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## **Allometric vs isometric growth in European stoneflies (Plecoptera)**

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In the present paper, we study the abdominal growth model (isometric vs. allometric) of  
15 nine species representing the seven European Plecoptera families, and discuss our  
results in the context of their biological differences (egg maturation phase, existence or  
not of adult feeding, size, etc.). Our data indicate that a linear or a power model best  
describes the relationship between abdomen length and total length, showing a  
relatively evident isometric growth for all the studied species. It was previously  
20 supposed that large-sized Perlodea 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 suggesting that also  
isometric growth could allow storing both mature gametes and reserve nutrients for  
adult life in nymphal abdomens.

**Key words:** Plecoptera, nymphal growth, biometry, adult feeding, gametic maturation.

## Introduction

The study of scaling, or of how shape and proportions change with size, is known as allometry (Gould 1966, Gayon 2000). Most body components scale allometrically, and this is a general pattern for many animals. These differences in the growth rates among body parts are referred to as allometric growth (Nijhout & Wheeler 1996).

The growth of most insects shows no general agreement neither with Brooks-Dyar's rule, that assumes that the dimension of a part of the insect body should increase at each moult by the same ratio as the body as a whole, ~~nor with Prizibram's rule, that states that weigh duplicate at each moult;~~ in fact, growth in most insects is allometric (Daly 1985, Gullan & Cranston 2005). This allometric growth along the ontogeny is a very interesting study matter because not only establishes the metric relationships among the different parts of the organism, but also reflects biological processes (Fenoglio et al. 2007).

Biometric studies in the order Plecoptera have recently investigated mass-length relationships (Burgherr & 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 & Zwick 1995). Moreover, the morphological differences between the first nymphal stage and all the following ones have been repeatedly cited in

literature (Hynes 1976, Zwick 1980, Lillehammer 1988). After the first moult, and from  
50 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.

55 For testing this hypothesis and obtaining a wider point of view on this topic in  
the Plecoptera group, we planned to study the growth of the abdomen and its  
relationship with nymphal size in species representing the seven European families.

Thus, the aim of this study is i) to analyze the growth patterns in different species; ii) to  
compare them; and iii) to discuss the results in the context of their biological differences  
60 (egg maturation previously or not to the emergence, existence or not of adult feeding,  
nymphal and adult size, etc.).

## Materials and Methods

65

Forty nymphs (belonging to several size categories representing all the size range,  
except the first instar) of each of the following species were studied:

Superfamily Perloidea:

70 1. *Dinocras cephalotes* (Curtis, 1827) [family Perlidae]. SPAIN, Granada, Sierra de  
Castril, Río Castril, 1220 m.a.s.l. López-Rodríguez, Marfil-Daza & Tierno de Figueroa  
leg.

2. *Perla bipunctata* Pictet, 1833 [family Perlidae]. SPAIN, Granada, Sierra de Castril, Río Castril, 1220 m.a.s.l. López-Rodríguez, Marfil-Daza & Tierno de Figueroa leg.
- 75 3. *Isoperla nevada* Aubert, 1952 [family Perlodidae]. SPAIN, Granada, Sierra Nevada, Río Válor, 2000 m.a.s.l. Sánchez-Ortega leg.
4. *Siphonoperla baetica* (Aubert, 1956) [family Chloroperlidae]. SPAIN, Cádiz, Streams in Southern Cádiz, 10-480 m.a.s.l. Ropero, Peña & Sánchez-Ortega leg.
- 80 Superfamily Nemouroidea:
5. *Rhabdiopteryx christinae* Theischinger, 1975 [family Taeniopterygidae]. SPAIN, Granada, Sierra de Huétor, Arroyo de las Perdices, 1380 m.a.s.l. López-Rodríguez & Tierno de Figueroa leg.
- 85 6. *Amphinemura triangularis* (Ris, 1902) [family Nemouridae]. SPAIN, Granada, Sierra de Huétor, Río Blanco, 1400 m.a.s.l. López-Rodríguez & Tierno de Figueroa leg.
7. *Nemoura lacustris* Pictet, 1865 [family Nemouridae]. SPAIN, Granada, Sierra de Huétor, Arroyo de las Perdices, 1380 m.a.s.l. López-Rodríguez & Tierno de Figueroa leg.
- 90 8. *Capnioneura libera* (Navás, 1909) [family Capniidae]. SPAIN, Granada, Sierra de Huétor, Arroyo de las Perdices, 1380 m.a.s.l. López-Rodríguez & Tierno de Figueroa leg.
9. *Leuctra fusca* (Linnaeus, 1758) [family Leuctridae]. SPAIN, Granada, Sierra Nevada, Río Aguas Blancas, 1300 m.a.s.l. Sánchez-Ortega leg.

95 All the individuals proceeded from the Plecoptera collection deposited in the Animal Biology Department (Granada University, Spain). We selected individuals

collected in monthly samplings of annual programs, guaranteeing the presence of nymphs of all different size classes.

In the laboratory, we measured total length (from the labrum to the last urite) and abdomen length of each nymph with an ocular micrometer (accuracy 0.1 mm) inserted into the eyepiece of an Olympus stereomicroscope (10 x). For a major accuracy, before measuring them, all individuals were positioned flat with a glass slide on.

Statistical analyses were performed with SPSS 14.0 (Lead Technologies Inc. 2005) and graphics were done in Statistica 7.1 (StatSoft 2005). **The null hypothesis we wanted to test was if there was an allometric and exponential relationship** between total body length and abdomen length. **As in any other study of regression, we checked out that the following statements were achieved: 1) that the residuals got from the regression model presented a normal distribution; 2) that homocedasticity existed in the residuals; 3) that no autocorrelation existed among the residuals, i.e. that they were independent (REFERENCE).** For this we first adjusted our data to several models, such as 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 ANOVA analysis for assessing 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. In order to check out if the ANOVA  $F$  could be properly used and its significant level, we tested the three statements mentioned above. The normality of the residuals was tested by means of a Kolmogorov-Smirnov analysis. The homocedasticity of the residuals was assessed graphically plotting the typified residuals against the typified prognosticated values. The existence or not of correlation among the residuals was evaluated using the

Durbin-Watson contrast. (REFERENCES). We also tested the differences in size between big Perlidae (*D. cephalotes* and *P. bipunctata*) and the rest of stoneflies by means of a non-parametric Kruskal-Wallis ANOVA, due to 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 (REFERENCES).

## Results and Discussion

When we studied the relation between abdomen length and 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 ( $y = ax^b$ ), as expected in allometry studies (Warton et al. 2006). For all the other studied species (*S. baetica*, *C. libera*, *A. triangularis* and *L. fusca*), the best fitting model is a linear ( $y = a + bx$ ) (Table I).

When evaluating the degree of allometry in abdomen growth, a tendency to isometric growth is detected for every species: this tendency was obvious in species fitting linear models and quite evident in power model ones, which slope values ranged from 1.033 to 1.138 (Fig. 1).

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 previously to the emergence the

145 adipose bodies tend to decrease when this occurs (Branham & 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 big Perloidea (family Perlidae and big Perlodidae), in which all  
the gametic maturation must occur in the last nymphal instars and the mature nymphs  
150 must store enough nutrients because the adults will not ingest food during this period of  
their life (Tierno de Figueroa & Sánchez-Ortega 1999, Tierno de Figueroa & Fochetti  
2001, Fausto et al. 2002).

This last idea seems to explain the results obtained by Fenoglio et al. (2007).  
Nevertheless, it does not apply to the present results, in which not only a clear  
155 allometric growth for the abdomen length was not found but also no differences were  
detected in this aspect between big Perloidea (*D. cephalotes* and *P. bipunctata*) and the  
remaining Plecoptera (the studied Nemouroidea, *I. nevada* and *S. baetica*) that present  
imaginal feeding and, in the case of Nemouroidea species, egg maturation in the adult  
stage (Hynes 1976, Tierno de Figueroa et al. 2003).

160 It is likely that the greater size of large Perloidea species (Kruskal-Wallis  
ANOVA  $H= 120.41$ ,  $p < 0.05$ , Fig. 2) is sufficient to store both mature gametes and  
reserve nutrients for the adult life, and no abdominal allometric growth is necessary.

Regarding this last topic, it is also usually accepted that the adult longevity is in  
average shorter in Perloidea (Zwick 1980), so an extra growth of the abdomen for  
165 storing reserves is not necessary (ponerlo?)

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Zwick P. 1991. Biometric studies of the growth and development of two species of  
225 *Leuctra* and *Nemurella pictetii* (Plecoptera: Leuctridae and Nemouridae). In: Alba-Tercedor J, Sánchez-Ortega A, editors. Overview and Strategies of Ephemeroptera and Plecoptera. Gainesville: Sandhill Crane Press. p 515-526. **Table I.** Best-fitting curve equation and regression parameters between abdomen length ( $y$ ) and total length ( $x$ ) for the nymphs of the studied species.

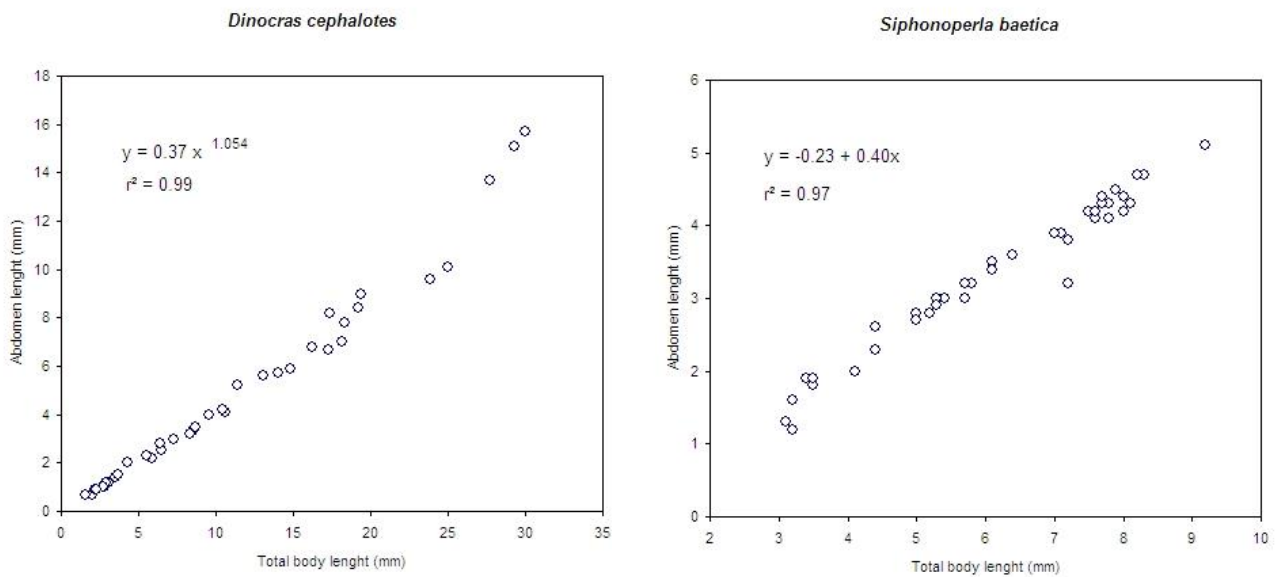
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Specie	Curve			
	equation	Slope ( $b$ )	Intercept ( $a$ )	$r^2$
<i>Dinocras cephalotes</i>	$y = ax^b$	1.054	0.370	0.992
<i>Perla bipunctata</i>	$y = ax^b$	1.084	0.368	0.988
<i>Isoperla nevada</i>	$y = ax^b$	1.134	0.325	0.976
<i>Siphonoperla baetica</i>	$y = a + bx$	0.581	-0.234	0.966
<i>Rhabdiopteryx christinae</i>	$y = ax^b$	1.033	0.418	0.990
<i>Capnioneura libera</i>	$y = a + bx$	0.516	-0.180	0.973
<i>Amphinemura triangularis</i>	$y = a + bx$	0.389	0.129*	0.931

<i>Nemoura lacustris</i>	$y = ax^b$	1.138	-0.134	0.894
<i>Leuctra fusca</i>	$y = a + bx$	0.493	0.238*	0.878

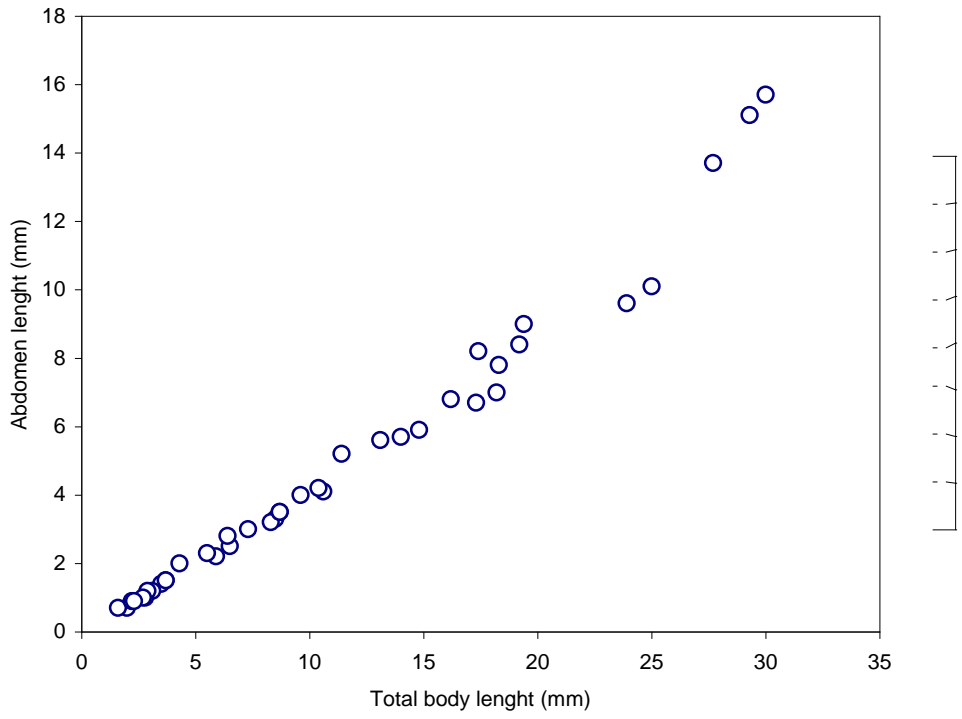
\* are not significant at a  $p$  level of 0.05

**Fig. 1.** Relationships between total body and abdomen lengths in species fitting power and linear models.



240 **Fig. 2.** Box plot showing nymphal total length of the studied species.

*Dinocras cephalotes*



Species