THE LIFE CYCLE OF THE MAYFLY *STENACRON INTERPUNCTATUM* (EPHEMEROPTERA: HEPTAGENIIDAE)[1]

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ABSTRACT

Larval growth and development of *Stenacron interpunctatum* was studied for a one year period at Wildcat Creek, Indiana. Analysis of developmental stages and size classes revealed three broods at different degrees of maturation at any one time of year. Broods emerged in early spring, mid-summer, and late summer-early fall, respectively; the former two overwintering in different stages of larval development, and the latter completing development in one growing season in warm temperatures and maturing at relatively smaller sizes. The population possessed a complex life cycle ranging from one generation per year to three generations every two years. General sampling over three growing seasons and controlled laboratory rearing support the conclusions.

Stenacron interpunctatum (Say) is often an abundant mayfly in streams and rivers in the eastern half of North America. Larvae graze on the undersides of rocks and large detritus during the daytime, and range freely over the upper surface of substrate at night (Wodsedalek, 1912; Lyman, 1945). The species may be an important fish food (Caucci and Nastasi, 1975), and may be useful in water quality assessment (Lewis, 1974).

Needham, et al. (1935) described postembryonic development in the laboratory, but no field data have previously been available. We describe the life cycle of *S. interpunctatum* primarily on the basis of its growth and development in a natural environment.

METHODS AND MATERIALS

Field studies were conducted from March, 1972, through September, 1974, on Wildcat Creek, a river in west central Indiana which drains a watershed of approximately 800 sq. mi. This river flows westerly and lies entirely within the Tipton Till Plain, emptying into the Wabash River at Lafayette. Regular benthic sampling was undertaken on its north fork upstream from the Kokomo Reservoir at Jerome, Howard County. Mean monthly discharge for the north fork ranges from less than 100 cfs in September and October to more than 1300 cfs during January (U.S.G.S. data).

Field rearing and collecting techniques were after Provonsha and McCafferty (1975). Laboratory rearing methods were after Huff and McCafferty (1974). Larvae were maintained at 22-24°C during transport and in the laboratory.

We studied larval development by regular, periodic sampling with artificial substrate samplers (Beak, et al., 1973), consisting of limestone filled 9X9X9 inch wire baskets left in the river for at least four weeks to ensure adequate colonization (Weber, 1973). Nine samples were taken between 21 July, 1973 and 13 July, 1974 (Fig. 1). Samplers were retrieved under water by capturing the entire rock basket in a canvas bag. Contents were washed, fixed in Pample's solution, and after sorting, transferred to 70% ethanol. A total of 531 larvae were sampled, measured, and categorized into developmental stages and size classes.

Since the number of instars in mayflies varies and the relationships of size and physiological development possibly vary with environmental conditions, developmental

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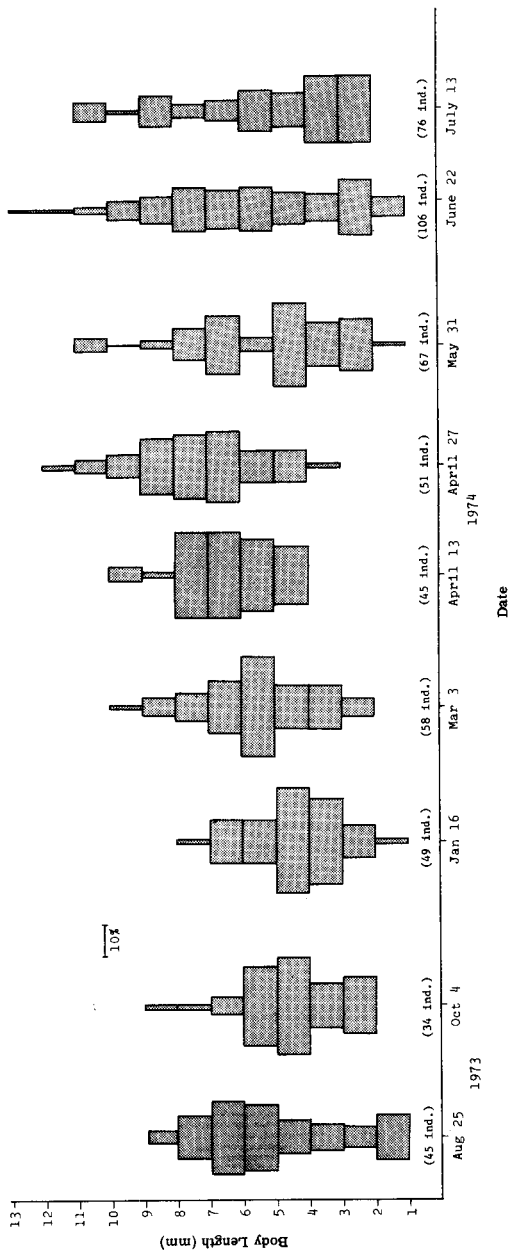

Fig. 1. Percent composition of *S. interpunctatum* larvae in millimeter size classes.

stages advocated by Pleskot (1962) rather than instars were used to determine larval development. The stages as defined below are somewhat arbitrary but are consistent and comparatively useful in ascertaining the relative degree of development toward maturation of the larvae. Instars were virtually impossible to determine from field samples. Since total length has previously been a useful measurement when sexes were treated separately (Clifford, 1970a, 1970b), body lengths exclusive of caudal filaments and antennae were measured and correlated with development.

Criteria for developmental stage classification were as follows: Stage I larvae possessed either thread-like gills or no gills at all; Stage II larvae possessed thickened gills but no wing pads; Stage III larvae possessed wing pads but the mesothoracic wing pads did not cover the metathoracic wing pads; Stage IV larvae possessed mesothoracic wing pads covering the metathoracic wing pads but not reaching beyond abdominal segment 1; Stage V larvae possessed longer wing pads than the latter but shorter than the distance between the pads and not extended beyond abdominal segment 2; Stage VI larvae possessed mesothoracic wing pads longer than the distance between them and extended beyond abdominal segment 2; Stage VII larvae possessed dark wing pads indicative of impending emergence. The presence or absence of developing male genitalia were used for sexing larvae. Sex could not be confidently determined for Stages I, II, and sometimes III.

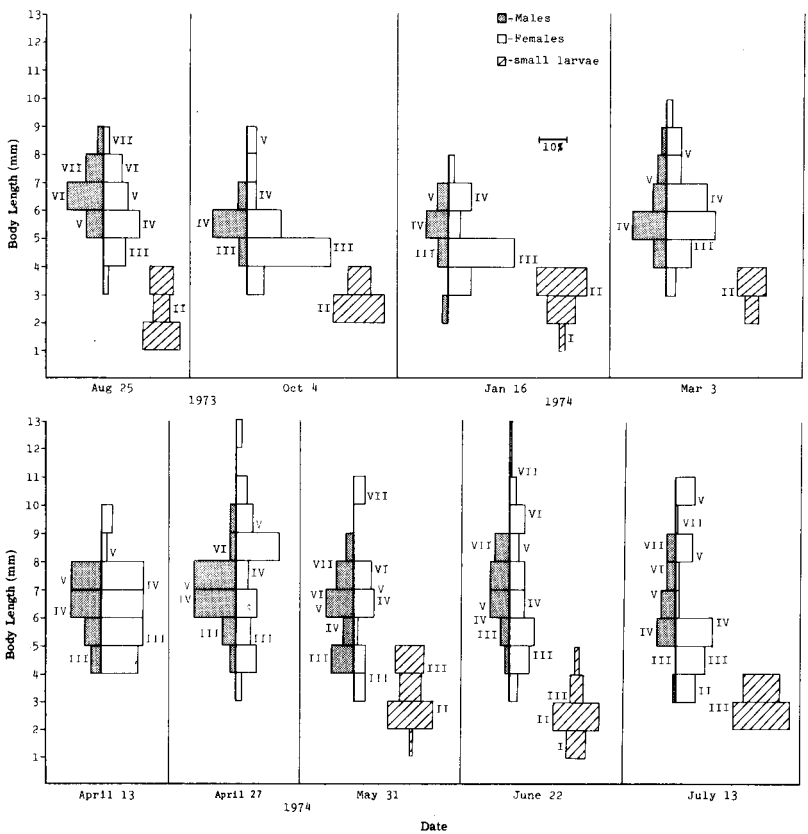

Fig. 2. Percent composition of male and female *S. interpunctatum* larvae in size classes (with developmental stages indicated at their mean size).

RESULTS AND DISCUSSION

Field data are summarized in Figures 1-5. There was no overall increase in size of larvae sampled from January through April (Fig. 2). Following adult emergence which began in May, the size class distribution varied considerably through July. Size became more evenly distributed as the emergence season progressed, especially in June and July.

When males and females were differentiated (Fig. 2), the distribution of size classes became skewed to varying degrees. The largest larvae were females. By indicating (Fig. 2) the distribution of developmental stages for each sex at points representing their mean size, it became apparent that females were also larger for each stage and exhibited a greater difference between successive stages. It was noted also that the mean size of mature larvae in May, June, and July, was greater than in late August. These relationships between sexes, and the size differences of mature larvae over the emergence period, have been reported for other aquatic insects (Hynes, 1970); and in mayflies somewhat similar size distributions have been found for *Leptophlebia cupida* (Clifford, 1970b), two species of *Epeorus* (Ide, 1935), and *Hexagenia bilineata* (Fremling, 1973).

Outlined areas (Figs. 3 and 4) are superimposed on the temporal distribution of developmental stages (including adults) and approximate three developing broods inferred from the data as follows. A group of very small larvae were found in the fall and winter, and represent progeny of adults emerging late in the emergence season. This brood (designated A), after overwintering as early developmental stages, began development at a rapid rate throughout spring and part of summer and emerged in late June, July, and early August. Another brood (B) began its larval development in June and early July, overwintered as Stage IV females and Stages IV to V males, continued larval development through the spring, and emerged from mid-May until July. A third brood (C) began larval development in May. These larvae developed rapidly throughout the summer and emerged

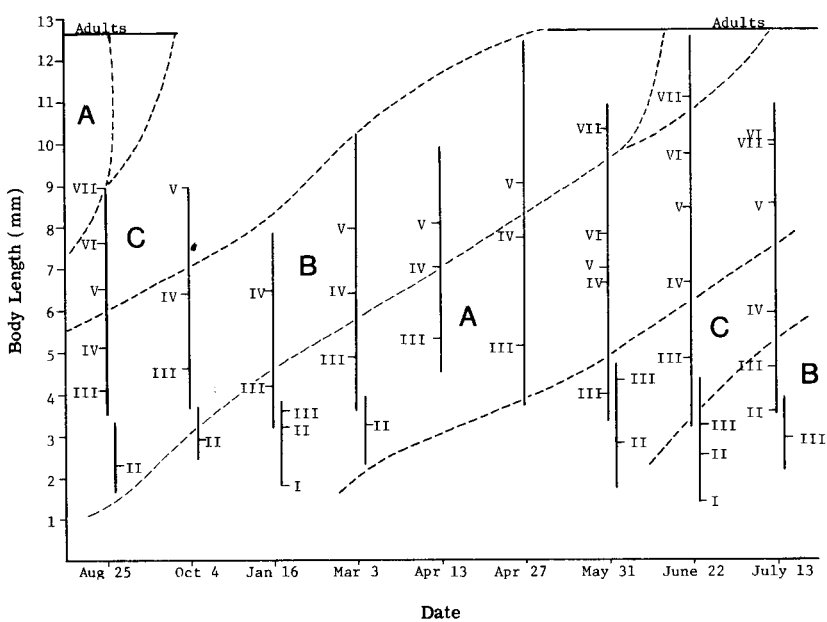

Fig. 3. Distribution of mean size of developmental stages of female *S. interpunctatum* larvae (with diagonal areas representing developing broods).

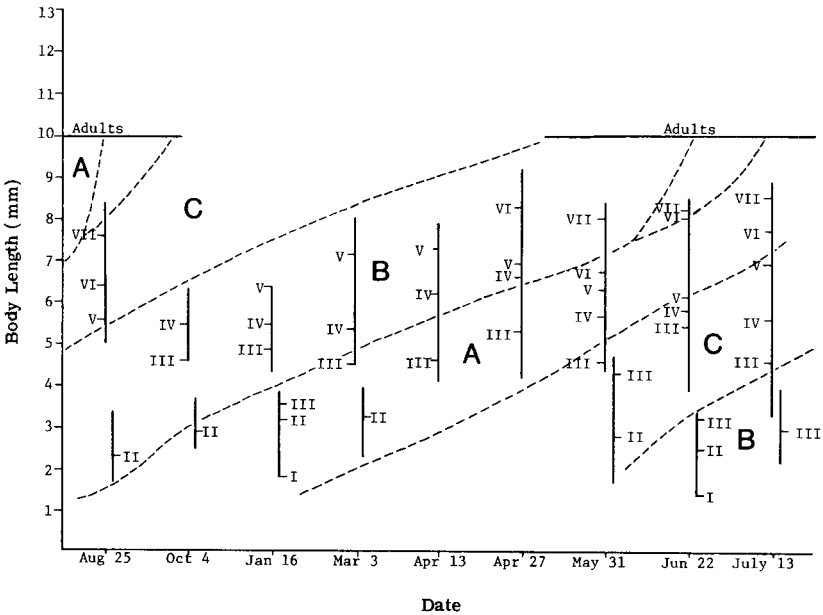

Fig. 4. Distribution of mean size of developmental stages of male *S. interpunctatum* larvae (with diagonal areas representing developing broods).

in late August and September as relatively small adults. We assume the above sequences to be similar from year to year. The fit between the last sample in July, 1974, and the first sample in August, 1973, would seem to substantiate this. Little growth apparently took place during periods of depressed winter temperatures, and from October through April no mature or Stage VI larvae were found. This population evidently does not overwinter as well developed larvae.

Broods A, B, and C were compared (Table 1) in terms of the mean time of development for Stage II to Stage VII larvae, the mean monthly water temperature for the period of this development, and the mean size of male and female Stage VII larvae. Brood C larvae were exposed to a longer continual period of relatively warmer water, and completed development in much less time than the other broods. Also, mature larvae were smaller, the females markedly so, in these "fast developers."

When reared from Stage II or III larvae at 22-24°C, individuals were consistently smaller than field samples as mature larvae and adults, and completed this development in 38-71 days. Fremling (1967 and personal communication) found that he could rear *Hexagenia bilineata* from eggs to adults in 79 days, and that these adults were always relatively very small.

Adult females were maintained in our laboratory for periods up to eight days; no data are available on adult longevity in the field. Needham, et al. (1935) reported eggs of *S. interpunctatum* hatching 13 to 15 days from time of oviposition in the laboratory. Ide (1935) found that eggs of three females of *S. interpunctatum*, all deposited at the same time and maintained under identical laboratory conditions, continued to hatch over a period of six weeks. Incubation time from 7 to 32 days at 18°C was recorded in our laboratory. Incubation time in the field is unknown.

The field and laboratory data suggest a complex life cycle (Fig. 5): The presence of three generations every two years at Wildcat Creek is indicated by Figures 3 and 4 since adults of Brood A would give rise to Brood B which subsequently overwinters; and Brood B would give rise to Brood C; and Brood C would give rise, at least in part, to Brood A

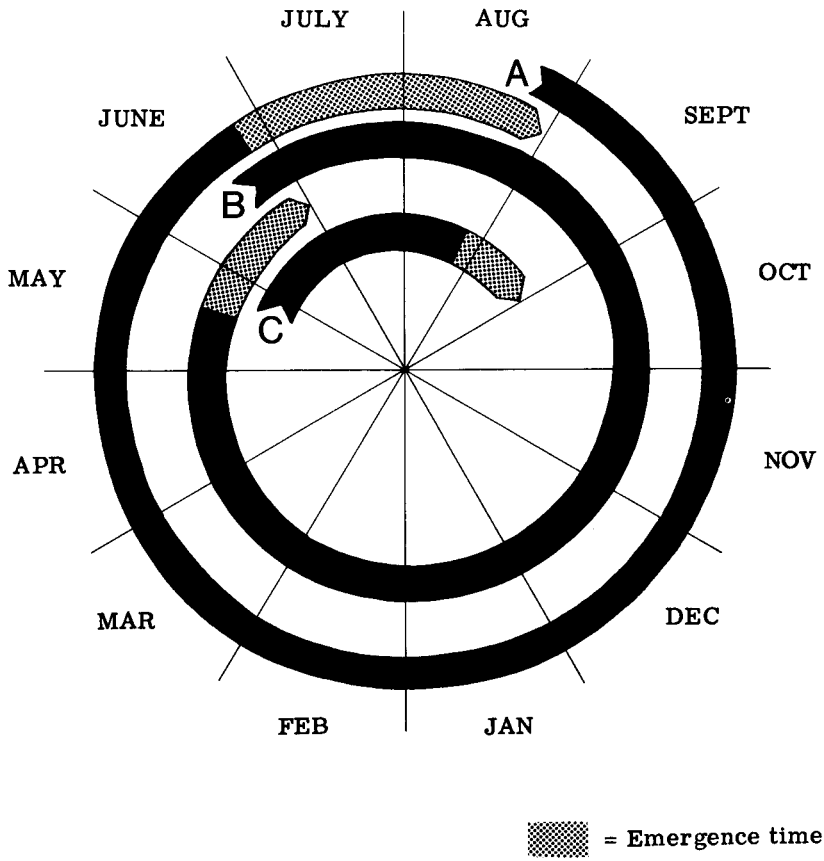

Fig. 5. Diagrammatic representation of the life cycle of *S. interpunctatum* at Wildcat Cr., Indiana.

Table 1. A Comparison of Developing Larval Broods of *S. interpunctatum* in Wildcat Creek, Indiana.

Brood	$\bar{X}$ Length of Development (Stage II to Stage VII)	$\bar{X}$ Monthly Water Temperature During Development (Range)	$\bar{X}$ Size ♂ Stage VII	$\bar{X}$ Size ♀ Stage VII
A	272 days	10.2 C (0.8-24.5 C)	8.33 mm	10.24 mm
B	355 days	11.9 C (0.8-24.5 C)	8.06 mm	10.66 mm
C	86 days	21.7 C (7.6-24.5 C)	7.56 mm	8.85 mm

which subsequently overwinters, etc. This is the type "D" life cycle of Landa (1968) and is similar to that described for *Baetis vagans* in New York by Murphy (1922). This classification may not be entirely satisfactory, however, because generation time estimation is complicated by factors of variable adult life span, length of egg incubation, and possible differential larval growth within broods. For example, it appears that the later maturing individuals of a brood (Figs. 3, 4, and 5) may also have some potential to give rise to individuals of the same brood the next year (see especially brood C). Also, there is evidently some potential for crossmating between broods (see adult overlap in Figs. 3, 4, and 5).

In conclusion, within the same geographic population there are population components contributing to three generations every two years, and concurrently, population components potentially contributing to one generation per year. This complex, interwoven life cycle would apparently guarantee considerable genetic mixing within the population over time. Any resource partitioning by different developmental stages being distributed in time throughout the year would theoretically reduce intraspecific competition. If length of brood development and water temperature are correlated, as data suggest, then the life cycle of *S. interpunctatum* populations may be expected to vary somewhat with climate and stream temperature regime within the broad latitudinal range of the species.

An interesting and potentially biosystematically significant by-product of this investigation was the preliminary observation that adult color variation is also apparently affected by length of brood development. This would tend to suggest that the previous use of historically typological color variants in recognizing several species or sympatric subspecies for *S. interpunctatum* is invalid. It also would help explain the preponderance of intermediate or "non-typical" color variants present in this and other North American populations of the species. We hope to test these hypotheses with controlled rearings and quantification of adult variability.

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