LIFE HISTORY OF *EPHEMERA DANICA* MÜLLER (Ephemeroptera) IN THE SIERRA MORENA OF SOUTH-WEST SPAIN.

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ABSTRACT

The growth and life history of *Ephemera danica* were studied in a permanent stream in the Sierra Morena. The following measurements of each nymph were made: body length, head length, head width, prothorax width, length of the wing pads and length of metafemur. Using standard and logarithmic transformed data, two principal component analyses were made for each sex. Multiple regression analysis were also made. These analyses indicate that during the course of development, the only deviation from almost isometric growth is in the wing pad size of both sexes. *E. danica* was univoltine in this locality.

INTRODUCTION

The life cycle of *Ephemera danica* Müller, 1764 has been studied in several European countries (Thibault, 1971; Svensson, 1977; Alba-Tercedor, 1990). It may have a one, two, or three year cycle, and two of these cycles are often present in the same habitat (Brittain, 1982). The aims of the present study were to determine the main characteristics of its life history in the Sierra Morena mountains of south-west Spain and to establish the most important body measurements useful for further studies of growth and development in this species. In aquatic insects allometric growth of wing pads has been noted by several authors (Corbert, 1955; Clifford *et al.*, 1979; Frutiger, 1987) as a useful character for field recognition of the final nymphal instar.

MATERIAL AND METHODS

The field study was carried out in a 150 m section of the stream, Bejarano (400 m a.s.l., 37° 56' N, 4° 52' W), a permanent watercourse whose width is between 1 and 3 m at the sampling site and whose mean water depth is 35 cm. Riparian vegetation was abundant (alder, *Alnus glutinosa*; elm, *Ulmus minor*; chestnut, *Castanea sativa*; hazel, *Corylus avellana*). The highest water temperature measured during the investigation was 18.5°C (21.8.1988), while the lowest was 13.0°C (20.11.1988 and 15.12.1988) (Fig. 1).

Between 8.2.1987 and 21.6.1989, forty-one benthic samples were taken using a hand net with a mesh size of 0.25 mm. In thirty-two samples, nymphs of *E. danica* were collected. The nymphs were fixed in 70% alcohol and examined under a stereomicroscope in the laboratory. Over the three years, 803 nymphs were colected. The following measurements were made: body length (bl), head capsule length (hl), head capsule width at base (hw), prothorax maximum width (pw), wing pad length (wl) and metafemur length (ml) (Fig. 2).

Using these measurements, for each sex two principal component analyses, using covariance matrix, have been carried out: firstly with standard data ($X - X / SD$) and secondly with logarithmic transformed data. In addition, several regression analysis - linear (multiplicative) ($Y = AX^{\circ}$) and exponential ($Y = \exp(A + BX)$) models- were made using all pairs of variables of the different body measurements.

RESULTS

Principal Component Analysis:

The spatial relationships of the six parameters considered are depicted for males, using standard data, in Figure 3. Factor loadings are listed in Table 1. The first two components accounted for 82.4% and 6.9%, respectively, of the variation. The first axis is defined by all variables with same level of significance, head capsule and prothorax maximum widths have the highest loadings; characters with important loadings on component two are head width, wing pad length and body length. The spatial relationships of the six parameters considered, for logarithmic transformed data, are depicted in Figure 4, while factor loading are listed in Table 2. The first two components accounted for 86.8% and 6.2%, respectively, of the variation. Only one character (wing pads length) gave a high value on component one. Wing pad length, head width and metafemur length were variables with important loadings on component two.

The results for females, were very similar to those of the males. Using standard data, the spatial relationships of six parameters considered are depicted in Figure 5, while factor loadings are listed in Table 3. The first two components accounted for 89.9% and 4.1%, respectively, of the variation. The first axis is defined by all variables with the same level of significe; prothorax and head width have the highest loadings. Using logarithmic transformed data, the spatial relationships of the six parameters considered are depicted in Figure 6. Factor loadings are listed in Table 4. The first two components accounted for 92.7% and 3.2%, respectively, of the variation. The first and second axis are defined as in the males.

Regression Analysis:

Linear (multiplicative), regression analyses were made with all pairs of variables. The slopes and correlation coefficients obtained by these analyses are given in Tables 5 and 6.

During the course of development, body proportions do not change to any great extent. High correlation coefficients and slopes near to one were obtained for several pairs of variables, both for males and for females. The only deviation from this almost isometric growth could be seen in the wing pads size of both sexes which grew disproportionately during the final stage of nymphal development. The slopes values for wing pads length (as dependent variable) with the remaining parameters were very different from one, especially for the pairs with head width, prothorax width and head length as the independent variable.

Applying the exponential model of regression analysis to pairs with wing pads length as dependent variable, and the other parameters as independent variable, high correlation coefficients were obtained, except for head length in males (Table 7).

Life cycle:

The nymphs were separated according to sex and head capsule width, and assigned to different size classes (class width 0.33 mm) (Fig. 7). In nymphs with allometric growth of the wing pads, the ratio wing pad length / head capsule width was always greater than two. (Fig. 8).

Our data indicate that *E. danica* is univoltine in the Sierra Morena. This is based on the following evidence: The majority of smaller nymphs (head capsule width = 1 mm) were collected between September and January; most nymphs showed allometric growth of their wing pads during April and May; exuviae and adults were collected in April and May; neither nymphs nor adults were collected between July and September.

DISCUSSION

A common approach to studying development is to analyze the progression of nymphs through the sequence of instars. However, instar number is know to be variable in mayflies (Brittain, 1982; Fink, 1984). For *E. danica*, the most useful body measurements were wing pad length, head width and prothorax width.

Although some species that occur over a wide geographic range have been shown to have a constant life cycle duration, for the majority of aquatic insects voltinism should be wiewed as a life history variable at the population level (Brittain, 1982). In the case of *E. danica* considerable variability exists in its voltinism (Thibault, 1971; Svensson, 1977). Some authors have suggested that the principal factors affecting the life cycle of *E. danica* are

are food supply and water temperature (see BAN & KAWAI, 1986); where food is abundant, a factor which may influence on this variability are minimum winter temperatures: while in a South Swedish stream the mean water temperature during the winter season are smaller than 5°C, and the individuals spent two-three years as nymph (Svensson, 1977), in the South Spain stream studied water temperature during the winter was always greater than 12°C, and the individuals spent less than one year as nymph.

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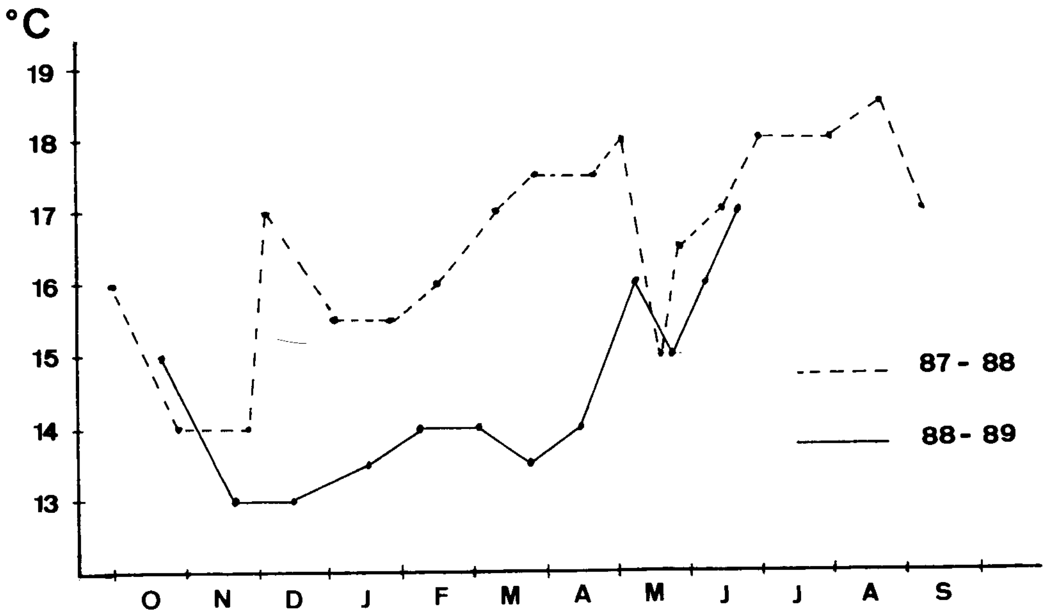

Fig. 1. Seasonal variation of water temperatures (°C) during the study period.

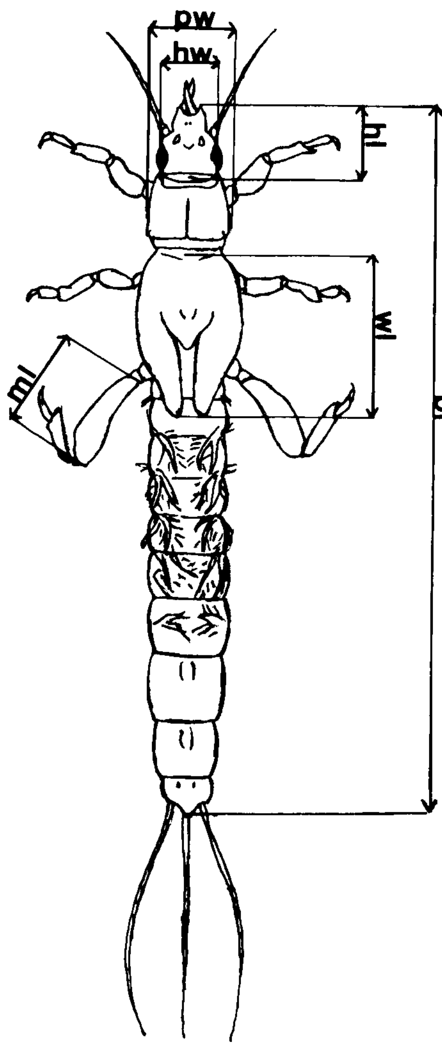

Fig. 2. Body measurements made: body length (bl), head capsule length (hl), head capsule width at base (hw), prothorax maximum width (pw), wing pad length (wl) and length of metafemur (ml).

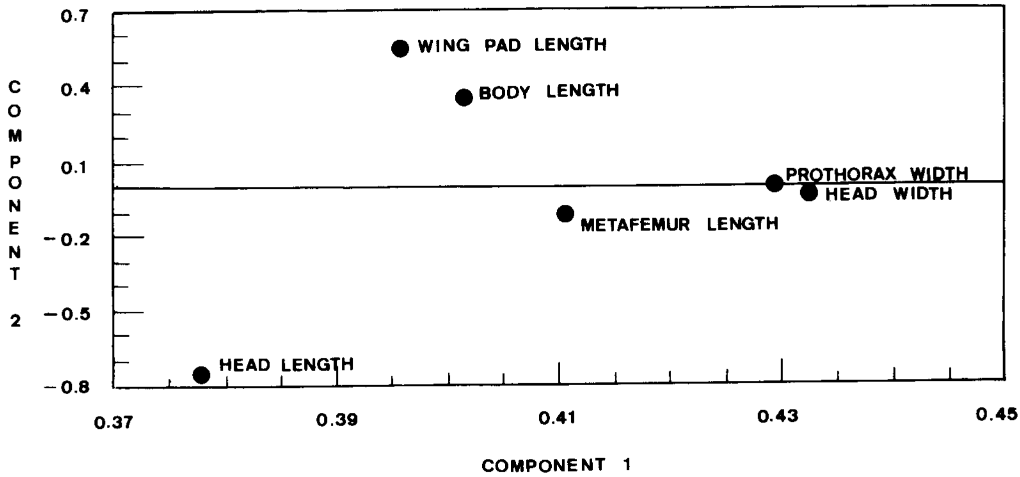

Fig. 3. Principal component analysis of males, using standard data. Location of the variables on the plane defined by axes I and II.

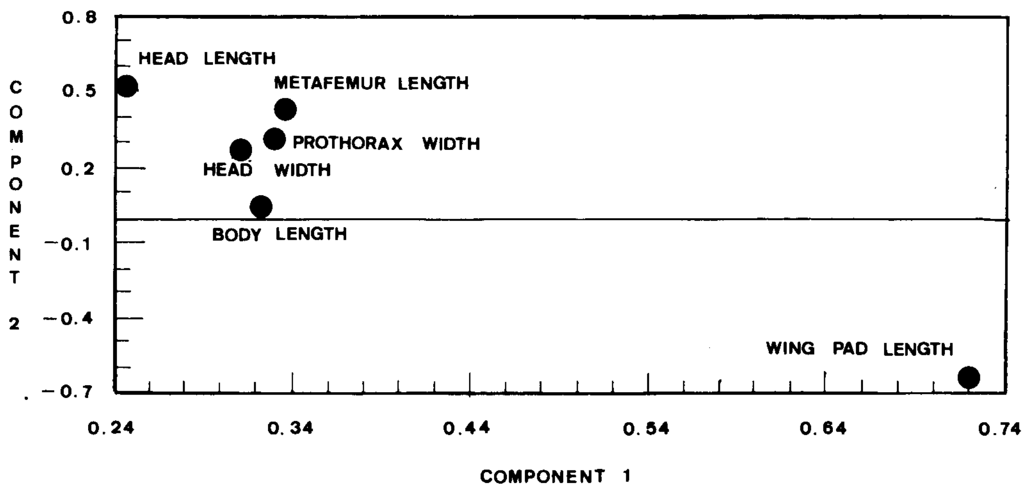

Fig. 4. Principal component analysis of males, using logarithmic transformed data. Location of the variables on the plane defined by axes I and II.

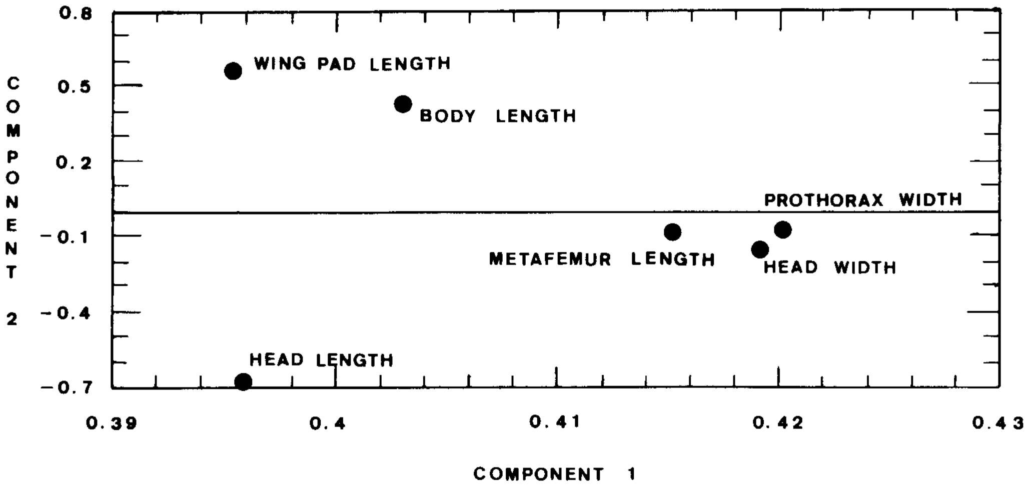

Fig. 5. Principal component analysis of females, using standard data. Location of the variables on the plane defined by axes I and II.

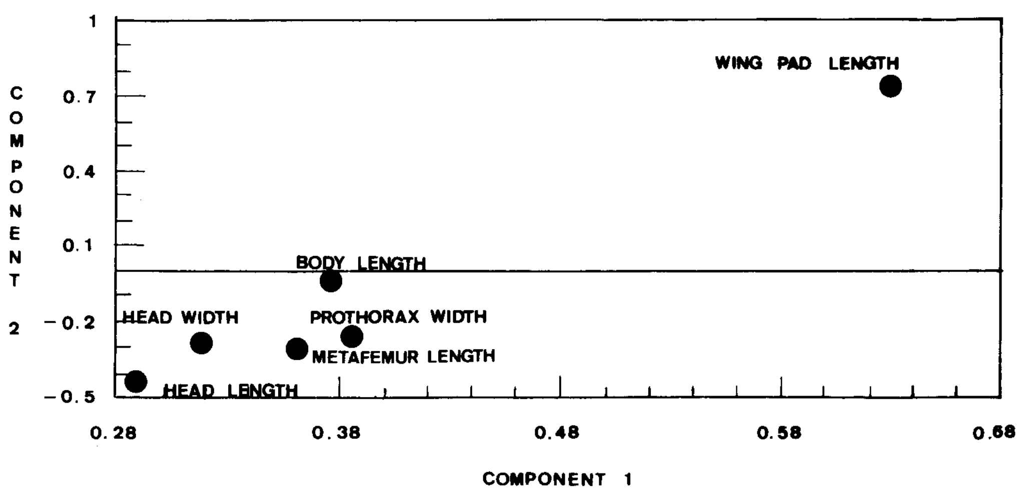

Fig. 6. Principal component analysis of females, using logarithmic transformed data. Location of the variables on the plane defined by axes I and II.

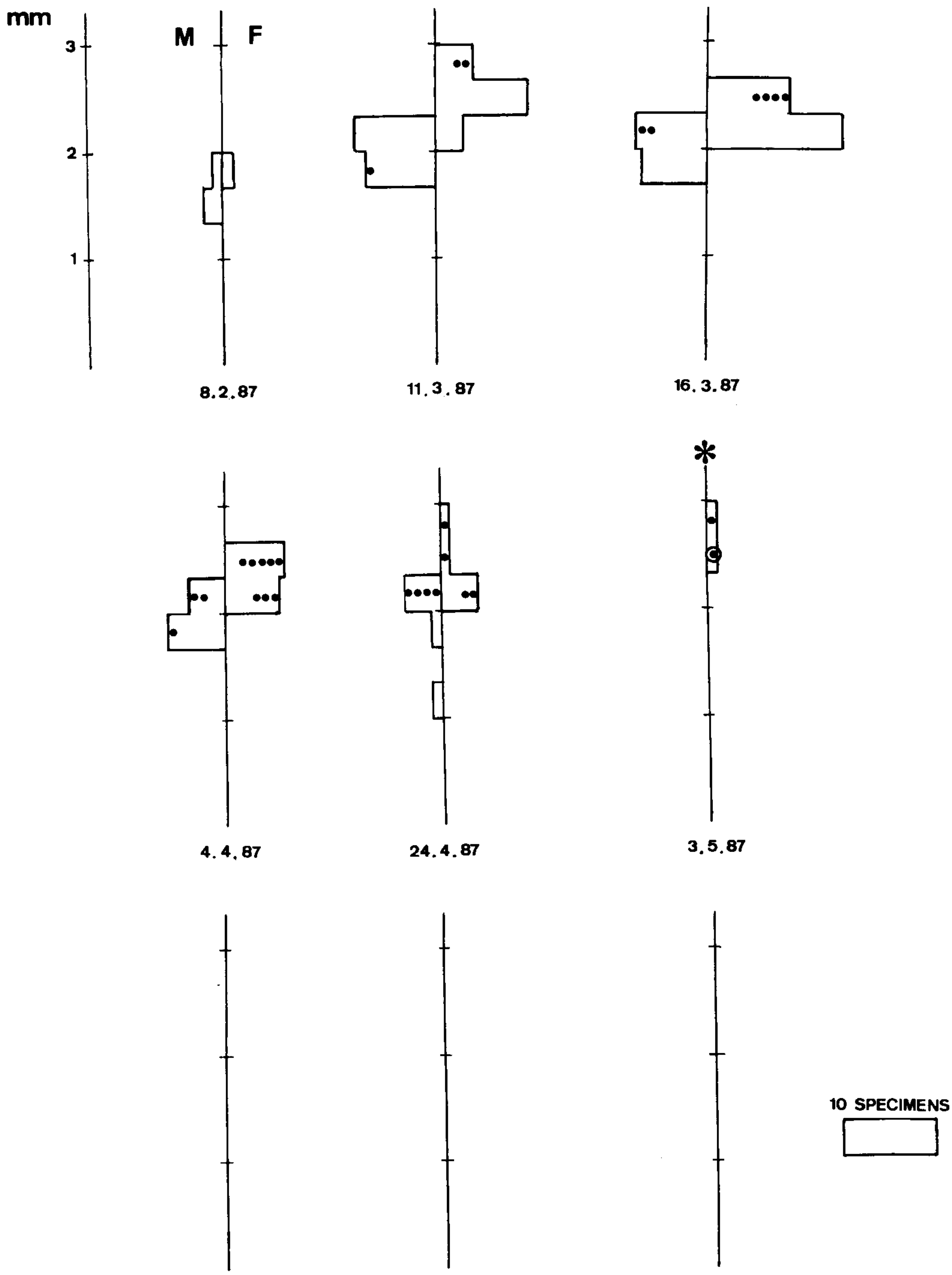

Fig. 7a. Seasonal changes in head width for males (M) and females (F) during the study period. ●, some nymphs with allometric growth; ✪, all nymphs with allometric growth; *, emergence.

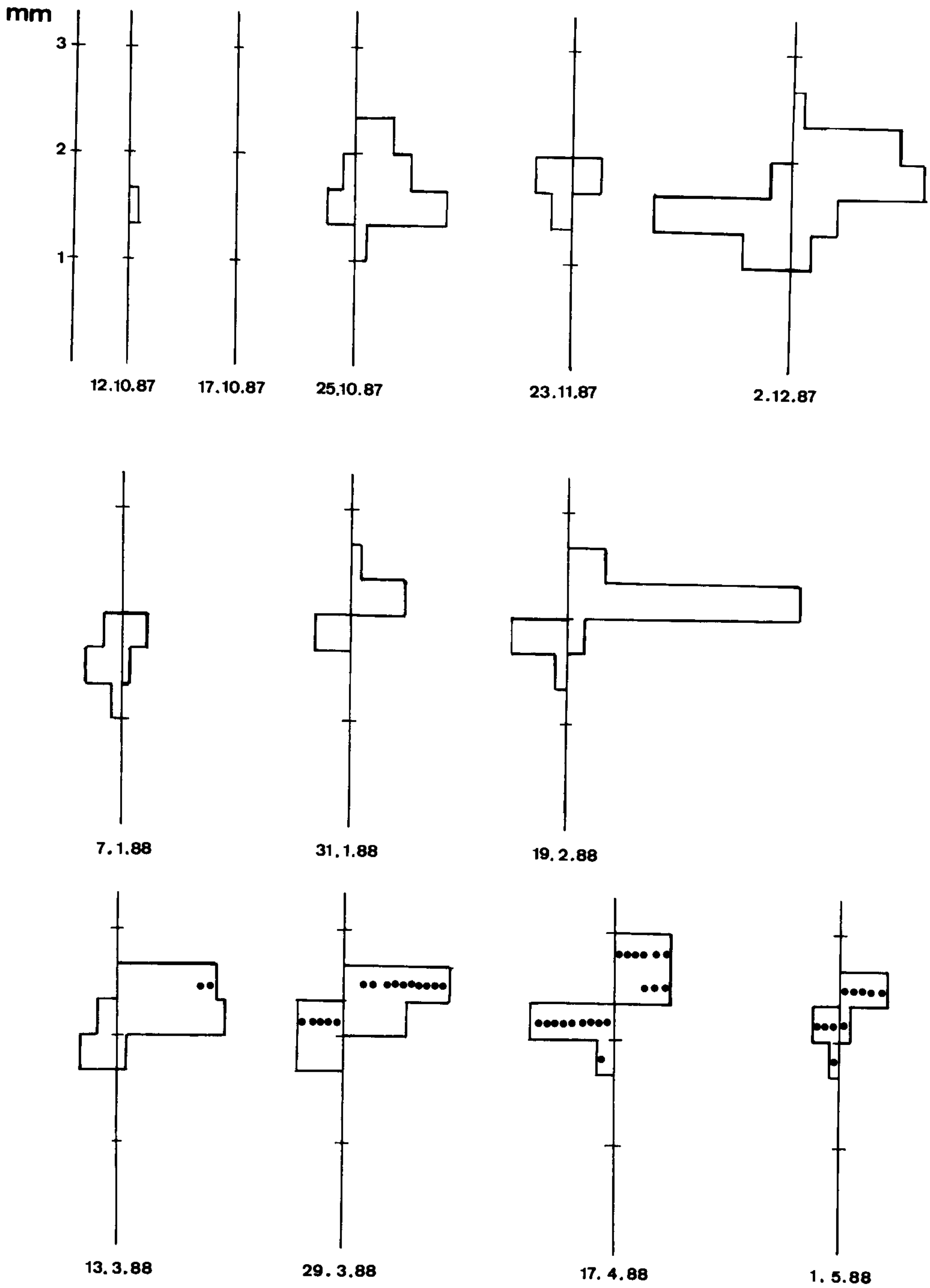

Fig. 7b. Seasonal changes in head width for males (M) and females (F) during the study period. ●, some nymphs with allometric growth; ✪, all nymphs with allometric growth; ✻, emergence.

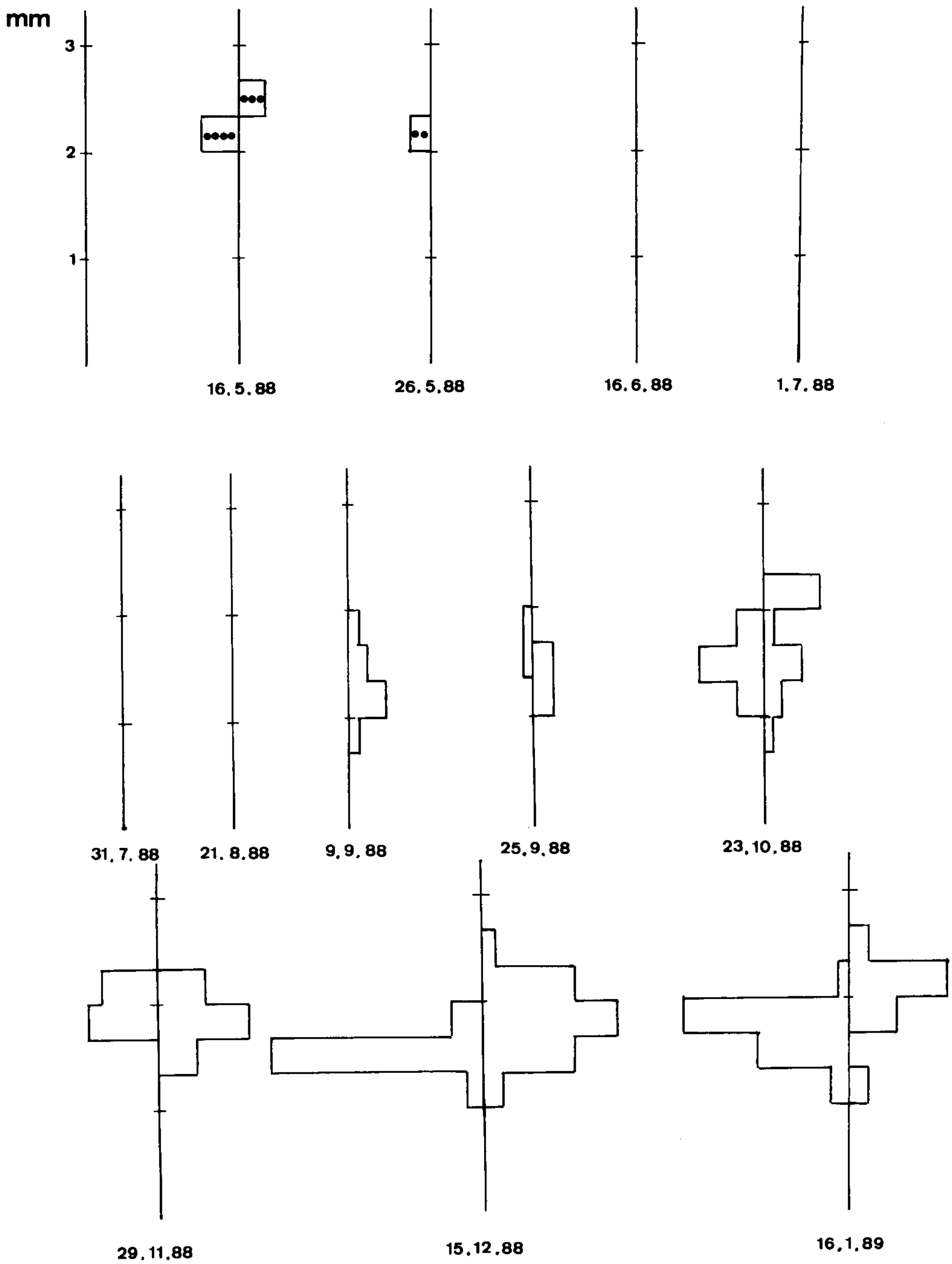

Fig. 7c. Seasonal changes in head width for males (M) and females (F) during the study period. ●, some nymphs with allometric growth; ✪, all nymphs with allometric growth; ✻, emergence.

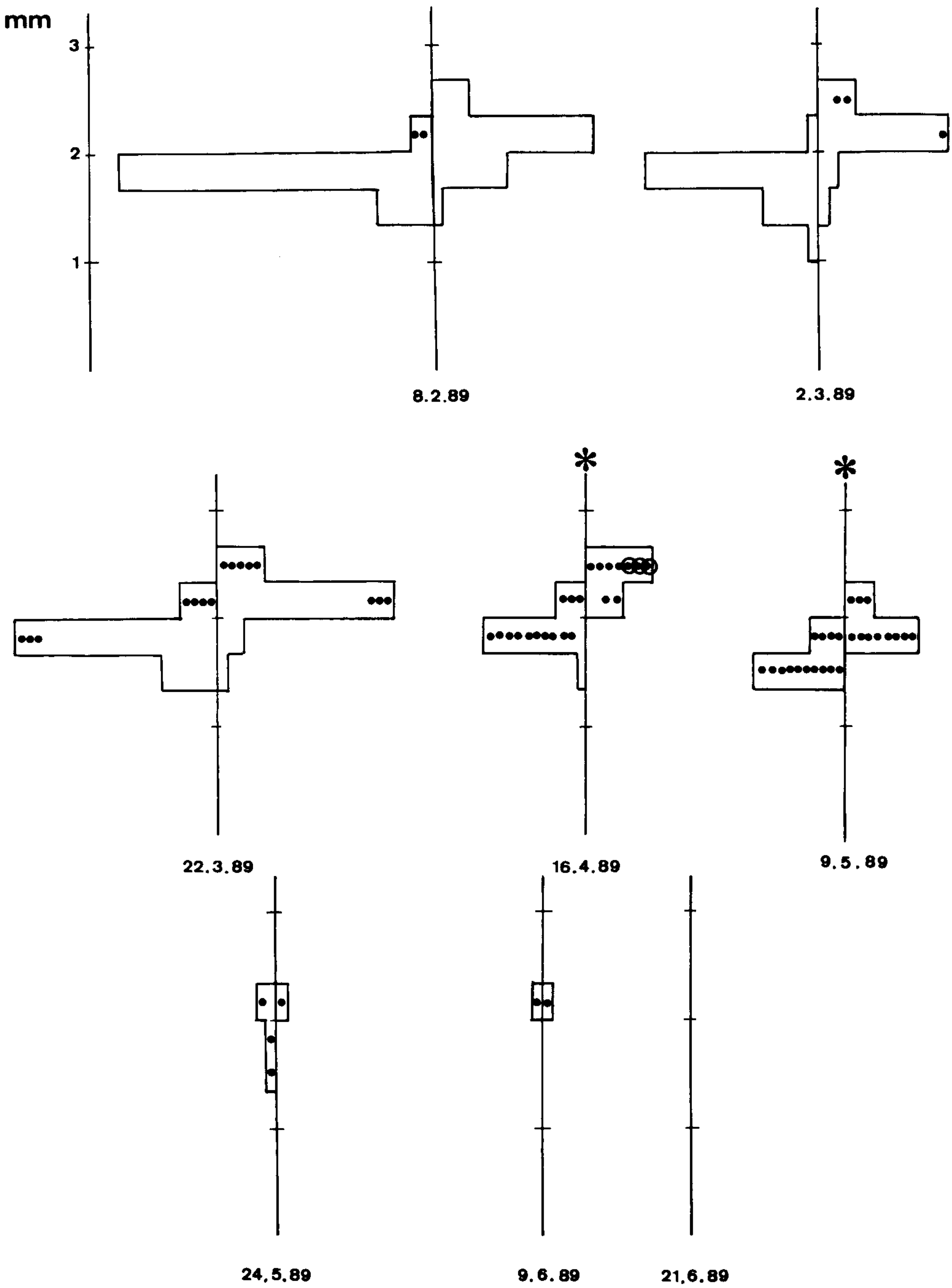

Fig. 7d. Seasonal changes in head width for males (M) and females (F) during the study period. ●, some nymphs with allometric growth; ✪, all nymphs with allometric growth; ✻, emergence.

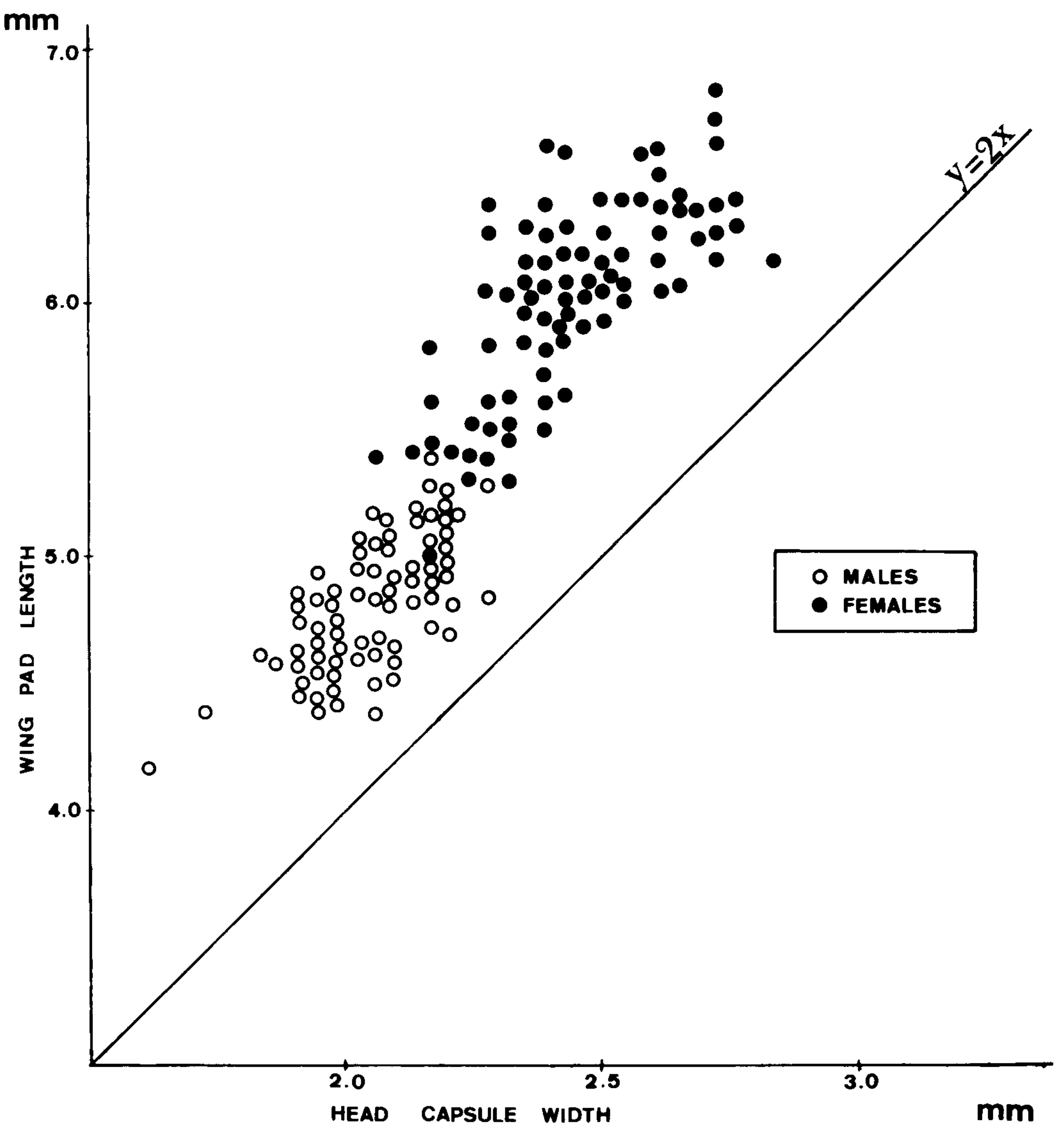

Fig. 8. Ratio wing pad length/head capsule width in nymphs with allometric growth of wing pads (final instar).

Table 1. Principal component analysis. Factor loadings of the six parameters studied, using standard data for males (1, body length; 2, head capsule length; 3, head capsule width; 4, prothorax maximum width; 5, wing pad length and 6, length of metafemur).

(1,1)	0.401	(1,2)	0.348	(1,3)	-0.670	(1,4)	0.248
(2,1)	0.377	(2,2)	-0.759	(2,3)	-0.268	(2,4)	-0.434
(3,1)	0.432	(3,2)	-0.023	(3,3)	-0.027	(3,4)	0.150
(4,1)	0.429	(4,2)	-4.421	(4,3)	0.072	(4,4)	0.395
(5,1)	0.395	(5,2)	0.533	(5,3)	0.210	(5,4)	-0.706
(6,1)	0.410	(6,2)	-0.126	(6,3)	0.653	(6,4)	0.265

Table 2. Principal component analysis. Factor loadings of the six parameters studied, using logarithmic transformed data for males. See Table 1 for explanation.

(1,1)	0.321	(1,2)	0.041	(1,3)	-0.788	(1,4)	-0.250
(2,1)	0.243	(2,2)	0.509	(2,3)	-0.032	(2,4)	0.802
(3,1)	0.312	(3,2)	0.265	(3,3)	-0.141	(3,4)	-0.075
(4,1)	0.329	(4,2)	0.302	(4,3)	-0.068	(4,4)	-0.265
(5,1)	0.719	(5,2)	-0.638	(5,3)	0.193	(5,4)	0.193
(6,1)	0.336	(6,2)	0.411	(6,3)	0.561	(6,4)	-0.423

Table 3. Principal component analysis. Factor loadings of the six parameters studied, using standard data for females. See Table 1 for explanation.

(1,1)	0.403	(1,2)	0.433	(1,3)	-0.561	(1,4)	-0.409
(2,1)	0.395	(2,2)	-0.682	(2,3)	0.274	(2,4)	-0.500
(3,1)	0.419	(3,2)	-0.124	(3,3)	-0.247	(3,4)	-1.368
(4,1)	0.420	(4,2)	-0.088	(4,3)	-0.233	(4,4)	0.320
(5,1)	0.395	(5,2)	0.561	(5,3)	0.693	(5,4)	-0.133
(6,1)	0.415	(6,2)	-0.089	(6,3)	0.109	(6,4)	0.679

Table 4. Principal component analysis. Factor loadings of the six parameters studied, using logarithmic transformed data for females. See Table 1 for explanation.

(1,1)	0.376	(1,2)	-0.053	(1,3)	-0.833	(1,4)	-0.068
(2,1)	0.288	(2,2)	-0.445	(2,3)	0.382	(2,4)	-0.662
(3,1)	0.318	(3,2)	-0.291	(3,3)	-0.114	(3,4)	-0.137
(4,1)	0.361	(4,2)	-0.313	(4,3)	-0.049	(4,4)	0.182
(5,1)	0.627	(5,2)	0.734	(5,3)	0.220	(5,4)	-0.120
(6,1)	0.386	(6,2)	-0.275	(6,3)	0.309	(6,4)	0.699

Table 5. Regression analysis, linear (multiplicative) model for males. The values of factors A and B, and R-squared (r°) are given. See figure 2 for explanation.

	b1	h1	hw	pw	w1	ml
b1	--------	A= 161.8 B= 0.820 r^2=0.485	A= 120.2 B= 0.920 r^2=0.727	A= 71.20 B= 0.864 r^2=0.716	A= 152.7 B= 0.406 r^2=0.696	A= 139.6 B= 0.687 r^2=0.523
h1	A= 0.091 B= 0.591 r^2=0.485	--------	A= 1.185 B= 0.741 r^2=0.653	A= 0.790 B= 0.689 r^2=0.631	A= 1.606 B= 0.283 r^2=0.470	A= 1.199 B= 0.619 r^2=0.588
hw	A= 0.033 B= 0.790 r^2=0.727	A= 1.396 B= 0.882 r^2=0.653	--------	A= 0.657 B= 0.870 r^2=0.844	A= 1.499 B= 0.384 r^2=0.726	A= 1.161 B= 0.755 r^2=0.735
pw	A= 0.052 B= 0.828 r^2=0.716	A= 2.679 B= 0.915 r^2=0.631	A= 2.084 B= 0.970 r^2=0.844	--------	A= 2.857 B= 0.404 r^2=0.720	A= 2.094 B= 0.818 r^2=0.774
w1	A= 3.95E-4 B= 1.713 r^2=0.696	A= 1.782 B= 1.656 r^2=0.470	A= 0.937 B= 1.888 r^2=0.726	A= 0.318 B= 1.779 r^2=0.720	--------	A= 0.989 B= 1.566 r^2=0.643
ml	A= 0.051 B= 0.760 r^2=0.523	A= 1.659 B= 0.949 r^2=0.588	A= 1.336 B= 0.972 r^2=0.735	A= 0.721 B= 0.945 r^2=0.774	A= 1.807 B= 0.410 r^2=0.643	--------

Table 6. Regression analysis, linear (multiplicative) model for females. The values of factor A and B, and R-squared (r^2) are given. See figure 2 for explanation.

	b1	h1	hw	pw	w1	m1
b1	----------	A= 137.7 B= 1.049 r^2=0.689	A= 100.0 B= 1.115 r^2=0.853	A= 59.15 B= 0.984 r^2=0.845	A= 130.9 B= 0.558 r^2=0.814	A= 116.6 B= 0.876 r^2=0.780
h1	A= 0.062 B= 0.657 r^2=0.689	----------	A= 1.019 B= 0.872 r^2=0.835	A= 0.680 B= 0.768 r^2=0.823	A= 1.336 B= 0.416 r^2=0.723	A= 1.101 B= 0.707 r^2=0.813
hw	A= 0.038 B= 0.765 r^2=0.853	A= 1.300 B= 0.956 r^2=0.835	----------	A= 0.669 B= 0.854 r^2=0.930	A= 1.415 B= 0.464 r^2=0.821	A= 1.196 B= 0.764 r^2=0.866
pw	A= 0.044 B= 0.859 r^2=0.845	A= 2.338 B= 1.071 r^2=0.823	A= 1.840 B= 1.087 r^2=0.930	----------	A= 2.511 B= 0.527 r^2=0.834	A= 2.032 B= 0.880 r^2=0.902
w1	A= 1.40E-3 B= 1.459 r^2=0.814	A= 1.358 B= 1.737 r^2=0.723	A= 0.914 B= 1.769 r^2=0.821	A= 0.379 B= 1.580 r^2=0.834	----------	A= 1.001 B= 1.465 r^2=0.835
m1	A= 0.022 B= 0.890 r^2=0.780	A= 1.300 B= 1.149 r^2=0.813	A= 0.528 B= 1.132 r^2=0.866	A= 0.588 B= 1.024 r^2=0.902	A= 1.389 B= 0.569 r^2=0.835	----------

Table 7. Regression analysis, exponential model. Values of R-squared (r^2) obtained using wing pads length as dependent variable. See figure 2 for explanation.

	bl	hl	hw	pw	ml	
wl	$r^2 = 0.698$	$r^2 = 0.471$	$r^2 = 0.758$	$r^2 = 0.732$	$r^2 = 0.677$	MALES
	$r^2 = 0.829$	$r^2 = 0.708$	$r^2 = 0.841$	$r^2 = 0.852$	$r^2 = 0.855$	FEMALES