Allometric Versus Isometric Growth in European Stoneflies (Plecoptera)

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ABSTRACT

We studied abdominal growth of nine species representing the seven European Plecoptera families. Our data indicate that a linear or a power model best describes the relationship between abdomen length and total length, showing an obvious isometric growth for all the nine species. It was previously supposed that large-sized Perloidea may present an abdominal allometric growth because of their particular energetic needs (egg maturation in nymphal stage and no feeding in the adults), but our data do not support this hypothesis, which suggests that isometric growth does provide sufficient storage for both mature gametes and reserve nutrients for adult life in the nymphal abdomen.

INTRODUCTION

The growth of most insects shows no general agreement with Brooks-Dyar's rule, that assumes that the dimension of a part of the insect body should increase at each molt by the same ratio as the body as a whole; in fact, growth in most insects is allometric (Daly 1985, Gullan and Cranston 2005). Biometric studies in the order Plecoptera have recently investigated mass-length relationships (Burgherr and Meyer 1997, Giustini et al. 2008), while studies on allometric growth mainly have analyzed the relationships between nymphal size and development of adult related characters, such as wing-pads (e.g. Brittain 1973, Zwick 1991, Beer-Stiller and Zwick 1995). Moreover, the morphological differences between the first nymphal stage and all the following ones have been repeatedly cited in the literature (Hynes 1976, Zwick 1980, Lillehammer 1988). After the first molt, and from the study of some species, the growth seems to show only minimum allometric structural modifications (Zwick 1980).

More recently, Fenoglio et al. (2007) showed in a tropical Plecoptera genus that the relationship between body and abdomen length was exponential and allometric, hypothesizing that this fact could be related to energetic and reproductive constrains. For testing this hypothesis and obtaining a wider point of view on this topic in the Plecoptera group, our purpose with this study was to examine the growth of the abdomen and its relationship with nymphal size in species representing the seven European families.

METHODS AND MATERIALS

Most specimens were obtained from the Plecoptera collection of the Animal Biology Department, Granada University. We selected individuals collected in monthly samplings of annual programs, guaranteeing the presence of nymphs of all different size classes. Forty nymphs of all size classes, except the first instar, of each of the following species were examined:

Dinocras cephalotes (Curtis, 1827) (Perlidae; Río Castril, Sierra de Castril, Granada, Spain; 1,220 m.a.s.l.; López-Rodríguez, Marfil-Daza and Tierno de Figueroa),

Perla bipunctata Pictet, 1833 (Perlidae; Río Castril, Sierra de Castril, Granada, Spain; 1,220 m.a.s.l.; López-Rodríguez, Marfil-Daza and Tierno de Figueroa),

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Isoperla nevada Aubert, 1952 (Perlodidae; Río Válor, Sierra Nevada, Granada, Spain; 2,000 m.a.s.l.; Sánchez-Ortega),

Siphonoperla baetica (Aubert, 1956) (Chloroperlidae; Streams in southern Cádiz, Spain; 10-480 m.a.s.l.; Ropero, Peña, and Sánchez-Ortega),

Rhabdiopteryx christinae Theischinger, 1975 (Taeniopterygidae; Arroyo de las Perdices, Sierra de Huétor, Granada, Spain; 1,380 m.a.s.l.; López-Rodríguez and Tierno de Figueroa),

Amphinemura triangularis (Ris, 1902) (Nemouridae; Río Blanco, Sierra de Huétor, Granada, Spain; 1,400 m.a.s.l.; López-Rodríguez and Tierno de Figueroa),

Nemoura lacustris Pictet, 1865 (Nemouridae; Arroyo de las Perdices, Sierra de Huétor, Granada, Spain; 1,380 m.a.s.l.; López-Rodríguez and Tierno de Figueroa),

Capnioneura libera (Navás, 1909) (Capniidae; Arroyo de las Perdices, Sierra de Huétor, Granada, Spain; 1,380 m.a.s.l.; López-Rodríguez and Tierno de Figueroa),

Leuctra fusca (Linnaeus, 1758) (Leuctridae; Río Aguas Blancas, Sierra Nevada, Granada, Spain; 1,300 m.a.s.l.; Sánchez-Ortega).

We measured total length (from the labrum to the last urite) and abdomen length of each nymph with an ocular micrometer. For accuracy, before measuring them, all individuals were positioned flat and held down with a glass slide.

Statistical analyses were performed with SPSS 14.0 (Lead Technologies Inc. 2005). Our null hypothesis was that there was an allometric and exponential relationship between total body length and abdomen length. We first fit our data to several models, including the linear ($y = a + bx$), the power ($y = ax^b$), the growth [$y = e^{(a+bx)}$], and the exponential ($y = ae^{bx}$). We obtained the values of their respective r^2 and performed an analysis of variance to assess the degree of significance of each model. We chose the model that presented the highest r^2 value and also the highest ANOVA F, when they were significant. The normality of the residuals was tested by means of a Kolmogorov-Smirnov analysis. The homocedasticity of the residuals was assessed graphically by plotting the typified residuals against the typified predicted values. The existence of correlation among the residuals was evaluated using the Durbin-Watson contrast. We also tested the differences in size between large Perloidea (*D. cephalotes* and *P. bipunctata*) and the rest of stoneflies by means of a non-parametric Kruskal-Wallis ANOVA (Zar 1999) because variables were not all normally distributed (Kolmogorov-Smirnov test with $p < 0.05$ in most cases). Particular differences between *D. cephalotes* and the other species and *P. bipunctata* and the other species were tested with a Mann-Whitney U test (Zar 1999).

Table 1. Best-fitting curve equations and regression parameters between abdomen length (*y*) and total length (*x*) for the nymphs of the nine plecopteran species. *= not significant at a *p* level of 0.05

Species	Curve equation	Slope (b)	Intercept (a)	r^2
Dinocras cephalotes	$y = ax^b$	1.054	0.370	0.992
Perla bipunctata	$y = ax^b$	1.084	0.368	0.988
Isoperla nevada	$y = ax^b$	1.134	0.325	0.976
Siphonoperla baetica	$y = a + bx$	0.581	-0.234	0.966
Rhabdiopteryx christinae	$y = ax^b$	1.033	0.418	0.990
Capnioneura libera	$y = a + bx$	0.516	-0.180	0.973
Amphinemura triangularis	$y = a + bx$	0.389	0.129*	0.931
Nemoura lacustris	$y = ax^b$	1.138	-0.134	0.894
Leuctra fusca	$y = a + bx$	0.493	0.238*	0.878

RESULTS AND DISCUSSION

When comparing abdominal length with total length, we observed that in the case of *D. cephalotes, P. bipunctata, I. nevada, R. christinae* and *N. lacustris* the best fitting curve was a power ($y = ax^b$). For all the other (*S. baetica, C. libera, A. triangularis,* and *L. fusca*), the best fitting model was linear ($y = a + bx$) (Table 1). Nevertheless, when evaluating the degree of allometry in abdominal growth, a tendency toward isometric growth was detected for every species. This tendency was obvious with those species fitting linear models and quite evident in power model ones, whose slope values ranged from 1.033 to 1.138 (Fig. 1).

Significant differences in total body length were found between large Perloidea (*D. cephalotes* and *P. bipunctata*) and the remaining species (Kruskal-Wallis ANOVA H= 120.41, p< 0.05, Fig. 2). Between *D. cephalotes* and *P. bipunctata,* no differences
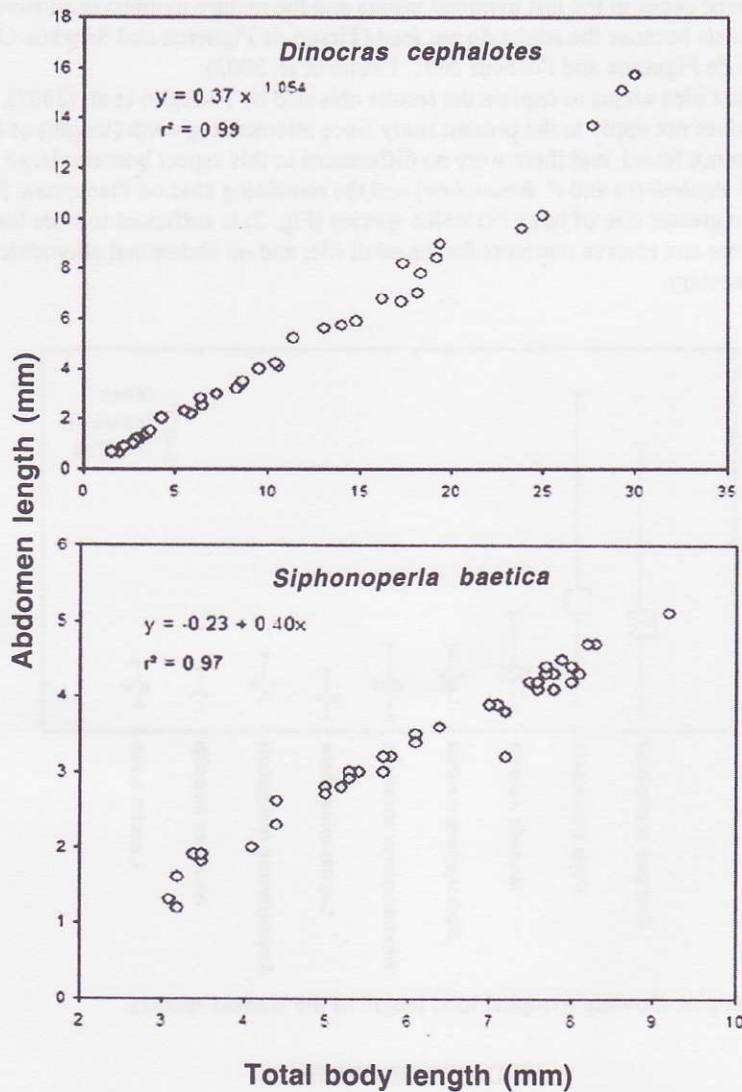

Figure 1. Relationships between total body and abdomen lengths in a species fitting power model (*Dinocras cephalotes*) and in a species fitting a linear model (*Siphonoperla baetica*).

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were found (Mann-Whitney U= 632.50, p> 0.05). When comparing both *D. cephalotes* and *P. bipunctata* with each of the remaining species, significant differences were detected (Mann-Whitney U with p< 0.05 in every case).

In insects, and particularly in Plecoptera, the abdomen is the tagma where gonads (and other reproductive structures) and the great parts of the gut are located. Moreover, the major part of food reserves is stored in the perivisceral fat bodies of the abdomen (Zwick 1980, Chapman 1998). In fact, it has been pointed out that the adipose bodies in stoneflies seem to reach the maximum expansion at the end of the nymphal growth, although in those species in which eggs mature prior to emergence, the adipose bodies tend to decrease when this occurs (Branham and Harthaway 1975, Zwick 1980). In relation to this, it could be hypothesized the existence of an allometric growth of this body region at the end of the nymphal development. This could be yet more important in the case of large Perloidea (family Perlidae and big Perlodidae), in which all the gametic maturation must occur in the last nymphal instars and the mature nymphs must store enough nutrients because the adults do not feed (Tierno de Figueroa and Sánchez-Ortega 1999, Tierno de Figueroa and Fochetti 2001, Fausto et al. 2002).

This last idea seems to explain the results obtained by Fenoglio et al. (2007). However, it does not apply to the present study since allometric growth (length) of the abdomen was not found, and there were no differences in this aspect between large Perloidea (*D. cephalotes* and *P. bipunctata*) and the remaining studied Plecoptera. It is likely that the greater size of large Perloidea species (Fig. 2) is sufficient to store both mature gametes and reserve nutrients for the adult life, and no abdominal allometric growth is necessary.
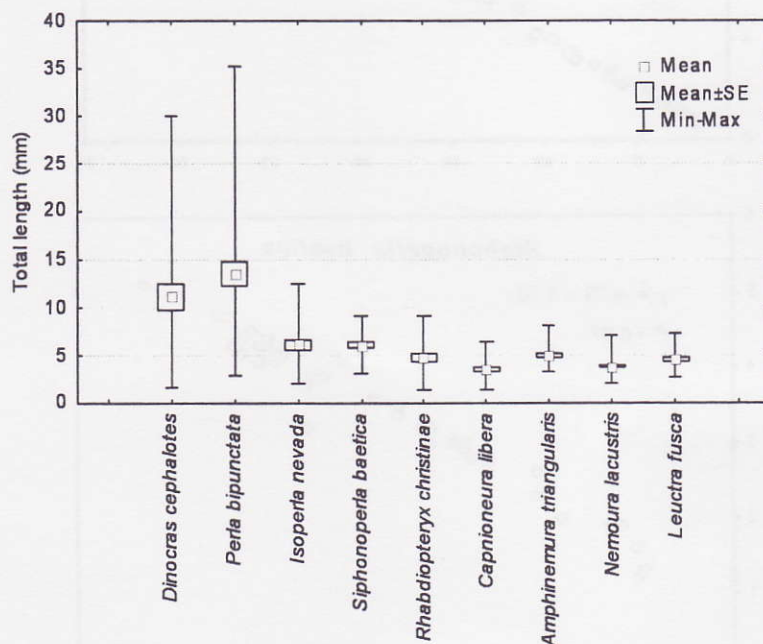

Figure 2. Box plot showing nymphal total length of the studied species.

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