The aims of this study were to determine which linear body dimensions are best suitable and which mathematical functions can be used to describe length–dry mass relationships for a population of *Phylloicus* sp. (Trichoptera: Calamoceratidae) larvae. We measured three linear body dimensions (body length, head capsule width and interocular distance) of 54 larvae to use as dry mass predictors. For the description of length–dry mass relationships we used linear, exponential and power function models. Body length provided the best fitted equations to estimate biomass, followed by head capsule width and interocular distance. The highest coefficients of determination were found in power function and exponential models. These relationships can be useful to determine the growth rate and/or secondary production of *Phylloicus* larvae in future laboratory experiments, as well as to understand the importance of these shredders in the energy flux of shaded tropical streams.

**Keywords:** size-mass equations; biomass estimation; linear body dimensions; *Phylloicus*; tropical shredders

**Introduction**

Biomass of aquatic macroinvertebrates is important to determine growth rates and/or secondary production, as well as to understand life histories, seasonal patterns and trophic relationships between functional feeding groups (Benke 1996; Burgherr and Meyer 1997). Data on macroinvertebrate biomass can also be useful in colonisation studies or quantifying the role of detritivores on leaf decomposition (Cressa 1999).

Among the different approaches to biomass determination, the most common is the direct weighing of individual specimens (Dermott and Paterson 1974; Smock 1980; Meyer 1989). However, this approach is often very time consuming, and prone to error if the insects have been previously stored in chemical preservatives (e.g. formalin or alcohol), which can cause alterations in their dry mass (Donald and Paterson 1977; Downing and Rigler 1984; Kato and Miyasaka 2007). Direct determination of dry mass has the added disadvantage of rendering the specimen
useless for further examination as a result of the drying process (Towers, Henderson and Veltman 1994).

An alternative to avoid such disadvantages is to estimate the biomass indirectly, using length–dry mass conversions (Gould 1966; Peters 1983; Burgherr and Meyer 1997; Benke, Huryn, Smock and Wallace 1997). Estimating dry mass indirectly from linear body dimensions (e.g. body length, head capsule width) is more rapid than direct mass determination, particularly for small invertebrates. Moreover, in laboratory experiments assessing invertebrate feeding behaviour, this approach allows the estimation of initial biomass without stressing and/or killing the organisms.

Length–dry mass relationships have been used to estimate the biomass of invertebrates from different geographical locations and of taxa with similar body shapes (Johnston and Cunjak 1999). Most of the length–dry mass relationships for stream invertebrates were estimated for North American and European taxa (Smock 1980; Meyer 1989) and, until now, only a few data were proposed for the tropical region. Furthermore, previous studies suggested the need to use taxa-specific relationships because they are more precise, once different taxa may differ in body shape and volume (Schoener 1980; Smock 1980; Gowing and Recher 1985; Cressa 1986).

Only few invertebrate taxa have been mentioned as shredders in neotropical streams. Among them, larvae of the genus *Phylloicus* Müller, 1880 (Trichoptera: Calamoceratidae) are well distributed throughout Latin America and, in some streams, can be found easily on leaf patches with low water current (Prather 2003). Because these larvae are also easy to manipulate and keep alive in laboratory conditions, they have been used in many experiments (e.g. feeding preference, growth, survival and case building) that aimed to better understand the behaviour of shredders and their influence on leaf decomposition in tropical streams (Grac¸a et al. 2001; Rincón and Martínez 2006).

In this study, we analysed the length–dry mass relationships for a population of *Phylloicus* sp. by using three different regression functions (linear, power and exponential) and three body dimensions in order to determine the best relationship.

**Materials and methods**

*Phylloicus* sp. larvae were collected on July 2007 in Taboões spring (20°03'38"S – 44°03'03"W), located in the Serra do Rola Moça State Park, Minas Gerais State, southeastern Brazil. The Taboões spring is inside a forest fragment, presenting a well developed riparian area, which forms a closed canopy. Leaves fall throughout the year and accumulate in the streambed.

Larvae were found visually, collected with a hand net, and taken to the laboratory in an isothermic box with stream water. In the laboratory, undamaged individuals of the same morphospecies were carefully removed from their cases and placed individually in Petri dishes. Three linear body dimensions were chosen among the most common used as biomass predictors: body length, head capsule width and interocular distance (Meyer 1989). Body length (BL) was measured as the distance from the anterior of the head to the posterior of the last abdominal segment. Head capsule width (HW) was measured across the widest section of the head. Interocular distance (ID) was measured as the minimum distance between eyes, parallel to head width. Body dimensions were measured to the nearest 0.1 mm with a Zeiss dissecting...
microscope fitted with an ocular micrometer (magnification: 8 x for BL measurements and 50 x for HW and ID measurements). Animals were then placed individually in pre-weighed aluminium foils, dried at 60°C for 48 h (Meyer 1989), left to cool in a desiccator, and their dry mass (DM) was measured to the nearest 0.1 mg.

Three regression models were calculated for the three *Phylloicus* body dimensions, using the method of least squares. The fit of regression equations was judged by the coefficient of determination ($r^2$), the significance level ($p$, obtained from regression ANOVA) and residual analysis. All statistical analyses were performed based on Zar (1999).

**Results**

Body dimensions measures and dry weights of 54 larvae were used for statistical analyses. *Phylloicus* dry mass presented the highest coefficient of variation, with values ranging from 1.3 to 26.6 mg (Table 1). Among body dimensions, body length presented higher range (10.4–28.9 mm) and coefficient of variation (Table 1).

The following regression models were chosen because they provided the best fits. Conversion of *Phylloicus* body dimensions to dry mass was determined by linear (1), exponential (2) and power function (3) models or its logarithmic equivalents:

\[
DM = a + b \cdot L 
\]

\[
DM = a \cdot e^{bL} \text{ (in linear form: } \ln DM = \ln a + b \cdot L) 
\]

\[
DM = a \cdot L^b \text{ (in linear form: } \ln DM = \ln a + b \cdot \ln L) 
\]

where $a/b$ are regression constants, DM is dry mass, $L$ is the linear body dimension (BL, HW, ID) and $e$ is a mathematical constant (Euler’s number: 2.718).

The parameters of Equations (1), (2) and (3) are listed in Table 2. All body dimensions showed a very high level of significance in the three models ($p < 0.01$). Body length provided the best relationships to estimate biomass (Table 2), followed by head capsule width and interocular distance. These relationships were best fitted by power function and exponential models that presented very similar coefficients of determination to each body dimension. Figure 1 shows the relations of dry mass as a function of body length, head capsule width and interocular distance for *Phylloicus* larvae. The regression lines and curves were given by power function.

Table 1. Ranges, mean, standard deviation (SD) and coefficient of variation (CV, in percentage) for body length, head capsule width, interocular distance (mm) and dry mass (mg) of *Phylloicus* sp. larvae; $n = 54$. CV = (SD/mean) $\times$ 100.

<table>
<thead>
<tr>
<th></th>
<th>Range</th>
<th>Mean</th>
<th>SD</th>
<th>CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body length</td>
<td>10.4–28.9</td>
<td>16.7</td>
<td>2.7</td>
<td>16.2</td>
</tr>
<tr>
<td>Head capsule width</td>
<td>0.8–1.5</td>
<td>1.3</td>
<td>0.2</td>
<td>14.0</td>
</tr>
<tr>
<td>Interocular distance</td>
<td>0.6–1.1</td>
<td>1.0</td>
<td>0.1</td>
<td>14.3</td>
</tr>
<tr>
<td>Dry mass</td>
<td>1.3–26.6</td>
<td>12.1</td>
<td>6.7</td>
<td>54.2</td>
</tr>
</tbody>
</table>
Discussion

Even though all relationships between body dimensions and biomass were highly significant, body length was the best predictor, explaining 75–76% of the variation in mass. This linear body dimension is widely used for determining length–dry mass relationships of aquatic invertebrates (e.g. Smock 1980; Towers et al. 1994; Burgherr and Meyer 1997) mainly because it has a broader measuring range. Body length also provides slightly higher coefficients of determination than head capsule width and interocular distance (González, Basaguren and Pozo 2002).

Although body length usually gives the best relationships, some authors (see Cressa 1999; Marchant and Hehir 1999; González et al. 2002) prefer to use other linear body dimensions, like head capsule width, case width, pronotum length or tarsus length. This probably owes to the fact that, among other reasons, these structures are sclerotised and less subject to distortion or breakage under manipulation than body length. In addition, Becker (2005) found that pronotum length is the best measurement to distinguish larval instars of Agapetus fuscipes (Trichoptera) in a German first-order stream. In the present study, larvae were measured on the same day they had been sampled. So, all measurements were done on fresh, undamaged and completely stretched animals, which allowed a precise and reliable determination of the three studied body dimensions.

The exponential and power function models did not differ between the body dimensions determined. Most authors found the highest fit between body length and dry mass when they use the power function model (e.g. Smock 1980; Meyer 1989; Burgherr and Meyer 1997) but exponential regressions have also been used by Dudgeon (1995) and Perán, Velasco and Millán (1999) for length–dry mass relationships of Hydrocyphon (Coleoptera) and Caenis luctuosa (Ephemeroptera), respectively. Wenzel, Meyer and Schwoerbel (1990) pointed out that differences between the results obtained using different regression models are low and they decrease when a higher number of animals is used. Although power function is more often used, the exponential model should not be discarded when looking for the best fit of length–dry mass relationships.

Table 2. Parameters (with 95% confidence intervals) of the linear, exponential and power function models for the relationship between a linear body dimension (L = body length [BL], head capsule width [HW] or interocular distance [ID], in mm) and dry mass (DM, in mg) of Phylloicus sp. larvae.

<table>
<thead>
<tr>
<th>Function</th>
<th>Conversion</th>
<th>a</th>
<th>ln a</th>
<th>b</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Linear</td>
<td>BL — DM</td>
<td>−20.24 ± 3.44</td>
<td>1.93 ± 0.20</td>
<td>0.64**</td>
<td></td>
</tr>
<tr>
<td>DM = a + b · L</td>
<td>HW — DM</td>
<td>−21.20 ± 4.58</td>
<td>26.49 ± 3.61</td>
<td>0.51**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>ID — DM</td>
<td>−19.97 ± 4.62</td>
<td>33.51 ± 4.78</td>
<td>0.49**</td>
<td></td>
</tr>
<tr>
<td>Exponential</td>
<td>BL — DM</td>
<td>−1.63 ± 0.32</td>
<td>0.23 ± 0.02</td>
<td>0.75*</td>
<td></td>
</tr>
<tr>
<td>ln DM =</td>
<td>HW — DM</td>
<td>−2.05 ± 0.40</td>
<td>3.45 ± 0.32</td>
<td>0.70**</td>
<td></td>
</tr>
<tr>
<td>ln a + b · L</td>
<td>ID — DM</td>
<td>−2.00 ± 0.39</td>
<td>4.48 ± 0.41</td>
<td>0.70**</td>
<td></td>
</tr>
<tr>
<td>Power</td>
<td>BL — DM</td>
<td>−7.73 ± 0.77</td>
<td>3.58 ± 0.28</td>
<td>0.76*</td>
<td></td>
</tr>
<tr>
<td>ln DM =</td>
<td>HW — DM</td>
<td>1.43 ± 0.09</td>
<td>3.95 ± 0.35</td>
<td>0.71**</td>
<td></td>
</tr>
<tr>
<td>ln a + b · ln L</td>
<td>ID — DM</td>
<td>2.50 ± 0.06</td>
<td>3.84 ± 0.34</td>
<td>0.71**</td>
<td></td>
</tr>
</tbody>
</table>

a, b = regression constants, r² = coefficient of determination (*p < 0.01, **p < 0.001). n = 54.
In practice, when interpreting a length–dry mass regression equation, “b” values represent the rate of increase (i.e. slope) of dry weight against length in a linear relationship, whereas the constant “a” only represents the dry mass of an organism at a unit length (i.e. 1 mm). It is known that for tropical aquatic insects the constant b falls short of the expected value of 3, which means that body mass of insects is more influenced by surface than by volume (Engelmann 1961). Our results support those from Cressa (1999) who found that *Phylloicus* sp. is one of the few taxa of tropical invertebrates whose slope is higher than 3, so it is possible that in this genus volume could influence body mass more than surface.

Figure 1. Scatter diagrams of (A) dry mass versus body length, (B) head capsule width and (C) interocular distance on normal coordinates (□) as well as on logarithmic coordinates (●) for *Phylloicus* sp. larvae. The regression equations (power function) are $\text{DM} = a \cdot L^b$ and $\ln \text{DM} = \ln a + b \cdot \ln L$. 
Some variations in length–dry mass relationships for the populations of the same species, but from different locations, can be caused by physical-chemical differences of the environment, trophic conditions or genetics. In this way, it is recommended to determine the relationships for populations under study or use relationships that were determined for populations from the same streams and/or regions. For example, Rincón and Martínez (2006), studying the growth rates of *Phylloicus* in laboratory experiments, used the empirical relationship described by Cressa (1999) who had studied populations from a similar region of Venezuela. On the other hand, length–dry mass relationships are not much affected by seasons, as shown by Kato and Miyasaka (2007). These authors suggested that it is not necessary to measure larvae in dry and wet seasons to have a consistent relationship.

When sampling organisms to determine length–dry mass relationships, one must be sure that organisms from different sizes (cohorts) have been collected. If not, only part of the logistic curve of population growth is quantified and the resulting relationships may not represent the whole population (Begon, Mortimer and Thompson 1996). In this study, if we consider Dyar’s law, an empirical law that suggests an increase of 1.5 in growth at each instar (Wigglesworth 1972), and the ranges of each body dimension measured, we can infer that only larvae from the last two instars were sampled. Based on this, our equations were determined with data from the right side of the curvilinear relationships between dry mass and body dimensions of this population of *Phylloicus* (see Majecki, Grzybkowska and Reddy 1997). On the other hand, as we have been monitoring this population for several months, larvae used in this study presented the same range of size of the ones that are found visually in most part of the year, suggesting that our equations were adequate to determine the dry mass of larvae destined to laboratory experiments.

In conclusion, the length–dry mass relationships presented here can be useful to determine the growth rate and/or secondary production of *Phylloicus*. Besides, our results also reinforce the necessity of more studies focusing on the life cycles of aquatic insects in the tropical region. We do hope that the present study encourages future research assessing the population dynamics of tropical shredders, as well as to understand the importance of these individuals on leaf processing, trophic relationships, colonisation rates, and even to compare populations within and between habitats.

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References


