

## Analysis of a northern mayfly (Ephemeroptera) population, with special reference to allometry of size

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Life history phenomena of the mayfly *Leptophlebia cupida* (Say) from a subarctic stream of Canada were found to be best interpreted by combining size-frequency distributions and developmental stage data. Autumn was a period of intense growth and uniform development; both growth and development were retarded but not completely stopped during the 6-month winter period; development accelerated rapidly after the spring breakup even though water temperatures were still near 0 °C. Total fecundity, average egg size, and total egg volume varied directly with the size of the female. Last instar nymphs and subimagos of a given length had about the same number and size of eggs, but imagos of the same length had larger eggs. Analysis of nymphal size allometry indicated that none of the investigated body parts of either sex was exhibiting isometric growth with that of total length. All female dimensions and some male dimensions deviated from simple size allometry when the nymphs were about 7 to 9 mm in total length; a hypothesis with biological implication is offered, accounting for these deviations. Length-volume biomass regression showed the nymphs conforming closely to the cube law; similar regressions for other stream invertebrates are also presented.

### Introduction

Considerable information about the life histories of North American mayflies (Ephemeroptera) has started to accumulate. The impetus for recent studies is due in part to the importance of mayfly nymphs as a component of stream drift and in part to the current trend of studying aquatic environments by the ecosystem approach. Mayfly life histories are usually assessed by size-frequency distributions. But the nymphs can exhibit features making it difficult to study accurately certain life history phenomena by size-frequency distribution alone. For example: the nymphs may have a variable number of molts, making it impossible to determine instar number from head capsule measurements; because of environmental factors, larger nymphs may be physiologically younger than smaller nymphs; continuous delayed hatching may tend to mask the true growth features of the population; and there are usually size differences between male and female nymphs.

In this study, in which both size-frequency distributions and developmental stage data are used, certain life history phenomena are analyzed (i.e. growth, development, and fecundity) of the mayfly *Leptophlebia cupida* (Say) from a subarctic stream of Canada. By using the allometric, or relative growth, method, information was also obtained on how the nymphs changed in form with change in size. The objective of the

allometric study was to associate changes in size of body parts, relative to changes in the total length, with the life history of *L. cupida* in its natural environment.

### Methods

#### Field Methods

From 1966, and as part of a continuing limnological program (Clifford 1969), *L. cupida* nymphs have been collected from one location of the Bigoray River, a brown-water (or muskeg) stream of west-central Alberta. During the ice-free season, usually May through October, samples were taken at about monthly intervals with a dip net having a mesh size of 16 meshes/cm. From November through April, samples were taken about every other month. To complete *L. cupida*'s life history it was also necessary to collect from an intermittent tributary. The tributary contained water after the snow melted in late spring, but it usually dried up completely by August of each year, and there was never water in the tributary during the winter months.

Nymphs were counted, measured (total length) to the nearest 0.5 mm excluding cerci, and separated into males and females by compound eye differentiation. For part of the study period, *L. cupida*'s total volume-biomass per sampling date was determined by standard liquid displacement methods (Welch 1948). Each measured nymph was grouped into one of four arbitrarily chosen developmental stages on the basis of the appearance and development of the mesothoracic wing pads (Fig. 1). Stage I nymphs lacked wing pads; stage II nymphs had wing pads, but their lengths were shorter than the distance separating the two wing pads; the wing pad length of stage III nymphs was greater than the distance separating the two wing pads; stage IV nymphs had darkened wing pads. A more advanced developmental stage represents an



length or width of the body part in question ( $Y$ ) against its total length ( $X$ ), using individual measurements of all nymphs. This procedure was repeated, but plotting included only the mean total length and mean of each body part for each of the 13 size classes. Generally, a power function adequately described both individual measurements and size class means.

Each body part was then related to total length by the power, or allometry equation

$$Y = bX^k$$

where the constant  $b$  is the value of  $Y$  when  $X$  equals one and the constant  $k$  is the ratio of the specific growth rates of  $Y$  and  $X$ . For simple allometry to hold, this ratio must remain constant throughout growth. Graphically,  $k$  is the slope of the line relating the part to the whole when expressed in log form. To shorten the calculation, the mean total length ( $X$ ) and the mean of each body part ( $Y$ ) of each size class were used. The allometry equation was treated in its log form

$$\log_e Y = \log_e b + k \log_e X$$

solving for  $k$  and  $b$  by both least square regression and Bartlett's "best fit" method (Simpson *et al.* 1960).

The allometry analysis of this study, where the nymphs were gathered more or less at random and placed into size groups without regard to true age, is that of allometry of size (or ontogenetic allometry of mass data, Gould 1966). This is in contrast to allometry of growth (ontogenetic allometry of longitudinal data) where measurements are made on recognized individuals throughout their postembryonic development.

### Results

#### Seasonal Cycle, Size, and Age

For most of the year, *L. cupida* is the dominant stream invertebrate, both in numbers (excluding Chironomidae) and biomass (Fig. 2). *L. cupida* is a univoltine species with an annual cycle; generations do not overlap, and the general features of the life history can be interpreted

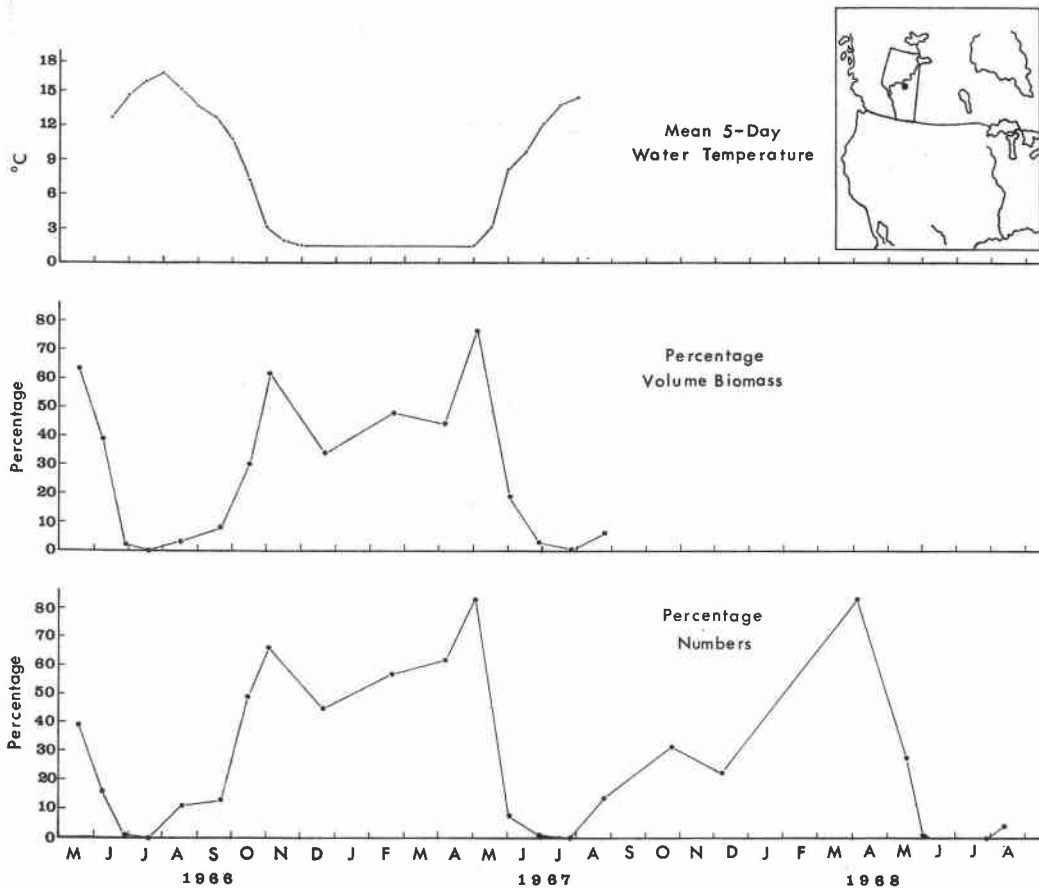


FIG. 2. Water temperatures of Bigoray River, and percentage (of total main stream fauna excluding Chironomidae) number and volume biomass of *Leptophlebia cupida* nymphs, with an insert showing the location of the stream.

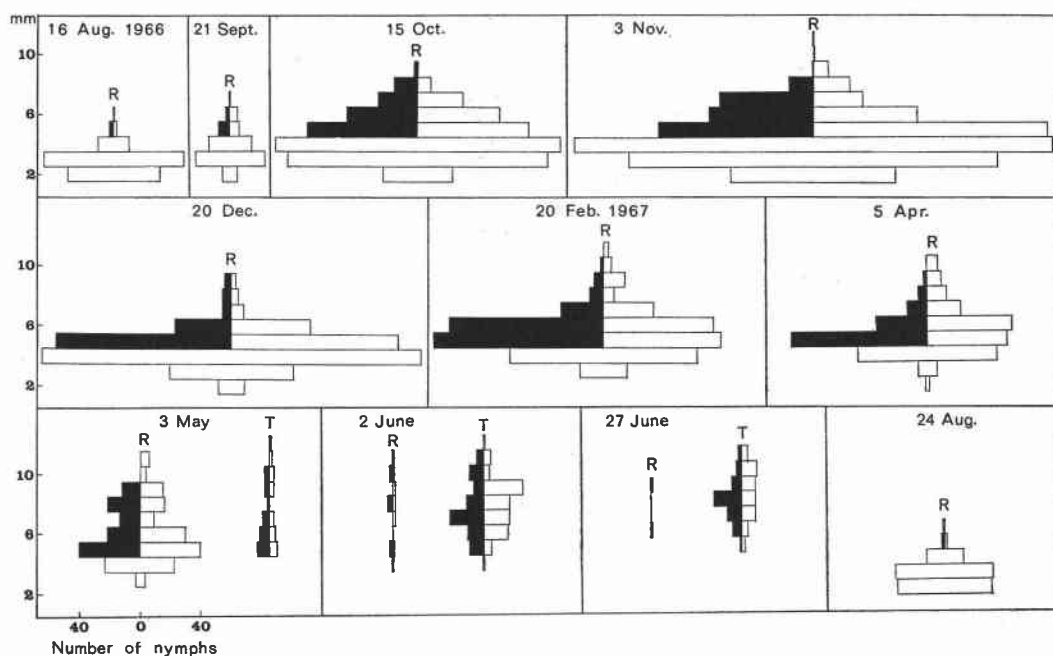


FIG. 3. Number of *Leptophlebia cupida* nymphs in mm-size classes from Bigoray River main stream (R) and tributary (T), 1966-1967. Nymphs shorter than 5 mm are centered; for those 5 mm and longer, females are on right of midline and males are darkened and on left of midline. The 2-mm size class also includes all nymphs smaller than 2 mm.

TABLE I

Percentage composition of *Leptophlebia cupida* nymphs in the four developmental stages, representing both river and tributary samples, June 1966 to August 1967

Collection date	Stage				Total number of specimens
	I	II	III	IV	
1966					
8 June	0	1	69	30	243
27 June	0	0	68	32	243
19 July	0	0	32	68	112
16 Aug.	99	1	0	0	179
21 Sept.	29	71	0	0	107
15 Oct.	4	95	1	0	859
3 Nov.	2	97	1	0	1302
20 Dec.	1	98	1	0	697
1967					
20 Feb.	0	90	10	0	639
5 Apr.	0	89	11	0	410
3 May	0	67	33	0	326
2 June	0	26	64	10	180
27 June	0	38	27	35	94
26 July	0	0	0	0	0
24 Aug.	84	16	0	0	155
Total length range, mm	2-6	2-11	5-12	7-13	

from seasonal size-frequency distributions (Fig. 3). Nymphs of the 1966–1967 generation were first collected in August. They grew rapidly during the remainder of the ice-free season, and by the time the stream froze over completely, during the first week of November, some nymphs appeared fully grown. There was a continuous influx of small nymphs into the population through December, indicating delayed hatching and masking the precise growth pattern of the population during the long winter.

In 1967, the ice broke up during the last 2 weeks of April. The nymphs moved into snow-melt tributaries and shallow marshy regions drained by the tributaries. Neave (1930) reported a similar migration of *L. cupida* in a Manitoba stream. The May 3 samples were taken at the beginning of the migration. By June 27, *L. cupida* was restricted almost entirely to the

tributaries and the nymphs were transforming at this time. The tributary from which samples were taken (and most of the surrounding marshy region) had dried up by the middle of July 1967, and no nymphs were found in the main stream

TABLE II

Number, observed range in mm-size classes, and mean total length of stage IV nymphs of the 1965–1966 and 1966–1967 generations, representing both river and tributary samples

	Number	Range, mm	Mean size, mm
1966			
8 June	71	7–13	9.9
27 June	78	7–11	8.3
19 July	76	7–10	8.2
1967			
2 June	17	8–11	9.8
27 June	25	8–11	9.2

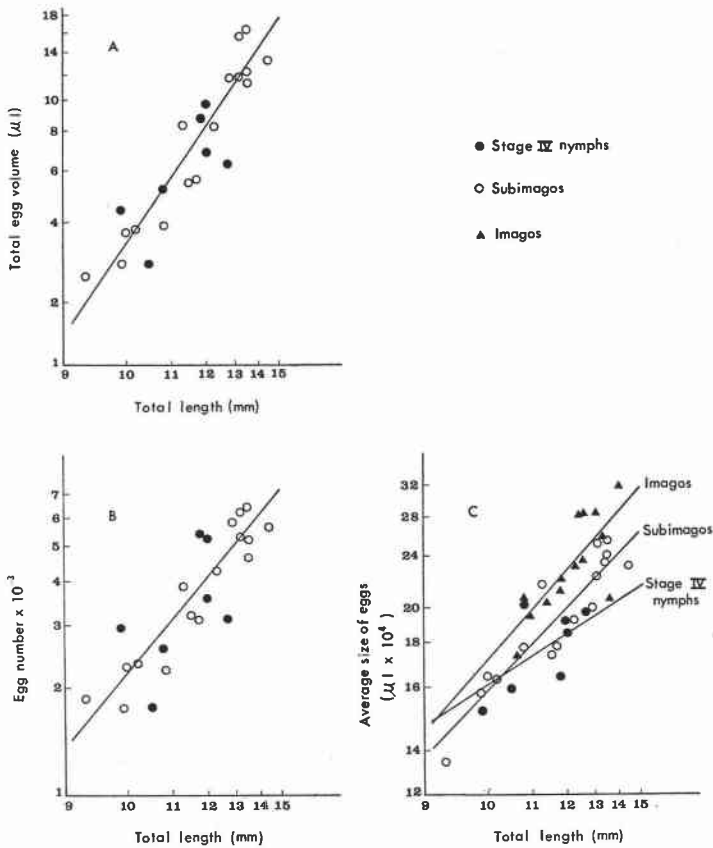


FIG. 4. Scatter diagrams, on logarithmic coordinates, of total egg volume (A), egg number (B), and average egg size (C) plotted against total length of *Leptophlebia cupida* nymphs, subimagos, and imagos. Subimaginal and nymphal data were combined to calculate the regressions of total egg volume and egg number.

at this time. The 1967–1968 generation appeared first in August 1967.

By separating *L. cupida* nymphs into developmental stages, the "age" structure of the population can be followed through the life cycle (Table I). *L. cupida* has a uniform developmental sequence for most of the annual cycle. After hatching in autumn of 1966 the new generation developed rapidly and quite uniformly. By 3 November, 97% of the population was in a single stage, stage II. Development during the 6-month winter period was retarded, but not completely stopped. The last winter sample, 5 April 1967, had 11% of the population in stage III compared to only 1% in stage III for the 3 November, 1966, sample. Water temperatures were still near 0 °C on 3 May, but nymphal development had speeded up and 33% of the population was in stage III. After the spring breakup, development proceeded rapidly and the clear-cut modality of the developmental stages became considerably damped. In late June, nymphs were still in all stages of development, except stage I. But this does not mean that the generally synchronous pattern of nymphal development had broken down. It is simply a consequence of most nymphs having emerged by this time.

There were large size ranges for each stage. A few nymphs 6 mm long had no wing pads

(stage I), whereas others (stage IV) were ready to transform into subimagos at 7 mm. Stage IV nymphs ranged in size from 7 to 13 mm and their average size decreased as the emergence period progressed (Table II). The rapid developmental period in spring acts against much growth for the larger nymphs at this time. For example: in autumn an 8-mm nymph, after one or more molts, would eventually grow to 9 mm and so on; but in spring an 8-mm nymph, after one or a few molts, would probably emerge.

#### Fecundity

Since mayflies have only one egg-laying cycle, all eggs must be formed (and possibly mature) by the time the subimagos transform. By examining subimagos or the last nymphal instar, one can estimate precisely the total fecundity of mayflies. For *L. cupida*, the total number of eggs per female (nymphs and subimagos combined) ranged from 1800 to 6400. Large females had more and larger eggs than small females (Fig. 4B and C). It was impossible to estimate accurately the total egg number of imagos; all imagos examined had less than 400 eggs, indicating they had in part oviposited.

Stage IV nymphs and subimagos of the same size had about the same number of eggs; the least square fitted regression for these combined data was  $\log_e Y = -6.205 + 3.039 \log_e X$ ,

TABLE III  
Number, mean total length of the 13 size classes, and percentage stage of *Leptophlebia cupida* nymphs used for the allometric size analysis

Sex	Number	Mean total length, mm	Stage			
			I	II	III	IV
Juveniles	5	1.63	100	—	—	—
Juveniles	10	2.37	100	—	—	—
Juveniles	11	3.42	27	73	—	—
Juveniles	10	4.73	—	100	—	—
Females	7	5.45	—	100	—	—
Males	8	5.63	—	100	—	—
Females	10	6.53	—	100	—	—
Males	7	6.51	—	100	—	—
Females	8	7.44	—	87	13	—
Males	7	7.55	—	100	—	—
Females	9	8.34	—	56	44	—
Males	9	8.49	—	56	44	—
Females	6	9.18	—	—	100	—
Males	7	9.36	—	—	71	29
Females	6	10.21	—	—	100	—
Males	7	10.32	—	—	71	29
Females	7	11.34	—	—	86	14
Males	5	11.24	—	—	100	—
Females	4	12.55	—	—	75	25
Females	5	13.60	—	—	60	40

where  $Y$  is egg number times  $10^{-3}$  and  $X$  is total length in millimeters. Separate regression lines were fitted to average egg size data: for imagos,  $\log_e Y = -0.748 + 1.557 \log_e X$ ; for subimagos,  $\log_e Y = -0.152 + 1.266 \log_e X$ ; and for stage IV nymphs,  $\log_e Y = 0.935 + 0.800 \log_e X$ , where  $Y$  is  $\mu\text{l}$  times  $10^4$  and  $X$  is total length in millimeters. Although the regression coefficients (slope of the lines) of average egg size were not significantly different from one another ( $t$  test) at the 95% level, the scatter diagram shows imagos for a given length having larger eggs than those of stage IV

nymphs and subimagos of the same length. Either *L. cupida*'s imago stage is considerably longer than the subimago stage, allowing the eggs to become completely mature in the adults, or I was measuring only the imagos' fertilized eggs, which, for unexplained reasons, might be larger than unfertilized eggs.

The total egg volume of a stage IV female nymph accounts for about 20% of the nymph's total volume-biomass, although this percentage varies slightly with the size of the nymph. This was arrived at by extrapolating total egg volume for a given size (Fig. 4A), where  $\log_e Y$  (in

TABLE IV

One-line allometric size constants for the mean values of the dimensional measurements ( $Y$ ) against mean total length ( $X$ ), as calculated by Bartlett's best fit method and by least square regression, with 95% confidence intervals (CI) for the latter.  
Both  $X$  and  $Y$  are in millimeters

	Bartlett's best fit		Least squares			
	$b$	$k$	$b$	95% CI	$k$	95% CI
Males						
Head length	0.210	0.865	0.212	0.207 0.217	0.870	0.798 0.943
Pronotum width	0.325	0.825	0.325	0.312 0.388	0.827	0.758 0.896
Mesonotum width	0.309	0.865	0.314	0.308 0.320	0.859	0.829 0.889
Mesonotum length	0.112	1.430	0.091	0.082 0.102	1.355	1.121 1.588
Abdomen width	0.263	0.951	0.271	0.261 0.280	0.940	0.881 0.999
Forceps length	<0.001	3.859	<0.001	—	3.665	1.788 5.541
Females						
Head length	0.252	0.806	0.222	0.214 0.231	0.823	0.762 0.883
Pronotum width	0.341	0.800	0.333	0.325 0.343	0.814	0.771 0.857
Mesonotum width	0.342	0.826	0.324	0.316 0.331	0.847	0.809 0.884
Mesonotum length	0.009	1.291	0.102	0.097 0.107	1.279	1.175 1.383
Abdomen width	0.269	0.958	0.269	0.258 0.281	0.951	0.883 1.020

$\mu l) = - 8.595 + 4.273 \log_e X$ , and then comparing this figure with the total volume-biomass of a nymph having the same size (Fig. 8); e.g. the total egg volume accounted for 17%, 21%, and 23% of the total volume-biomass of 10-mm, 11-mm, and 12-mm nymphs respectively.

*Allometry Analysis*

Table III gives the numbers, mean total lengths, and percentage stages of nymphs used

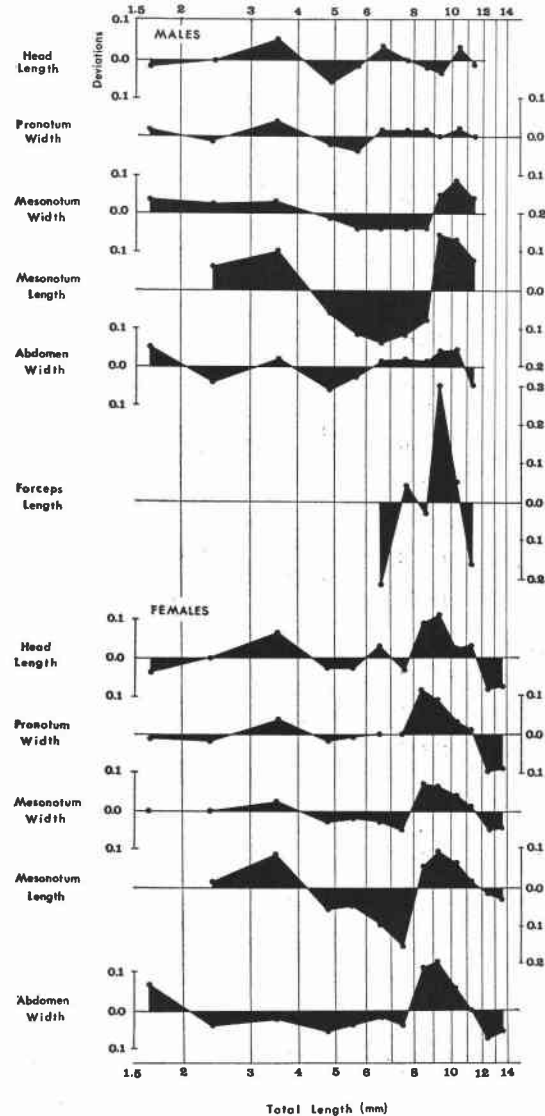


FIG. 5. Deviations of the dimensional measurements' observed values from the theoretical values as predicted by the calculated  $k$  slopes, when all body parts were fitted by single allometric functions. (See text for further explanation.)

in the allometry of size analysis. The results of solving for the constants  $b$  and  $k$  in the allometry equation by both least square analysis and the Bartlett's best fit method are given in Table IV. For *L. cupida*, both methods lead to the same inference: the nymphs are changing shape as they increase in total length. As indicated by the 95% confidence intervals, none of the body parts, with the possible exception of female abdominal width, exhibited isometric growth ( $k = 1$ ) with that of total length. With the exception of mesonotum length and forceps length, all body parts increased in length or width relatively more slowly than did total length ( $k < 1$ ).

The premise for making the one-line calculations is that  $k$  for a given body part is a single straight line when plotted on log coordinates; i.e. the relationship of the part to the whole does not deviate from simple allometry. To determine possible deviations for *L. cupida*, I used the graphic method of Richards and Kavanagh (1945), which is further elaborated by Simpson *et al.* (1960). For a particular dimension, the one-line slope of simple allometry is calculated; then the natural logs of the calculated ordinal values are subtracted from the natural logs of

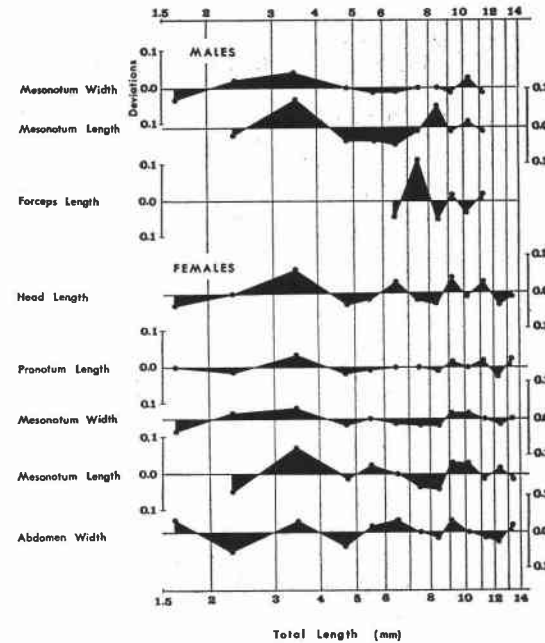


FIG. 6. Deviations of the dimensional measurements' observed values from the theoretical values for those body parts each fitted by two allometric functions.

actual ordinal values. The resulting values, called deviations, are then plotted around a line (equal to zero deviation) corresponding to their abscissal (total length) position. If there is deviation from simple allometry, the resulting points will exhibit a methodical trend or curve, a trend not accounted for by simple random variations.

For *L. cupida*, there are definite trends and large deviations for certain body parts (Fig. 5). The female nymphs exhibit consistent and systematic deviations for all body parts, with the most striking deviations taking place between mean total lengths of 7.4 and 8.3 mm. For male nymphs there are large and systematic deviations for mesonotum length and forceps length, and also a methodical trend for mesonotum width; the largest deviations for these body parts are between 8.5 and 9.4 mm.

All female body parts and male mesonotum length, mesonotum width, and forceps length were considered deviating from simple size

allometry. Two separate allometric functions were then calculated for each of these body parts, covering mean total length ranges of 1.63 to 8.49 mm and 9.36 to 11.24 mm for males, and 1.63 to 7.44 mm and 8.34 to 13.60 mm for females. These functions were then fitted to the actual values and their deviations calculated as for the one-line functions (Fig. 6). This eliminated most of the systematic trends and greatly reduced the magnitude of the deviations, seemingly justifying the premise that female nymphs are deviating from simple size allometry at an average size of about 8 mm and the male nymphs at an average size of about 9 mm. Table V gives the values of the size constants and their confidence intervals for those dimensions fitted by two functions. Figure 7 shows the functions fitted to the actual values for all body parts.

Assuming that the slopes adequately represent the allometry of size relationships, the following inferences can be made about relative growth of *L. cupida* nymphs.

TABLE V  
Allometric size constants and their 95% confidence intervals, for those dimensions fitted by two functions as calculated by least square regression

	<i>b</i>	95% CI	<i>k</i>	95% CI	<i>b</i>	95% CI	<i>k</i>	95% CI
Males								
Lower line (1.63-8.49 mm)				Upper line (9.36-11.24 mm)				
Mesonotum width	0.323	0.316 0.330	0.827	0.788 0.866	0.340	0.276 0.418	0.850	-1.922 3.623
Mesonotum length	0.115	0.110 0.121	1.182	1.060 1.305	0.250	0.226 0.278	0.970	-0.412 2.352
Forceps length	<0.001	—	4.223	-5.155 13.560	0.036	0.028 0.049	0.976	-2.688 4.640
Females								
Lower line (1.63-7.44 mm)				Upper line (8.34-13.60 mm)				
Head length	0.220	0.209 0.230	0.824	0.722 0.926	0.543	0.524 0.563	0.452	0.238 0.575
Pronotum width	0.320	0.264 0.335	0.822	0.784 0.860	1.001	0.975 1.025	0.355	0.206 0.504
Mesonotum width	0.321	0.313 0.328	0.837	0.791 0.883	0.592	0.581 0.604	0.596	0.481 0.711
Mesonotum length	0.123	0.117 0.130	1.128	0.988 1.268	0.203	0.196 0.211	0.995	0.774 1.216
Abdomen width	0.279	0.269 0.289	0.910	0.839 0.981	0.786	0.761 0.812	0.511	0.322 0.699

(1) None of the body parts exhibits isometric growth with total length, and hence total length cannot be accurately extrapolated from body part measurements without applying a correction for allometry. For both sexes, pronotum width is, with respect to total length, increasing in size least rapidly, and mesonotum length most rapidly; the latter is the only dimension of both sexes exhibiting positive allometry ( $k > 1$ ). A comparison of individual  $k$  values of males with those of females is somewhat biased because the same juveniles were used in calculating both the  $k$  slopes of males and females. The tendency is for the male dimensions to have larger  $k$  values than those of females.

(2) For the entire range of total lengths, simple size allometry holds only for male head length, pronotum width, and abdomen width. All female body parts and male mesonotum width, mesonotum length, and forceps length are considered to deviate from simple allometry.

Deviations are especially striking for female abdomen width and for male mesonotum length and forceps length.

(3) The deviations have been drawn as discontinuities, or "breaks," dividing the nymphs into two allometric size stanzas. An alternate approach would have been to separate the nymphs into three allometric size stanzas, with a short middle stanza between 7 and 9 mm showing strong positive allometry. Regardless of the type of departure from simple size allometry, there are striking changes taking place in allometry of size, between 7 and 9 mm, and the ultimate direction of these deviations is generally towards a lesser slope.

#### *Length-Volume Biomass*

If body form remained constant throughout nymphal life, volume (or weight) would increase as the cube of length and hence the  $k$  value in the power equation would be 3. For both male and

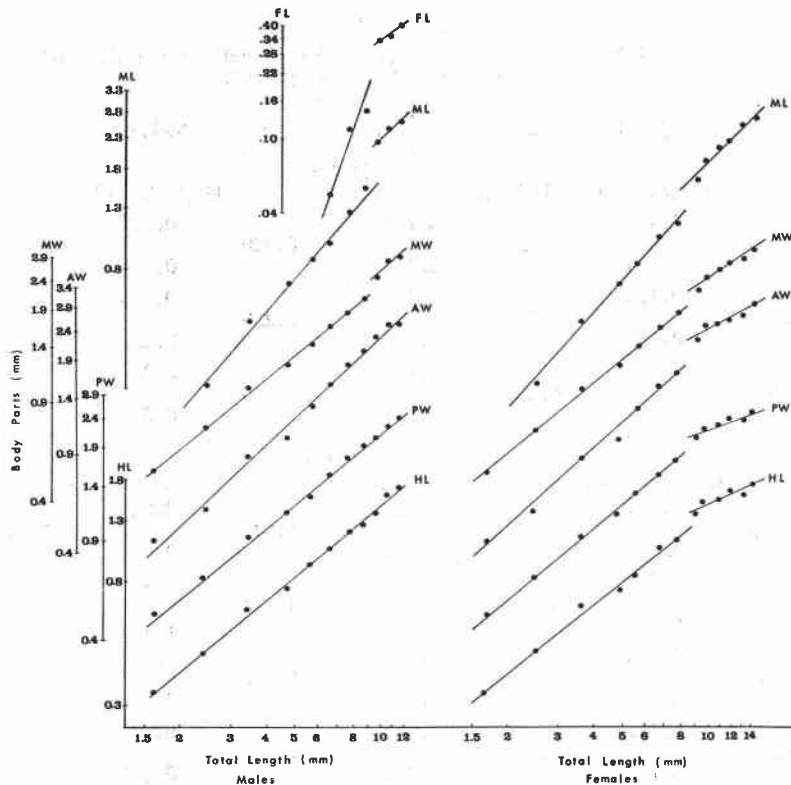


FIG. 7. Scatter diagrams of the mean linear measurements of body parts plotted against mean total length; both variates plotted logarithmically. Body parts: head length (HL), pronotum width (PW), abdomen width (AW), mesonotum width (MW), mesonotum length (ML), and male forceps length (FL).

female *L. cupida* nymphs, deviations from the cube were relatively slight (Table VI). Male and female *k* values (including the same juveniles in both calculations) were not significantly different from each other at the 95% level. The length-volume biomass regression calculated from the combined data of both sexes is shown in Fig. 8. The *k* value here, as was found for the separate male and female calculations, was not significantly different from 3. With the exception of *Hydropsyche* spp., none of the least square calculated *k* values for other stream invertebrates of the Bigoray River was significantly different from 3 (Table VI).

### Discussion

The allometry analysis indicates that simple size allometry holds for the various body parts

of *L. cupida* nymphs until the nymphs are about 7 to 9 mm in total length; then, for some of the male dimensions and all the female dimensions, there are deviations from simple size allometry. Can biological significance be inferred from these deviations? It is possible that the deviations are artifacts resulting from increasingly larger random variations in the size of the body parts (*Y*) over short intervals of total length (*X*) as the nymphs increase in total length, even though much of the scatter would have been reduced because class means were plotted. However, the deviations appear suddenly, are systematic in trend (substantiated by the graphic deviation method of Richard and Kavanagh 1945), and are not apparent in all dimensions. Also the fitting of a second allometric function to each of those dimensions exhibiting deviations seemingly satisfies the allometric relationship again.

TABLE VI

Allometric constants and their 95% confidence intervals for the length-volume biomass relationship, where *Y* is in microliters and *X* is in millimeters, calculated for *L. cupida* and some other Bigoray River invertebrates

	<i>b</i>	95% CI	<i>k</i>	95% CI
Ephemeroptera				
<i>Leptophlebia cupida</i> (males)	0.009	0.007 0.011	3.37	2.47 4.27
<i>Leptophlebia cupida</i> (females)	0.011	0.010 0.012	3.24	2.99 3.49
<i>Leptophlebia cupida</i> (combined)	0.010	0.009 0.012	3.28	2.70 3.86
<i>Callibaetis coloradensis</i> Banks	0.006	0.005 0.007	3.41	2.91 3.90
<i>Siphonurus alternatus</i> (Say)	0.0006	0.0004 0.0008	3.58	2.58 4.58
<i>Baetis tricaudatus</i> Dodds	0.013	0.008 0.022	3.05	1.64 4.47
Plecoptera				
<i>Nemoura cinctipes</i> Banks	0.0002	0.0001 0.0003	4.50	2.91 6.09
Trichoptera				
<i>Hydropsyche</i> spp.	0.073	0.058 0.091	2.37	1.90 2.83
Amphipoda				
<i>Gammarus lacustris</i> Sars	0.058	0.006 0.011	2.52	1.88 3.17

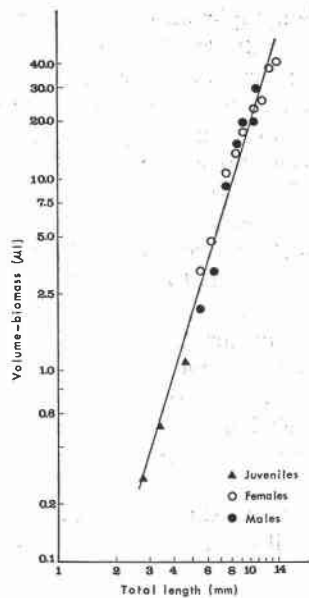


FIG. 8. Total length-volume biomass relationship of *Leptophlebia cupida* nymphs; both variates plotted logarithmically.

If the deviations are not accounted for by random variation, it is possible they have biological significance. It is suggested that the nymphs, when they are about 7 to 9 mm in total length, pass from an "immature" stage to a "mature" stage; and the deviations from simple size allometry for certain body parts at this time reflect this *transitory*, or critical, period. The deviations therefore are accounted for by the changing ratios of the specific growth rates due to the induction or speeding-up of the development of adult structures. Shortly after achieving the "mature" stage, the nymphs are ready to transform regardless of size. Just how long the nymphs remain in the "mature" stage before transforming, and hence continue to grow, depends on environmental factors, although not necessarily the same one(s) that initiate the transitory period. The overall result is to accumulate nymphs in the "mature" stage, and therefore emergence tends to be synchronized.

This hypothesis is based on (1) the striking deviations from simple allometry in those body

parts that would be expected to reflect the development of adult structures, e.g. forceps length (accessory genitalia of males), male and female mesonotum length (flight muscles), and female abdomen width (egg development); (2) the accelerated changes in the percentage composition of developmental stages (even though these are arbitrarily chosen stages) when the nymphs are about 7 to 9 mm in total length (Table III); (3) for the field population, the accelerated changes in percentage composition of developmental stages being at least casually related to the spring breakup of ice and hence a sudden change in photoperiod, the nymphs having been in almost complete darkness for about 6 months (Table I); and (4) the general agreement of the hypothesis with what Khoo (1968) found in a controlled laboratory study of a capniid stonefly (Plecoptera) nymph: lengthening photoperiod initiates the development of adult structures, and decreasing water temperatures retard growth.

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