trichoptera were not significantly different from one another, but all were significantly lower (4.0–8.5%) than the ash content for Gastropoda (18.9%, without shell).

Discussion

Our compilation and analysis of invertebrate length-mass regressions for North America en-

abled us to describe the variability in such relationships within and among taxonomic groups, and to provide other investigators with equations that may prove useful in their own studies. Therefore, we will attempt to explain some of the observed variability and offer some guidance in the use of these equations.

Variability in length-mass constants among macroinvertebrates

Inspection of the equations for all invertebrate groups reveals that the exponent b is often close to a value of 3 (Appendices 1, 2, and 3). The shape of the animals and their specific gravity must remain exactly the same throughout larval development for the expected value of b to be exactly 3. However, the shape of virtually all aquatic invertebrates changes somewhat as they grow, and specific gravity does not remain constant. For insects, the mean value of b for body length is actually somewhat <3 for all orders (Table 2), most families (Table 4), and most individual taxa (Appendix 1). Previous compilations of length-mass equations for aquatic insects are consistent with the generalization that mean b values for insect orders are <3 (Smock 1980, Meyer 1989, Towers et al. 1994, Burgherr and Meyer 1997).

There are 2 basic reasons why the mean value of b would be consistently <3 : 1) insects become proportionately narrower as body length increases, or 2) specific gravity declines with size. Schoener (1980) noted that b values are usually <3 for length-mass regressions of terrestrial insects (mixed species) and suggested that this was caused by a tendency for longer species to be relatively thinner. Our 1st reason is somewhat different than Schoener's explanation because it applies to a larva changing shape as it grows rather than differences in shape among species of different adult lengths.

To illustrate why b values may be >3 or <3 , we have created 6 hypothetical examples using cuboid shapes that grow through 4 size classes (Table 5). In example 1, body shape remains constant with increasing size and $b = 3$, as expected. In contrast, example 2 shows that when width and height increase by a factor smaller than length (i.e., animal becomes narrower with increasing size), $b < 3$. Example 3 illustrates that when body shape remains constant (as in example 1), b will be <3 if specific gravity declines

with size. We do not know whether progressive changes in shape or specific gravity are the most likely reasons for mean b values being <3 for most aquatic insects. Whichever is the case, however, it cannot apply to all taxa because some b values are >3 (Appendix 1).

The mean values of b for head width of insect orders may be >3 or <3 (Table 3). One possible reason for head-width regressions having b values >3 (e.g., Ephemeroptera), is that head width might be proportionately higher in early instars than late instars. Example 4 in Table 5 illustrates an otherwise constant body shape, but a head width that is increasing at a slower rate than other body dimensions. Thus, the length-mass regression for head width has a b value >3 . Where $b < 3$ (e.g., Diptera, Table 3), it suggests that head width may be proportionately smaller in early instars than in later instars.

It has been suggested that b is likely to be closer to a value of 2 for organisms that are relatively flattened; i.e., those that are more 2-dimensional than 3-dimensional (e.g., Wenzel et al. 1990, Towers et al. 1994). This suggestion only would be true if the flattened dimension (height) remained constant or changed very little as the other 2 dimensions increased (example 6 in Table 5), although we are unaware of this situation in any invertebrate group. If all dimensions increased in the same proportions through time, the volume should increase in a cubic fashion regardless of shape (note that examples 1 and 5 in Table 5 produce a value of $b = 3$, even though example 5 represents a more flattened shape). Comparison of b values for body length between non-heptageniid mayflies and the more flattened heptageniids (Appendix 1) showed no significant difference in the means (t -test, $p > 0.3$).

Decapods were unusual among all the invertebrate groups considered in that their b values for carapace length or total length were consistently >3 (Appendix 1, Table 2). As implied above, when b is >3 for any invertebrate, it may mean that it is becoming proportionately wider as length increases or that its specific gravity increases with size. In the case of decapods, however, it also may mean that their chelipeds increase in size more rapidly than their body length. Mason (1975) suggested that males of the crayfish *Pacifastacus* (Decapoda) weigh more than females of the same length because of accelerated development of their chelipeds. The

TABLE 4. Higher-level length-mass equations ($DM = a L^b$, where DM is dry mass [mg], L is total body length [mm], and a and b are constants) for Turbellaria (class), crustaceans (order), and insect larvae (family). For Decapoda, L = carapace length. All a and b values are means calculated from individual taxa within a group (Appendix 1). n = the number of equations used in calculating the mean. Note that several equations are based on only a single equation from Appendix 1 (i.e., $n = 1$). See Appendix 1 for details.

Taxon	$b \pm 1 \text{ SE}$	$a \pm 1 \text{ SE}$	n
Turbellaria	2.168 \pm 0.016	0.0082 \pm 0.0013	3
Crustacea			
Amphipoda	3.015 \pm 0.087	0.0058 \pm 0.0014	7
Decapoda	3.626 \pm 0.084	0.0147 \pm 0.0030	9
Isopoda	2.948 \pm 0.163	0.0054 \pm 0.0018	2
Ephemeroptera			
Ameletidae	2.588	0.0077	1
Baetidae	2.875 \pm 0.131	0.0053 \pm 0.0010	9
Baetiscidae	2.905	0.0116	1
Caenidae	2.772 \pm 0.069	0.0054 \pm 0.0008	4
Ephemerellidae	2.676 \pm 0.131	0.0103 \pm 0.0025	8
Ephemeridae	2.764 \pm 0.043	0.0034 \pm 0.0009	4
Heptageniidae	2.754 \pm 0.039	0.0108 \pm 0.0014	15
Isonychiidae	3.043 \pm 0.124	0.0031 \pm 0.0000	2
Leptophlebiidae	2.686 \pm 0.082	0.0047 \pm 0.0006	5
Polymitarcyidae	3.050	0.0020	1
Siphlonuridae	3.446 \pm 0.455	0.0027 \pm 0.0025	3
Tricorythidae	3.194 \pm 0.028	0.0061 \pm 0.0032	2
Odonata			
Aeshnidae	2.813	0.0082	1
Calopterygidae	2.742	0.0050	1
Coenagrionidae	2.785 \pm 0.119	0.0051 \pm 0.0036	2
Cordulegastridae	2.782	0.0067	1
Corduliidae	2.787 \pm 0.050	0.0096 \pm 0.0015	3
Gomphidae	2.787 \pm 0.147	0.0088 \pm 0.0025	5
Libellulidae	2.809 \pm 0.134	0.0076 \pm 0.0019	5
Plecoptera			
Capniidae	2.562 \pm 0.100	0.0049 \pm 0.0004	3
Chloroperlidae	2.724	0.0065	1
Leuctridae	2.719 \pm 0.025	0.0028 \pm 0.0003	2
Nemouridae	2.762 \pm 0.107	0.0056 \pm 0.0010	3
Peltoperlidae	2.737 \pm 0.116	0.0170 \pm 0.0029	2
Perlidae	2.879 \pm 0.092	0.0099 \pm 0.0030	13
Perlodidae	2.742 \pm 0.043	0.0196 \pm 0.0118	7
Pteronarcyidae	2.573 \pm 0.273	0.0324 \pm 0.0260	2
Taeniopterygidae	2.655 \pm 0.058	0.0072 \pm 0.0012	4
Hemiptera			
Corixidae	2.904	0.0031	1
Gerridae	2.596	0.0150	1
Veliidae	2.719 \pm 0.058	0.0126 \pm 0.0043	2
Megaloptera			
Corydalidae	2.873 \pm 0.069	0.0037 \pm 0.0009	5
Sialidae	2.753 \pm 0.048	0.0037 \pm 0.0006	2
Trichoptera			
Brachycentridae	2.818 \pm 0.317	0.0083 \pm 0.0056	3
Glossosomatidae	2.958 \pm 0.070	0.0082 \pm 0.0017	2
Helicopsychidae (case width)	3.096	0.0125	1
Hydropsychidae	2.926 \pm 0.151	0.0046 \pm 0.0007	10
Lepidostomatidae	2.649	0.0079	1
Leptoceridae	3.212	0.0034	1

TABLE 4. Continued.

Taxon	$b \pm 1 \text{ SE}$	$a \pm 1 \text{ SE}$	n
Limnephilidae	2.933 \pm 0.065	0.0040 \pm 0.0008	4
Odontoceridae	2.988 \pm 0.253	0.0077 \pm 0.0005	2
Philopotamidae	2.511 \pm 0.074	0.0050 \pm 0.0000	3
Phryganeidae	2.811	0.0054	1
Polycentropodidae	2.705 \pm 0.174	0.0047 \pm 0.0024	2
Psychomyiidae	2.873	0.0039	1
Rhyacophilidae	2.480	0.0099	1
Sericostomatidae	2.741	0.0074	1
Lepidoptera			
Pyralidae	2.918	0.0033	1
Coleoptera			
Chrysomelidae	3.111	0.039	1
Elmidae	2.879 \pm 0.177	0.0074 \pm 0.0025	6
Psephenidae	2.906 \pm 0.023	0.0123 \pm 0.0041	2
Ptilodactylidae	3.100	0.0012	1
Diptera			
Athericidae	2.586	0.0040	1
Blephariceridae	3.292	0.0067	1
Ceratopogonidae	2.469 \pm 0.213	0.0025 \pm 0.0011	3
Chironomidae	2.617 \pm 0.067	0.0018 \pm 0.0004	17
Empididae	2.546 \pm 0.110	0.0054 \pm 0.0012	2
Sciariidae	2.091	0.0042	1
Simuliidae	3.011 \pm 0.153	0.0020 \pm 0.0006	8
Tabanidae	2.591	0.0050	1
Tipulidae	2.681 \pm 0.055	0.0029 \pm 0.0007	9

relatively high b values for decapod equations in Appendix 1 suggest that both male and female chelipeds may have accelerated growth, although rates would be greater in males than females. Finally, most b values for molluscs were close to 3, with several slightly above or slightly below 3, suggesting little change in shape or specific gravity relationships described above.

It is difficult to compare our a values with those from the literature because a probably is not independent of b . However, comparisons of the plotted lines themselves provide some interpretive value. Our mean values of a (0.0064) and b (2.788) for all insects (Table 2) produced a line that was reasonably similar to the line for all aquatic insects ($a = 0.019$, $b = 2.46$) generated by Smock (1980) from North Carolina (Fig. 5). Predicted values tend to converge toward the larger length categories (i.e., 10–50 mm). The line for all aquatic insects ($a = 0.0027$, $b = 2.79$) generated by Burgherr and Meyer (1997) for Central Europe has a slope that is identical to our own (Fig. 5). However, their lower a value results in a line that falls below our line and the

one produced by Smock (1980), and would estimate a lower mass for a given length. This discrepancy may be a result of differences in the individual taxa that were used to generate the regressions, and should serve as a warning that generalized equations may be inaccurate if applied to individual taxa.

Our all-insects regression line and those of Smock (1980) and Burgherr and Meyer (1997) each fell below the regression line for terrestrial (presumably adult) insects ($a = 0.0305$, $b = 2.62$) produced by Rogers et al. (1976). Other general length-mass regressions for adult terrestrial insects by Schoener (1980), Sample et al. (1993), and Hódar (1996) also were above our regression for aquatic insects. The higher mass predicted by regressions for terrestrial insects suggests either a higher specific gravity or a broader body than is found in aquatic insects. A higher specific gravity for terrestrial adults could be a result of heavier sclerotization. Alternatively, morphological differences between adults and larvae, such as the presence of wings and genitalia, could partially account for heavier adults.

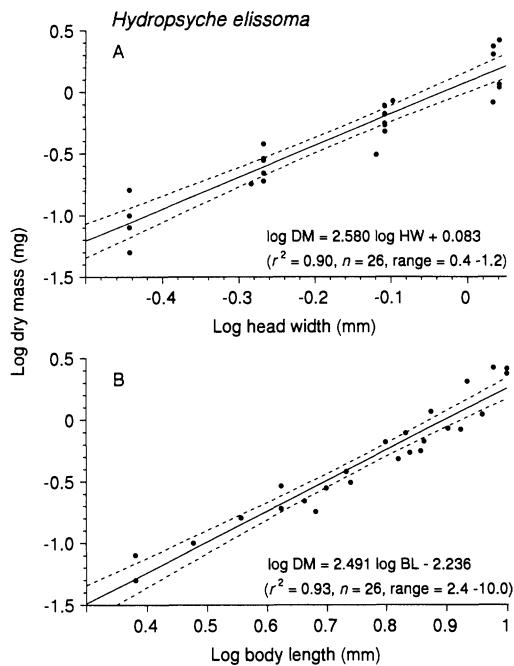


FIG. 3. Length-mass regressions for head width (A) and body length (B) for *Hydropsyche elissoma* from the Satilla River, Georgia. n = number of data points, range = range of values for length or width, DM = dry mass, HW = head width, and BL = body length. Dashed lines represent 95% confidence limits.

Variability of mass for a given linear dimension

It is important to recognize that when freshwater arthropods molt, they suddenly increase their body volume without increasing their DM (the cast exuviae actually represents a loss of mass). This phenomenon introduces variability into length-mass regressions, because animals collected for weighing may have just molted or be close to molting. Thus, animals of the same body dimensions may vary considerably in their DM. In spite of this natural variability, the value of b will not necessarily deviate from 3 unless there is a progressive change in average specific gravity with size.

Insect larvae belonging to the holometabolous orders (= Endopterygota) generally have greater within-instar variability in DM than those in the hemimetabolous orders (= Exopterygota), because most Holometabola tend to have fewer instars and thus increase more in linear dimensions (and mass) from 1 instar to the next than the Hemimetabola (Cole 1980, Butler 1984,

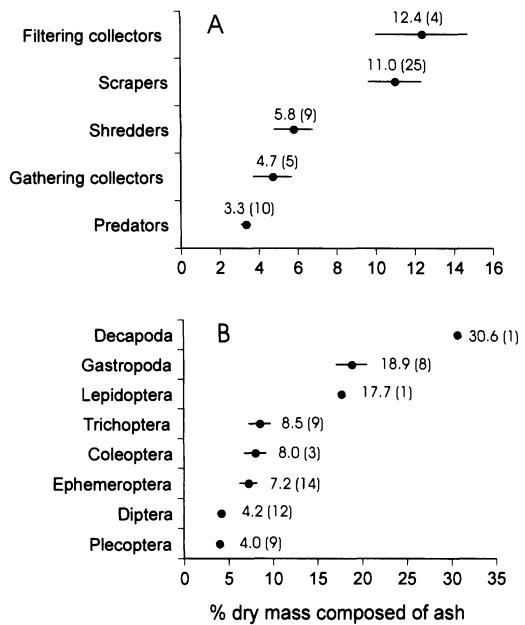


FIG. 4. Percentage of dry mass composed of ash for aquatic invertebrates in different functional feeding groups (A), and in different taxonomic groups (B). Data are from Appendices 1, 2, and 3. Error bars are ± 1 SE. Value associated with each data point is mean % ash and n is in parentheses.

Hutchinson et al. 1997). To accomplish the large increase in mass after molting, much of the cuticle of holometabolous insects remains unsclerotized and undifferentiated. For example, when larval caddisflies molt, the initially soft cuticle of their heads rapidly reaches its instar-specific width and quickly hardens (Fig. 3A), but the undifferentiated cuticle of their abdomen is somewhat extensible and facilitates more continuous growth and as much as a tripling of mass (Fig. 3B). Sclerotized cuticle such as the head capsule is lost at molting, but the unsclerotized cuticle (i.e., endocuticle) is largely reabsorbed, which is energetically economical for larval development (Chapman 1982). In contrast to the Holometabola, most growth of the more completely sclerotized Hemimetabola occurs at molting when new soft cuticle is produced. For example, dragonflies usually have ~10–12 instars, increase their linear dimensions by ~28% at each molt, and approximately double their volume (A. C. Benke, unpublished data). Mayflies usually have 15–25 instars (Butler 1984). If they increase their linear dimensions by ~10% at each molt, volume only increases by ~33%.

TABLE 5. Hypothetical examples of the effect of changes in body shape and specific gravity (mass/volume) on the exponent (slope) of length-mass equations, $M = a L^b$, where M = body mass, L = body length (or head width in example 4), a = constant coefficient, and b = exponent. Mass is calculated from linear dimensions as width \times height \times length, assuming a cuboid shape, and assuming specific gravity = 1 unless otherwise specified. Examples are: 1) constant body shape in which all dimensions increase by a factor of 1.2 from one size class (1, 2, 3, 4) to the next, 2) changing body shape in which width and height increase by a factor smaller than length, 3) constant body shape in which specific gravity declines with body size, 4) an equation based on head width, with a constant body shape, except that head width increases by a factor smaller than body length, 5) constant, but flattened, body shape in which all dimensions increase by a factor of 1.2, and 6) flattened body in which height is constant, but length and width increase by a factor of 1.2.

	Size class			
	1	2	3	4
1) Constant body shape				
Length ($\times 1.2$)	5.00	6.00	7.20	8.64
Width ($\times 1.2$)	1.00	1.20	1.44	1.73
Height ($\times 1.2$)	1.00	1.20	1.44	1.73
Mass	5.00	8.64	14.93	25.80
	$a = 0.040$	$b = 3.000$		
2) Declining body width and height				
Length ($\times 1.2$)	5.00	6.00	7.20	8.64
Width ($\times 1.1$)	1.00	1.10	1.21	1.33
Height ($\times 1.1$)	1.00	1.10	1.21	1.33
Mass	5.00	7.26	10.54	15.28
	$a = 0.187$	$b = 2.040$		
3) Constant shape, declining specific gravity				
Length ($\times 1.2$)	5.00	6.00	7.20	8.64
Width ($\times 1.2$)	1.00	1.20	1.44	1.73
Height ($\times 1.2$)	1.00	1.20	1.44	1.73
Volume	5.00	8.64	14.93	25.80
Mass/volume ($\times 0.98$)	1.100	1.078	1.056	1.035
Mass	5.500	9.31	15.77	26.70
	$a = 0.053$	$b = 2.899$		
4) Constant shape, declining head width				
Head width ($\times 1.15$)	1.2	1.38	1.59	1.83
Length ($\times 1.2$)	5.00	6.00	7.20	8.64
Width ($\times 1.2$)	1.00	1.20	1.44	1.73
Height ($\times 1.2$)	1.00	1.20	1.44	1.73
Mass	5.00	8.64	14.93	25.80
	$a = 2.465$	$b = 3.886$		
5) Constant (flat) body shape				
Length ($\times 1.2$)	5.00	6.00	7.20	8.64
Width ($\times 1.2$)	2.00	2.40	2.88	3.46
Height ($\times 1.2$)	0.40	0.48	0.58	0.69
Mass	4.00	6.92	11.94	20.64
	$a = 0.032$	$b = 3.000$		
6) Flattened body, constant height				
Length ($\times 1.2$)	5.00	6.00	7.20	8.64
Width ($\times 1.2$)	2.00	2.40	2.88	3.46
Height ($\times 1.0$)	0.40	0.40	0.40	0.40
Mass	4.00	5.76	8.29	11.94
	$a = 0.160$	$b = 2.000$		

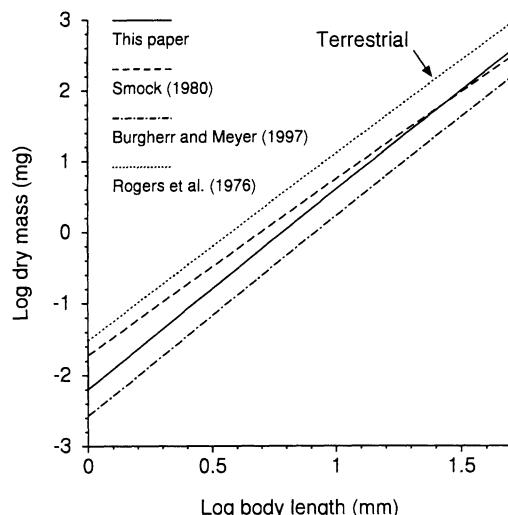


FIG. 5. Comparison of general length-mass equations of insects, including aquatic insects from North Carolina (Smock 1980), Central Europe (Burgherr and Meyer 1997), and North America (this paper), and terrestrial insects from a North American grassland in Washington state (Rogers et al. 1976). All equations are of the form $\log_{10} \text{DM} = b \log_{10} \text{BL} + \log_{10} a$, where DM = dry mass, BL = body length, and a and b are fitted constants. Values of a and b for each equation are presented in the text.

Thus, it is important to recognize that the deviation of individual data points from the length-mass regression line (as indicated by r^2) is partly the result of inherent variability within an instar rather than measurement error. Furthermore, using a length-mass regression to estimate mass for a single individual of a holometabolous taxon may result in a 50–100% error. For example, the highest value (2.65 mg) of the 5th instar used in the head-width regression for *Hydropsyche elissoma* is 71% higher than the value (1.55 mg) predicted by the regression (Fig. 3A). Variation of mass within a hemimetabolous instar also can be substantive, but is likely to be smaller than for holometabolous orders. For example, Wenzel et al. (1990) warned that a 20% error from a length-mass regression can be expected because of within-instar variation in mass for Ephemeroptera. Considering such potential errors, caution should be exercised if such regressions are used for estimating mass of an individual animal. In contrast, their utility is greater for studies in which one is seeking a

mean value for large numbers of animals found in a single length class.

Dry mass vs AFDM

We believe that equations based on AFDM are more accurate than those using DM (which includes ash content). The use of AFDM eliminates the possibility that some gut contents may contain inorganic materials or that inorganic silt may adhere to exoskeletons, biasing mass determinations with material that is not tissue. However, estimating AFDM is more time consuming than estimating DM, and most investigators do not go to the extra trouble. Whether the extra work involved is worth the effort is certainly debatable. Our % ash estimates (Fig. 4) should enable anyone to convert values estimated from a DM equation to AFDM values and vice versa. There appeared to be better discrimination of % ash among taxonomic groups than among functional groups. However, the functional group conversions may prove useful as well, particularly for species where taxonomic conversions are missing. Most of our % ash estimates were somewhat lower than the 10% approximated by Waters (1977) for zoobenthos and zooplankton.

Although most investigators use units of DM or AFDM, approximate conversions to energy, wet mass, and C are available (e.g., Waters 1977). More recently, Wenzel et al. (1990) estimated that % C ranged from 45.1 to 48.2% of DM for mayflies in Germany. If AFDM is ~93% of DM for mayflies (Fig. 4), then the Wenzel et al. (1990) estimate of % C would range from 48.5 to 51.8% of AFDM. In addition, A. D. Huryn (unpublished data) estimated that the mean C content of AFDM was 47.8% for various freshwater invertebrates (molluscs, oligochaetes, amphipods, and insects) in New Zealand. Thus, mean C content of AFDM appears to be consistently close to 50% for freshwater invertebrates. A. D. Huryn (unpublished data) also estimated that AFDM consisted of 10.4% N.

Usefulness of published length-mass regressions

We hope that our compilations of equations are helpful to other investigators in their own research, but we urge caution in their application. How does one select the most appropriate equation? Species- and genus-level regressions

are certainly preferable to family- or order-level equations. However, in the absence of a genus-level equation, a family-level equation should provide a reasonable, but less accurate estimate (Table 4). Family-level equations should be most representative when they are based on multiple taxa and a relatively high number of equations. Order-level equations should be the last resort (Table 2).

Given a choice of equations at a particular taxonomic level, how does one decide on the best equation? One should 1st consider whether the a and b coefficients seem reasonable, particularly in comparison to equations of closely related taxa. For example, mean b values among orders are ~ 3 , but examination of individual equations shows that b is sometimes <2 and >4 (see ranges in Table 2, and individual values in appendices). We believe that the true relationship between length and mass probably falls reasonably close to 3 in most aquatic insects (i.e., >2.4 and <3.6). As indicated above, however, this generalization does not apply to crayfish whose b values are commonly >3.6 . Therefore, we urge some caution in using any regression for insects in which b deviates considerably from these values. We should also point out that true values of b close to 2 are quite possible, as Nolte (1990) showed in a careful analysis of chironomid length-mass relationships.

If several equations of a given taxon have reasonable a and b values, then r^2 , the number of replicates, the range of lengths used in the regression, and geographic location all should be taken into account. If several equations have reasonably good values (e.g., *Baetis* spp., where $b > 2.4$, $r^2 > 0.80$, $n > 30$, Appendix 1), then geographic location (i.e., using the equation derived from the closest population) should be the deciding factor, in our opinion.

Some variation in length-mass relationships for populations of the same species in different locations is likely to be caused by differences in the physical-chemical environment, trophic conditions, or genetics, and should be considered a potential source of error when using the equations presented here. Various authors have suggested that regressions developed for the same taxa from different geographic regions may have significant differences in length-mass relations, and recommended caution in their application (e.g., Smock 1980, Meyer 1989, Wenzel et al. 1990, Burgherr and Meyer 1997). However,

in cases where different investigators developed equations for the same taxa in different regions, it is possible that investigator-related biases in weighing or measurement rather than geographic location could be responsible for these differences. Readers should make their own comparisons of regressions for a given taxon in Appendices 1, 2, and 3, and judge for themselves which is most acceptable for use in their own systems.

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Literature Cited

- ALDRIDGE, D. W., AND R. F. McMAHON. 1978. Growth, fecundity and bioenergetics in a natural population of the asiatic freshwater clam *Corbicula manilensis* Phillipi from north central Texas. *Journal of Molluscan Studies* 44:49-70.
- ALLAN, J. D. 1984. The size composition of invertebrate drift in a Rocky Mountain stream. *Oikos* 43:68-76.
- BALFOUR, D. L., AND L. A. SMOCK. 1995. Distribution, age structure, and movements of the freshwater mussel *Elliptio complanata* (Mollusca: Unionidae) in a headwater stream. *Journal of Freshwater Ecology* 10:255-268.
- BASSET, A., AND D. S. GLAZIER. 1995. Resource limitation and intraspecific patterns of weight \times length variation among spring detritivores. *Hydrobiologia* 316:127-137.
- BENKE, A. C. 1993. Concepts and patterns of invertebrate production in running waters. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* 25:15-38.
- BENKE, A. C., AND D. I. JACOBI. 1994. Production dynamics and resource utilization of snag-dwelling mayflies in a blackwater river. *Ecology* 75:1219-1232.
- BROWN, A. V., AND L. C. FITZPATRICK. 1978. Life his-

- tory and population energetics of the dobson fly, *Corydalus cornutus*. *Ecology* 59:1091–1108.
- BURGHERR, P., AND E. I. MEYER. 1997. Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. *Archiv für Hydrobiologie* 139:101–112.
- BUTLER, M. G. 1984. Life histories of aquatic insects. Pages 24–55 in V. H. Resh and D. M. Rosenberg (editors). *The ecology of aquatic insects*. Praeger, New York.
- CAMERON, C. J., I. F. CAMERON, AND C. G. PATERSON. 1979. Contribution of organic shell matter to biomass estimates of unionid bivalves. *Canadian Journal of Zoology* 57:1666–1669.
- CHAPMAN, R. F. 1982. *The insects: structure and function*. 3rd edition. Harvard University Press, Cambridge, Massachusetts.
- COLE, B. J. 1980. Growth ratios in holometabolous and hemimetabolous insects. *Annals of the Entomological Society of America* 73:489–491.
- DERMOTT, R. M., AND C. G. PATERSON. 1974. Determining dry weight and percentage dry matter of chironomid larvae. *Canadian Journal of Zoology* 52:1243–1250.
- DIXON, R. W. J., AND F. J. WRONA. 1992. Life history and production of the predatory caddisfly *Rhyacophila vao* Milne in a spring-fed stream. *Freshwater Biology* 27:1–11.
- EDWARDS, R. T., AND J. L. MEYER. 1987. Bacteria as a food source for black fly larvae in a blackwater river. *Journal of the North American Benthological Society* 6:241–250.
- EGGERT, S. L., AND T. M. BURTON. 1994. A comparison of *Acroneuria lycorias* (Plecoptera) production and growth in northern Michigan hard- and soft-water streams. *Freshwater Biology* 32:21–31.
- FOE, C., AND A. KNIGHT. 1985. The effect of phytoplankton and suspended sediment on the growth of *Corbicula fluminea* (Bivalvia). *Hydrobiologia* 127:105–115.
- FRANCE, R. L. 1993. Production and turnover of *Hyalella azteca* in central Ontario, Canada compared with other regions. *Freshwater Biology* 30:343–349.
- GIBERSON, D. J., AND T. D. GALLOWAY. 1985. Life history and production of *Ephoron album* (Say) (Ephemeroptera: Polymitarcyidae) in the Valley River, Manitoba. *Canadian Journal of Zoology* 63: 1668–1674.
- GRIFFITH, M. B., S. A. PERRY, AND W. B. PERRY. 1993. Growth and secondary production of *Paracapnia angulata* Hanson (Plecoptera; Capniidae) in Appalachian streams affected by acid precipitation. *Canadian Journal of Zoology* 71:735–743.
- HANSON, J. M., W. C. MACKAY, AND E. E. PREPAS. 1988. Population size, growth, and production of a unionid clam, *Anodonta grandis simpsoniana*, in a small, deep Boreal Forest lake in central Alberta. *Canadian Journal of Zoology* 66:247–253.
- HAWKINS, C. P. 1986. Variation in individual growth rates and population densities of ephemerellid mayflies. *Ecology* 67:1384–1395.
- HÓDAR, J. A. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecologica* 17:421–433.
- HORNBACH, D. J., T. DENEGA, B. S. PAYNE, AND A. C. MILLER. 1996. Shell morphometry and tissue condition of *Amblema plicata* (Say, 1817) from the upper Mississippi River. *Journal of Freshwater Ecology* 11:233–240.
- HORST, T. J., AND G. R. MARZOLF. 1975. Production ecology of burrowing mayflies in a Kansas reservoir. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* 19:3029–3038.
- HOWMILLER, R. P. 1972. Effects of preservatives on weights of some common macrobenthic invertebrates. *Transactions of the American Fisheries Society* 101:743–746.
- HUDSON, P. L., AND G. A. SWANSON. 1972. Production and standing crop of *Hexagenia* (Ephemeroptera) in a large reservoir. *Studies in Natural Sciences* 1(4):1–42. (Available from: Eastern New Mexico University, Portales, New Mexico 88130 USA)
- HURYN, A. D., J. W. KOEBEL, AND A. C. BENKE. 1994. Life history and longevity of the pleurocerid snail *Elimia*: a comparative study of eight populations. *Journal of the North American Benthological Society* 13:540–556.
- HURYN, A. D., AND J. B. WALLACE. 1987. Production and litter processing by crayfish in an Appalachian mountain stream. *Freshwater Biology* 18: 277–286.
- HUTCHINSON, J. M. C., J. M. McNAMARA, A. I. HOUSTON, AND F. VOLLRATH. 1997. Dyar's rule and the investment principle: optimal moulting strategies if feeding rate is size-dependent and growth is discontinuous. *Philosophical Transactions of the Royal Society of London, Series B* 352:113–138.
- JIN, H.-S. 1995. Life history and production of *Glossosoma nigrior* (Trichoptera: Glossosomatidae) in two Alabama streams associated with different geology. MS Thesis, University of Alabama, Tuscaloosa.
- JOHNSON, M. G. 1988. Production of the amphipod *Pontoporeia hoyi* in South Bay, Lake Huron. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 617–624.
- JOP, K. M., AND K. W. STEWART. 1987. Annual stonefly (Plecoptera) production in a second order Oklahoma Ozark stream. *Journal of the North American Benthological Society* 6:26–34.
- JORGENSEN, J. K., H. E. WELCH, AND M. F. CURTIS. 1992. Response of Amphipoda and Trichoptera to lake fertilization in the Canadian Arctic. *Canadian*

- an Journal of Fisheries and Aquatic Sciences 49: 2354-2362.
- KAWABATA, K., AND J. URABE. 1998. Length-weight relationships of eight freshwater planktonic crustacean species in Japan. Freshwater Biology 39: 199-206.
- KOESEL, J. W. 1994. The life history, secondary production, food habits, and prey electivity of *Corydalus cornutus* (Megaloptera) in a small southeastern stream. MS Thesis, University of Alabama, Tuscaloosa.
- LAURITSEN, D. D., AND S. C. MOZLEY. 1983. The freshwater asian clam *Corbicula fluminea* as a factor affecting nutrient cycling in the Chowan River, N.C. Report No. UNC-WRRI-83-192. Water Resources Research Institute of the University of North Carolina, Chapel Hill.
- LAUZON, M., AND P. P. HARPER. 1988. Seasonal dynamics of a mayfly (Insecta: Ephemeroptera) community in a Laurentian stream. Holarctic Ecology 11:220-234.
- LEUVEN, R. S. E. W., T. C. M. BROCK, AND H. A. M. VAN DRUTEN. 1985. Effects of preservation on dry- and ash-free dry weight biomass of some common aquatic macro-invertebrates. Hydrobiologia 127:151-159.
- MAIER, K. J., P. KOSALWAT, AND A. W. KNIGHT. 1990. Culture of *Chironomus decorus* (Diptera: Chironomidae) and the effect of temperature on its life history. Environmental Entomology 19:1681-1688.
- MARCHANT, R., AND H. B. N. HYNES. 1981. Field estimates of feeding rate for *Gammarus pseudolimnaeus* (Crustacea: Amphipoda) in the Credit River, Ontario. Freshwater Biology 11:27-36.
- MARTIEN, R. F., AND A. C. BENKE. 1977. Distribution and production of two crustaceans in a wetland pond. American Midland Naturalist 98:162-175.
- MASON, J. C. 1975. Crayfish production in a small woodland stream. Freshwater Crayfish 2:449-479.
- MATHIAS, J. A. 1971. Energy flow and secondary production of the amphipods *Hヤalella azteca* and *Crangonyx richmondensis occidentalis* in Marion Lake, British Columbia. Journal of the Fisheries Research Board of Canada 28:711-726.
- MCCAULEY, E. 1984. The estimation of abundance and biomass of zooplankton in samples. Pages 228-265 in J. A. Downing and F. H. Rigler (editors). A manual on methods for the assessment of secondary productivity in fresh waters. 2nd edition. Blackwell, Oxford, UK.
- MCCULLOUGH, D. A., G. W. MINSHALL, AND C. E. CUSHING. 1979a. Bioenergetics of a stream "collector" organism, *Tricorythodes minutus* (Insecta: Ephemeroptera). Limnology and Oceanography 24:45-58.
- MCCULLOUGH, D. A., G. W. MINSHALL, AND C. E. CUSHING. 1979b. Bioenergetics of lotic filter-feeding insects *Simulium* spp. (Diptera) and *Hydropsyche occidentalis* (Trichoptera) and their function in controlling organic transport in streams. Ecology 60:585-596.
- MERRITT, R. W., AND K. W. CUMMINS (EDITORS). 1996. An introduction to the aquatic insects of North America. 3rd edition. Kendall/Hunt, Dubuque, Iowa.
- MERRITT, R. W., D. H. ROSS, AND G. L. LARSON. 1982. Influence of stream temperature and seston on the growth and production of overwintering larval black flies (Diptera: Simuliidae). Ecology 63: 1322-1331.
- MEYER, E. 1989. The relationship between body length parameters and dry mass in running water invertebrates. Archiv für Hydrobiologie 117:191-203.
- MORIN, A., C. BACK, A. CHALIFOUR, J. BOISVERT, AND R. H. PETERS. 1988. Effect of black fly ingestion and assimilation on seston transport in a Quebec lake outlet. Canadian Journal of Fisheries and Aquatic Sciences 45:705-714.
- MUTCH, R. A., AND G. PRITCHARD. 1984. The life history of *Zapada columbiana* (Plecoptera: Nemouridae) in a Rocky Mountain stream. Canadian Journal of Zoology 62:1273-1281.
- NOLTE, U. 1990. Chironomid biomass determination from larval shape. Freshwater Biology 24:443-451.
- PAYNE, B. S., AND A. C. MILLER. 1996. Life history and production of filter-feeding insects on stone dikes in the lower Mississippi River. Hydrobiologia 319: 93-102.
- PETRUS, K. T. 1993. Comparative life history of an aquatic insect detritivore in two streams with different water chemistry. MS Thesis, University of Alabama, Tuscaloosa.
- PHILLIPS, E. C. 1997a. Life history and energetics of *Ancyronyx variegata* (Coleoptera: Elmidae) in northwest Arkansas and southeast Texas. Annals of the Entomological Society of America 90:54-61.
- PHILLIPS, E. C. 1997b. Life cycle, survival, and production of *Macronychus glabratus* (Coleoptera: Elmidae) in northwest Arkansas and southeast Texas streams. Invertebrate Biology 116:134-141.
- PICKARD, D. P., AND A. C. BENKE. 1996. Production dynamics of *Hyalella azteca* (Amphipoda) among different habitats in a small wetland in the southeastern USA. Journal of the North American Benthological Society 15:537-550.
- PIERCE, C. L., P. H. CROWLEY, AND D. M. JOHNSON. 1985. Behavior and ecological interactions of larval Odonata. Ecology 66:1504-1512.
- RABENI, C. F. 1992. Trophic linkage between stream centrarchids and their crayfish prey. Canadian Journal of Fisheries and Aquatic Sciences 49:1714-1721.
- ROGERS, L. E., W. T. HINDS, AND R. L. BUSCHBOM. 1976.

- A general weight vs. length relationship for insects. Annals of the Entomological Society of America 69:387–389.
- ROSEMOND, A. D., P. J. MULHOLLAND, AND J. W. ELWOOD. 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. Ecology 74:1264–1280.
- ROSS, D. H. 1982. Production of filter-feeding caddisflies (Trichoptera) in a southern Appalachian stream system. PhD Dissertation, University of Georgia, Athens.
- ROWE, L., AND M. BERRILL. 1989. The life cycles of five closely related mayfly species (Ephemeroptera: Heptageniidae) coexisting in a small southern Ontario stream pool. Aquatic Insects 11:73–80.
- SAMPLE, B. E., R. J. COOPER, R. D. GREER, AND R. C. WHITMORE. 1993. Estimation of insect biomass by length and width. American Midland Naturalist 129:234–240.
- SCHOENER, T. W. 1980. Length-weight regressions in tropical and temperate forest-understory insects. Annals of the Entomological Society of America 73:106–109.
- SEPHTON, T. W., AND C. G. PATERSON. 1986. Production of the chironomid *Procladius bellus* in an annual drawdown reservoir. Freshwater Biology 16:721–733.
- SICKEL, J. B. 1976. An ecological study of the Asiatic clam, *Corbicula manilensis* (Phillipi, 1841), in the Altamaha River, Georgia, with emphasis on population dynamics, productivity and control methods. PhD Dissertation, Emory University, Atlanta, Georgia.
- SIEGFRIED, C. A., AND A. W. KNIGHT. 1978. Aspects of the life history and growth of *Acroneuria (Calineuria) californica* in a Sierra foothill stream. Annals of the Entomological Society of America 71:149–154.
- SMOCK, L. A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biology 10:375–383.
- SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry. 3rd edition. W. H. Freeman and Company, New York.
- STELZER, R. S., AND T. M. BURTON. 1993. Growth and abundance of the crayfish *Orconectes propinquus* in a hard water and a soft water stream. Journal of Freshwater Ecology 8:329–340.
- STITES, D. L., A. C. BENKE, AND D. M. GILLESPIE. 1995. Population dynamics, growth, and production of the Asiatic clam, *Corbicula fluminea*, in a black-water river. Canadian Journal of Fisheries and Aquatic Sciences 52:425–437.
- STOUT, B. M., E. F. BENFIELD, AND J. R. WEBSTER. 1993. Effects of a forest disturbance on shredder production in southern Appalachian headwater streams. Freshwater Biology 29:59–69.
- SULLIVAN, D. M., AND M. S. TOPPING. 1984. Secondary production in *Isonychia bicolor* (Ephemeroptera: Oligoneuriidae). Transactions of the Missouri Academy of Science 18:17–24.
- TOWERS, D. J., I. M. HENDERSON, AND C. J. VELTMAN. 1994. Predicting dry weight of New Zealand aquatic macroinvertebrates from linear dimensions. New Zealand Journal of Marine and Freshwater Research 28:159–166.
- WALDE, S. J., AND R. W. DAVIES. 1987. Spatial and temporal variation in the diet of a predaceous stonefly (Plecoptera: Perlodidae). Freshwater Biology 17:109–115.
- WALLACE, J. B., AND M. E. GURTZ. 1986. Response of *Baetis* mayflies (Ephemeroptera) to catchment logging. American Midland Naturalist 115:25–41.
- WATERS, T. F. 1977. Secondary production in inland waters. Advances in Ecological Research 10:91–164.
- WENZEL, F., E. MEYER, AND J. SCHWOERBEL. 1990. Morphology and biomass determination of dominant mayfly larvae (Ephemeroptera) in running waters. Archiv für Hydrobiologie 118:31–46.
- WINNELL, M. H., AND D. S. WHITE. 1984. Ecology of shallow and deep water populations of *Pontoporeia hoyi* (Smith) (Amphipoda) in Lake Michigan. Freshwater Invertebrate Biology 3:118–138.

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APPENDIX 1. Length-mass regression equations based on total body length (unless otherwise indicated in parentheses). Equations are of the form $DM = aL^b$, where DM = dry mass (mg), L = body length (mm), and a and b are fitted constants. * indicates that ash-free dry mass (AFDM) was used instead of DM; for these regressions, % ash content of DM is given. f = female, m = male, and A = adult (Coleoptera only). Other abbreviations (FR, BC, PR; see source paper) represent different collection sites. All regressions are significant at $p < 0.05$. n = number of individuals included in regression, range = range of body lengths (mm) included in regression, state = state or province where individuals were collected, source = reference or individual (unpublished); ADH = Alexander D. Smock, LAS = Leonard A. Smock, ACB = Arthur C. Benke, BW = Bruce Wallace.

APPENDIX 1. Continued.

APPENDIX 1. Continued.

Taxon	$a \pm 1 \text{ SE}$	$b \pm 1 \text{ SE}$	r^2	n	Range	$\% \text{ ash} \pm 1 \text{ SE}$	State	Source
<i>Drunella</i> sp.	0.0257 ± 0.0025	2.252 ± 0.352	0.62	28	2.4–9.8		VA	LAS
<i>Drunella</i> sp.	0.0019	3.46	0.91	256			OR	Hawkins 1986
<i>Ephemerella</i> sp.	0.0097 ± 0.0003	2.663 ± 0.104	0.89	84	2.7–8.8		GA	ACB
<i>Ephemerella</i> sp.	0.0128 ± 0.0014	2.444 ± 0.266	0.81	46	2.1–7.7		VA	LAS
<i>Eurylophella temporalis</i>	0.0080 ± 0.0011	2.663 ± 0.210	0.94	74	1.7–6.1		VA	LAS
<i>E. verisimilis</i>	0.0051	2.442					QC	Lauzon and Harper 1988
<i>Serratella</i> sp.	0.0088 ± 0.0015	2.584 ± 0.479	0.76	24	2.3–8.0		VA	LAS
<i>Serratella</i> sp.*	0.0103 ± 0.0010	2.903 ± 0.072	0.99	10	0.6–7.1	4.2 ± 0.5	NC	ADH and JBW
Ephemeridae								
<i>Ephemerella</i> sp.*	0.0021 ± 0.0003	2.737 ± 0.079	0.99	14	0.9–22.4	18.8 ± 3.2	AL	ADH
<i>Hexagenia limbata</i>	0.0025	2.718	0.94				KS	Horst and Marzolf 1975
<i>H. limbata</i>	0.0024	2.710	0.98	32			SD/NE	Hudson and Swanson 1972
<i>H. munda</i>	0.0062 ± 0.0003	2.891 ± 0.113	0.79	21	3.3–24.6		NC	Smock 1980
	0.0249	2.73	0.98	85			ON	Rowe and Berrill 1989
Heptageniidae								
<i>Epeorus cf. dispar</i> *	0.0121 ± 0.0021	2.667 ± 0.125	0.98	10	0.5–9.1	4.7 ± 0.5	NC	ADH and JBW
<i>E. pleuralis</i> *	0.0119 ± 0.0010	2.824 ± 0.058	0.99	14	0.5–9.0	6.0 ± 0.5	NC	ADH and JBW
<i>Epeorus</i> sp.	0.0056 ± 0.0020	2.926 ± 0.355	0.55	18	1.3–11.6		VA	LAS
<i>Heptagenia</i> sp.	0.0180 ± 0.0010	2.326 ± 0.040	0.72	90	1.3–9.7		NC	Smock 1980
<i>Heptagenia</i> sp.	0.0087 ± 0.0005	2.731 ± 0.198	0.95	11	2.8–9.8		GA	ACB
<i>Leucrocuta</i> sp.*	0.0110 ± 0.0007	2.761 ± 0.051	1.00	9	1.5–6.5	9.7 ± 1.4	NC	ADH and JBW
<i>Nixe</i> sp.*	0.0080 ± 0.0008	2.919 ± 0.079	0.99	9	1.1–5.9	6.4 ± 0.7	NC	ADH and JBW
<i>Stenacron carolina</i> *	0.0057 ± 0.0009	2.782 ± 0.102	0.99	10	0.7–10.5	6.9 ± 0.8	NC	ADH and JBW
<i>S. inter punctatum</i>	0.0067 ± 0.0008	2.807 ± 0.087	0.88	45	1.0–10.9		NC	Smock 1980
<i>S. meririvulanum</i> *	0.0101 ± 0.0004	2.891 ± 0.021	1.00	10	0.7–12.3	5.3 ± 0.7	NC	ADH and JBW
<i>Stenonema modestum</i>	0.0078 ± 0.0002	2.871 ± 0.027	0.88	128	0.8–12.1		NC	Smock 1980
<i>S. modestum</i>	0.0101 ± 0.0016	2.636 ± 0.186	0.81	52	1.0–10.7		VA	LAS
<i>S. modestum</i>	0.0047	2.819					QC	Lauzon and Harper 1988
<i>Stenonema</i> spp.	0.0128 ± 0.0008	2.616 ± 0.151	0.84	59	2.0–12.7		GA	ACB
Isonychiidae								
<i>Isonychia</i> sp.	0.0031 ± 0.0007	3.167 ± 0.023	0.88	107	2.2–13.2		NC	Smock 1980
<i>Isonychia</i> spp.	0.0031	2.918	0.97	123	2.6–12.9		GA	Benke and Jacobi 1994
Leptophlebiidae								
<i>Habrophlebia vibrans</i> *	0.0047 ± 0.0006	2.566 ± 0.113	0.99	7	0.9–5.7	6.0 ± 0.7	NC	ADH and JBW
<i>H. vibrans</i>	0.0028	2.488					QC	Lauzon and Harper 1988
<i>Leptophlebia</i> sp.	0.0054 ± 0.0009	2.836 ± 0.222	0.78	25	1.2–8.4		VA	LAS
<i>Paraleptophlebia</i> spp.*	0.0038 ± 0.0006	2.918 ± 0.119	0.99	8	0.9–7.4	7.5 ± 0.5	NC	ADH and JBW
<i>Paraleptophlebia</i> sp.	0.0061 ± 0.0005	2.624 ± 0.189	0.88	55	1.0–7.8		VA	LAS

APPENDIX 1. Continued.

Taxon	<i>a</i> ± 1 SE	<i>b</i> ± 1 SE	<i>r</i> ²	<i>n</i>	Range	% ash ± 1 SE	State	Source
Polymitarcyidae								
<i>Ephoron album</i>	0.002	3.05	0.89	5–14			MB	Giberson and Galloway 1985
Siphlonuridae								
<i>Siphlonica aerotromia</i> *	0.0002 ± 0.0002	3.610 ± 0.272	0.90	20	6.0–21.0	8.4 ± 0.8	ME	ADH
<i>Siphlonurus</i> sp.*	0.0001 ± 0.0000	4.140 ± 0.150	0.96	30	5.4–18.0	4.0 ± 0.8	ME	ADH
Tricorythidae								
<i>Tricorythodes minutus</i>	0.0092	3.222		200			ID	McCullough et al. 1979a
<i>Tricorythodes</i> sp.	0.0029 ± 0.0040	3.165 ± 0.253	0.77	19	1.7–7.1		VA	LAS
ODONATA								
Zygoptera								
Calopterygidae								
<i>Calopteryx</i> sp.	0.0050 ± 0.0008	2.742 ± 0.222	0.87	25	2.0–16.1		VA	LAS
Coenagrionidae								
<i>Argia</i> spp.	0.0086 ± 0.0018	2.666 ± 0.130	0.83	23	4.1–15.2		NC	Smock 1980
<i>Ischnura</i> spp.	0.0015 ± 0.0001	2.904 ± 0.180	0.96	13	2.9–13.3		SC	ACB
Anisoptera								
Aeshnidae								
<i>Boyeria villosa</i>	0.0082 ± 0.0021	2.813 ± 0.087	0.94	11	3.3–35.4		NC	Smock 1980
Cordulegastridae								
<i>Corduleoester maculata</i>	0.0067 ± 0.0012	2.782 ± 0.242	0.81	18	3.2–38.1		VA	LAS
Corduliidae								
<i>Epitheca cynosura</i>	0.0090 ± 0.0004	2.757 ± 0.103	0.94	48	2.5–19.7		SC	ACB
<i>E. semiaquae</i>	0.0074 ± 0.0007	2.720 ± 0.359	0.76	17	4.2–29.3		VA	LAS
<i>Neurocordulia molesta</i>	0.0124 ± 0.0006	2.884 ± 0.142	0.89	54	3.0–19.0		GA	ACB
Gomphidae								
<i>Dromogomphus</i> sp.	0.0180 ± 0.0016	2.239 ± 0.317	0.83	12	8.5–19.0		SC	ACB
<i>Gomphius</i> spp.	0.0044 ± 0.0006	3.124 ± 0.297	0.85	9	4.8–26.6		NC	Smock 1980
<i>Gomphius</i> spp.	0.0060 ± 0.0008	2.847 ± 0.388	0.90	24	3.0–37.1		VA	LAS
<i>Lanthus vernalis</i> *	0.0097	2.895	0.98	9	0.9–16.0		NC	ADH
<i>Progomphus obscurus</i>	0.0057 ± 0.0012	2.831 ± 0.322	0.74	28	3.9–23.0		VA	LAS
Libellulidae								
<i>Celithemis fasciata</i>	0.0058 ± 0.0003	2.877 ± 0.098	0.95	44	2.1–16.3		SC	ACB
<i>Erythemis simplicicollis</i>	0.0061 ± 0.0009	3.089 ± 0.411	0.89	9	4.2–12.5		SC	ACB
<i>Ladona deplanata</i>	0.0072 ± 0.0003	2.618 ± 0.117	0.94	37	6.5–23.8		SC	ACB
<i>Libellula</i> spp.	0.0151 ± 0.0013	2.393 ± 0.262	0.83	19	6.3–16.5		SC	ACB

APPENDIX 1. Continued.

Taxon		<i>a</i> ± 1 SE	<i>b</i> ± 1 SE	<i>r</i> ²	<i>n</i>	Range	% ash ± 1 SE	State	Source
<i>Plathenius hydia</i>		0.0040 ± 0.0003	3.068 ± 0.285	0.85	22	7.0–18.9		SC	ACB
PLECOPTERA									
Capniidae									
<i>Allocapnia</i> spp.		0.0047 ± 0.0004	2.761 ± 0.156	0.79	29	1.4–6.7		NC	LAS
<i>Allocapnia</i> spp.		0.0057 ± 0.0003	2.439 ± 0.199	0.92	25	1.3–7.0		VA	LAS
<i>Allocapnia</i> spp.*		0.0040 ± 0.0006	2.487 ± 0.122	0.98	10	0.7–6.9	4.7 ± 1.0	NC	ADH and JBW
Chloroperlidae									
<i>Sueetsa</i> sp.*		0.0062 ± 0.0019	2.724 ± 0.213	0.95	10	0.7–8.6	3.9 ± 1.3	NC	ADH and JBW
Leuctridae									
<i>Leuctra</i> sp.		0.0025 ± 0.0003	2.744 ± 0.100	0.88	34	2.2–7.2		VA	LAS
<i>Leuctra</i> sp.*		0.0030 ± 0.0003	2.694 ± 0.065	1.00	9	0.6–7.7	4.9 ± 0.7	NC	ADH and JBW
Nemouridae									
<i>Amphinemura wui</i> *		0.0071 ± 0.0008	2.678 ± 0.084	0.99	9	0.8–6.5		NC	ADH and JBW
<i>Amphinemura</i> spp.		0.0040 ± 0.0005	2.975 ± 0.178	0.88	62	1.0–6.9		VA	LAS
<i>Prostoa completa</i>		0.0055 ± 0.0003	2.633 ± 0.126	0.96	38	0.9–6.2		VA	LAS
Peltoperlidae									
<i>Tallaperla maria</i>		0.0141	2.62	0.89	289			Stout et al. 1993	
<i>Tallaperla</i> sp.*		0.0194 ± 0.0014	2.853 ± 0.058	1.00	12	0.6–9.9	2.6 ± 0.5	NC	ADH
Perlidae									
<i>Acroneuria abnormis</i>		0.0061 ± 0.0005	3.000 ± 0.420	0.94	22	4.2–26.1		NC	LAS
<i>A. hycorias</i> (FR)		0.0129	2.8	0.97				MI	Eggert and Burton 1994
<i>A. hycorias</i> (PR)		0.0101	2.9	0.97				MI	Eggert and Burton 1994
<i>Acroneuria</i> spp.		0.0019 ± 0.0001	3.232 ± 0.160	0.89	52	3.4–17.0		GA	ACB
<i>Agnetaia capitata</i>		0.0144 ± 0.0015	2.688 ± 0.322	0.76	21	3.0–11.2		VA	LAS
<i>Beloneraia georgiana</i> *		0.0079 ± 0.0007	2.844 ± 0.050	1.00	11	1.3–18.7	3.9 ± 0.9	NC	ADH and JBW
<i>B. georgiana</i>		0.0094 ± 0.0011	2.766 ± 0.262	0.86	31	3.3–19.5		VA	LAS
<i>Ecceptura xanthenes</i>		0.0030 ± 0.0003	3.232 ± 0.185	0.96	18	5.8–20.0		NC	LAS
<i>Neoperla clymene</i>		0.0429 ± 0.0051	1.950 ± 0.356	0.67	17	3.8–14.0		GA	ACB
<i>Paragnetina kansensis</i>		0.0093 ± 0.0006	2.797 ± 0.167	0.82	63	4.0–22.0		GA	ACB
<i>Perlestia placida</i>		0.0030 ± 0.0001	3.020 ± 0.143	0.85	83	3.7–10.2		GA	ACB
<i>Perlestia</i> sp.		0.0037 ± 0.0003	3.080 ± 0.150	0.81	15	2.5–11.5		NC	Smock 1980
<i>Perlinella drymo</i>		0.0034 ± 0.0003	3.123 ± 0.203	0.81	18	3.3–16.9		VA	LAS
Perlodidae									
<i>Clioperla clio</i>		0.0037 ± 0.0002	2.931 ± 0.213	0.83	26	2.4–13.2		NC	LAS
<i>C. clio</i>		0.0054 ± 0.0005	2.762 ± 0.290	0.77	50	2.9–14.3		VA	LAS

APPENDIX 1. Continued.

APPENDIX 1. Continued.

Taxon	<i>a</i> ± 1 SE	<i>b</i> ± 1 SE	<i>r</i> ²	<i>n</i>	Range	% ash ± 1 SE	State	Source
<i>Brachycentrus etowahensis</i>	0.0025 ± 0.0008	3.443 ± 0.037	0.98	224	2.0–13.0	11.7 ± 0.5	GA	JBW
<i>Brachycentrus</i> sp.	0.0025 ± 0.0005	2.600 ± 0.421	0.66	26	2.2–10.4	VA	LAS	
<i>Micrasema</i> sp.*	0.0181 ± 0.0019	2.410 ± 0.087	0.97	22	1.0–5.4	7.2 ± 0.6	AL	ADH
Glossosomatidae								
<i>Glossosoma nigrior</i> *	0.0065	3.028	0.98	61	0.7–6.3	6.6 ± 0.5	AL	Jin 1995
<i>Glossosoma</i> sp.*	0.0092 ± 0.0015	2.888 ± 0.134	0.96	20	1.2–5.8	4.3 ± 1.2	AL	ADH
Helicopsychidae								
<i>Helicopsyche</i> sp.* (case width)	0.0120 ± 0.0014	3.096 ± 0.129	0.96	28	1.3–4.3			
Hydropsychidae								
<i>Cheumatopsyche</i> spp.	0.0049 ± 0.0006	2.620 ± 0.308	0.69	58	1.4–12.0	NC	LAS	
<i>Cheumatopsyche</i> spp.	0.0045 ± 0.0005	2.721 ± 0.300	0.83	47	1.1–11.8	VA	LAS	
<i>Hydropsyche elisoma</i>	0.0058 ± 0.0003	2.491 ± 0.143	0.93	26	2.4–10.0	GA	ACB	
<i>H. incommoda</i>	0.00053 ± 0.00003	4.179 ± 0.179	0.90	43	2.6–9.0	GA	ACB	
<i>H. occidentalis</i>	0.0041	2.970	0.69	50		ID	McCullough et al. 1979b	
<i>H. sparna</i> *	0.0074 ± 0.0010	2.666 ± 0.073	0.99	20	1.0–14.4	10.7 ± 0.6	AL	ADH
<i>Hydropsyche</i> spp.	0.0051 ± 0.0007	2.824 ± 0.289	0.79	122	1.6–15.1	NC	LAS	
<i>Hydropsyche</i> spp.	0.0060 ± 0.0009	2.708 ± 0.323	0.71	36	1.3–14.3	VA	LAS	
<i>Macrosteleum carolina</i>	0.0026 ± 0.0003	3.117 ± 0.263	0.88	16	1.8–15.0	NC	LAS	
<i>M. carolina</i>	0.0039 ± 0.0003	2.966 ± 0.217	0.73	71	4.0–13.5	GA	ACB	
Lepidostomatidae								
<i>Lepidostoma</i> sp.	0.0079 ± 0.0009	2.649 ± 0.135	0.78	33	1.0–9.1	VA	LAS	
Leptoceridae								
<i>Ocetis</i> spp.	0.0034 ± 0.0006	3.212 ± 0.251	0.71	23	1.2–8.0	VA	LAS	
Limnephilidae								
<i>Ironoquia parvula</i>	0.0041 ± 0.0004	2.933 ± 0.199	0.61	18	2.5–17.3	VA	LAS	
<i>Limnephilus</i> sp.*	0.0015 ± 0.0008	3.115 ± 0.214	0.87	32	5.6–19.2	10.7 ± 0.9	ME	ADH
<i>Pycnopsyche luculentta</i>	0.0052 ± 0.0003	2.832 ± 0.111	0.92	47	2.8–17.9	VA	LAS	
<i>P. scabripennis</i>	0.0049 ± 0.0003	2.850 ± 0.282	0.87	27	3.1–23.8	VA	LAS	
Odontoeridae								
<i>Psilotreta</i> sp.	0.0082 ± 0.0010	2.735 ± 0.200	0.76	18	1.5–13.0	VA	LAS	
<i>Psilotreta</i> sp.*	0.0064 ± 0.0008	3.241 ± 0.091	0.99	19	0.9–9.1	11.3 ± 2.1	AL	ADH
Philopotamidae								
<i>Chimarra</i> sp.	0.0049 ± 0.0008	2.480 ± 0.205	0.78	34	1.6–10.2	NC	LAS	
<i>Chimarra</i> sp.	0.0050 ± 0.0009	2.401 ± 0.598	0.64	29	1.8–9.4	VA	LAS	
<i>Chimarra</i> sp.*	0.0044 ± 0.0006	2.652 ± 0.092	0.97	27	0.8–11.2	12.1 ± 1.5	AL	ADH

APPENDIX 1. Continued.

APPENDIX 1. Continued.

Taxon	<i>a</i> ± 1 SE	<i>b</i> ± 1 SE	<i>r</i> ²	<i>n</i>	Range	% ash ± 1 SE	State	Source
DIPTERA								
<i>Anchyrtarsus bicolor*</i>	0.0011 ± 0.0003	3.100 ± 0.139	0.95	25	1.6–15.2	9.3 ± 2.1	AL	ADH
Athericidae	0.0038 ± 0.0022	2.586 ± 0.279	0.79	24	3.3–15.8	4.8 ± 0.3	AL	ADH
<i>Atherix</i> sp.*	0.0064 ± 0.0015	3.292 ± 0.188	0.98	8	0.9–4.7	4.3 ± 0.6	AL	ADH
Blephariceridae	0.00022 ± 0.00003	2.871 ± 0.255	0.91	15	2.2–10.8		ACB	
<i>Blepharicera</i> sp.*	0.00033 ± 0.0002	2.392 ± 0.163	0.66	18	1.0–7.3		NC	Smock 1980
Ceratopogonidae	0.0039 ± 0.0007	2.144 ± 0.531	0.71	33	1.4–7.0		VA	LAS
<i>Palpomyia</i> spp. group	0.0006	2.770	0.86	91	0.9–12.1		NC	ADH
<i>Palpomyia</i> spp. group	0.0059 ± 0.0009	2.099 ± 0.235	0.88	50	1.7–10.8		VA	LAS
Chironomidae*	0.0051 ± 0.0004	2.322 ± 0.124	0.88	61	1.8–7.3		NC	Smock 1980
Chironominae/Orthocladiinae	0.0007 ± 0.00009	2.952 ± 0.118	0.93	51	1.0–6.7		AL	ACB
Chironomini	0.00083	2.86	0.96	105			CA	Maier et al. 1990
<i>Chironomus</i> decorus	0.00068 ± 0.00004	2.620 ± 0.112	0.96	26	2.0–13.7		AL	ACB
<i>Chironomus</i> spp.	0.0010 ± 0.00008	2.606 ± 0.189	0.94	15	1.0–4.6		AL	ACB
<i>Cladopeltma</i> sp.	0.00059 ± 0.00005	3.142 ± 0.312	0.87	17	2.6–6.7		AL	ACB
<i>Dicrotendipes</i> sp.	0.0010 ± 0.00005	2.761 ± 0.110	0.98	18	1.3–5.7		AL	ACB
<i>Polyptilum</i> spp.	0.0008 ± 0.0012	2.728 ± 0.197	0.67	45	1.3–5.3		VA	LAS
Tanytarsini	0.0012 ± 0.00013	2.294 ± 0.317	0.81	14	1.6–5.8		AL	ACB
<i>Tanytarsus</i> spp.	0.0020 ± 0.0006	2.254 ± 0.396	0.74	39	1.6–5.0		VA	LAS
Orthocladiinae	0.0026 ± 0.0005	2.503 ± 0.458	0.81	46	2.3–8.2		VA	LAS
Tanypodinae	0.0038 ± 0.0006	2.411 ± 0.130	0.85	12	2.0–9.0		NC	Smock 1980
Tanypodinae	0.0010 ± 0.00009	2.884 ± 0.166	0.94	20	0.8–7.5		AL	ACB
<i>Ablabesmyia</i> sp.	0.0012	2.597		123			ON	Sephton and Peterson 1986
<i>Procladius bellus</i>	0.00077 ± 0.00006	2.693 ± 0.154	0.91	32	1.0–9.8		AL	ACB
<i>Procladius</i> spp.	0.0066 ± 0.0010	2.436 ± 0.434	0.69	16	1.6–8.0		VA	LAS
Empididae	0.0040 ± 0.0015	2.655 ± 0.261	0.93	9	1.4–9.9		ADH and JBW	
Empididae*	0.0040 ± 0.0013	2.091 ± 0.218	0.94	7	1.5–7.4		NC	Smock 1980
Sciariidae	0.0048 ± 0.0007	2.550 ± 0.132	0.72	26	1.6–7.7		MI	Merritt et al. 1982
Simuliidae	0.0012 ± 0.0002	3.190 ± 0.080	0.94	612				
<i>Prosimulium mixtum/</i> <i>fuscum</i>	0.00119 ± 0.00059	2.692 ± 0.303	0.89	15			QC	Morin et al. 1988
<i>Simulium decorum</i>	0.00025 ± 0.00013	3.342 ± 0.093	0.95	70			QC	Morin et al. 1988
<i>S. tuberosum</i>	0.00055 ± 0.00012	3.036 ± 0.081	0.98	38			QC	Morin et al. 1988

APPENDIX 1. Continued.

Taxon	<i>a</i> ± 1 SE	<i>b</i> ± 1 SE	<i>r</i> ²	<i>n</i>	Range	% ash ± 1 SE	State	Source
<i>Simulium</i> spp.*	0.0031	2.64	0.90	24				Edwards and Meyer 1987
<i>Simulium</i> spp.*	0.0040 ± 0.0005	2.807 ± 0.122	0.99	9	0.7–5.2	7.9 ± 0.7	GA	ADH and JBW
<i>Stegopterna mutata</i>	0.00042 ± 0.00011	3.830 ± 0.140	0.94	169			NC	Merritt et al. 1982
Tabanidae							MI	
<i>Chrysops / Tabanus</i> spp.	0.0050 ± 0.0006	2.591 ± 0.105	0.81	20	1.9–16.4		VA	LAS
Tipulidae								
<i>Dicranota</i> sp.*	0.0027 ± 0.0007	2.637 ± 0.164	0.97	9	1.2–9.2	3.4 ± 0.6	NC	ADH and JBW
<i>Hexatoma</i> spp.*	0.0042 ± 0.0007	2.596 ± 0.108	0.97	19	1.0–12.6	3.0 ± 0.3	NC	ADH and JBW
<i>Lipsothrix</i> sp.*	0.0006 ± 0.0006	2.745 ± 0.388	0.92	5	2.8–16.0	3.5 ± 1.1	NC	ADH and JBW
<i>Molophilus</i> sp.*	0.0016 ± 0.0005	2.914 ± 0.194	0.97	8	1.2–9.5	5.3 ± 2.0	NC	ADH and JBW
<i>Pedicia</i> sp.*	0.0013 ± 0.0005	2.851 ± 0.221	0.96	8	2.2–16.0	3.5 ± 0.6	NC	ADH and JBW
<i>Pilaria</i> sp.*	0.0014 ± 0.0003	2.667 ± 0.124	0.98	8	2.6–11.1	2.4 ± 0.2	NC	ADH and JBW
<i>Tipula abdominalis</i>	0.0015 ± 0.0002	2.810 ± 0.190	0.88	27	4.0–31.1	VA	LAS	
<i>T. abdominalis</i>	0.0054 ± 0.0003	2.463 ± 0.133	0.92	36	4.3–38.1	NC	LAS	
<i>Tipula</i> sp.*	0.0064 ± 0.0034	2.443 ± 0.199	0.95	9	4.3–28.3	4.5 ± 0.6	NC	ADH and JBW

APPENDIX 2. Length-mass regression equations for Mollusca based on shell length or width. Equations are of the form $DM = a L^b$, where DM = dry mass of soft tissue (mg), L = maximum shell length (mm), and a and b are fitted constants. W indicates that maximum shell width was used instead of shell length. AW indicates that maximum shell width at aperture was used instead of shell length. * indicates that ash-free dry mass (AFDM) was used instead of DM; for these regressions, % ash content of DM (soft tissue) and % ash of total mass (including shell) are given. Sampling seasons are indicated by sum. = summer and spr. = spring. All other numbers or acronyms represent different collection sites (e.g., 10A, 10B; see source papers). For *Elimia* species, AG = Alligator Creek, CH = Choccolocco Creek, HM = Hendrick Mill Branch, MA = Marys Creek, RO = Rocky Branch, TE = Terrapin Creek; *Elimia* equations are revised from Huryn et al. (1994). All regressions are significant at $p < 0.05$. n = number of individuals included in regression, range = range of body lengths (mm) included in regression, state = state or province where individuals were collected, source = reference or individual (unpublished); ADH = Alexander D. Huryn, LAS = Leonard A. Smock, ACB = Arthur C. Benke.

Taxon	$a \pm 1 \text{ SE}$	$b \pm 1 \text{ SE}$	r^2	n	Range	% ash $\pm 1 \text{ SE}$ (soft)	% ash $\pm 1 \text{ SE}$ (+ shell)	State	Source
BIVALVIA									
Corbiculidae									
<i>Corbicula fluminea</i>	0.0204	2.45	0.91	185				GA	Stites et al. 1995
<i>C. fluminea</i>	0.0055	3.18	0.99	66				GA	Sickel 1976
<i>C. fluminea</i>	0.0078	3.12	0.99	20				TX	Aldridge and McMahon 1978
<i>C. fluminea</i> (spr.)*	0.0089	3.34	0.97	26				CA	Foe and Knight 1985
<i>C. fluminea</i> (sum.)*	0.0058	3.45	0.99	18				CA	Foe and Knight 1985
<i>C. fluminea</i> (spr.)	0.0141	3.01	0.97	21				NC	Lauritsen and Mozley 1983
<i>C. fluminea</i> (sum.)	0.0209	2.77	0.87	35				NC	Lauritsen and Mozley 1983
Sphaeriidae									
<i>Pisidium</i> sp.	0.0163 ± 0.0013	2.477 ± 0.187	0.87	104	1.7–10.3			VA	LAS
Unionidae									
<i>Amblema plicata</i> (10A)	0.0144	2.782	0.96					IA/WI	Hornbach et al. 1996
<i>A. plicata</i> (10B)	0.0102	2.852	0.95					IA/WI	Hornbach et al. 1996
<i>A. plicata</i> (11)	0.0041	3.042	0.97					IA/WI	Hornbach et al. 1996
<i>A. plicata</i> (14)	0.0086	2.863	0.96					IA/IL	Hornbach et al. 1996
<i>A. plicata</i> (17)	0.0028	3.133	0.96					IA/IL	Hornbach et al. 1996
<i>A. plicata</i> (18)	0.0052	2.972	0.96					IA/IL	Hornbach et al. 1996
<i>A. plicata</i> (19U)	0.0055	2.992	0.89					IA/IL	Hornbach et al. 1996
<i>A. plicata</i> (19L)	0.0009	3.394	0.89					IA/IL	Hornbach et al. 1996
<i>A. plicata</i> (24)	0.0166	2.741	0.70					MO/IL	Hornbach et al. 1996
<i>A. plicata</i> (25)	0.0091	2.854	0.95					MO/IL	Hornbach et al. 1996
<i>A. plicata</i> (26)	0.0179	2.724	0.44					MO/IL	Hornbach et al. 1996
<i>A. plicata</i> (10A)*	0.0236	2.618	0.95					IA/WI	Hornbach et al. 1996
<i>A. plicata</i> (10B)*	0.0194	2.640	0.96					IA/WI	Hornbach et al. 1996
<i>A. plicata</i> (11)*	0.0068	2.842	0.98					IA/WI	Hornbach et al. 1996

APPENDIX 2. Continued.

Taxon	<i>a</i> ± 1 SE	<i>b</i> ± 1 SE	<i>r</i> ²	<i>n</i>	Range	% ash ±1 SE (soft)	% ash ±1 SE (+ shell)	State	Source
<i>A. plicata</i> (14)*	0.0205	2.588	0.95					IA/IL	Hornbach et al. 1996
<i>A. plicata</i> (17)*	0.0146	2.685	0.95					IA/IL	Hornbach et al. 1996
<i>A. plicata</i> (18)*	0.0300	2.489	0.93					IA/IL	Hornbach et al. 1996
<i>A. plicata</i> (19U)*	0.0123	2.749	0.84					IA/IL	Hornbach et al. 1996
<i>A. plicata</i> (19L)*	0.0037	2.992	0.90					IA/IL	Hornbach et al. 1996
<i>A. plicata</i> (24)*	0.2033	2.091	0.72					MO/IL	Hornbach et al. 1996
<i>A. plicata</i> (25)*	0.0124	2.702	0.95					MO/IL	Hornbach et al. 1996
<i>A. plicata</i> (26)*	0.0638	2.358	0.50					MO/IL	Hornbach et al. 1996
<i>Anodontia cataracta</i> (ML)	0.0038	2.915 ± 0.094		154	10–100			NB	Cameron et al. 1979
<i>A. cataracta</i> (LL)	0.0142	2.729 ± 0.059		249	20–120			NS	Cameron et al. 1979
<i>A. grandis simpsoniana</i>	0.00042	3.42 ± 0.044		170	18–80			AB	Hanson et al. 1988
<i>Elliptio complanata</i>	0.0023	3.156	0.97	67	22–104			VA	Balfour and Smock 1995
<i>E. complanata</i>	0.0067	2.770 ± 0.089	0.94	281	10–80			NB	Cameron et al. 1979
<i>Lampsilis ochracea</i>	0.0075	2.931 ± 0.148		186				NB	Cameron et al. 1979
GASTROPODA									
Pleuroceridae									
<i>Elimia cahawbensis*</i> (AW) (HM)	0.0331 ± 0.0026	2.851 ± 0.042	0.99	49	0.6–10.7	16.2 ± 2.1	90.3 ± 0.3	AL	ADH
<i>E. cahawbensis*</i> (HM)	0.0037 ± 0.0011	3.320 ± 0.126	0.96	30	2.7–14.6			AL	ADH
<i>E. cahawbensis*</i> (AW) (AG)	0.0238 ± 0.0016	3.091 ± 0.038	0.99	51	0.8–11.7	29.7 ± 3.6	92.0 ± 0.3	AL	ADH
<i>E. cahawbensis*</i> (AG)	0.0033 ± 0.0005	3.232 ± 0.065	0.99	30	4.6–20.2			AL	ADH
<i>E. cahawbensis*</i> (AW) (RO)	0.0324 ± 0.0029	3.074 ± 0.052	0.99	50	0.8–12.3	15.1 ± 1.5	89.1 ± 0.4	AL	ADH
<i>E. cahawbensis*</i> (RO)	0.0074 ± 0.0019	3.022 ± 0.111	0.96	30	1.9–19.3			AL	ADH
<i>E. carinifera*</i> (AW) (HM)	0.0701 ± 0.0069	2.420 ± 0.059	0.97	56	0.2–11.2	14.0 ± 1.6	92.5 ± 0.4	AL	ADH
<i>E. carinifera*</i> (HM)	0.0055 ± 0.0018	2.761 ± 0.131	0.94	30	2.2–21.3			AL	ADH
<i>E. clavaeformis*</i> (W)	0.0123	3.984	0.96	50				TN	Rosemond et al. 1993
<i>E. fascinans*</i> (AW)(CH)	0.0224 ± 0.0021	3.051 ± 0.049	0.98	61	0.7–12.7	16.9 ± 2.0	93.0 ± 0.3	AL	ADH
<i>E. fascinans*</i> (CH)	0.0203 ± 0.0030	2.521 ± 0.069	0.97	36	1.0–21.7			AL	ADH
<i>E. fascinans*</i> (AW) (MA)	0.0229 ± 0.0028	3.013 ± 0.066	0.98	52	0.8–11.3	19.1 ± 2.4	93.5 ± 0.3	AL	ADH
<i>E. fascinans*</i> (AW) (TE)	0.0248 ± 0.0032	2.971 ± 0.068	0.97	51	0.8–12.3	21.5 ± 2.8	93.9 ± 0.3	AL	ADH
<i>E. variata*</i> (AW) (AG)	0.0247 ± 0.0025	2.994 ± 0.057	0.98	52	0.8–12.8	18.3 ± 3.0	93.2 ± 0.3	AL	ADH
<i>E. variata*</i> (AG)	0.0058 ± 0.0012	3.151 ± 0.095	0.97	30	2.7–17.2			AL	ADH

APPENDIX 3. Length-mass regression equations based on head width. Equations are of the form $DM = aHW^b$, where DM = dry mass (mg), HW = head width (mm), and a and b are fitted constants. * indicates that ash-free dry mass (AFDM) was used instead of DM. Where indicated, the following are substituted for $HW:HL$ = head length, TW = telson width, IOW = interocular width, PW = pronotal width (all units are mm). Other abbreviations represent different collection sites (see source paper). All regressions are significant at $p < 0.05$. n = number of individuals included in regression, range = range of head widths or otherwise) included in regression, state = state or province where individuals were collected, source = reference or individual (unpublished); ADH = Alexander D. Huryn, LAS = Leonard A. Smock, ACB = Arthur C. Benke, JBW = J. Bruce Wallace.

APPENDIX 3. Continued.

Taxon	$a \pm 1 \text{ SE}$	$b \pm 1 \text{ SE}$	r^2	n	Range	$\% \text{ ash} \pm 1 \text{ SE}$	State	Source
<i>Baetisca</i> sp.	0.3240 ± 0.313	3.461 ± 0.294	0.74	51	0.7–2.6		GA	ACB
Caenidae								
<i>Caenis diminuta</i>	0.2667 ± 0.0128	2.764 ± 0.100	0.96	30	0.1–1.1		AL	ACB
<i>Caenis</i> sp.	0.7293 ± 0.2008	3.109 ± 0.815	0.64	14	0.3–1.2		NC	LAS
<i>Caenis</i> sp.	0.8642 ± 0.1899	3.011 ± 0.268	0.63	35	0.2–1.4		VA	LAS
Ephemerellidae								
<i>Drunella coloradensis</i>	0.450	3.476	0.94	46			CO	Allan 1984
<i>Drunella</i> sp.	1.2840 ± 0.3692	2.960 ± 0.656	0.60	28	0.3–1.8		VA	LAS
<i>Drunella</i> spp.	0.434	3.62	0.92	256			OR	Hawkins 1986
<i>Ephemerella</i> sp.	0.5481 ± 0.1545	3.303 ± 0.728	0.56	46	0.2–1.6		VA	LAS
<i>Ephemerella</i> spp.	0.584 ± 0.0196	3.592 ± 0.154	0.86	85	0.7–1.8		GA	ACB
<i>Eurylophella temporalis</i>	0.9336 ± 0.2000	3.122 ± 0.287	0.86	74	0.2–1.5		VA	LAS
<i>Serratella</i> sp.	0.7255 ± 0.2626	3.325 ± 0.525	0.72	24	0.3–1.6		VA	LAS
Heptageniidae								
<i>Cinygmulia</i> sp.	0.182	2.886	0.83	43			CO	Allan 1984
<i>Epeorus longimanus</i>	0.060	4.111	0.92	36			CO	Allan 1984
<i>Epeorus</i> sp.	0.1321 ± 0.0374	3.303 ± 0.565	0.81	18	0.3–3.8		VA	LAS
<i>Heptagenia</i> sp.	0.1610 ± 0.0121	3.134 ± 0.277	0.93	11	1.0–2.8		GA	ACB
<i>Stenacron interpunctatum</i>	0.1099 ± 0.0211	3.569 ± 0.318	0.90	45	0.3–3.6		NC	LAS
<i>Stenonema modestum</i>	0.1824 ± 0.0193	3.221 ± 0.230	0.98	128	0.3–4.1		NC	LAS
<i>S. modestum</i>	0.1116 ± 0.0245	3.358 ± 0.464	0.74	52	0.4–3.8		VA	LAS
<i>Stenonema</i> spp.	0.1837 ± 0.0115	3.035 ± 0.170	0.83	67	0.8–3.3		GA	Benke and Jacobi 1994
Isonychiidae								
<i>Isonychia bicolor</i>	0.7879	3.915	0.99	40			MO	Sullivan and Topping 1984
<i>Isonychia</i> sp.	0.8390 ± 0.3202	3.421 ± 0.348	0.66	107	0.4–2.0		NC	LAS
<i>Isonychia</i> spp.	0.5510	3.268 ± 0.219	0.96	123	0.5–2.0		GA	ACB
Leptophlebiidae								
<i>Leptophlebia</i> sp.	0.4571 ± 0.0961	3.724 ± 0.761	0.81	25	0.4–2.2		VA	LAS
<i>Paraleptophlebia</i> sp.	0.5264 ± 0.2777	3.038 ± 0.558	0.76	55	0.4–1.7		VA	LAS
Siphlonuridae								
<i>Siphlonisca aerodromia</i> *	0.2830 ± 0.0528	3.982 ± 0.337	0.88	20	0.9–2.6	8.4 ± 0.8	ME	ADH
<i>Siphlonura</i> sp.*	0.2361 ± 0.0285	4.244 ± 0.220	0.93	30	0.8–2.7	4.0 ± 0.8	ME	ADH
Tricorythidae								
<i>Tricorythodes</i> sp.	0.7777 ± 0.1767	3.252 ± 0.483	0.81	19	0.3–1.4		VA	LAS

APPENDIX 3. Continued.

Taxon	$a \pm 1 \text{ SE}$	$b \pm 1 \text{ SE}$	r^2	n	Range	$\% \text{ ash} \pm 1 \text{ SE}$	State	Source
Zygoptera								
Calopterygidae								
<i>Calopteryx</i> sp.	0.3828 \pm 0.0821	2.488 \pm 0.400	0.87	25	0.2–3.4		VA	LAS
Coenagrionidae								
<i>Argia</i> spp.	0.4727 \pm 0.1665	2.455 \pm 0.421	0.85	23	0.3–3.9		NC	LAS
<i>Enallagma aspersum</i>	0.0400	3.520	0.77	20			TN	Pierce et al. 1985
<i>E. traviatum</i>	0.0748	2.760	0.72	16			TN	Pierce et al. 1985
<i>Ischnura</i> sp.	0.1189 \pm 0.0080	3.000 \pm 0.173	0.97	13	0.7–2.8		SC	ACB
Anisoptera								
Cordulegastridae								
<i>Cordulegaster maculata</i>	1.0025 \pm 0.3440	2.401 \pm 0.583	0.67	18	0.9–8.6		VA	LAS
Corduliidae								
<i>Epitheca cynosura</i>	0.2028 \pm 0.0077	3.026 \pm 0.096	0.92	85	0.9–5.7		SC	ACB
<i>E. semiaquae</i>	0.7491 \pm 0.1111	2.681 \pm 0.731	0.76	17	0.6–5.8		VA	LAS
<i>Neurocordulia molesta</i>	0.3214 \pm 0.0159	3.002 \pm 0.142	0.90	54	1.0–6.2		GA	ACB
Gomphidae								
<i>Dromogomphus</i> sp.	0.7396 \pm 0.0514	2.416 \pm 0.260	0.90	12	1.6–3.5		SC	ACB
<i>Gomphus</i> spp.	0.8177 \pm 0.0934	2.454 \pm 0.204	0.94	24	1.1–6.6		VA	LAS
<i>Progomphus obscurus</i>	0.6964 \pm 0.1400	2.646 \pm 0.666	0.72	28	0.7–4.3		VA	LAS
Libellulidae								
<i>Celithemis fasciata</i>	0.0826 \pm 0.0031	3.252 \pm 0.071	0.97	70	0.5–5.5		SC	ACB
<i>Erythemis simplicollis</i>	0.0995 \pm 0.0083	3.592 \pm 0.229	0.95	15	1.5–4.8		SC	ACB
<i>Ladonia deplanata</i>	0.2080 \pm 0.0083	3.180 \pm 0.111	0.94	56	1.5–4.7		SC	ACB
<i>Libellula</i> spp.	0.2393 \pm 0.0161	2.909 \pm 0.152	0.94	24	0.7–4.2		SC	ACB
<i>Plathemis lydia</i>	0.4613 \pm 0.0413	3.019 \pm 0.307	0.83	22	1.6–4.6		SC	ACB
PLECOPTERA								
Capniidae								
<i>Allocapnia</i> spp.	0.7121 \pm 0.1902	3.250 \pm 0.813	0.61	29	0.3–0.8		NC	LAS
<i>Allocapnia</i> spp.	0.5438 \pm 0.1353	3.255 \pm 0.520	0.85	25	0.3–0.7		VA	LAS
<i>Paracapnia angulata</i> (SFR)	0.497	2.43					WV	Griffith et al. 1993
<i>P. angulata</i> (WS4)	0.549	3.09					WV	Griffith et al. 1993
<i>P. angulata</i> (WS3)	0.712	3.51					WV	Griffith et al. 1993
<i>P. angulata</i> (HSR)	0.364	2.44					WV	Griffith et al. 1993
Leuctridae								
<i>Leuctra</i> sp.	0.8496 \pm 0.1234	3.201 \pm 0.254	0.90	34	0.4–0.8		VA	LAS

APPENDIX 3. Continued.

Taxon	<i>a</i> ± 1 SE	<i>b</i> ± 1 SE	<i>r</i> ²	<i>n</i>	Range	% ash ± 1 SE	State	Source
Nemouridae								
<i>Amphinemura delosa</i>	1.496	2.587	0.99	113	0.3–0.7	OK	Jop and Stewart 1987	
<i>Amphinemura</i> spp.	0.4373 ± 0.0965	2.966 ± 0.686	0.72	62	0.4–1.2	VA	LAS	
<i>Prostoia completa</i>	0.5263 ± 0.1826	2.762 ± 0.599	0.66	38	0.3–1.4	VA	LAS	
<i>P. completa</i>	2.323	3.34	0.96	63	0.4–1.1	OK	Jop and Stewart 1987	
<i>Zapada columbiana</i>	0.45	3.10	0.98	70	AB	Mutch and Pritchard 1984		
<i>Z. hayesi</i>	0.512	2.934	0.87	40	CO	Allan 1984		
Peltoperlidae								
<i>Tallaperla anna</i> complex (HMB)	0.47	4.00	0.98	42	AL	Petrus 1993		
<i>T. anna</i> complex (YC)	0.56	3.75	0.98	42	AL	Petrus 1993		
Perlidae								
<i>Acroleuria abnormis</i>	0.3208 ± 0.0284	3.189 ± 0.276	0.96	22	0.7–5.1	NC	LAS	
<i>A. evoluta</i> (IOW)	0.592	3.745	0.99	151	0.3–3.2	OK	Jop and Stewart 1987	
<i>Acroleuria</i> spp.	0.1563 ± 0.0063	3.242 ± 0.119	0.93	52	0.8–4.0	GA	ACB	
<i>Agnetina capitata</i>	0.2698 ± 0.0506	3.063 ± 0.658	0.61	21	0.6–3.2	VA	LAS	
<i>A. capitata</i> (IOW)	1.125	3.233	0.99	152	0.4–2.9	OK	Jop and Stewart 1987	
<i>Beloneuria georgiana</i>	0.5671 ± 0.1255	2.724 ± 0.565	0.81	31	0.4–4.3	VA	LAS	
<i>Calineuria californica</i>	0.12	3.81	0.96	180	CA	Siegfried and Knight 1978		
<i>Ecoptura xanthenes</i>	0.2444 ± 0.0660	3.326 ± 0.956	0.61	18	0.4–3.3	NC	LAS	
<i>Neoperla clymene</i>	0.6825 ± 0.0767	2.000 ± 0.333	0.71	17	0.9–2.8	GA	ACB	
<i>Neoperla</i> spp. (IOW)	1.169	2.551	0.99	88	0.3–1.9	OK	Jop and Stewart 1987	
<i>Pangonetina kansensis</i>	0.2650 ± 0.0172	3.205 ± 0.189	0.83	63	1.1–5.6	GA	ACB	
<i>Perlinella drymo</i>	0.5500 ± 0.1358	2.929 ± 0.821	0.72	18	0.5–3.4	VA	LAS	
<i>Perlestia placida</i>	0.2466 ± 0.0085	3.616 ± 0.181	0.83	83	0.8–2.3	GA	ACB	
<i>Perlestia</i> sp.	0.4012 ± 0.1835	2.802 ± 0.898	0.61	15	0.4–3.3	NC	LAS	
Perlodidae								
<i>Cliperla clio</i>	0.4027 ± 0.0366	2.987 ± 0.305	0.94	26	0.6–3.3	NC	LAS	
<i>C. clio</i>	0.5462 ± 0.0621	2.826 ± 0.381	0.85	50	0.4–3.3	VA	LAS	
Isogenus group	0.7234 ± 0.1833	2.641 ± 0.705	0.64	32	0.5–2.8	NC	LAS	
<i>Isoperla bilineata</i>	0.5462 ± 0.1445	2.826 ± 0.465	0.76	33	0.5–2.5	VA	LAS	
<i>I. namata</i>	1.167	2.472	0.99	125	0.4–1.7	OK	Jop and Stewart 1987	
<i>Kogotus nonus</i>	0.72	3.61	0.87	150	AB	Walde and Davies 1987		
Pteronarcidae								
<i>Pteronarcys dorsata</i>	0.8057 ± 0.0524	3.167 ± 0.211	0.86	36	1.6–5.2	GA	ACB	

APPENDIX 3. Continued.

Taxon	$a \pm 1 \text{ SE}$	$b \pm 1 \text{ SE}$	r^2	n	Range	% ash $\pm 1 \text{ SE}$	State	Source
Taeniopterygidae								
<i>Strophopteryx</i> sp.	0.4388 \pm 0.1202	3.921 \pm 0.932	0.64	26	0.3-1.4		VA	LAS
<i>Taeniopteryx lita</i>	0.4236 \pm 0.0211	2.683 \pm 0.193	0.93	16	0.4-0.9		GA	ACB
<i>Taeniopteryx</i> spp.	0.7444 \pm 0.1285	3.482 \pm 0.764	0.81	44	0.4-1.7		NC	LAS
MEGALOPTERA								
Corydalidae								
<i>Corydilus cornutus</i>	1.4942 \pm 0.2222	2.586 \pm 0.323	0.85	41	0.8-9.2		NC	LAS
<i>C. cornutus</i>	1.0962 \pm 0.3894	2.652 \pm 0.500	0.72	21	0.7-10.1		VA	LAS
<i>C. cornutus</i>	0.5315 \pm 0.0304	3.025 \pm 0.079	0.95	82	0.4-9.5		GA	ACB
<i>C. cornutus</i>	0.321	3.256	0.97	90	0.6-11.5		AL	Koebel 1994
<i>C. cornutus</i>	0.273	2.87	0.92	445			TX	Brown and Fitzpatrick 1978
Nigroniidae								
<i>Nigronia serricornis</i>	1.1666 \pm 0.2311	2.474 \pm 0.564	0.79	34	0.8-6.3		NC	LAS
<i>N. serricornis</i>	0.9367 \pm 0.2806	2.635 \pm 0.721	0.69	26	0.6-6.7		VA	LAS
Sialidae								
<i>Sialis aequalis</i>	0.4861 \pm 0.1865	3.108 \pm 0.640	0.77	36	0.3-3.5		VA	LAS
<i>Sialis</i> sp.	0.5428 \pm 0.1102	2.936 \pm 0.862	0.69	25	0.4-3.4		NC	LAS
TRICHOPTERA								
Brachycentridae								
<i>Brachycentrus</i> sp.	2.221 \pm 0.2330	3.349 \pm 0.402	0.88	26	0.3-1.4		VA	LAS
Hydropsychidae								
<i>Cheumatopsyche</i> spp.	1.362 \pm 0.3711	2.284 \pm 0.658	0.61	58	0.2-1.5		NC	LAS
<i>Cheumatopsyche</i> spp.	0.984 \pm 0.2630	2.814 \pm 0.471	0.83	47	0.2-1.4		VA	LAS
<i>Hydropsyche elissoma</i>	1.2106 \pm 0.0831	2.580 \pm 0.179	0.89	26	0.4-1.2		GA	ACB
<i>H. incornuta</i>	1.5955 \pm 0.1438	3.621 \pm 0.281	0.80	43	0.3-1.1		GA	ACB
<i>H. orris</i> (IOW)	1.702	2.773	0.97				MS	Payne and Miller 1996
<i>Hydropsyche</i> spp.	1.180 \pm 0.2852	2.886 \pm 0.888	0.69	122	0.2-1.8		NC	LAS
<i>Hydropsyche</i> spp.	1.265 \pm 0.1622	2.747 \pm 0.284	0.87	36	0.2-1.7		VA	LAS
<i>Macrostelemum carolina</i>	1.301 \pm 0.1888	2.726 \pm 0.390	0.92	16	0.2-1.7		NC	LAS
<i>M. carolina</i>	0.9474 \pm 0.0561	3.009 \pm 0.138	0.87	71	0.5-2.1		GA	ACB
Lepidostomatidae								
<i>Lepidostoma</i> sp.	1.666 \pm 0.1555	2.987 \pm 0.222	0.94	33	0.2-1.3		VA	LAS
Leptoceridae								
<i>Nectopsycie</i> sp.	2.644 \pm 0.3665	3.297 \pm 0.522	0.74	16	0.4-0.8		GA	ACB
<i>Oecetis</i> spp.	1.913 \pm 0.5983	3.300 \pm 0.637	0.67	23	0.2-1.0		VA	LAS

APPENDIX 3. Continued.

Taxon	<i>a</i> ± 1 SE	<i>b</i> ± 1 SE	<i>r</i> ²	<i>n</i>	Range	% ash ± 1 SE	State	Source
Limnephilidae								
<i>Apatania zonella</i>	5.812	4.102			0.2–1.2		NT	Jorgenson et al. 1992
<i>Grensia</i> sp.	1.486	3.856			0.3–2.0		NT	Jorgenson et al. 1992
<i>Ironoquia parvula</i>	1.645 ± 0.3491	3.220 ± 0.780	0.66	18	0.4–2.0		VA	LAS
<i>Pycnopsyche luculenta</i>	1.823 ± 0.4729	3.114 ± 0.950	0.64	47	0.3–2.1		VA	LAS
<i>P. scabripennis</i>	2.024 ± 0.3655	3.109 ± 0.436	0.85	27	0.3–2.3		VA	LAS
Odontoceridae								
<i>Psilotreta</i> sp.	1.941 ± 0.5008	3.366 ± 0.521	0.79	18	0.3–1.6		VA	LAS
Philopotamidae								
<i>Chimarra</i> sp.	1.465 ± 0.3913	3.087 ± 0.666	0.66	34	0.3–1.1		NC	LAS
<i>Chimarra</i> sp.	1.106 ± 0.2555	3.143 ± 0.762	0.64	29	0.2–1.2		VA	LAS
Phryganeidae								
<i>Ptilostomis</i> sp.	2.042 ± 0.4896	3.333 ± 0.920	0.61	20	0.5–2.5		VA	LAS
Polycentropodidae								
<i>Neureclipsis</i> sp.	0.6852 ± 0.0718	4.580 ± 0.767	0.63	23	0.8–1.5		GA	ACB
<i>Polycentropus</i> spp.	1.568 ± 0.2050	3.302 ± 0.352	0.90	25	0.2–1.3		VA	LAS
Psychomyiidae								
<i>Lype diversa</i>	1.732 ± 0.1591	3.384 ± 0.307	0.96	28	0.2–1.3		VA	LAS
<i>L. diversa</i> *	2.173 ± 0.424	3.664 ± 0.183	0.94	28	0.2–0.7	1.6 ± 0.2	NC	ADH and JBW
Rhyacophilidae								
<i>Rhyacophila vao</i>	6.80	4.123	0.78	613	0.2–0.9		AB	Dixon and Wrona 1992
<i>Rhyacophila</i> spp.	1.750 ± 0.2486	3.522 ± 0.879	0.73	32	0.4–1.5		VA	LAS
Sericostomatidae								
<i>Agarodes libalis</i>	1.566 ± 0.3636	2.982 ± 0.520	0.85	41	0.3–1.4		VA	LAS
<i>Fattigia pele</i>	1.003 ± 0.095	3.309 ± 0.151	0.98	10	0.3–1.9	12.2 ± 3.0	NC	ADH and JBW
COLEOPTERA								
Chrysomelidae								
<i>Galerucella nymphaea</i>	14.981 ± 9.310	3.670 ± 0.168	0.80	120	0.2–0.6	7.1 ± 0.3	GA	JBW
Elmidae								
<i>Ancyromyx variegata</i>	2.0181 ± 0.4009	3.468 ± 0.600	0.74	37	0.2–0.5		VA	LAS
<i>A. variegata</i>	3.8971	2.804 ± 0.427	0.92	800	0.2–0.6		AR	Phillips 1997a
<i>A. variegata</i>	3.2589	2.645 ± 0.419	0.91	800	0.2–0.6		TX	Phillips 1997a
<i>Macromyces glabratus</i>	1.6041 ± 0.6005	3.499 ± 0.903	0.64	38	0.2–0.5		NC	LAS
<i>M. glabratus</i>	1.7685 ± 0.3845	3.357 ± 0.755	0.81	54	0.1–0.5		VA	LAS
<i>M. glabratus</i>	3.7289	2.758 ± 0.303	0.95		0.2–0.7		AR	Phillips 1997b

APPENDIX 3. Continued.

Taxon	$a \pm 1 \text{ SE}$	$b \pm 1 \text{ SE}$	r^2	n	Range	% ash $\pm 1 \text{ SE}$	State	Source
<i>M. glabratus</i>	3.8620	2.793 \pm 0.281	0.96		0.2–0.7		TX	Phillips 1997b
<i>Stenelmis</i> spp.	1.4040 \pm 0.3123	3.794 \pm 0.844	0.60	46	0.2–0.6		NC	LAS
DIPTERA								
Ceratopogonidae								
<i>Palpomyia</i> spp. group	1.0431 \pm 0.3625	2.383 \pm 0.630	0.72	18	0.1–0.3		NC	LAS
<i>Palpomyia</i> spp. group	1.3044 \pm 0.3999	2.359 \pm 0.632	0.79	33	0.1–0.4		VA	LAS
Chironomidae	2.7842 \pm 0.7005	2.835 \pm 0.399	0.90	73	0.1–0.4		NC	LAS
Chironominae	1.9574 \pm 0.3297	2.589 \pm 0.403	0.81	50	0.1–0.5		VA	LAS
Chironominae/	2.7802 \pm 0.7666	2.841 \pm 0.293	0.88	61	0.1–0.4		NC	LAS
Orthocladiinae								
Tanytarsini	1.6660 \pm 0.4450	2.484 \pm 0.521	0.71	45	0.1–0.3		VA	LAS
Orthocladiinae	1.7899 \pm 0.6622	2.311 \pm 0.566	0.64	39	0.1–0.4		VA	LAS
Tanypodinae	2.1694 \pm 0.5630	2.623 \pm 0.377	0.85	46	0.1–0.4		VA	LAS
Tanypodinae	2.8046 \pm 0.7109	2.955 \pm 0.570	0.85	12	0.1–0.4		NC	LAS
Empididae	0.9888 \pm 0.6388	2.602 \pm 0.924	0.60	16	0.2–0.6		VA	LAS
Simuliidae	1.3824 \pm 0.3644	3.161 \pm 0.508	0.76	26	0.2–0.7		NC	LAS
<i>Prosimulium</i> spp.	2.553	4.347	0.88	34			CO	Allan 1984