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Biometric studies of some stoneflies and a mayfly (Plecoptera and Ephemeroptera)

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Abstract

Aspects of the nymphal/adult developmental change were investigated in biometric studies of several species of Plecoptera: Nemouridae near Schlitz, Hesse, Germany. Preliminary information on the mayfly, *Baetis vernus* Curtis, is also provided. Nemourid nymphs pass through 3 wing bearing stages before reaching adulthood. Instars can be identified by their characteristic shapes, as expressed by the wing length/head width (WL/HW) ratio. Size does not allow instar discrimination, mainly due to sexual size differences. HW is *ca* 10% larger in last instar female than in male nemourid nymphs; exuviae shed at the moult to adult represent about 14% of nymphal ash free dry weight (AFDW). Biomass lost with exuviae during the many larval moults should be accounted for in estimates of production. Freshly emerged nemourid females are about 6% larger and 30% heavier than males. The HW/AFDW relationship is the same in both sexes. Through terrestrial feeding during adult life, males double their weight on average. Mature females are up to three times heavier than freshly emerged ones. They invest about 30% of their final AFDW in reproduction.

Shape of last instar nymphal *Baetis* was expressed as the ratio wing length/mesonotum length. It is size-dependent, a characteristic, instar-specific shape may not occur in this mayfly. Nymphal and subimaginal exuviae together represent about 14% of last instar nymphal dry weight. Females of *Baetis* are about 55% heavier than males. Unlike in Plecoptera, the size/weight (ML/AFDW) relationship differs between sexes.

Introduction

Growth and development of hemimetabolous insects are often described as a series of molts for growth accompanied by continuous and gradual change. However, recent work on single species of Plecoptera has revealed stepwise developmental change and a fixed number of well defined morphs leading to the adult moult. Whether this is the rule in Plecoptera, and if so, if other hemimetabolous insect groups, e.g., Ephemeroptera, are similar in this respect remains to be established.

The development of aquatic hemimetabolous insects passing through a large and often variable number of instars is not well known. While the pupal stage of holometabolous insects is recognized as a distinct life phase, mayflies and stoneflies are usually treated as though their entire larval period was available for growth and biomass gain. Final adult size (which determines reproductive capacity, e.g. Harvey *et al.*, 1979; Kondratieff & Voshell, 1980; Oberndorfer & Stewart, 1977; Sheldon, 1972; Sweeney & Vannote, 1981) depends on available food, thermal and other abiotic conditions, but there are obviously additional important influencing factors connected with initiation of metamorphosis and developmental mode (Zwick, 1992). Such information is relevant for the understanding of life cycle adaptations as well as for studies of stream insect production.

The present paper quantitatively describes several aspects of development, exuvial weight loss at moults, and of adult weight gain and reproductive investment in some species of Plecoptera; it also provides preliminary information on some of these aspects for the mayfly *Baetis vernus* Curtis.

At least in a few species of Plecoptera, late development is known to follow a regular pattern once some (presently not precisely known) environmental cues initiate metamorphosis (Zwick, 1991), thereby adding developmental change to growth. Increase of size at moults is the same throughout development, and during metamorphosis leading to the winged adult. Morphological change is completed in three moults exhibiting distinctive steps of wing development (Zwick, 1991). This means that final adult size is pre-determined by the size at the onset of metamorphosis. A recent study of *Leuctra prima* Kempny (Zwick, 1992) provides an example of the combined effects of environment and pre-defined change during metamorphosis, under field conditions. In this paper we describe similar developmental patterns for species in several additional genera of stoneflies.

Most central European Plecoptera belong to superfamily Nemouroidea and have to feed in the adult stage. Terrestrial adult biomass gain may contribute a very substantial proportion of mature adult biomass, but has been demonstrated in very few species so far (Zwick, 1989). We show similar relations for additional species of stoneflies, and for the first time estimate the proportion of adult female biomass invested into reproduction, *i.e.*, returned to the stream as eggs.

Our data on Ephemeroptera are limited, but we present them because even less is known about the same aspects for mayflies. They were analysed for allometry during growth (Campbell, 1991; Clifford, 1970a, b), but so far without attempt to derive general, instar-related patterns. When instar numbers of mayflies were determined by Fink (1984), for example, particular morphologically defined stages during metamorphosis were not described, also not in the account of developmental processes in *Dolania americana* (Harvey *et al.*, 1979). However, it is not clear whether such distinct stages did not exist or were just not considered.

Study area, material and methods

Study area

The present study was conducted from May to October 1989, in the sandstone foothills near the township of Schlitz, Hesse, Germany, between 200–300 m a.s.l.

Mayflies were collected at a rapid in the epipotamal region of the Fulda River at Schlitz-Hutzdorf, in August and September. At this station, the river is β -mesosaprobic and supports a rather diverse fauna.

Spent females of the stonefly *Protonemura nitida* were obtained in October, along the epirhithral of the Fulda river above Obernhausen, Hesse, Rhön Mts, *ca* 700 m a.s.l. Detailed descriptions of both sites are available (Illies, 1953; H. Zwick, 1974; Marten, 1983; Pitsch, 1983).

All other stoneflies were collected along the lower course of the Breitenbach, an unpolluted, small (mean annual discharge: about 15 l s^{-1}) eastern tributary of the Fulda river between Schlitz-Pfordt and Schlitz-Fraurombach. The Breitenbach flows through a narrow strip of grassland in its forested catchment area. Detailed habitat descriptions are available, e.g., Illies (1971, 1978), Gümbel (1976) and Sandrock (1978).

Collecting, rearing, preservation

Freshly emerged *Baetis* adults were collected with a handnet. Mayfly nymphs were individually picked from the river. Adult Plecoptera were mainly handpicked from littoral vegetation. Plecoptera nymphs were either picked individually, or sorted from random kick samples of the benthic fauna collected with an 0.5 mm mesh net.

Nymphs of both groups visibly approaching adulthood were laboratory-reared, using methods described by Marten & Zwick (1989). They were kept singly, to safely associate exuviae and adults. Distinction of sexes was possible only in last instar nymphs, by morphology of the genital region.

Additional nymphs, including small ones, were preserved in a 96%-ethanol/4%-formaldehyde solution; nymphal size was measured (see below). Ash-free dry weight (AFDW) was later determined as the difference between dry weight at 105 °C, and ash weight after 3 hr combustion at 500 °C. All weights were determined to the nearest μ g on a 'Sartorius' ultra-micro-scale.

Adults were treated similarly. In addition, condition of field collected adults was rated (see below).

Measurements

Measurements were made with a WILD M5 dissecting microscope combined with a digitizing tablet (Werneke & Zwick, 1992); repeated measurements of the same object differed by at most 0.26%.

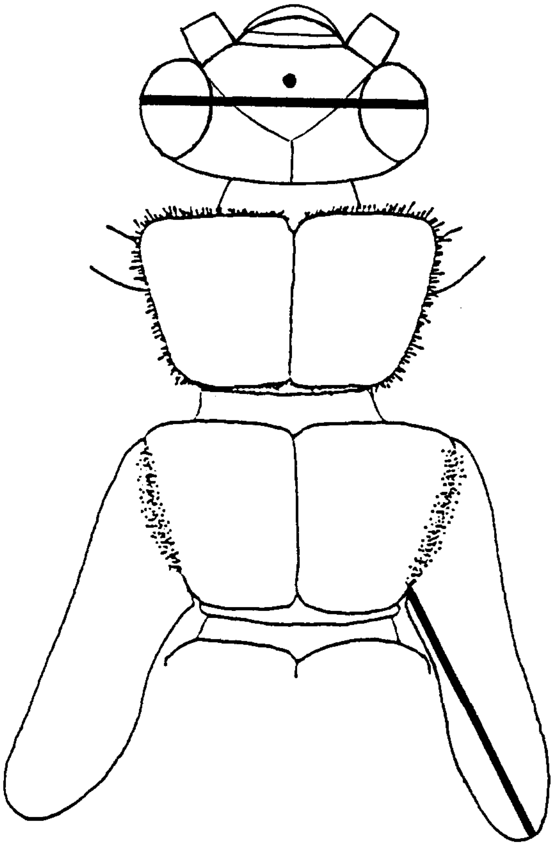

Fig. 1. Nymphal head and thorax of *Protonemura intricata*, bars showing measurement of head width and wing pad length, respectively.

Plecopteran size was expressed as head capsule width across the compound eyes (HW). Because *Baetis* have sexually dimorphic heads, length of mesonotum along the middorsal line was used instead. Adult wing length (WL) was determined as the distance between the tip of the front wing and the base of a major wing vein, the costa. In nymphs, WL actually is wing pad length which we determined as distance between tip of wing pad and medial point of contact between pad and mesonotum (Fig. 1).

Data analysis

Least square regressions between variables were calculated from sets of individual measurements of size (HW or ML) and AFDW. This made it possible to correct individual readings for size, and to compare weight between stages, sexes and adult in different conditions (defined below), even though of course no single specimen was ever weighed more than once.

Curtosis and skewness were used to test for normal distribution of data; data significantly deviating from normal distribution were excluded from further analysis. Significance of differences between means for individual sexes or species, respectively, was examined by the Wilcoxon-Mann-Whitney U-test (Sachs, 1984).

Categories of adult condition

Field collected plecopteran females were assigned to the following categories:

1. fresh: just emerged, not fully pigmented, abdomen not extended by large oocytes, no sperm mass visible through the transparent body wall;
2. mature: fully pigmented females before first oviposition, abdomen full of large oocytes, their contours often apparent on outside of body; Malpighian tubules pressed against body wall by egg mass, visible from outside through the transparent body wall; often, the full receptacles apparent as pale spots inside sternum 8/9;
3. spent: fully pigmented females with shrivelled and contracted abdomens.

Since adult Ephemeroptera cannot feed, only categories 1 and 3 apply to them.

Species studied

Plecoptera studied were: *Nemoura cambrica* (Stephens), *N. cinerea* (Retzius), *N. flexuosa* (Aubert), *N. marginata* (Pictet), *Protonemura auberti* (Illies), *P. intricata* (Ris) and *P. nitida* (Pictet); none was available in all stages. Therefore, species are identified by different symbols in the illustrations; results for congeners agreed closely, we have therefore calculated regressions for the combined species.

Only one mayfly species, *Baetis vernus* Curtis, was studied. Numbers of spent females were insufficient for analysis.

Table 1. Mean AFDW [mg±s.d.] of last instar nymphs and exuviae, respectively, of some Nemouridae and of *Baetis vernus*, respectively

Taxon		Number	AFDW
Nemouridae			
P. auberti,	males	25	0.616±0.159
P. auberti,	females	11	0.784±0.258
P. intricata,	males	15	0.405±0.060
P. intricata,	females	34	0.537±0.128
P. auberti,	exuviae	60	0.088±0.022
P. intricata,	exuviae	28	0.067±0.021
Nemoura spp.,	exuviae	9	0.138±0.069
Baetis vernus			
male,	nymphal exuviae	20	0.054±0.005
male,	subimaginal exuviae	20	0.047±0.006
female,	nymphal exuviae	20	0.070±0.076
female,	subimaginal exuviae	20	0.045±0.009

Results

Plecoptera

Metamorphosis and instar discrimination

Nymphs of *Protonemura auberti* and *P. intricata* exhibited continuous variation of both HW and WL and could not be grouped into instars by either one of these variables. Sexual size differences were marked, mean female exceeding mean male size by 9–10%.

In plots of WL against HW, data points form discrete groups, corresponding to ante-penultimate (L_{n-2}), penultimate (L_{n-1}) and last instar (L_n), respectively. Linear regressions were fitted to these data on logarithmic scales (Fig. 2). Regression parameters for *P. auberti* are shown in the figure inset, the regressions for *P. intricata* are very similar:

$$L_n : y = 0.84x + 142,14; r^2 = 0.73$$

$$L_{n-1} : y = 0.65x + 151,28; r^2 = 0.74$$

$$L_{n-2} : y = 0.38x + 122,67; r^2 = 0.42$$

Late larval instars are distinguished by characteristic shapes, the WL/HW-ratio can be used to identify the last 3 stages and is independent of specimen size (Fig. 3); slopes of regressions for the data points do not significantly differ from zero.

Table 2. Percentage of last instar nymphal dry weight lost as exuvial weight at the moult to adult stage in two species of *Protonemura*, of *Nemoura* spp., and all Nemouridae, collectively.

Taxon	Number	% exuvial weight
P. auberti	61	13.9
P. intricata	28	14.7
Nemoura spp.	9	12.0
Nemouridae genn. spp.	97	14.0

Size-weight relationship in the last instar

Absolute size and weight of *Protonemura* spp. vary considerably, means differed significantly between the sexes (Table 1). However, the relation of AFDW to size (*i.e.*, HW) was the same for all species (Table 3).

Exuvial biomass lost

Biomass lost with exuviae was determined at the adult moult for *P. auberti*, *P. intricata* and *Nemoura* spp. (Table 1).

AFDW of shed exuviae varied between 8.1 and 18.5% of nymphal AFDW, and losses by females were smaller than those by males (*P. auberti*: 0.3%; *P. intricata*: 0.8%; *Nemoura* spp.: 1.2%; significant at the 0.05% level). Overall mean loss is 14.0% of nymphal AFDW; means of individual species vary between 12.0 and 14.7%, but differences were not significant (Table 2).

Changes in size-weight relationships during adult life

The size-weight relationship of freshly emerged adults was linear on logarithmic scales. It was the same for *Protonemura* and for *Nemoura* spp., even though specific differences in absolute size were obvious (Table 3). On average, HW of females was 6% greater than HW of males, and females were 31% heavier than conspecific males.

The initially uniform size-weight relationship disappears during adult life, when weight is gained through feeding in the terrestrial environment. Individual variation is marked but on average mature females are 2.5 times (*Nemoura* spp.) to 3 times (*Protonemura* spp.) (Fig. 4; note specific differences in absolute size and weight) heavier than fresh females of similar HW (Table 3). The size-weight relationship of mature females was the same for all nemourid species stud-

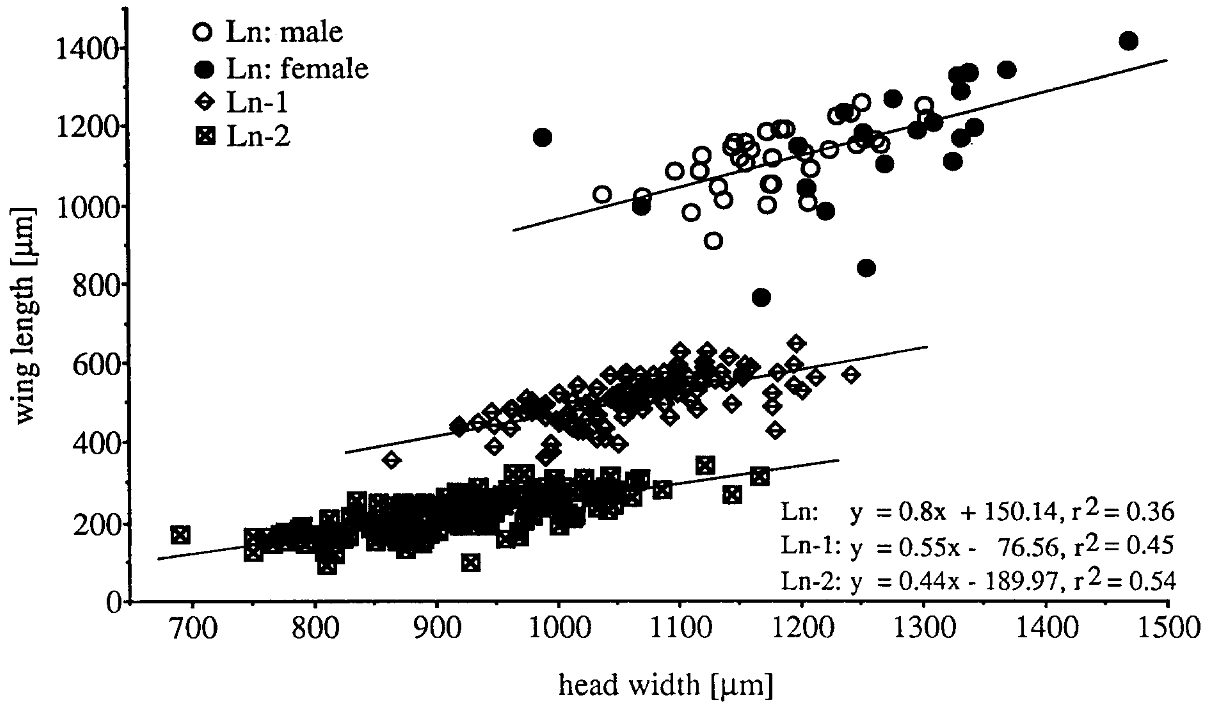

Fig. 2. *Protonemura auberti*, relation between head width and wing pad length in the last three nymphal instars (Ln = last instar; Ln-1 = penultimate instar; Ln-2 = antepenultimate instar). Correlation coefficients of regressions are at the 0.1% level.

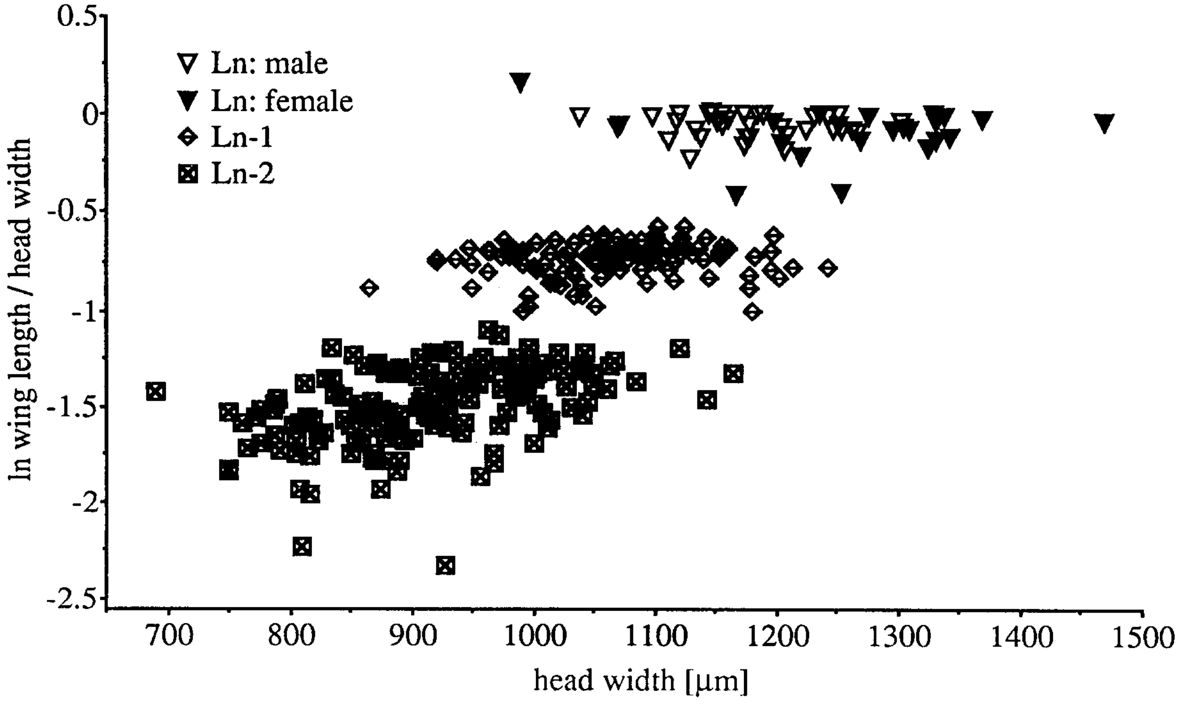

Fig. 3. *Protonemura auberti*, instar-specific relations between wing length and head width, independent of absolute size. Instar definitions as in Fig. 1, logarithmic scale of ordinate chosen only for better graphical resolution.

Table 3. Regression parameters between ln head width (X) and ln ash free dry weight (AFDW, in mg; Y) for nymphs and adults, respectively, of some Nemouridae and of *Baetis vernus*, respectively. Correlation coefficients of regressions are at the 0.1% level.

Taxon	Number	Slope	Intercept	r^2
P. auberti & intricata, unsexed nymphs	84	2.92	−21.21	0.75
P. auberti, P. intricata, N. cambrica, N. cinerea, freshly emerged males	39	2.82	−20.89	0.75
P. auberti, P. intricata, N. cambrica, N. cinerea, freshly emerged females	58	3.50	−25.68	0.91
P. auberti, P. intricata, P. nitida, mature females (max. weight)	100	3.31	−23.14	0.71
P. auberti, P. intricata, P. nitida, freshly emerged females (young)	52	3.49	−25.76	0.85
P. auberti, P. intricata, P. nitida, N. cambrica, N. cinerea, N. flexuosa N. marginata, aged females	138	3.57	−25.13	0.73
B. vernus, female nymphs	20	1.60	−11.66	0.59
B. vernus, male nymphs	20	1.61	−12.03	0.51

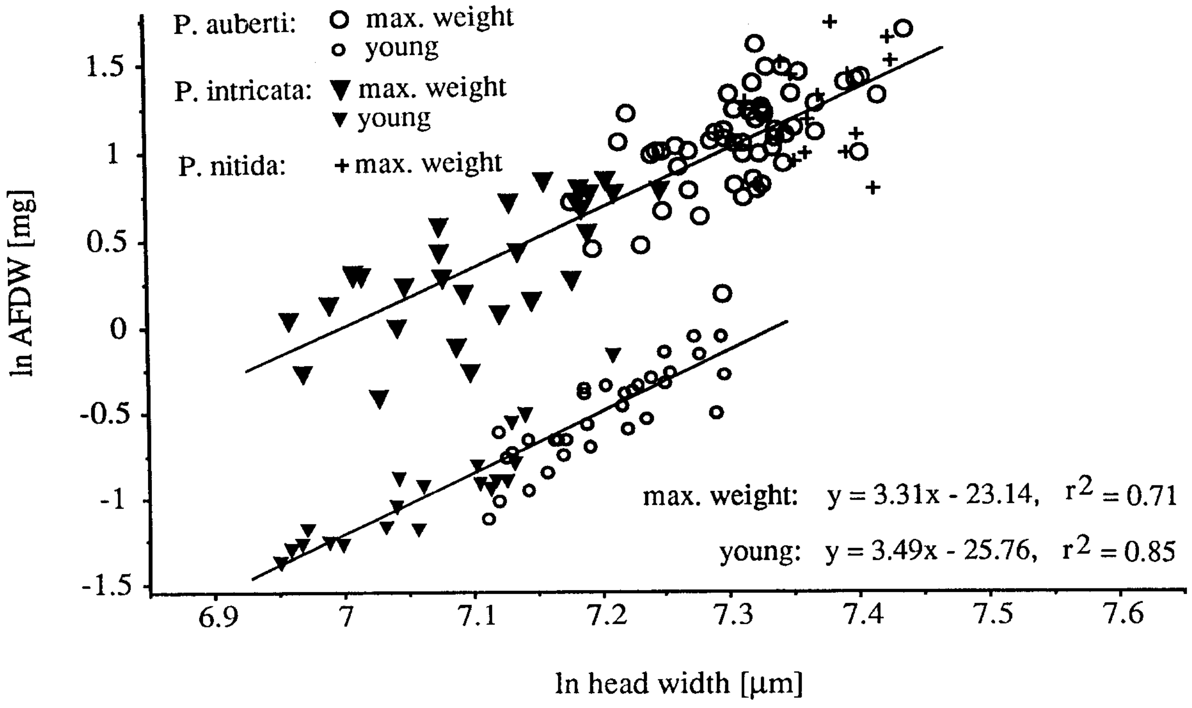

Fig. 4. Relationship, for several species of Nemouridae, between maximum AFDW and head width in freshly emerged (young) and aged females (max. weight) that have fed in the terrestrial environment; see text for species names.

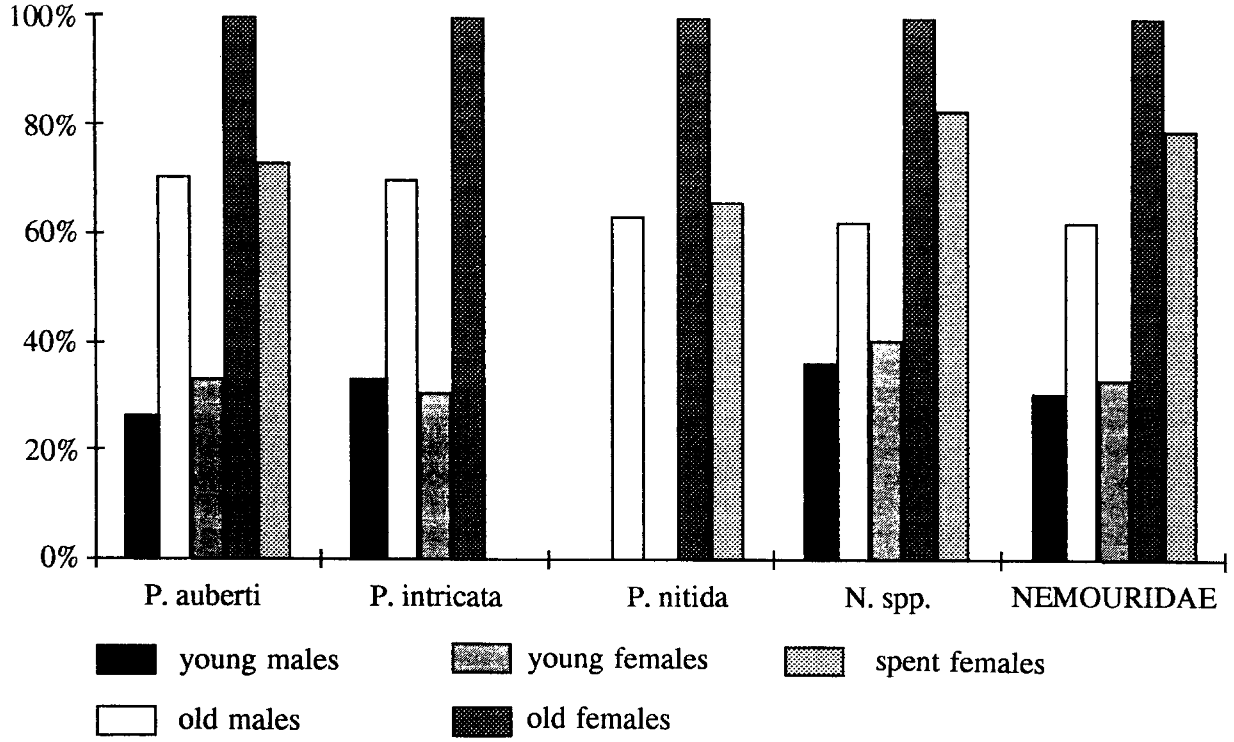

Fig. 5. Change of biomass of average specimens during phases of adult life in several species of Nemouridae; see text for species names. AFDW at a particular head width was read from the independently determined regressions for the different life phases and expressed as percentages of maximum weight attained by aged females.

ied (Table 3). On average, males double weight during terrestrial adult life (Fig. 5).

Biomass invested in reproduction

On average, fully fed mature females were 30% heavier than spent ones. This difference is considered to correspond to the egg mass laid, *i.e.*, to reproductive investment. Note, that spent females are still much heavier than freshly emerged ones.

Ephemeroptera

Metamorphosis and instar discrimination

Only last instar nymphs were examined. Absolute length of wing pad increases with size (expressed as mesonotum length); sexes differ, females have longer wings than males of the same mesonotum length. Shape (expressed as the relation between wing length and mesonotum length) of last instar specimens does not seem to be uniform but to vary with size (Fig. 6): the larger a specimen is, the relatively shorter are its wing pads.

Size-weight relationship in adults

The relationship between specimen size and specimen weight differed between sexes: slope was similar, but intercept was not (Table 4). Females of a given mesonotum length weighed about 55% more than males of the same mesonotum length.

Exuvial biomass lost

During transformation from nymph to adult, mayflies shed nymphal and preimaginal exuviae; both were weighed (Table 1). Exuvial and corresponding adult weights were compared. Regardless of sex, the two exuviae together weighed on average 0.1 mg, corresponding to 11 and 17% of female and male weight at emergence, respectively (Table 4).

Discussion

Wing development in the species of *Protonemura* and *Nemoura* studied here agrees with data on *Leuctra* and *Nemurella* (Zwick, 1991). Three distinctly winged

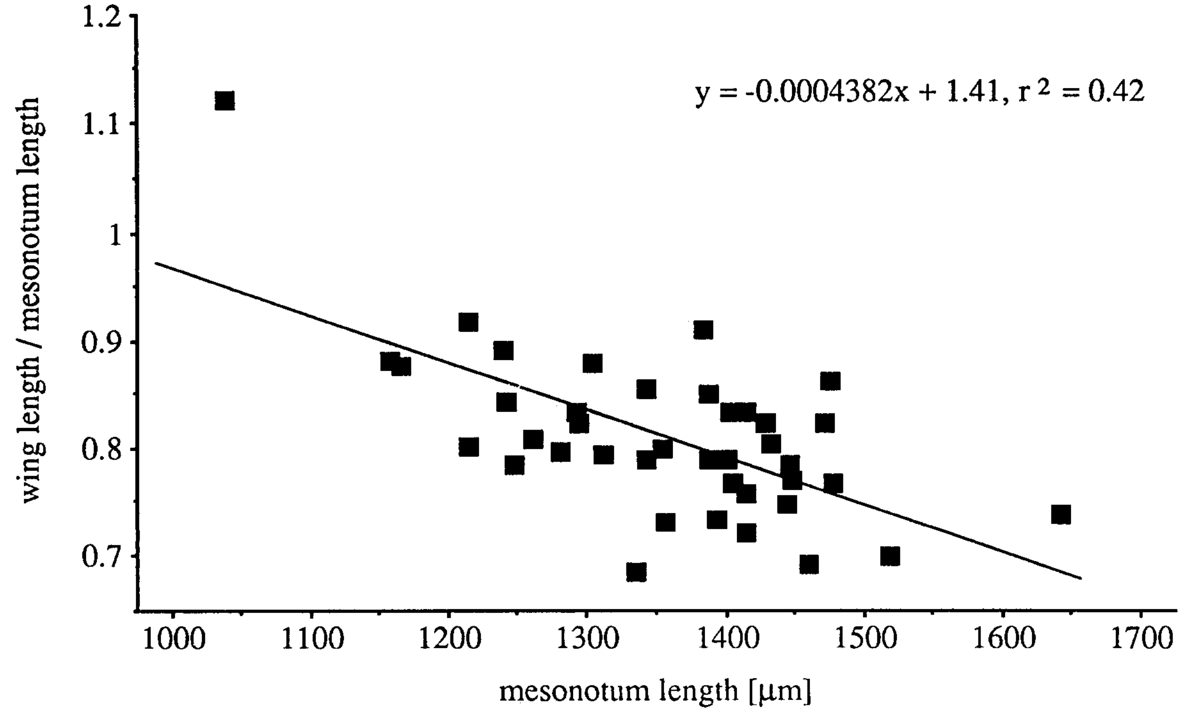

Fig. 6. *Baetis vernus*, last instar nymphs: dependence of shape (described by the quotient winglength/mesonotum length) on size (expressed as mesonotum length).

nymphal instars were also described for other very distantly related plecopteran taxa, e.g. *Pteronarcys proteus* (Newman) (Holdsworth, 1942) and *Dictyogenus alpinum* (Pictet) (Zwick, 1982), and this number may well be typical of the order.

In the present study, instar L_{n-2} is better delimited from L_{n-1} than it was in earlier studies, but the separation is still not entirely satisfactory. Distinction of the very differently sized sexes would perhaps have helped, but was impossible. Since L_{n-2} is the only group of data points in Fig. 3 with an, albeit vague, dependence of WL/HW on size (Fig. 3), this group may in fact be heterogeneous, and comprise more than a single instar. The first external indication of beginning wing development, which is angular shape of thoracic nota but no defined wingpad yet, was observed as early as instar L_{n-3} in *Dictyogenus*.

Mayfly metamorphosis still needs investigation. It should be noted that within the last instar of *Baetis vernus*, shape (described by the quotient wing length/mesonotum length) seemed to depend on size (expressed as mesonotum length; Fig. 6), whereas in Plecoptera the corresponding WL/HW quotient was constant in a given instar (Fig. 3), *i.e.*, there was no evidence of allometry of shape in the last instar.

A study of the stonefly *Taeniopteryx nivalis* (Knight *et al.*, 1976) suggested that last instar nymphal weight was somewhat greater than the total of nymphal plus exuvial dry weights; this may be explained by metabolic losses, or dissolved material in fluids lost during the moult. For comparison with exuviae, we nevertheless took last instar nymphal weight to correspond to the sum of exuvial weight plus weight of the emerging adult.

Exuviae represented on average 14% of the AFDW of last instar nymphal nemourids. In *Dictyogenus alpinum* (Perlodidae), exuvial weight corresponds to 15.8 and 14.1% of nymphal AFDW, for males and females, respectively (Zwick, unpublished data). In another perlodid stonefly, *Hydroperla crosbyi* (Needham & Claassen), (Oberndorfer & Stewart, 1977; their Table 1) give 21 and 8% exuvial weight losses.

Since percent size increase at moults is the same throughout development of Plecoptera (Zwick, 1991), and since there is no major change of body form during development, exuvial weight probably represents a similar proportion of nymphal biomass at each of the

Table 4. Percentage of last instar nymphal dry weight lost as exuvial weight at the moult to subimaginal and imaginal stage, respectively, in *Baetis vernus*.

Taxon	Number	% larval exuvial weight	% subimaginal exuvial weight
B. vernus male	20	9.0	7.8
B. vernus female	20	6.2	5.0

numerous moults. This aspect deserves further attention; we feel that biomass lost with exuviae should not be neglected in estimates of stonefly production.

Harvey *et al.* (1980) made this same point for Ephemeroptera. They found that *Dolania americana* loses about 10–15% of its dry weight at each of its about 13 moults. The energy content of the exuviae was 'only about 15–20% lower than for the larvae themselves'. *Dolania* is no exception, in *Baetis*, the two exuviae shed during transformation to adulthood together also weighed about 14% of last instar body weight.

In contrast, much smaller exuvial weights, about 2% of the total, were reported for *Agapetus fuscipes* Curtis, a soft-skinned caddisfly (Benedetto, 1975) protected in a case.

Sexual size and weight differences observed in the present study are in line with previous observations on related taxa, in accordance with different life cycle strategies. Mayfly females accumulate biomass required for egg maturation during aquatic nymphal life and are, upon emergence, much heavier than males; however, mesonotum length is not generally greater than in males (Table 3). In *Baetis rhodani* Pictet, Bengtsson (1988) noticed also no significant size differences between sexes.

Many Plecoptera with reduced adult mouthparts, e.g. most Systellognatha, also accumulate biomass needed for reproduction during nymphal life (see Zwick, 1980, for references). Females are much heavier and larger than males.

In contrast, nemourid adults feed extensively. Upon emergence, females are larger, *i.e.*, have greater HW's, but not heavier than corresponding males. The same was observed for *Leuctra prima* (Zwick, 1990). Evidently, females provide empty storage capacity for terrestrial biomass gains. Such gains were even greater in the present nemourids studied. Reproduction depends on this terrestrial biomass contribution, which underlines the prime importance of the usually ignored terrestrial adult life phase of aquatic insects.

Nemourid males also gain considerable weight during adult life, despite the fact that male plecopteran reproductive organs are always well developed in the last nymphal instar (Zwick, 1980). However, the only records of completed spermatogenesis in the last instar (Matthey & Aubert, 1947) concern Systellognatha; information on Nemouroidea is lacking. In any case, Hynes (1942) has shown that feeding before copulation is indispensible in nemourids.

Assessing reproductive investment as weight difference between mature and spent female Plecoptera presupposes that females are uniparous. There is indeed no evidence for a second gonotrophic cycle, after additional adult feeding. Instead, field observations (Zwick, unpublished) suggest that nemourid females unable to lay all eggs in a single batch may produce several successively smaller egg masses within a short time, probably during a single day, after which females are spent and die. Assumed uniparity of nemourids is also supported by the fact that oviposition activity occurs only once in the field and extends roughly over a period of time that equals the interval during which females previously emerged; compare figures 2, 3, 5 of Zwick (1990). This does not necessarily apply to all nemouroid Plecoptera, several ovarial cycles were reported in the winter stonefly genus *Allocapnia* (Harper & Hynes, 1972).

Oberndorfer & Stewart (1977) found that *Hydroperla crosbyi* (Perlodidae) invested about 50% of adult dry weight into its egg mass. Our estimate of a 30% reproductive investment in nemourids may therefore be conservative; specimens rated as spent by external appearance may still have contained part of their egg load, resulting in low values for investment. However, because adult specimens needed to be weighed, dissection to evaluate condition more precisely was impractical. We critically excluded many specimens as 'intermediate' which were fully pigmented, but exhibited neither of the two striking shapes of abdomen used to define 'mature' and 'spent' stages. In fact, single eggs sometimes stuck to abdomen or wings of 'intermediate' specimens; these had obviously started, but not yet completed, ovipositing when they were caught.

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