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LIFE HISTORY, DEVELOPMENTAL PROCESSES, AND ENERGETICS OF THE BURROWING MAYFLY *Dolania americana*

MASTER

by

R. S. Harvey

Savannah River Laboratory
E. I. du Pont de Nemours and Company
Aiken, South Carolina 29801

Robin L. Vannote and B. W. Sweeney

Stroud Water Research Center
Academy of Natural Sciences of Philadelphia
R.D. 1
Avondale, Pennsylvania 19311

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DISCLAIMER

INTRODUCTION

Dolania americana Edmunds and Traver is a burrowing mayfly known only from three coastal plain streams in the southeastern United States (Peters and Peters, 1977). In Upper Three Runs, a spring-fed blackwater stream in South Carolina (33° 23' N; 81° 37' W), *D. americana* is the dominant mayfly species inhabiting the sandy substrate. Larvae are very distinct morphologically, being highly adapted for burrowing in sandy substrate (Edmunds and Traver, 1959). *D. americana* are predators and feed mainly on midge larvae (Diptera: Chironomidae).

Aside from brief field notes accompanying the original taxonomic description of *D. americana* (Edmunds and Traver, 1959), only the adult habits and emergence patterns have been reported (Peters and Peters, 1977). This paper describes quantitatively: (1) the bioenergetics and developmental dynamics of the larval stage; (2) adult emergence and fecundity; and (3) biochemical characteristics of the eggs. These data are used to delineate both the life history of *D. americana* and the overall importance of this species to energy flow in Upper Three Runs.

METHODS

Larvae were taken at random from all potential habitats throughout the year. Larval collections were made at about two week intervals from September 1972 through August 1974 and also from June 1978 through September 1978. Small larvae (dry weight (< 2,0 mg), which were most abundant in fine to coarse (0.1 - 1.0 mm) sand near the stream edge, were obtained by hand picking through sand collected with a dip net. Large larvae (dry weight > 2.0 mg) were usually collected with a modified Needham scraper (5.0 mm mesh) from coarse sand and fine gravel (11-34 mm) adjacent to the thalweg. Figure 1, derived from transect core samples from Upper Three Runs, shows that *D. americana* are more likely to occur where the sand size is small. Sample size ranged from $\geq$ 50 when larvae were small to ca. 20 for large larvae.

Larval respiration was measured with a Differential Submarine Respirometer (Gilson, 1963). Larvae were collected from the stream, placed immediately in test vessels containing 1.5 cm of washed stream sand and 7 ml of filtered (0.45 μm) stream water, and accliminated to test conditions for 2 h. Test temperatures were within 0.5°C of ambient stream water at the time of collection. One larva was placed in each vessel and oxygen uptake was measured at 30 min intervals for 3 h. Carbon dioxide which evolved during respiration was absorbed by a 20% KOH solution. Following the 3 h experiment at ambient (AMB) stream temperature, the respirometer water bath was gradually increased 5.0°C over a 48 h period. Respiration was then measured at 30 min intervals for 3 h at the AMB + 5.0°C temperature. Larvae used in metabolic studies were killed in ETOH,* sexed, dried at 100°C for 24 h, and weighed to the nearest 0.1 mg.

*The amount of weight loss from ETOH was inversely related to size and ranged from 6.8 to 21.7%. Percent weight loss (y) can be predicted from initial dry weight (x) by: $y = 24.4 - 0.845x$, correlation coefficient (r^2) = 0.82.

Adult emergence was monitored by: (1) light trapping at the stream edge; (2) surface drift samples of terminal instar larval molt skins; and (3) drift collections of exhausted male and female adults. Drift nets (1 mm mesh) were 1 m wide and filtered the top 15 cm of the stream. Two drift nets were deployed: one about 3 m from the stream edge (net 1) and the other at mid-channel (net 2). Drift was sampled daily from 0400 to 0700 hours during peak emergence.

Caloric values for eggs, larvae, subimagoes and adults were estimated using a Phillipson microbomb calorimeter. The lipid, protein, and carbohydrate contents of eggs were estimated by the following methods: (1) lipid-weight loss following a 24 h hot (50°C) chloroform:methanol (2:1) extraction solvent in a Soxyhlet apparatus; (2) protein-modified Lowry (1952) technique (Price, 1965); (3) carbohydrate-a phenol-sulfuric acid extraction (Dubois, 1956).

Energy budgets were constructed according to the following equation:

$$A = G + M + R$$

where

A = assimilation = energy consumed in food - energy lost by egestion, excretion, and secretion

G = total change in energy value of body materials

M = energy accumulated in molt skins (exuviae)

R = energy metabolically used or released in all ways for all purposes

Growth was measured by changes in biomass and converted to calories using different conversion factors which varied according to size and sex of larvae (see results below). Relative growth rates (mg/mg/day) for each sampling period and season were calculated using an exponential model:

$$\text{Growth Rate} = (\ln W_f - \ln W_i) / t$$

where

W_f = weight at the end of the time period

W_i = weight at the beginning of the time period

t = duration of time period

Molt skin losses during the larval period were estimated by assuming that: (1) each male and female larva molts 13 times (T. Fink, personal communication) while growing from 0.1 mg to about 11 and 25 mg respectively; (2) the first larval molt occurs at 0.15 mg dry weight for both sexes; (3) each larva grows exponentially; (4) larval weight for each successive molt (m + 1) can be predicted from the weight of the previous molt (m) by the following equations: males: $Wt_{(m+1)} = Wt_{(m)}\, e^{0.336}$, female: $Wt_{(m+1)} = Wt_{(m)} e^{0.383}$, where 0.336 and 0.383 are the average instantaneous growth rates for the entire larval growth period of the fastest growing male and female respectively; and (5) each molt skin weighs about 15% of the larva's dry weight at the time of molting. Molt skin losses were converted to calories separately for males and females by using a caloric equivalent of 4.935 cal mg^{-1} dry weight.

Respiration costs were estimated for a given size animal and stream temperature using empirically derived regression equations. Total respiration for a given period was obtained by summing daily oxygen consumption for an animal of median weight. Oxygen consumption ($\mu\ell O_2$) was converted to calories by using the oxycaloric equivalent of 4.825×10^{-3} cal per $\mu\ell O_2$ (Brody, 1945).

The energy budget reported is for the fastest growing male and female larvae in the subpopulation of Upper Three Runs. For each larval collection, we assumed that the average of the three largest larvae approximated the weight of the fastest growing female and the average larval weight for the entire collection represented the fastest growing male. These assumptions appear valid for *D. americana* because: (1) large (> 3.5 mg) larvae are easily sexed and observations on winter and spring collections (when most larvae generally exceed 3.5 mg) bear out our assumptions; and (2) rearing data for other mayfly species show that the largest and average size larvae for each collection made early in the larval growth period are always the largest female and male respectively (Sweeney 1977, Sweeney and Schnack 1977).

The energy budget only includes periods of positive growth. For example, if the mean larval weight decreases or remains the same in consecutive samples then the time interval for calculating growth, respiration, and molt loss is lengthened sequentially until a sample is obtained that exhibits an increase in mean larval weight. This avoids entering negative values for growth into the budget.

RESULTS

Life History

It appears that *D. americana* has a two year life cycle in Upper Three Runs. Adult emergence and egg deposition in 1978 began on June 1 and continued through June 19. Bottom samples collected on June 2 with fine (500 μm) mesh nets revealed many small (0.1 - 0.5 mg) larvae (Fig. 2A). It is hypothesized that these larvae were not first instar, but rather had hatched in the early spring of 1978 because: (1) dry weight measurements of eggs indicate that first instar larvae weigh at most 0.1 mg; (2) larvae weighing 0.5 mg were present on the date of first adult emergence; and (3) instantaneous growth rates of small ($<$ 1.0 mg) larvae in June or July (when stream temperatures are highly favorable for growth; Fig. 2) suggest that a least five weeks would be needed for larvae to grow from 0.1 to 0.5 mg.

The above hypothesis was tested by dissecting eggs in June 1978 from newly emerged females, fertilizing them with sperm stripped from adult males, and incubating the eggs in glass jars (5.5 cm OD, 6.5 cm deep) containing 100 ml of filtered (0.45 μm) stream water. Jars were kept in a constant temperature water bath at the Stroud Laboratory that was adjusted weekly to trace approximately the average annual thermal regime of Upper Three

Runs. Mature embryos were observed by November, but eggs did not begin hatching until April 4, 1979. Egg hatch continued through May 25, with first instar larvae being about 0.06 mg dry weight.

Collections made after June indicate that larvae weight increases exponentially during the warm months and growth ends by the following May. Maximum larval weights at emergence were 12 and 34 mg for males and females respectively. Adult emergence was synchronous with most adults on wing during the early part of June. A few intermediate size (range: 2.5 - 6.0 mg) larvae failed to emerge with the main cohort in June (see Fig. 2B). These remaining larvae showed no indication of adult maturation (e.g. wing bud development, darkened cuticle, etc.) and disappeared from the stream by early August. These larvae apparently contribute little if any to population recruitment in Upper Three Runs because: (1) drift net samples indicate that they probably do not emerge, and (2) female size would be below the threshold for egg production (i.e. ca. 9 mg).

Calorimetry of Life History Stages

The caloric content of *D. americana* varies substantially with its developmental state (Table 1). Eggs have the highest caloric content (ca 6.18 ca/mg) while newly hatched larvae have the fewest calories (ca. 5.33 cal/mg). Caloric content per unit weight increases with larval growth due probably to accumulation of stored lipid materials. Mature female larvae contain more lipid material per unit weight than mature male larvae and thus have a higher energy content. Stored energy in mature female larvae is represented largely by mature eggs whose lipid content per unit weight is apparently higher than any other developmental stage.

The energy content of larval molt skins, both male and female, is only about 15-20% lower than for the larvae themselves. This suggests that molting may represent a large energy loss expecially since *D. americana* molts about 13 times during larval growth (T. Fink, personal communication) and each molt skin is about 10-15% of the molting larva's dry weight.

Larval Respiration

Respiration rates were correlated positively with temperature (between 6° and 23°C), but inversely related to body size for any specific temperature (Fig. 2A). Regression coefficients of fitted equations did not vary significantly over the range of test temperatures (Analysis of Covariance: $F_{6,879} = 2.03$*, $P > 0.05$; Table 2). This suggests that the metabolism of small and large larvae responds similarly to changes in temperature. Sex did not appear to alter respiration rates significantly when males and females of similar weight were compared ($P > 0.05$).

For increasing stream temperatures, + 5°C above ambient, weight specific respiration increased for large animals but decreased for small animals (Figure 3B). This reflects a general

*Although this F value borders on significance at the 0.05 level, most of the variance in the analysis can be attributed to the 19-20.9°C data. Elimination of the 19-20.9°C data, which do not yield a significant regression anyway, results in more convincing statistics showing that the regression coefficients do not vary significantly (Analysis of Covalence: $F_{5\ 795} = 0.85$, $P > 0.5$).

tendency for regression coefficients to shift from negative values at ambient temperatures to zero (or even positive values) at ambient plus 5°C. These results do not suggest a form of overcompensation or acclimation by small larvae, but rather a type of metabolic collapse associated with stress, particularily among small individuals. The stress involved may be due to the short-term increase in temperature or other factors associated with the experimental design (e.g. food deprivation, build-up of waste materials in test vessels or prolonged exposure to artificial test conditions.

Larval Growth

Larval growth appeared continuous for *D. americana,* although seasonal differences in the amount of growth occurred (Table 3). The magnitude and efficiency of growth were greatest in non-winter months when stream temperatures exceeded 15°C. Females generally grew more efficiently and faster than males during all seasons. The daily caloric requirement per female larva was usually about twice the amount estimated for male larvae. Instantaneous growth rates appeared to be inversely related to body size and positively correlated with stream temperatures for both sexes. Energy lost from respiration greatly exceeded that used in net production (growth plus exuviae) for most time periods. Net production efficiency was highest for small animals growing at temperatures above 20°C. Maximum net production (cal/day) per individual occurs in spring for both sexes. The data do not show when maximum net production occurs for the sub population as a unit in Upper Three Runs because larval density estimates were not made.

Adult Emergence

Drift collections of larval molt skins which are shed during emergence suggest that metamorphosis was highly synchronous with 98% of the individuals emerging within a seven day period (Table 4). This synchrony of adult emergence probably results from an environmental cue stimulating the development of adult tissues within both small and large larvae almost simultaneously in late spring. Peters and Peters (1977) suggest that temperature is important in stimulating and/or suppressing metamorphosis. Our data neither refutes not supports this hypothesis.

Adult emergence in Upper Three Runs began at about 0530 hours (sunrise) and ended about 0615 hours. Observations support Peters and Peters (1977) contention that *D. americana* are sensitive to small changes in light intensity occurring just before sunrise. During the peak emergence period, nine flow-through microcosm streams were stocked with mature male and female larvae. Emergence among microcosms was synchronous and could be initiated earlier in the morning than normal by artificial illumination (Table 5). On June 6, two distinct adult emergences (at 0237 and 0533 hours) were obtained by artifically lighting the microcosms for one hour early in the morning, then darkening them again, and re-exposing the trays to sunrise.

The sex ratio at emergence in Upper Three Runs was skewed towards males for drifting larval skins, but towards females for drifting adults (Table 4). The skewed sex ratio for drifting adults has also been reported for other *D. americana* subpopulations (Peters and Peters, 1977). A higher proportion of drifting female adults may be an artifact, however, due to a failure of many adult males to return to the river after the mating swarm. This failure to return could result because: (1) susceptibility of adult males to predation (bats, birds, etc.) appears much greater than females since males must emerge, alight on terrestrial vegetation or river bank for molting into imago stage*, return to the river, and patrol up and down the river in search of females; (2) many males may not successfully complete the subimaginal molt and remain terrestrial.

The skewed sex ratio of drifting cast skins is difficult to rationalize. It is possible, however, that female skins sink after floating a shorter distance than males due to their heavier weight (avg. = 2.787 vs. 1.804 mg). We suggest, therefore, that skewed sex ratios based on drifting adults and larval skins may not be realistic, especially since larval collections made prior to emergence indicate a 1:1 sex ratio for mature larvae.

The mean weight of drifting larval skins appears to decrease for both sexes during the emergence period (Fig. 4). Since larval skin weight is correlated positively with the weight of the larva (and thus emerging adult), these data suggest that adult size of both sexes decreases through the

*Peters and Peters (1977) suggest that males may molt to the subimago while drifting downstream. We have not observed this nor have we obtained significant numbers of cast subimago skins in drift collections.

emergence period. Thus, the relative contribution of the last emerging females to population recruitment may be decreased considerably by: (1) reduced size and fecundity; and (2) decreased probability of mating successfully.

Adult Fecundity

The number of eggs per female averaged about 77 and ranged from 44 to 148 (Table 6). There was no significant difference between mature larvae and subimagoes when comparing the average number of eggs, weight per egg, and total egg weight. The quantity of nonreproductive tissue appeared higher in female larvae than adults (10.086 vs. 7.201 mg); but when the average weight of the cast larval skin (2.787 mg) is subtracted, the differences are negligible (7.299 vs. 7.201 mg). About 56% of the total dry weight of an emerging female is eggs. After ovipositing, adult females weigh about the same as adult males.

A highly significant linear relationship was observed for fecundity as a function of female dry weight (Fig. 5). Since there were no significant differences between the fecundity dry weight regressions for subimagoes and larvae (Analysis of Covariance: $F_{1,37} = 0.73$, $P > 0.05$), the two data sets were combined into a single regression. Although *D. americana* produces fewer eggs per female than has been reported for any other mayfly, individual eggs are at least 10 fold larger and heavier than reported for any other species.

The adaptive significance of a low fecundity-large egg reproductive strategy is unclear, but may be related more to the species trophic habit (i.e. predator) than to the shifting, sandy nature of the habitat.

Egg Quality

Biochemical analysis revealed that eggs were mainly protein (50.3%) and lipid (25.5%) by weight, with small amounts of carbohydrate (9.0%; Table 7). Although similar data on other aquatic species are not available for comparison, the results agree well with the limited published data for terrestrial insects (Singh and Sinha 1977). Assuming the non-lipid dry component is used primarily for synthesis rather than respiration and the average dry weight of one egg is 0.12 mg (see Table 6), the maximum dry weight of first instar larvae would be 0.08 mg.

DISCUSSION

Although a two year life cycle has been suggested for other species of burrowing mayflies (Bartholomae and Meier 1977, Hynes 1970), the two years are spent mainly in the larval stage. In contrast, *D. americana* seems to remain in the egg for most of the first year and as a larva the second. The adaptive significance of a ten month embryonic period is unclear, particularly since the substrate of Upper Three Runs is loose, shifting sand. One might deduce that an optimum strategy would be to spend as short a time as possible in the egg stage which seems very susceptible to physical disruption by the abrasive sand, to being covered with thick deposits of silt or sand, etc. The egg of *D. americana*, however, appears highly adapted to endure a prolonged embryonic period because: (1) eggs are big (relative to other mayflies) and contain a large supply of nutrient chemicals needed for embryonic development; (2) the chorion is thick and seems very resistant to mechanical breakage or puncturing; and (3) the intact chorion is not readily infected by aquatic fungi. The largeness of the egg may also be adaptive because it yields a large first instar larva. This assumes that larval mortality is inversely related to size and increased larval size expands the size range of potentially exploitable prey.

For most insect species, egg quantity and quality are generally considered to be highly adaptive characteristics which are related directly to the probability of the average animal to survive during the period between egg deposition one year and oviposition two years later. Our analyses of the size and number of eggs for *D. americana* suggests that individual mortality for eggs and larvae is probably extremely low relative to other mayfly species. Since egg mortality due to predation, fungal attack, physical disruption, etc. would seem to be correlated positively with the duration of the egg stage, one might expect strong selection against a prolonged egg diapause. Our results however, on the bioenergetics of larval development indicate that larvae hatching in June (as opposed to April) would never achieve sufficient growth by the following June to emerge with more than a few eggs if they could emerge at all. The intermediate sized larvae which fail to emerge with the remaining subpopulation of Upper Three Runs may result from a few individuals; each generation failing to undergo an embryonic diapause.

Although annual or seasonal production of *D. americana* was not estimated in Upper Three Runs, the resource requirements of individual larvae can be obtained from the energy budget. We estimate the minimum daily caloric intake (i. e. assimilation/day) of a male and female larva growing during the summer - fall - winter - spring period to be 0.88 - 1.46 - 1.35 - 2.68 and 1.77 - 2.65 - 2.13 - 5.49 cal/day, respectively. Assuming *D. americana* eat mainly chironomid larvae that average about 0.15 mg and have a caloric equivalent of about 5.0 cal/mg, the number of prey consumed per day would range from 1.2 to 3.5 for males and 2.3 to 7.3 for females depending on the season and stage of larval development.* Although the daily caloric intake per animal increases during larval development (except in winter), resource exploitation by the subpopulation as a whole may actually decrease or remain in a quasi-equilibrium throughout the year. To approach an

*These values may be quite conservative because in this analysis we did not include the energy expended in the actual search and capture of prey.

equilibrium, larval mortality would have to be about 75% during the growing season. Higher mortality, which seems reasonable, would decrease the amount of resource used by large larvae relative to earlier stages.

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TABLE 1

Caloric Content (Caloric Content (Calories per mg Ash Free Dry Weight) of Various Developmental Stages and Tissue Types for *Dolania americana*

Sample Type	*n*	*Mean*	*S.D.*	*Range*
Small larvae (♂ & ♀)	2	5.33	0.22	5.17-5.49
Intermediate larvae (♂ & ♀)	1	5.80	-	-
Mature ♂ larvae	3	5.68	0.29	5.38-6.08
♂ larval molt skin	3	5.09	0.32	4.90-5.48
♂ Subimago	3	5.86	0.14	5.72-6.00
♂ Subimago molt skin	1	4.63	-	-
Mature ♀ larvae	3	6.09	0.12	5.97-6.26
♀ larval molt skin	5	5.16	0.23	4.91-5.52
♀ Subimago (pre-oviposition)	3	6.03	0.30	5.77-6.36
♀ Subimago (post-oviposition)	2	5.55	0.01	5.54-5.55
Eggs	5	6.18	0.21	5.90-6.43

TABLE 2

Regression Equations (log Y = b log X + log a) for Weight Specific Metabolism (μl O_2 mg^{-1} h^{-1}) of *Dolania americana* at Various Temperature Intervals

Temperature °C	*b Y X*	*log a*	*Degrees of freedom*	*Level of significance*
6-7.9	-0.316	0.074	1,022	0.002
10-12.9	-0.371	0.380	1.093	< 0.001
13-15.9	-0.346	0.592	1.229	< 0.001
16-18.9	-0.266	0.590	1.269	< 0.001
19-20.9	-0.087	0.499	1,085	0.112
21-22.9	-0.238	0.721	1,158	< 0.001
23-23.9	-0.284	1.004	1.030	0.024

TABLE 3. Partial Energy Budget for the Fastest Growing Male and Female Larvae of *Dolania americana* in Upper Three Runs*

MALE LARVAE

°C			*Mg*		*Total calories per median size larva*				*%*	$mg\ mg^{-1}\ d^{-1}$
Date	*Average Temp.*	*No. Days*	*Average Weight (s.d.)*	*Median Weight*	*Growth*	*Respiration*	*Exuvia*	*Assimilation*	*Net Production Efficiency*	*Instantaneous Growth Rate*
June 7			0.314 (0.101)							
	20.8	15		0.354	0.419	2.127	0.291	2.837	24.9	0.015
June 22			0.395 (0.169)							
	21.1	15		0.529	1.436	5.625	0.414	7.475	24.7	0.034
July 7			0.663 (0.324)							
	21.7	15		0.870	2.205	8.221	0.577	11.003	25.2	0.032
July 22			1.077 (0.441)							
	23.0	31		1.334	2.770	33.598	1.999	38.367	12.4	0.013
Aug. 22			1.591 (0.988)							
	20.8	31		2.155	6.212	28.031	1.687	35.980	22.0	0.017
Sept. 22			2.721 (1.563)							
June 7 - Sept. 22	21.6	107		1.517	13.042	77.602	4.968	95.612	18.8	0.020
Sept. 22			2.721 (1.563)							
	20.4	15		3.180	4.817	15.740	2.294	22.851	31.1	0.019
Oct. 7			3.641 (1.822)							
	17.3	15		3.890	2.509	18.341	0.000	20.850	12.0	0.008
Oct. 22			4.139 (1.855)							
	15.4	16		4.321	1.656	17.688	3.072	22.419	21.1	0.005
Nov. 7			4.504 (2.463)							
	14.4	30		5.129	6.308	39.543	0.000	45.851	13.7	0.008
Dec. 7			5.755 (2.979)							
Sept. 22 - Dec. 7	16.4	76		4.238	15.293	91.312	5.366	111.971	18.4	0.009
Dec. 7			5.755 (2.979)							
	12.9	62		6.234	5.024	79.015	4.441	88.425	10.7	0.003
Feb. 7			6.893 (3.501)							
	12.1	28		7.610	6.179	27.783	0.000	33.957	18.2	0.006
March 7			8.328 (4.289)							
Dec. 7 - March 7	12.7	90		7.038	11.203	106.793	4.441	122.434	12.7	0.004
March 7			8.328 (4.289)							
	16.1	46		8.493	1.172	94.761	6.292	102.225	7.3	0.001
April 22			8.659 (6.155)							
	18.4	30		9.913	11.895	81.677	8.261	101.833	19.7	0.008
May 22			11.168 (6.784)							
March 7 - May 22		76		9.748	13.067	176.438	14.554	204.058	18.3	0.004

* Net production efficiency (%) was obtained by dividing the sum of growth and exuvia energy by total assimilation for a given period. See text for description of other parameters.

TABLE 3. (Continued)
Partial Energy Budget for the Fastest Growing Male and Female Larvae of *Dolania americana* in Upper Three Runs*

FEMALE LARVAE

°C			Mg		Total calories per median size larva				%	mg mg^{-1} d^{-1}
Date	Average Temp.	No. Days	Average Weight (s.d.)	Median Weight	Growth	Respiration	Exuvia	Assimilation	Net Production Efficiency	Instantaneous Growth Rate
June 7			0.574 (0.018)							
	20.8	15		0.677	1.084	3.844	0.503	5.431	29.2	0.020
June 22			0.781 (0.079)							
	21.1	15		1.155	4.038	10.205	0.740	14.983	31.9	0.044
July 7			1.530 (0.090)							
	21.7	15		1.739	2.184	13.937	1.110	17.231	19.1	0.016
July 22			1.948 (0.112)							
	23.0	31		3.124	12.862	61.269	3.997	78.129	21.5	0.025
Aug. 22			4.300 (0.360)							
	20.8	31		5.333	11.508	59.802	3.405	74.715	19.9	0.012
Sept. 22			6.366 (0.550)							
June 7 - Sept. 22	21.6	107			31.676	149.057	9.755	190.488	21.7	0.022
Sept. 22			6.366 (0.550)							
	20.4	15		7.366	10.938	33.951	0.000	44.889	24.3	0.018
Oct. 7			8.366 (1.101)							
	17.3	15		8.499	1.468	32.533	4.885	38.886	16.3	0.002
Oct. 22			8.633 (1.106)							
	15.4	16		9.616	10.855	31.814	0.000	42.669	25.4	0.012
Nov. 7			10.600 (1.757)							
	14.4	30		10.933	3.664	64.867	7.402	75.933	14.5	0.002
Dec. 7			11.266 (1.193)							
Sept. 22 - Dec. 7	16.4	76			26.925	163.165	12.287	202.377	19.4	0.007
Dec. 7			11.266 (1.193)							
	12.9	62		13.649	2.640	131.984	10.363	144.987	8.9	<0.001
Feb. 7			16.033 (1.877)							
	12.1	28		16.249	2.540	44.901	0.000	47.441	5.3	<0.001
March 7			16.466 (2.369)							
Dec. 7 March 7	12.7	90			5.180	176.885	10.363	192.428	8.1	0.004
March 7			16.466 (2.369)							
	16.1	46		19.999	41.907	175.486	0.000	217.393	19.3	0.007
April 22			23.533 (2.357)							
	18.4	30		24.364	9.762	172.289	17.910	199.961	13.8	0.002
May 22			25.196 (0.600)							
March 7 - May 22		76			51.669	347.775	17.910	417.354	16.5	0.006

* Net production efficiency (%) was obtained by dividing the sum of growth and exuvia energy by total assimilation for a given period. See text for description of other parameters.

TABLE 4

Number and Sexual Composition of Cast Larvae Molt Skins and Dead Adults Collected in Drift Nets on the Upper Three Runs. Net #1 - Near Right Bank; Net #2 = Mid-Channel

	Larval Skins					*Adults*			
	Net #1		*Net #2*		*Net #2*	*Net #1*		*Net #2*	
Date	*Male*	*Female*	*Male*	*Female*	*Cumulative %*	*Male*	*Female*	*Male*	*Female*
6-3-78	18	4	28	15	1.5	-	-	-	-
6-4-78	47	45	279	187	17.8	-	-	51	60
6-5-78	1	-	30	-	18.9	-	-	1	-
6-6-78	290	240	329	264	39.7	-	-	45	61
6-7-78	(discontinued)		5	8	40.2	(discontinued)		-	-
6-8-78			821	626	91.1			160	199
6-9-78			121	93	98.6			12	18
6-10-78			5	4	98.9			-	-
6-11-78			7	11	99.5			-	-
6-12-78			2	-	99.6			-	-
6-13-78			4	2	99.8			1	-
6-14-78			3	1	99.9			-	-
6-15-78			-	-				-	-
6-16-78			-	-				-	-
6-19-78			1	-	100.0			-	-
Totals	356	289	1635	1211		-	-	269	338

TABLE 5.

Influence of Artificial and Natural Lighting on the Onset of Diel Emergence for *Dolania americana*

	Laboratory Trays		*Upper Three Runs*	
Date	*Lights*	*First Emergence*	*Sunrise*	*First Emergence*
6-3-78	0400	0401	0518	0534
6-4-78	0330	0333	0518	0540
6-5-78	0416	0417	0518	0536
6-6-78	0230(0530)	0233(0533)	0518	0542

TABLE 6

Dry Weight (mg) and Fecundity of *Dolania americana* Females Collected from Upper Three Runs from June 3 through June 6

Animal Number	*Stage*	*Non-Reproductive Tissue Weight*	*Egg Weight*	*Total Weight*	*Number of Eggs*	*Weight per Egg*
1	Subimago	8.696	14.684	23.380	102	0.143
2	Subimago	8.228	9.540	17.771	76	0.125
3	Subimago	5.032	7.740	12.770	65	0.119
4	Subimago	9.668	8.130	17.798	60	0.135
5	Subimago	6.420	5.512	11.932	47	0.117
6	Subimago	7.480	7.412	14.892	70	0.106
7	Subimago	5.768	6.888	12.666	62	0.111
8	Subimago	7.836	9.816	17.652	84	0.117
9	Subimago	6.788	12.310	19.098	100	0.123
10	Subimago	6.060	10.524	16.584	82	0.128
11	Subimago	5.210	7.736	12.946	66	0.117
12	Subimago	7.128	12.052	19.180	99	0.122
13	Subimago	5.772	8.472	14.244	66	0.128
14	Subimago	8.190	6.796	14.986	50	0.136
15	Subimago	6.484	13.572	20.066	123	0.110
16	Subimago	5.968	8.868	14.840	70	0.127
17	Subimago	7.540	6.080	13.620	52	0.117
18	Subimago	11.356	9.244	20.600	76	0.122
19	Larva	13.300	10.824	24.124	93	0.116
20	Larva	9.988	9.802	19.790	85	0.115
21	Larva	10.516	7.216	17.732	56	0.129
22	Larva	11.652	8.964	20.616	84	0.107
23	Larva	10.040	8.248	18.288	70	0.118
24	Larva	14.404	12.992	27.396	104	0.125
25	Larva	15.184	19.252	34.436	148	0.130
26	Larva	9.336	9.084	18.420	72	0.126
27	Larva	11.108	11.388	22.496	96	0.119
28	Larva	10.964	9.132	20.096	68	0.134
29	Larva	11.056	9.936	20.992	89	0.112
30	Larva	9.804	9.760	19.564	79	0.124
31	Larva	7.968	9.522	17.490	63	0.151
32	Larva	11.600	12.628	24.228	102	0.123
33	Larva	8.288	9.332	17.620	74	0.126
34	Larva	6.564	8.500	15.064	77	0.110
35	Larva	12.698	14.868	27.566	122	0.121
36	Larva	8.248	4.484	12.732	44	0.101
37	Larva	7.592	6.032	13.624	56	0.107
38	Larva	8.978	7.068	16.046	57	0.124
39	Larva	7.312	6.050	13.362	54	0.112
40	Larva	5.400	5.688	11.088	50	0.113

Subimago: Avg.	7.201	9.182	16.390	75	0.122
(Std. dev.)	(1.628)	(2.580)	(3.238)	(20)	(0.009)
Nymph: Avg.	10.086	9.581	19.671	79	0.120
(Std. dev.)	(2.489)	(3.304)	(5.521)	(25)	(0.011)

TABLE 7

Chemical Composition of *D. americana* Eggs

Nutrient Chemical	*n*	*Mean %*	*Range*
Carbohydrate	5	9.0	7.6-12.8
Lipid	2	25.5	25.5-25.6
Protein	11	50.3	47.6-54.3

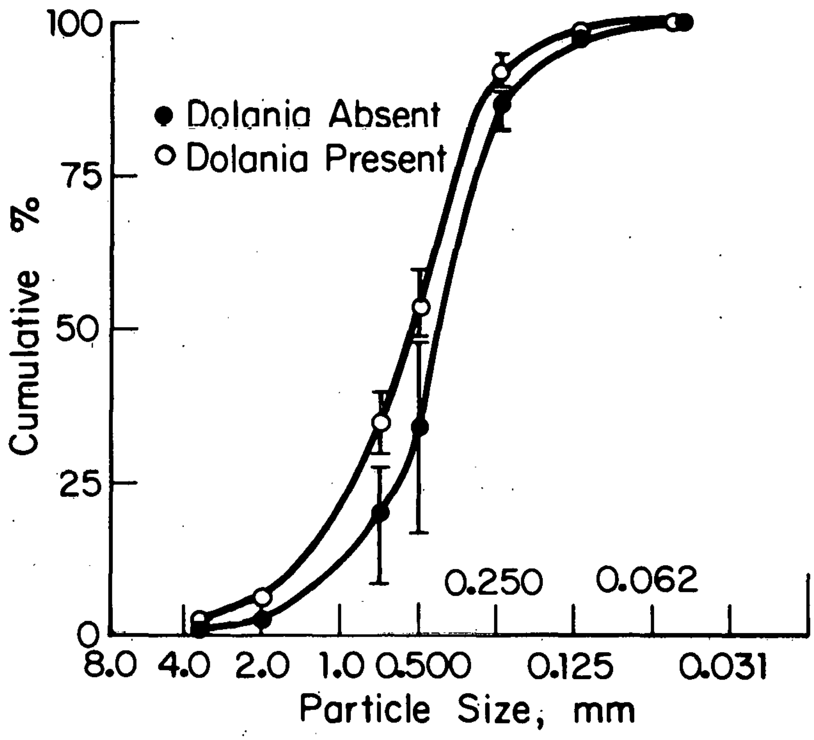

FIGURE 1. Size Distribution of Sand From Stream Transect Samples

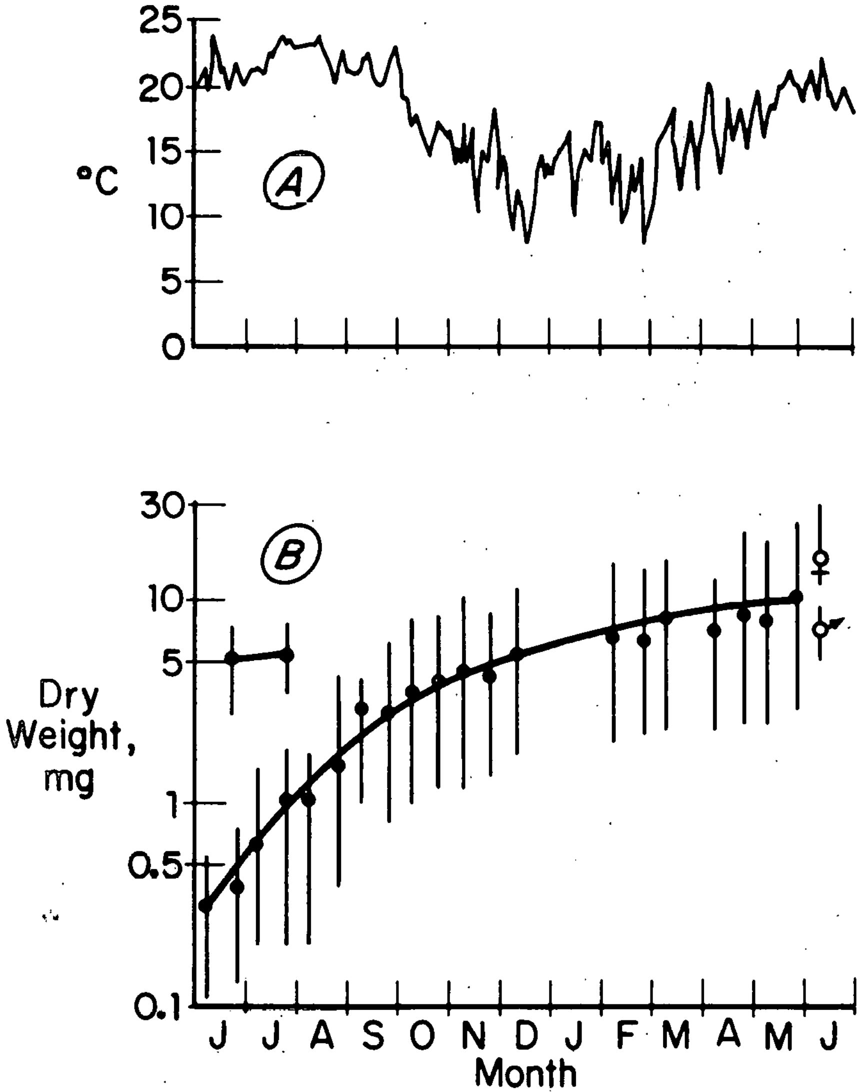

FIGURE 2. (A)-Daily temperature recordings for Upper Three Runs from June 1973-June 1974. (B)-Larval growth of *Dolania americana* in Upper Three Runs. Solid dots = mean weight of each collection; vertical lines indicate the range. Male and female signs designate the mean weight and range of male and female subimagos, respectively. Line drawn through sample means is described by: y = 0.027x - 0.244 where y is average weight and x is number of days since June 1.

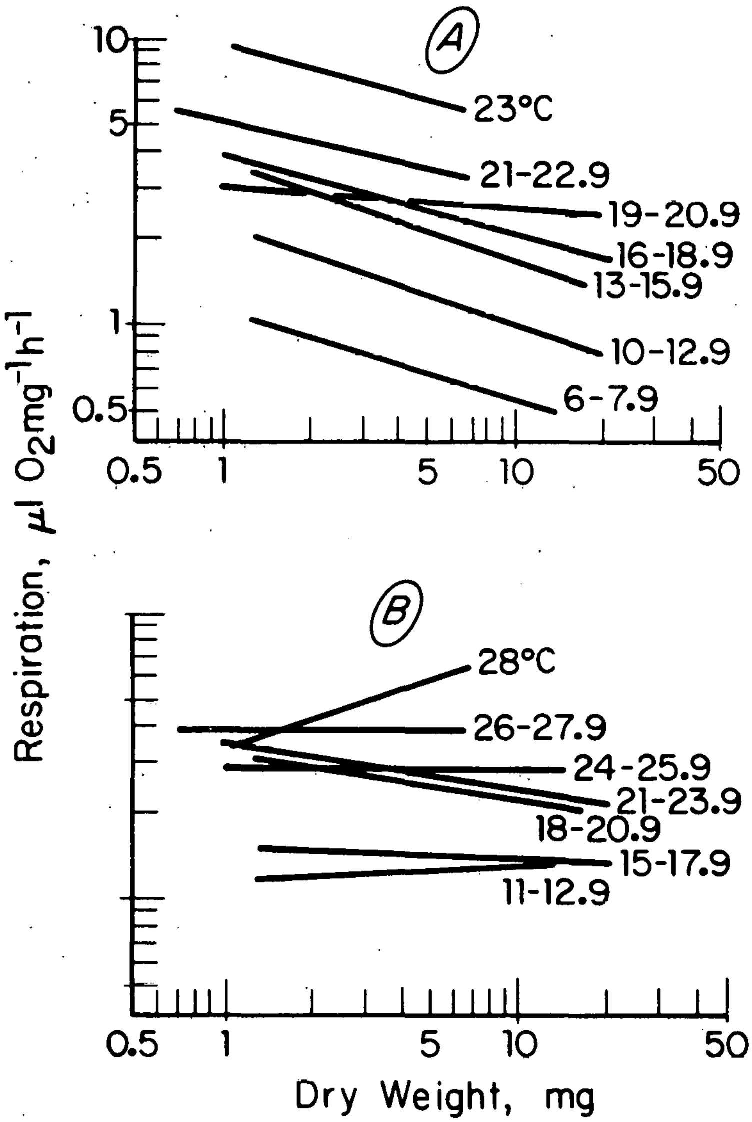

FIGURE 3. Weight Specific Respiration Rate for *Dolania americana* Larvae. Larvae were collected, placed in respiration vessels at ambient stream temperatures, and oxygen uptake measured (Figure 2A); larvae were then gradually acclimated over a 48 hour period to ambient +5°C before taking further measurements (Figure 2B). Two or more experiments within a given temperature range were combined for the regression analysis.

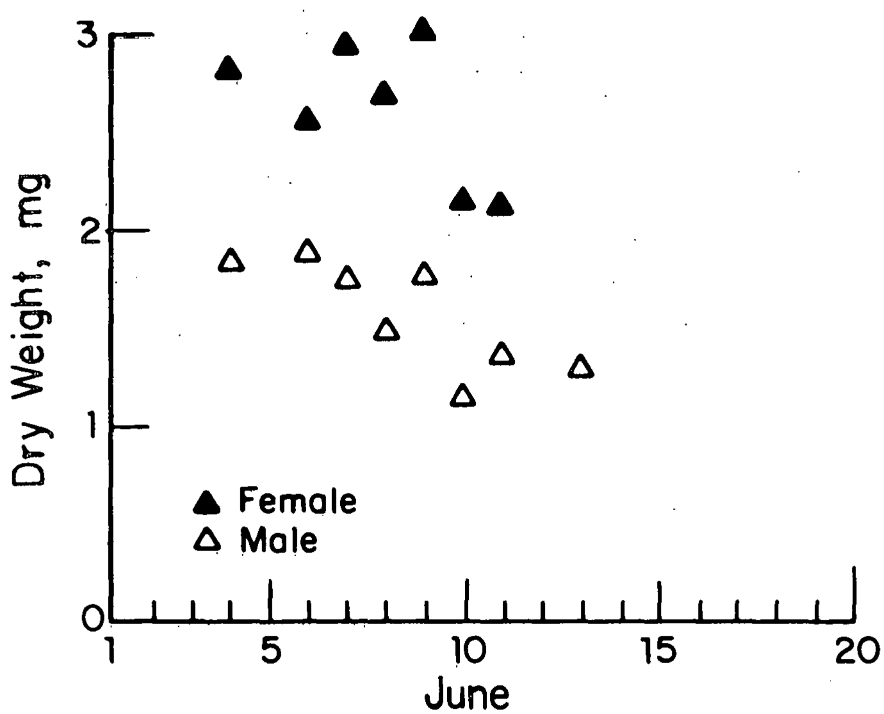

FIGURE 4. Average weight of male (△) and female (▲) larval molt skins collected from Upper Three Runs in drift nets during the adult emergence period. Molt skins were counted and weighed collectively for each date; the variance of each mean is unknown.

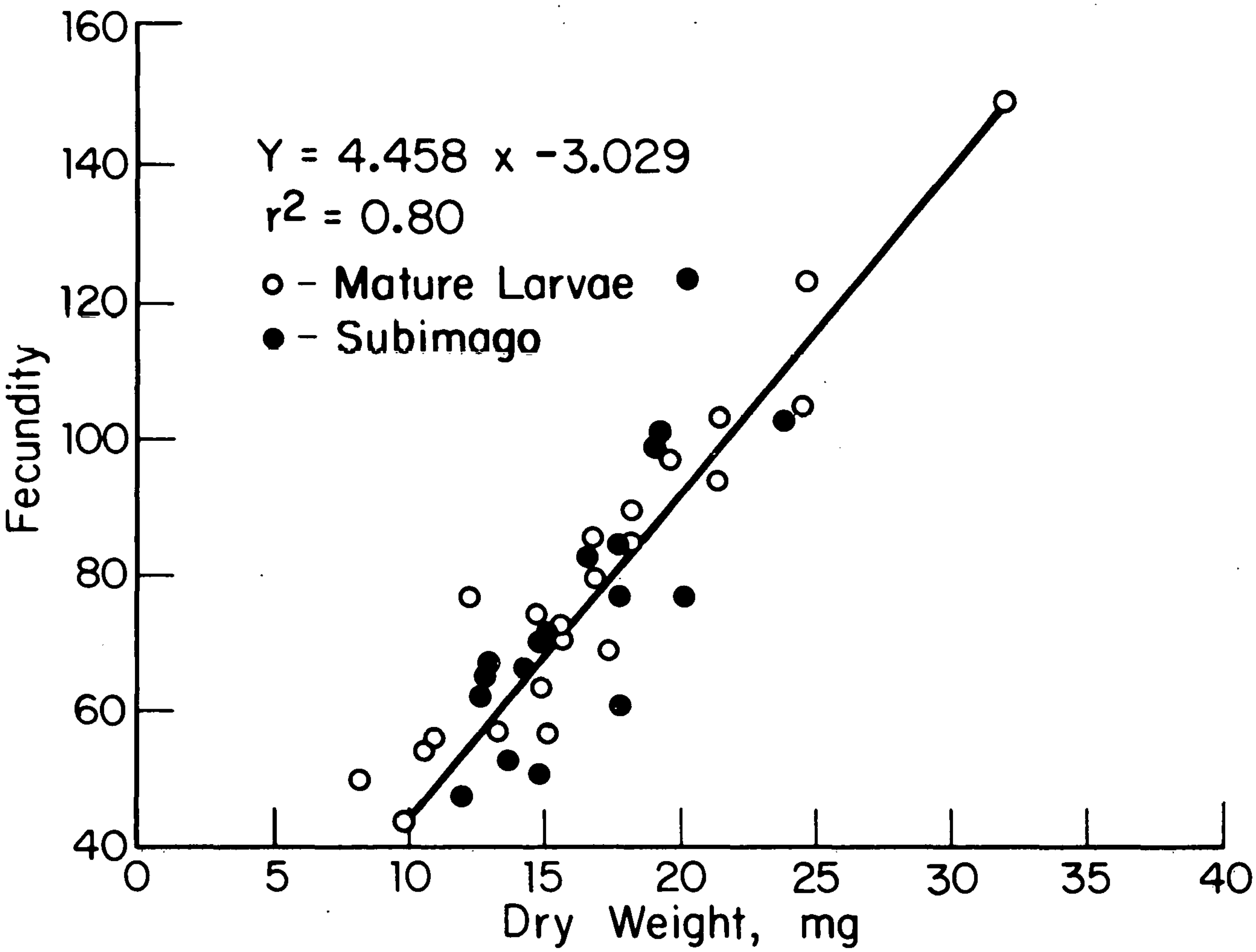

FIGURE 5. Fecundity of *Dolania americana* as a function of individual dry weight. Open circles = mature larvae; closed circles = subimago.