Effects of Developmental Thermal Regimes on Two Mayfly Species and Their Taxonomic Interpretation[1]

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Ann. Entomol. Soc. Am. 77: 69–87 (1984)

ABSTRACT *Hexagenia limbata* and *Stenacron interpunctatum* were studied to determine the source and significance of intraspecific variabiltity. Life cycles at two study sites in Indiana were complex, with at least two cohorts each. Maturation times determined in the laboratory for test groups of single populations decreased with warmer experimental temperature gradients (escalating developmental thermal regimes of 6 to 26°C, 12 to 26°C, 18 to 26°C, and 24 to 26°C, respectively). Degree-day accumulation was important for *H. limbata* emergence at the two colder regimes, whereas a minimum water temperature of 18°C was necessary for *S. interpunctatum* emergence. Reared adults varied in those phenotypic characters previously thought to have delimited multiple species or subspecies. Variability was either significantly correlated with developmental thermal regime or temperature independent and apparently individual. Size, intensity of color, and maculation were temperature dependent and increased as maturation time increased. Museum specimens from throughout the species ranges reflect the relationship between color types and thermal regimes. We conclude that subspecific classifications of both species are not tenable, and variants, for the most part, represent ecophenotypes.

THE MAYFLIES *Hexagenia limbata* (Serville), a burrowing form in the family Ephemeridae, and *Stenacron interpunctatum* (Say), a flatheaded form in the family Heptageniidae, have a number of associated features in common. Both are among the most commonly taken, variable, and relatively widespread of North American mayflies. Investigators have reported complex life cycles for both (Neave 1932, Hunt 1953, Hudson and Swanson 1972, McCafferty and Huff 1978). Each has historically been classified as several species and most recently as several subspecies (Spieth 1941, 1947, Edmunds et al. 1975). McCafferty (1975) summarized the complex nomenclatural history of *H. limbata*, and Spieth (1947), Lewis (1974), and Jensen (1974) reviewed that of *S. interpunctatum*. These species are also similar in that subspecific interpretations have become increasingly difficult to accommodate because of a confusing array of atypical or intermediate forms being discovered (Spieth 1941, 1947, McCafferty 1975, Lehmkuhl 1980) and seasonal variability being found within single geographic populations (Neave 1932, Ide 1935, McCafferty and Huff 1978, Edmunds, personal communication).

A large number of original descriptions of North American mayflies (most around the turn of this century) were made without benefit of large series, associated metamorphic stages, or adequate comparative material from broad geographic areas. Thus, many species descriptions were inevitably typological. The lack of a clear understanding of intraspecific variation, as has been shown in certain well studied genera, can result in inflated species numbers and taxonomic anomalies (Bednarik and McCafferty 1979, Morihara and McCafferty 1979, Kondratieff and Voshell, personal communication). Typological subspecies could, of course, lead to analogous problems.

Diagnoses and keys for distinguishing *H. limbata* and *S. interpunctatum* subspecies have involved characters of body and structural size, color, and maculation patterns of adults (Traver 1931, 1935, Spieth 1941, 1947, Burks 1953). Demonstrations that such characters sometimes vary with postembryological developmental history (Spieth 1938, Kondratieff and Voshell, personal communication) make their taxonomic reliability questionable.

A consideration of all the above, together with our long experienced taxonomic difficulties with *H. limbata* and *S. interpunctatum*, led to the hypothesis that many of the characters used to distinguish subspecies (species of some) were environmentally controlled and that described variants were essentially ecophenotypes. These differences could be manifested as a result of different developmental regimes at different locations and as a result of different cohorts at single locations being subject to different seasonal regimes. Temperature could be the controlling factor, particularly because developmental temperatures have been shown to affect adult size in several mayflies (Ide 1940, Clifford and Boerger 1974, Sweeney and Vannote 1978, Vannote and Sweeney 1980).

Phenotypic variation, with the exception of body length, has not been quantitatively correlated with

[1] Purdue Agric. Exp. Stn. Journal No. 9426.

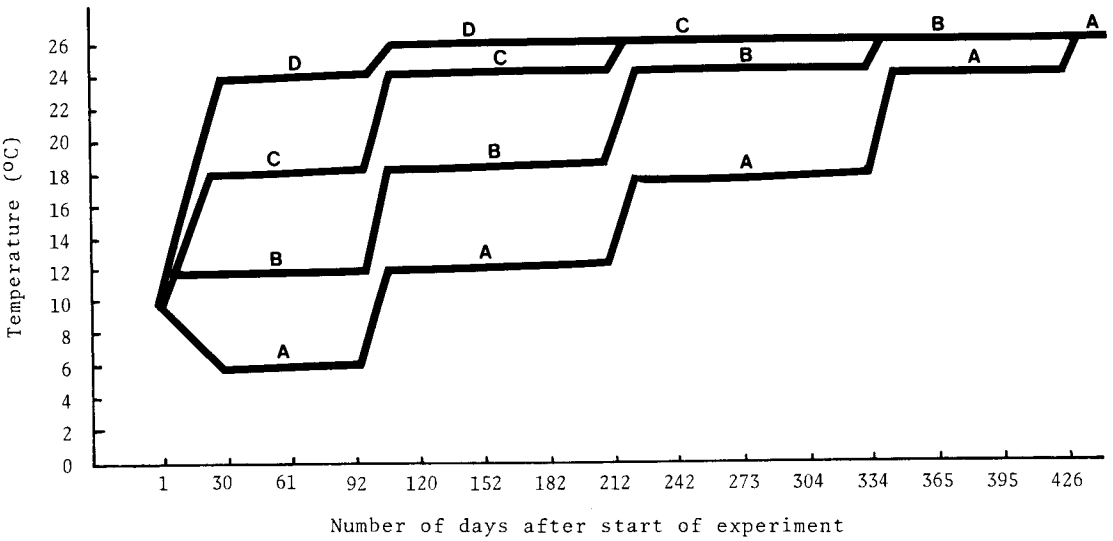

Fig. 1. Schedule of experimental thermal regimes (A–D) for *H. limbata*.

developmental thermal regime. We have attempted to demonstrate experimentally the degree to which adult phenotypes (describable in terms of taxonomically implicated characters) are affected by differences in developmental thermal regimes that simulate the primary range of environments encountered in nature by these species. Such information could help resolve obvious taxonomic problems.

Procedure

Study Sites. Local populations of the test species found in the vicinity of Purdue University (West Lafayette, Indiana) were used for field and laboratory studies. *H. limbata* was sampled from Little Pine Creek, a small stream draining agricultural farmland. Larvae were collected from a 15-m, silt-bottomed stretch of stream 16 km west of West Lafayette, at State Road 26. Samples of *S. interpunctatum* were collected from the Tippecanoe River, 11 km east of Brookston, Ind., at State Road 18. A sampling area of 50 m^2 was situated close to the bank and was 0.25 to 0.38 m deep with riffles and numerous stones and dense periphyton growth.

Field Study. Mayfly life history studies appear most reliable when larval development is determined by a predictable sequence of morphological changes that parallel development (Pleskot 1962). For *H. limbata*, the following developmental stages were found to adequately represent the sequence of development: Stage I, wing pads absent; Stage II, only fore wing pads present; Stage III, fore wing pads and hind wing pads present, the former do not cover the latter; Stage IV, fore wing pads completely cover hind wing pads; Stage V, wing pads blackened. For *S. interpunctatum*, analogous developmental stages established by McCafferty and Huff (1978) were adopted.

Life cycles of *H. limbata* and *S. interpunctatum* were studied from larvae collected monthly from October 1980 to September 1981. No samples were taken from December to February because of ice. Body length and developmental stage were determined, and larvae were arranged in monthly length-frequency histograms.

Laboratory Study. Three hundred *H. limbata* larvae in the 8 to 10 mm size range and 300 larvae of *S. interpunctatum* in the 3 to 8 mm size range were recruited in October. Larvae were acclimated for a week in the laboratory at a temperature similar to their respective sample sites. Larvae of each species were then divided into four test groups, and these were placed into separate rearing facilities. Based on the distributions of *H. limbata* and *S. interpunctatum* and USGS water temperature data, the following thermal regimes (A–D) were selected to reflect a spectrum of different thermal gradients encountered in nature by the two species: A, 6 to 26°C; B, 12 to 26°C; C, 18 to 26°C; D, 24 to 26°C. The temperatures were adjusted through these gradients during the course of the experiment according to the schedules shown in Fig. 1 and 2.

Regimes A and B were in calibrated Living Stream environmental tanks (Frigid Units, Model No. MT 500). Each rectangular tank had two separate chambers (61 by 64 by 36 cm) on either side of a filtering water chiller unit (filters were replaced every 3 months). Regimes C and D were maintained in aquaria (81 by 38 by 36 cm), each equipped with thermostat heaters and aerators. Water was filtered once a week. Photoperiod was unaltered.

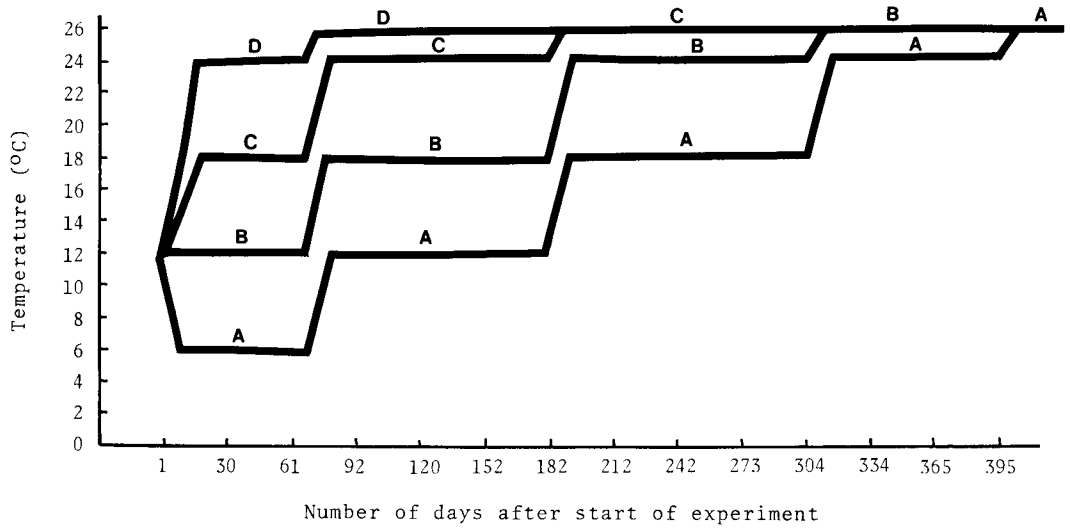

Fig. 2. Schedule of experimental thermal regimes (A–D) for *S. interpunctatum*.

Mud used as substrate collected from the sample site was emptied into each *H. limbata* rearing tank to a depth of 15 cm. *Hexagenia limbata* larval diets consist of detritus, diatoms, and other algae contained in mud substrates. Mud was therefore replaced each month (excluding December to March) so each rearing tank would have presumably similar diets. Lab-cultivated periphyton was added to rearing tanks each week. Stones with dense periphyton growth taken from the sampling site were provided for *S. interpunctatum* as substrate and replaced every month (excluding December to March) because larvae feed mainly on diatoms and detritus scraped from hard substrates. Laboratory grown periphyton was also added every week. Temperature could possibly affect growth and developmental results indirectly by limiting dietary items; however, every attempt was made to maximize food availability at each regime. Only at the coldest regime for *H. limbata* were dietary items difficult to maintain at high levels and of possible consequence in interpreting results.

Each rearing tank was covered with an elevated net for holding emerging subimagos and adults. Subimagos of *H. limbata* were transferred to a smaller chamber above the rearing tank in order to prevent possible drowning. Successful molting to the adult was obtained when the subimagos were positioned hanging down and away from a support surface. Subimagos of *S. interpunctatum* were allowed to remain in the rearing tanks, where they would fly to the top of the net and remain until the final molt. Numbers of successful emergents for each of the test groups are given in Table 1 and represent sample sizes on which data and analyses are based. The sample sizes are not repeated in subsequent tables.

For phenotypic character examination, adults were killed and placed in 95% acetone for 10 to 15 h before drying (a process recommended by Berté [1979] for preserving color patterns). Each adult was allowed to live approximately 15 h and was completely mature before being killed. Specimens placed in acetone were positioned for study with the wings flattened out horizontally. The first 25 individuals were examined for coloration and extent of maculation and measured for body size before treating in acetone. These data were later compared with results obtained after fixing in acetone. Only eye color was affected (most turned white), and therefore eye color before fixation was recorded.

All characters previously used by investigators as taxonomic characters of specific and subspecific importance for the test species were recorded. The number of measurements made for each character at each temperature regime sometimes varied, because only those specimens in suitable condition were considered. At the coldest regime, many *H. limbata* adults molted unsuccessfully with the posterior end of the abdomen attached to the subimaginal pellicle, or the fore legs were not intact. As a result no statistical tests on the affected characters of *H. limbata* could be carried out for this regime.

To quantify base body coloration of *H. limbata*, the range of color was represented by five adult forms (almost white, yellow, bright yellow, yellow-brown, and brown) mounted in sequence and used as a color reference standard. Abdominal maculation was quantified by making similar reference standards using four individuals. This eunomic series was made by selecting the two extremes represented in the test individuals—i.e., one that was "slightly maculated" and one that was "intensely maculated." The two other intermediate reference

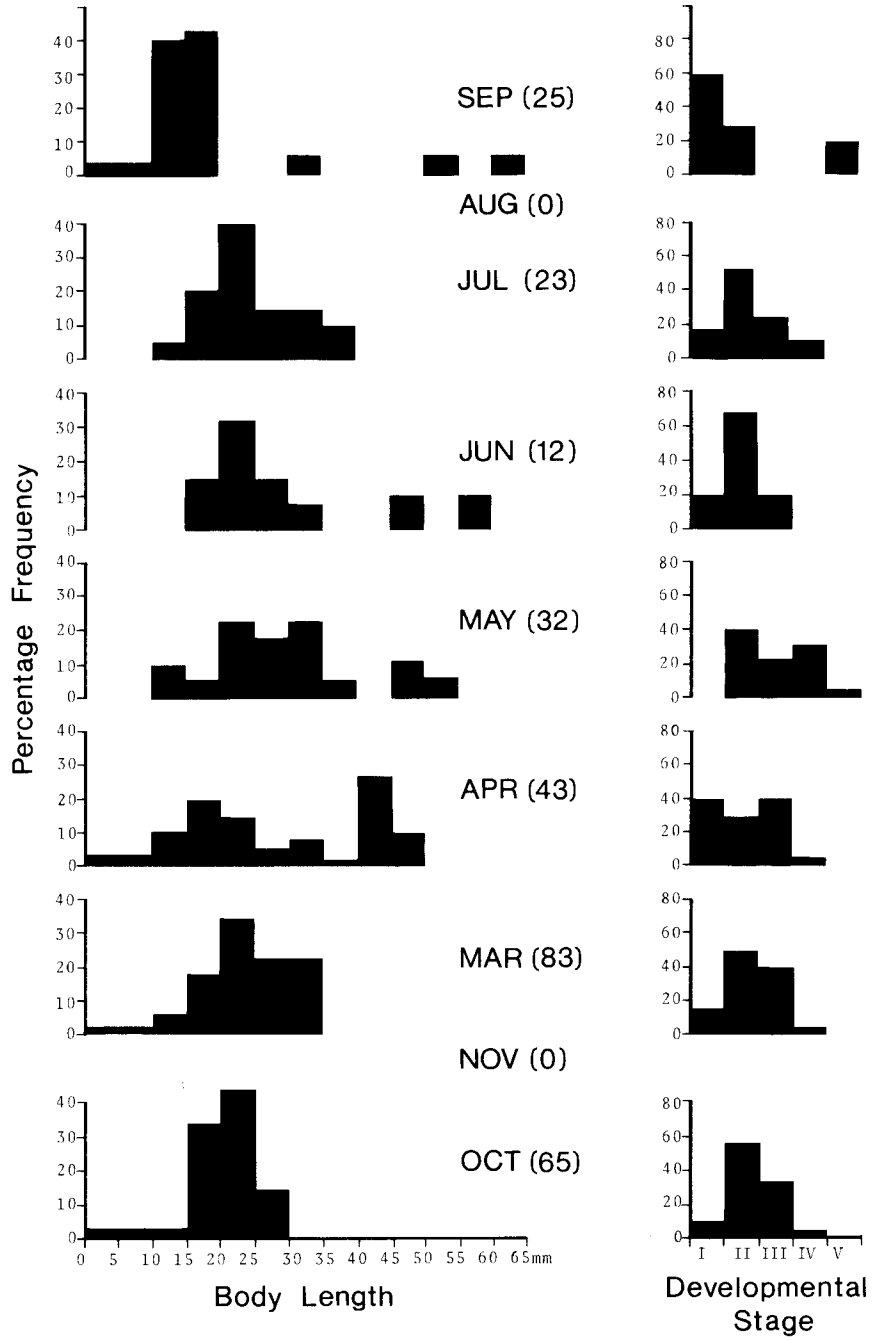

Fig. 3. Percent body length and developmental stage frequency of *H. limbata* larvae at Little Pine Creek, October 1980 to September 1981 (sample number parenthetical).

individuals were selected from the range of specimens that showed intermediate degrees of maculation—i.e., "moderately maculated" and "heavily maculated"—but were clearly distinct from each other and the extremes. Degrees of maculation that slightly exceeded the extremes found in the test individuals are rarely represented in nature by these species. Reference standards were selected similarly for base body coloration and abdominal maculation of *S. interpunctatum* adults.

Male genitalia of both species were slide mounted with Canada balsam. An elevated cover slip

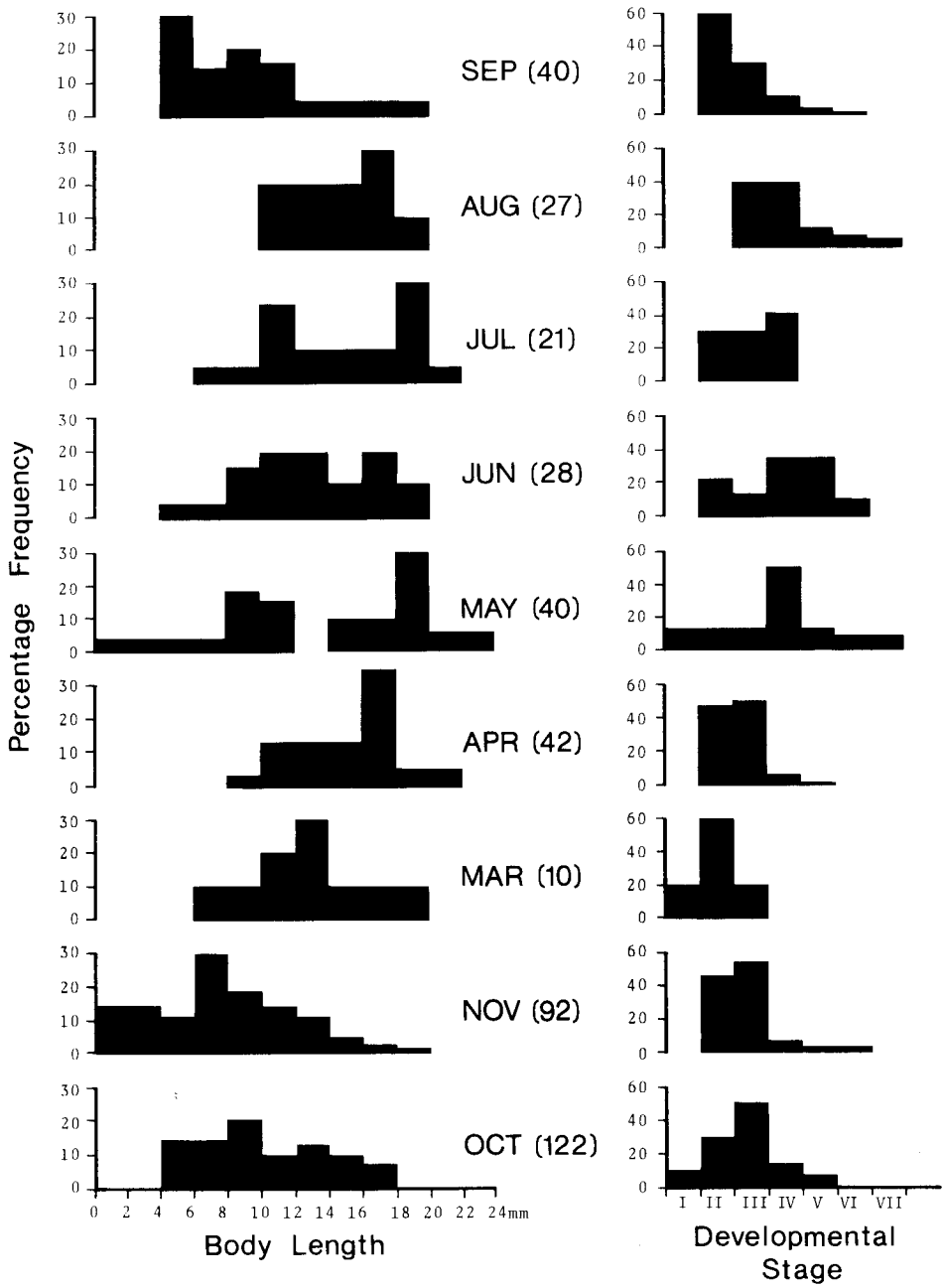

Fig. 4. Percent body length and developmental stage frequency of *S. interpunctatum* larvae at Tippecanoe River, October 1980 to November 1981 (sample number parenthetical).

was used so the three-dimensional nature of the penes would not be distorted (Bednarik and McCafferty 1979).

Adults of *S. interpunctatum* collected in the field were preserved in a manner similar to the above. A total of 87 adults was collected and phenotypic characters were examined for comparison with the laboratory test individuals.

Data were subjected to analysis of variance. Measurements of mean values obtained at different thermal regimes were tested for significance using a two-tailed t test. Tests for independence were determined by χ^2 goodness-of-fit ($\alpha = 0.05$).

Over 300 museum specimens of adult *H. limbata* were examined for abdominal maculation from California, Idaho, Illinois, Indiana, Iowa,

Table 1. Numbers of emergents of *H. limbata* and *S. interpunctatum* from different developmental thermal regimes

	Regime A	Regime B	Regime C	Regime D
H. limbata				
Male	14	25	20	25
Female	12	31	24	26
S. interpunctatum				
Male	22	27	26	33
Female	20	32	30	35

Maine, Manitoba, Mexico, Michigan, Minnesota, North Carolina, Ohio, Oklahoma, Oregon, Pennsylvania, Texas, Virginia, and Wisconsin. Over 1,400 adult specimens of *S. interpunctatum* were examined from Arkansas, Illinois, Indiana, Maine, Manitoba, Minnesota, Virginia, and Wisconsin. These areas included northern and southern range extremes of both species. All specimens were preserved in alcohol (some for over 2 decades). Because some fading may have occurred, only the relative degree of maculation was recorded. Specimens were on loan from Freshwater Institute-Manitoba, Illinois Natural History Survey, Oregon State University, Purdue University, U.S. National Museum, and Virginia Polytechnic Institute and State University.

Phenology

The life cycle of *H. limbata* at our sampling site was complex with at least two apparent cohorts. There were 0 to 2 mm and stage I larvae in March and April, and September and October (Fig. 3). A third cohort beginning development in midsummer may also exist because stage I larvae were also collected in June and July. Although data presently do not allow the life cycle pattern to be defined further, it is apparent that cohorts hatching from eggs at different times of the year experience differences in environmental conditions (e.g., thermal regimes) over time.

The life cycle of *H. limbata* is not only complex but variable through its range. Hunt (1953) found two cohorts of *H. limbata* present at any one time in some southern Michigan lakes. A main cohort completed development in 1 year and emerged in late summer, whereas a smaller cohort took approximately 20 to 22 months to develop and emerged in summer of the next year. Hudson and Swanson (1972) reported 1 and 2 year cohorts in some lakes in Texas and that life cycle was dependent on the time of hatching. Neave (1932) reported a 2-year life cycle in Lake Winnipeg. Larvae did not grow appreciably in winter but mostly in August. Lyman (1940) found that newly hatched larvae in Douglas Lake, Michigan appeared in August and were three-fourths grown by late summer of that year and emerged in June and July of the 2nd year. Spieth (1941) observed that in northern Indiana larvae hatched in July and reached an average length of 11.3 mm in 3 months.

The life cycle of *S. interpunctatum* at our study site was also complex with two major identifiable cohorts (Fig. 4). The early spring cohort had a peak emergence in May, whereas the late summer cohort had a peak emergence in August. Because adults were collected in the field from May to October, overlap between cohorts was apparent. Emergence occurred in the field only when water temperatures were above 16°C. Eggs apparently hatch in early fall and early spring, because stage I larvae were collected in November and May. McCafferty and Huff (1978) observed three cohorts in Wildcat Creek, Indiana.

Little is currently known about control of growth and maturation in Ephemeroptera, although temperature is evidently responsible for some phenological variation (Elliott 1967, Ulfstrand 1968, Radford and Hartland-Rowe 1971, Vannote and Sweeney 1980). A certain threshold is necessary for development to proceed, and development is greatest at an optimum threshold level (Richards 1959). Below this threshold, growth and maturation do not occur, and beyond the optimum level the rates of these two processes gradually decrease.

Laboratory rearing at various thermal regimes indicated that as temperature increased, mean maturation time decreased (Table 2); however, approximately similar maturation times for *H. limbata* were found at the two intermediate regimes. For *S. interpunctatum*, there was relatively less

Table 2. Mean maturation rates (days) for *H. limbata* and *S. interpunctatum* adults reared from different thermal regimes

	Regime A	Regime B	Regime C	Regime D
H. limbata				
Male	262	191	221	155
Female	287	217	223	170
Male + female	278 (128–393)	208 (93–283)a	222 (142–301)a	163 (91–324)a
S. interpunctatum				
Male	251	193	110	87
Female	203	197	118	90
Male + female	257 (210–306)	195 (176–245)	114 (104–163)	89 (60–104)

Values followed by the same letter are not significantly different ($\alpha = 0.05$). Values in parentheses are ranges.

Table 3. Mean degree-day quotas for *H. limbata* and *S. interpunctatum* adults reared from different thermal regimes

	Regime A	Regime B	Regime C	Regime D
H. limbata				
Male	2,386	2,473	3,969	4,342
Female	2,599	2,753	4,008	4,620
Male + female	2,526a	2,652a	3,992	4,500
	(1,435–3,878)	(1,574–3,570)	(2,823–5,237)	(3,289–7,041)
S. interpunctatum				
Male	4,239	3,999	3,632	3,192
Female	4,733	3,939	3,833	3,290
Male + female	4,469	3,968	3,725	3,246
	(3,666–5,586)	(3,711–4,481)	(3,552–4,732)	(2,730–3,600)

Values followed by the same letter are not significantly different ($\alpha = 0.05$). Values in parentheses are ranges.

variation, and adults emerged in a more synchronized manner, with smaller standard deviations and well defined modes.

Certain studies of growth rate of aquatic macroinvertebrates (Thorup 1963, Anderson 1969, Fahy 1973) have demonstrated a degree-day dependence of growth. The threshold temperature for *H. limbata* larvae was determined by Hunt (1953) to be approximately 10°C, and, because our field data are consistent with his observation, this value was used as the base for calculating degree days. Mean number of degree-days for maturation (determined by emergence of adults) at different thermal regimes (Table 3) indicated no significant difference between the A and B regimes. For these cold regimes an overall mean minimum degree-day quota of 2,588 was accumulated before emergence. At the C and D regimes, however, higher quotas are evidently needed for emergence, possibly because of higher levels of metabolism at these temperatures.

No data have been published on the threshold temperature of *S. interpunctatum* larvae. From our field data we assumed it to be approximately 4°C, and this was used as the base value for calculating degree days. Humpesch (1980) found the threshold temperatures for four species of the related genus *Ecdyonurus* to be between 3.5 and 4°C. Larvae having accumulated the highest degree-day quota were reared at the coldest regime and vice versa (Table 3). These are different from the results obtained for *H. limbata* where emergence time appeared to be independent of water temperature (emergence was observed even when the water temperature was 12°C). Below 18°C, *S. interpunctatum* did not emerge even though developing larvae had accumulated a degree-day quota equivalent to successful emergents reared at the warmest regime (ca. 2,800 degree-days).

The fact that a certain critical temperature (ca. 18°C) is necessary for emergence of *S. interpunctatum* but a certain minimum degree-day quota is necessary for *H. limbata* is in agreement with other mayfly studies demonstrating that, depending on the species, emergence is related to one or the other factor (Sprules 1947, Macan and Maudsley 1966, Fahy 1973, Brittain 1976). It is evident that development of both *H. limbata* and *S. interpunctatum* is strongly influenced by temperature. Complex life cycles of these species may be expected to vary in detail as a result of prevailing temperatures and, as shown within single multicohort populations, as a result of seasonal temperatures.

Phenotypic Variation

Body Length. Mean body lengths obtained experimentally for both species were temperature dependent. Table 4 shows that mean size of male and female adults of *H. limbata* decreased as temperature increased at the B, C, and D regimes, but it also decreased at the coldest regime, perhaps owing to an inadequate diet. Although there was an average decrease of 6.5% between B and D regimes, a wide range of body lengths was found in each test group. A large variation in size of *H. limbata* adults reared from a single brood of eggs under identical conditions was observed by Hunt (1953). Maximum body size of *S. interpunctatum* was obtained at the lowest temperature regime, with size progressively smaller at warmer regimes. The average decrease in size between the A and D regimes was 27%.

Investigators have generally noted size reduc-

Table 4. Mean body lengths (mm) of *H. limbata* and *S. interpunctatum* reared from different thermal regimes

	Regime A	Regime B	Regime C	Regime D
H. limbata				
Male	19.25	21.43	20.42	18.78
	(15–26)	(17–25.5)	(18–23)	(17–24)
Female	25.33	26.44	25.71	25.52
	(21.5–28)	(22.5–29.5)	(22–29)	(16.5–29)
S. interpunctatum				
Male	9.87	8.91	8.25	7.49
	(8.3–11.1)	(7–9.5)	(7–9)	(6.5–8.5)
Female	10.7	9.25	8.5	7.57
	(9.6–11.5)	(8–10.5)	(8–10)	(7–9)

Values in parentheses are ranges.

Table 5. Mean structure ratios for *H. limbata* adult males reared from different thermal regimes compared with available published data

	FWL (mm)	FWL:BL	FL:BL	F:Tb	Tb:t	3t:2t
Thermal regime						
A	15.6a	—	—	—	—	—
B	16.0a	0.7619	0.6012	0.5693b	0.8295c	0.7932d
C	16.9a	0.7867	—	—	—	—
D	16.1a	0.7659	0.6154	0.6095b	0.8293c	0.7825d
Nominal subspecies						
H. l. californica	(17–18)	—	—	—	—	—
H. l. limbata	(18–20)	—	—	—	—	—
H. l. occulta	(18–19)	—	1.0	0.5882	0.8333	0.8333
H. l. venusta	(11–15)	—	0.7692	0.5556	0.8333	1.0
H. l. viridescens	18.0	—	1.0	0.5882	0.7692	0.8333

FWL, Fore wing length; BL, body length; FL, fore leg length; F, fore femur length; Tb, fore tibia length; t, fore tarsus length; 3t and 2t, third and second fore tarsal segment length, respectively. Nominal subspecies are from Traver (1931) and Spieth (1941). a, b, c, and d, Not significantly different ($\alpha = 0.05$) from others similarly marked.

tion of adults of several mayfly species as the season progressed, with later emergents being smaller (e.g., Fremling 1973, McCafferty and Huff 1978, Vannote and Sweeney 1980). In our field studies of the two test species (Fig. 3 and 4), we found noticeable size differences of stage V larvae within and between cohorts that appeared to be related to the different developmental regimes of the larvae. Observed decreases in body size with increase in temperature may be a result of one or more effects of temperature on larval development as has been discussed by Vannote and Sweeney (1980).

Structural Size. Traver (1931, 1935) and Spieth (1941) regarded fore wing length of *H. limbata* as taxonomically important. Although we found that body length decreased with temperature, fore wing length was not significantly different between test groups (Table 5), but significant differences were observed for mean ratio of fore wing length to body length. The ratios ascribed to species (=Spieth's subspecies) or subspecies by Traver (1931) and Spieth (1941) are included in Table 5. We found similar relationships for *S. interpunctatum* (Table 6), except that no significant difference existed for FWL:BL between B and C regime individuals.

Spieth (1947) used ratios of fore wing length to first tarsal segment to differentiate subspecies of *S. interpunctatum* males. We found a significant difference only between the coldest and warmest regimes.

Traver (1931) tabulated ratios involving male fore leg segments used in differentiating *Hexagenia* species (=Spieth's subspecies of *limbata*). We measured these for only the B and D regimes, because too few emergents from the A and C regimes had fore legs intact. Means for femur to tibia, tibia to tarsus, third tarsal to second tarsal segment, and fore leg to body length ratios are given and compared to Traver's data in Table 5. Our values (except fore leg segments to body length) were not significantly different between B and D regimes. We do not know if Traver's differentiating mean ratios were significantly different.

Fore leg to body length of *S. interpunctatum* adult males differed significantly only in the warmest thermal regime. The ratio of the second tarsal segment to the first was used by Spieth (1947) to differentiate males of *S. interpunctatum* subspecies, and these values are compared with our results in Table 6.

Table 6. Mean structure ratios for *S. interpunctatum* adult males reared from different thermal regimes compared with available published data

	FWL (mm)	FWL:BL	FWL:1t	FL:BL	2t:1t
Thermal regime					
A	9.53a	0.95	9.3c	0.9196e	2.3514
B	9.67a	1.05b	8.4c,d	0.9482e	1.9889f
C	9.68a	1.11b	8.1c,d	0.9748e	1.5996f,g
D	9.56a	1.29	7.6d	1.0836	1.6547g
Nominal subspecies					
S. i. canadense	8.96	—	9.08	—	2.34
S. i. frontale	9.38	—	9.96	—	2.37
S. i. interpunctatum	7.98	—	9.37	—	2.63
S. i. heterotarsale	7.59	—	5.48	—	1.57

FWL, Fore wing length; BL, body length; 1t and 2t, first and second fore tarsal segments, respectively; FL, fore leg length. Nominal subspecies are from Spieth (1947). a, b, c, d, e, f, and g, Not significantly different ($\alpha = 0.05$) from others similarly marked.

Table 7. Percent frequency of base body colorations observed in *H. limbata* adults reared from different thermal regimes

Color	Thermal regime			
	A	B	C	D
Pale cream-white	0	23	0	10
Yellow	18	38	62	42
Bright yellow	27	19	31	32
Yellow-brown	36	15	8	10
Reddish-brown	18	6	0	6

Male Genitalia. Although subtle differences in the shape of the adult penes were described by Spieth (1941) for his subspecies of *H. limbata*, we could not detect differences in adults from any regime. The curvature of the penes consistently resembled Spieth's drawing of *H. l. limbata*. Spieth's differences were evidently an artifact of slide preparation technique. We could find false differences by slide mounting genitalia in euparal as Spieth had done, because such mounting variously distorts penes shape.

Size, shape, and color of *S. interpunctatum* male genitalia did not significantly differ among our test groups. Medial spines were often slightly asymmetrical and shorter on one side. Lateral spines were present in all individuals, with the numbers varying between 7 and 15. No apical or distal spines were present, but two spines on the dorsal side of the penal lobes posterior to the lateral spines were often present. Spieth (1947) noted similar variation but regarded it as individual rather than taxonomic.

Base Body Coloration. The base body coloration of reared adults of *H. limbata* varied from a pale cream-white to reddish brown and included the color descriptions given by Spieth (1941) for *H. limbata* subspecies. The frequency of base color types varied with experimental thermal regimes (Table 7). Cold-regime (slow-maturing) larvae developed into yellow to reddish brown adults, whereas warmest regime (fast-maturing) larvae developed into a broader range of adults, including cream-white, but were dominated by yellow and bright yellow individuals. Although most grades were present in all thermal regimes, base color and thermal regimes were not independent.

Base body coloration of *S. interpunctatum* adults from the B, C, and D regimes ranged from bright yellow to almost white. Spieth (1947) described *S. i. interpunctatum*, *S. i. frontale*, and *S. i. heterotarsale* as having a general chrome-yellow color, faintly tinged with green. We did not find any green tinge, even before acetone treatment. Spieth's *S. i. canadense* was described as typically yellow with an enormous amount of piceous color, and corresponded to what we observed in the A regime test group. Field-collected adults ranged similarly, with those at the beginning of the emergence season being pale yellow (with the exception of one female). Individuals collected from June to August were yellow; those from early September were bright yellow.

Abdominal Maculation. Spieth (1941) used abdominal color patterns to distinguish subspecies of *H. limbata*. Maculations of our reared adults showed a strong correlation with developmental temperature (Fig. 5–8; Table 8). Comparison of Spieth's figures of male dorsal abdomens with Fig. 5 reveals that his *venusta* corresponds to our "slightly maculated"; *limbata* to our "moderately maculated"; *occulta* to our "heavily maculated"; and *occulta-viridescens* to our "intensely maculated." Table 8 gives the percentage frequency with which these maculations were obtained. Heavy to intense dorsal maculation was most predominate in the coldest regime group, became progressively less frequent in B and C test groups, and, again, increased in frequency in the D regime test group. Dorsal and ventral maculation showed similar correlations, although the greatest frequency of ventrally slightly maculated forms occurred in the B test group.

Maculation patterns in reared *S. interpunctatum* adults (Fig. 9) corresponded to Spieth's (1947) description of subspecies as follows: our "slightly

Table 8. Percent frequency of dorsal and ventral (Dor/Ven) abdominal maculation patterns observed in *H. limbata* adults reared from different thermal regimes

Maculation pattern	Thermal regime			
	A (Dor/Ven)	B (Dor/Ven)	C (Dor/Ven)	D (Dor/Ven)
Male				
Slightly maculated	0/8	35/40	55/20	12/13
Moderately maculated	9/17	38/32	25/60	16/13
Heavily maculated	55/8	23/16	20/20	44/27
Intensely maculated	36/67	4/12	0/0	28/47
Female				
Slightly maculated	0/9	19/33	17/0	11/15
Moderately maculated	9/9	26/17	58/21	22/50
Heavily maculated	9/9	32/30	17/38	41/15
Intensely maculated	82/73	23/30	8/41	26/20

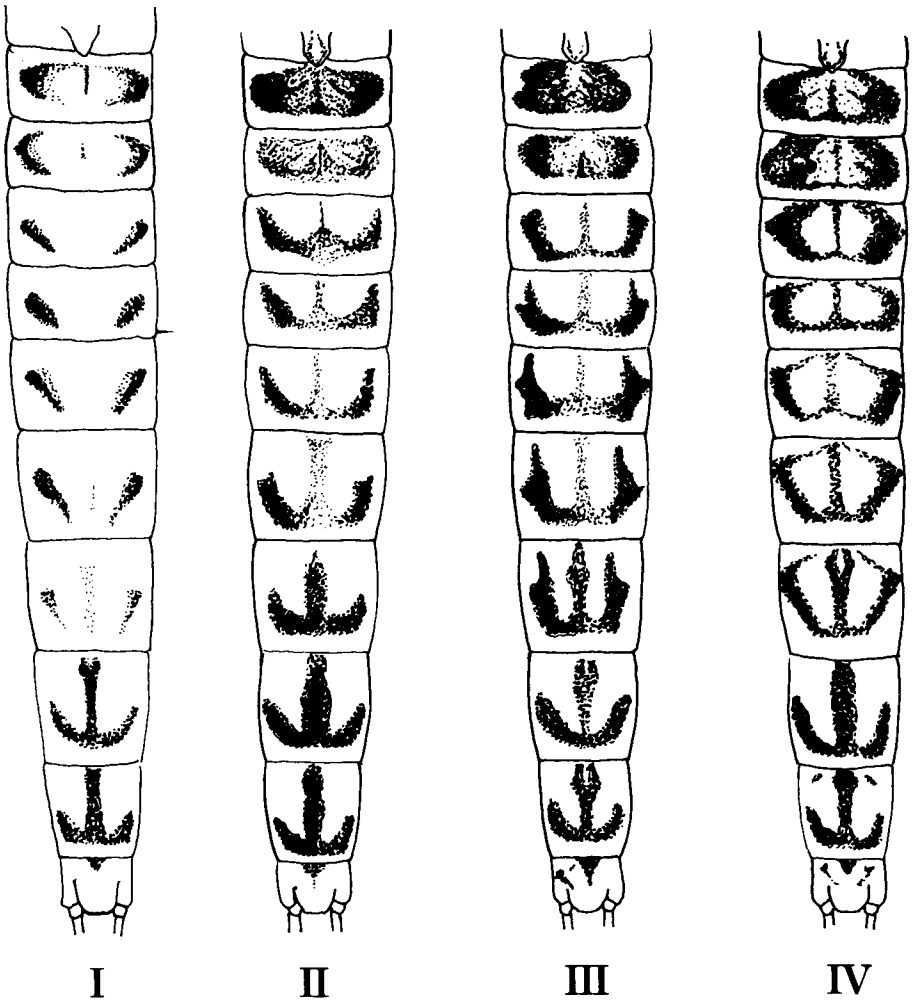

Fig. 5. Dorsal abdominal maculation of *H. limbata* adult males reared from different thermal regimes (I, slightly maculated; II, moderately maculated; III, heavily maculated; IV, intensely maculated).

maculated" corresponds to *heterotarsale* and *interpunctatum*; our "moderately maculated" to *frontale*; and our "heavily maculated" to *canadense*. Results given in Table 9 indicate that slightly maculated forms increased in frequency from the coldest to warmest regime. Heavily and intensely maculated adults occurred only in the A and B regime groups. Thus, Spieth's *heterotarsale* and *interpunctatum* pattern were obtained mainly from larvae reared at warmer regimes. His *canadense* pattern was obtained only at colder regimes. Maculation pattern was not independent of thermal regime. Spieth (1947) described stigmal spots for *S. i. frontale*, and these were observed in ca. half of the A and B regime adults, but were otherwise absent.

About 50% of the adults collected in the field in May had a heavily maculated pattern and approximately 40% were slightly maculated. In June, July, and August, 60% were slightly maculated and the remainder were either moderately maculated or heavily maculated. In September, approximately 80% were slightly maculated. Thus, adults emerging in spring (overwintered as mature larvae) have more maculation than those of other cohorts.

Wing Coloration. A correlation was found between thermal regime and some of the wing characteristics that Spieth (1941) and Traver (1931) used to differentiate *H. limbata* at the species and subspecies level. Fore wing membranes were hyaline and ranged from colorless to tinged with yellow-brown (Table 10). Wings tinged with pale yellow were most common, but the frequency of yellow and yellow-brown was greatest in the coldest regime group and was least in the warmest regime group. Costal and subcostal membranes had various degrees of brown pigment in most specimens of all four test groups. Costal crossveins were

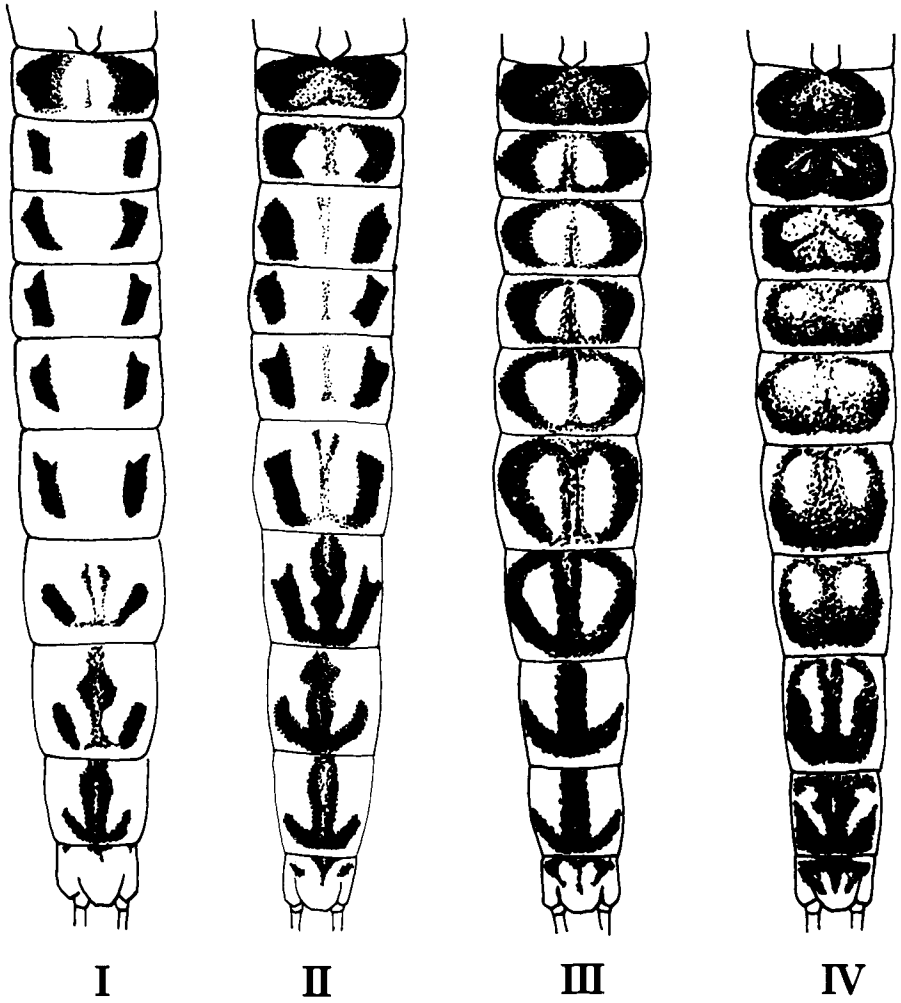

Fig. 6. Dorsal abdominal maculation of *H. limbata* adult females reared from different thermal regimes (I, slightly maculated; II, moderately maculated; III, heavily maculated; IV, intensely maculated).

marginated in all individuals, and most crossveins anterior to MP_1 were marginated in males.

The frequency distribution of infuscation of the hind wing margin of reared adults is also given in Table 10. According to Spieth (1941), males of all subspecies possess such infuscation except *H. l. occulta*, which may or may not possess it. Two-thirds or more of males from each regime possessed heavy infuscation. Most females lacked infuscation, and although some from the A and B regimes possessed light or heavy infuscation, this characteristic was independent of thermal regime.

Fore wings of all reared *S. interpunctatum* adults were hyaline with the subcostal and costal membrane a pale yellow-brown basally and darker brown distally beyond the bulla. The tip of the fore wings also had four to five marginal veins infuscated with brown-black. The bulla consisted of one to three crossveins (more often two or three) infuscated with a brown-black dash. This infuscation was symmetrical in the left and right wings of 65% of the individuals. Hind wings were infuscated distally with the margin varying from a faint brown-black to a distinct black. The above characters and thermal regime were not correlated and were randomly expressed in field-collected individuals also.

Leg Coloration. Spieth (1941) ascribed color characteristics for adult male fore femora and tibiae (ranging from brown to black) to his subspecies of *H. limbata*. We found all these variations in reared males, but their frequency was not significantly correlated with thermal regime. Spieth (1947) described the adult males of *S. i. canadense* and *S. i. frontale* as having dark middle and distal bands on the hind femora, and the middle band as absent in *S. i. interpunctatum* and *S. i. heterotarsale*. We found the middle band in 58, 31, 52,

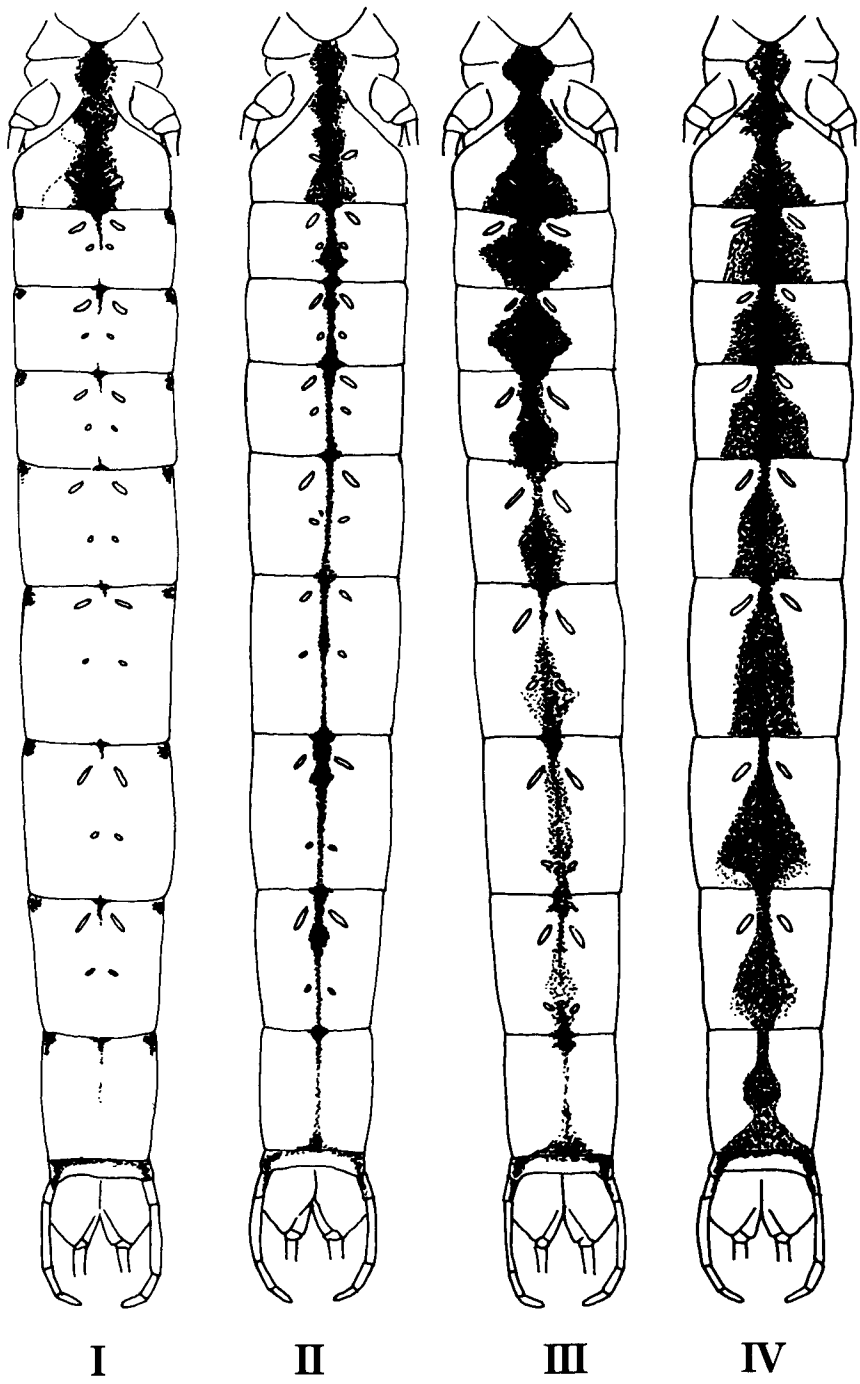

Fig. 7. Ventral abdominal maculation of *H. limbata* adult males reared from different thermal regimes (I, slightly maculated; II, moderately maculated; III, heavily maculated; IV, intensely maculated).

and 40% of the A, B, C, and D regime adults, respectively, and this characteristic was independent of thermal regime. The frequency of adults from the field study possessing this character did not vary significantly through the emergence period.

Cerci Coloration. The cerci of most male *H. limbata* adults from all test groups were yellow with dark brown at the joinings. Although the yellow was dominated by brown in a few individuals (giving a darker color to the entire length of the cerci), this variation was independent of thermal regimes. This variation was used by Traver (1931) to describe *Hexagenia* species that were later rel-

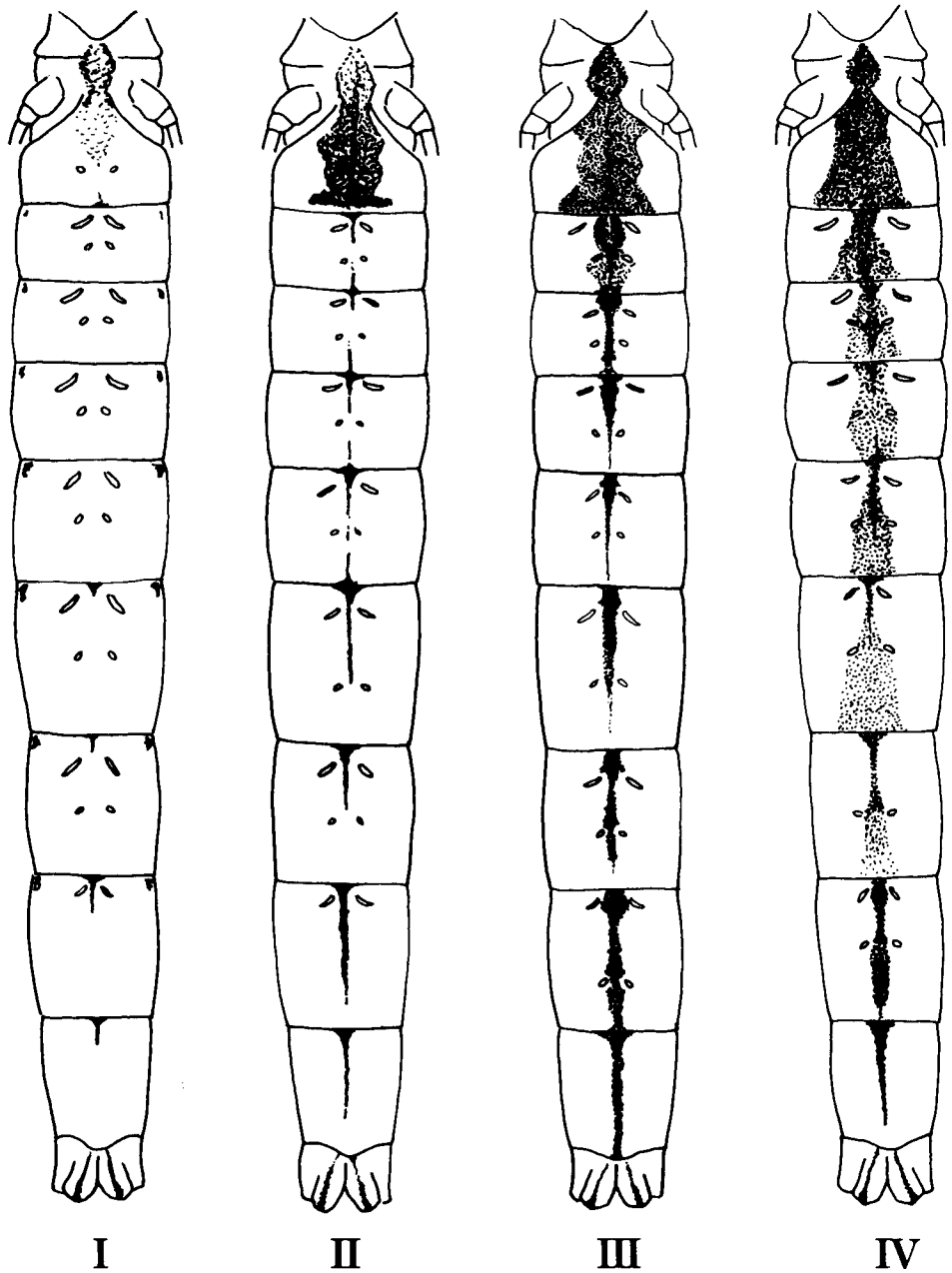

Fig. 8. Ventral abdominal maculation of *H. limbata* adult females reared from different thermal regimes (I, slightly maculated; II, moderately maculated; III, heavily maculated; IV, intensely maculated).

egated to subspecific status by Spieth (1941). The cerci of reared females were faintly ringed with brown at the joinings of a few individuals only. The rest had cerci that were almost creamy white to pale yellow. Cerci of reared *S. interpunctatum* adults were pale gray to light brown, but variation was not correlated with thermal regime.

Compound Eye Coloration. Traver (1931) used compound eye color for differentiating *H. limbata*. Our reared *H. limbata* males had compound eyes that were black ventrally, and the dorsal aspect varied between brown, yellow-brown, and green. No correlation existed between eye color and thermal regime. Compound eyes of our reared *S. interpunctatum* males varied from yellow-brown to green, again independent of thermal regime.

Head Color Pattern. Maculation of the adult clypeus was used by Spieth (1947) to characterize subspecies of *S. interpunctatum*. All the variations

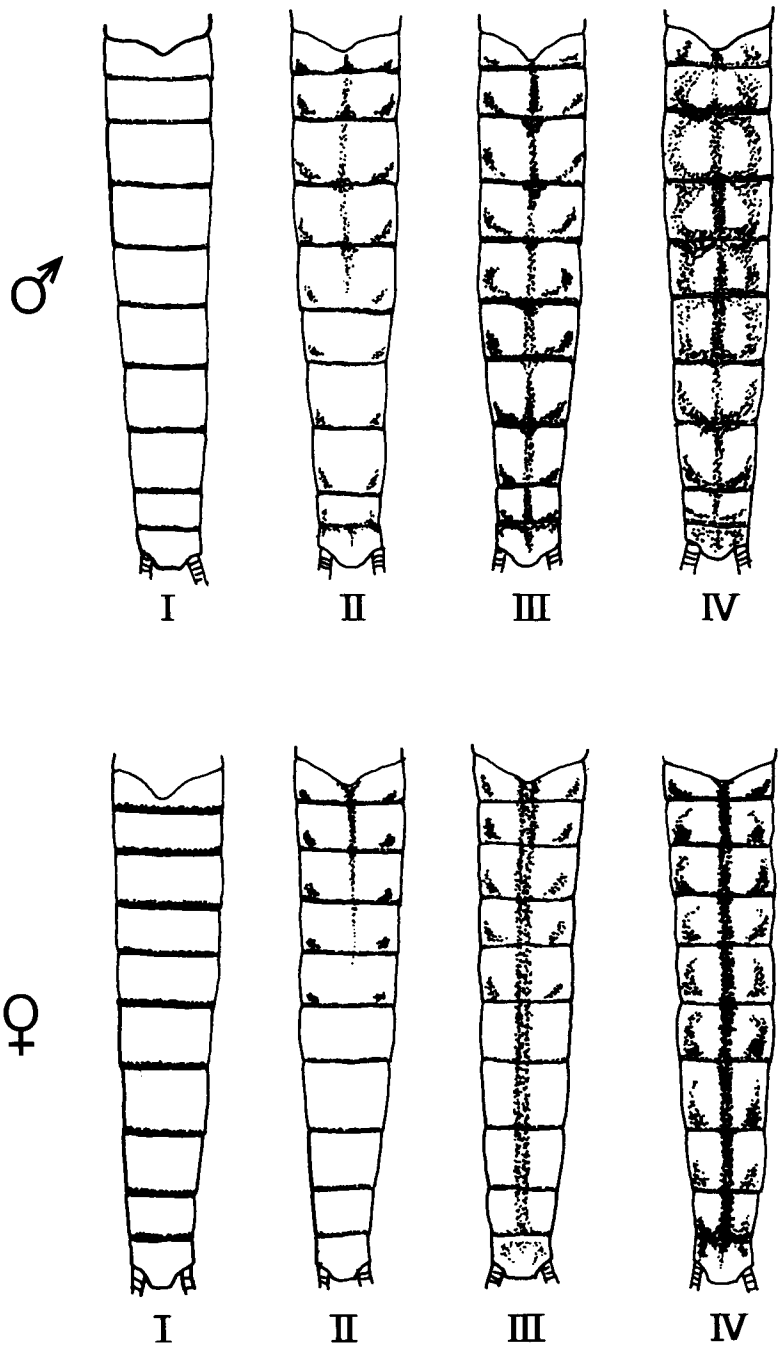

Fig. 9. Dorsal abdominal maculation of *S. interpunctatum* adults reared from different thermal regimes (I, slightly maculated; II, moderately maculated; III, heavily maculated; IV, intensely maculated).

of this character were found in reared individuals (Fig. 10). Spieth's description of the subspecies *heterotarsale* corresponds to our "not maculated"; *interpunctatum* to our "slightly maculated"; *frontale* to our "moderately maculated"; and *canadense* to our "heavily maculated." Frequencies of these variations in the test regime groups (Table 11) show maculation significantly decreases with warmer and shorter developmental regimes. An even stronger correlation was observed in the mac-

Table 9. Percent frequency of dorsal abdominal maculation patterns observed in *S. interpunctatum* adults reared from different thermal regimes

Maculation pattern	Thermal regime			
	A	B	C	D
Male				
Slightly maculated	46	56	92	97
Moderately maculated	36	26	8	3
Heavily maculated	9	14	0	0
Intensely maculated	9	4	0	0
Female				
Slightly maculated	45	59	70	96
Moderately maculated	35	25	30	4
Heavily maculated	10	13	0	0
Intensely maculated	10	3	0	0

Table 10. Percent frequency of fore wing coloration and hind wing infuscation observed in *H. limbata*

	Thermal regime			
	A	B	C	D
Fore wing color				
Colorless	11	20	7	27
Pale yellow tinged	27	50	49	62
Yellow tinged	31	23	19	11
Yellow-brown tinged	31	7	25	0
Hind wing infuscation	♂/♀	♂/♀	♂/♀	♂/♀
Heavy	100/9	67/10	80/0	70/0
Light	0/14	25/13	20/17	15/7
Absent	0/77	8/77	0/83	15/93

ulation of the vertex (Fig. 10; Table 11). Degree of vertex maculation has not been used taxonomically in *S. interpunctatum* but has been used widely in mayfly taxonomy. All clypeal and vertex maculation types were found in the field samples, but a correlation with emergence time was not evident. Head patterns have not been used taxonomically for *H. limbata*, and the slight variations in the clypeus and vertex observed in reared adults were not correlated with thermal regime.

Pronotum Color Pattern. Reared *S. interpunctatum* adults had three distinct pronotal patterns (Fig. 10). Our "not maculated" corresponds to Spieth's (1947) *heterotarsale*; our "moderately maculated" to *interpunctatum*; and our "heavily maculated" to *canadense* and *frontale*. Frequencies show an inverse correlation between degree of maculation and developmental thermal regime (Table 11). Approximately 70% of early emerging field-sampled adults had heavily maculated pronota, and the remainder had moderately maculated pronota. Toward the end of the emergence period, 17% had heavily maculated pronota and 67% had moderately maculated pronota.

Meso- and Metathoracic Color Pattern. The pleura of 95% of *S. interpunctatum* adults reared from the warmest regime were unmarked, whereas 96% reared at the coldest regime had a dark brown oblique marking. Also, adults emerging in spring at the field site possessed this marking, but summer emergents did not. This marking was described by Spieth (1947) as absent in *heterotarsale* and *interpunctatum* and present in *frontale* and *canadense*. The mesonota of coldest regime males were an intense brown, but those of the warmest regime males were light. Metanota of all individuals were relatively unmarked as were the meso- and metasterna.

Maculation in Museum Specimens. Our experimental data indicated that maculation patterns, as expressed rather dramatically on the abdomen, are related to developmental thermal regime (a cooler regime evidently resulting in a longer maturation time and greater deposition of melanic pigment). We tested this hypothesis by studying museum specimens collected from other geographical areas generally reflective of differing thermal regimes within the species ranges. Abdominal pattern had been heavily relied on by identifiers, and it can usually be studied satisfactorily in preserved specimens.

Although no geographic gradient was evident, there were distinct differences in frequencies of individuals between extreme north and extreme south parts of ranges, with slightly maculated individuals more common in the south, and heavily maculated individuals more common in the north. Maculation was, however, highly variable throughout the ranges.

Taxonomy

Phenotypic characters observed in adults of *H. limbata* and *S. interpunctatum* reared at different thermal regimes can be grouped into three sets: (i) variable characters significantly affected by thermal regimes, (ii) variable characters randomly expressed in that they were not correlated with thermal regimes, or (iii) characters not variable among thermal regimes. Characters used by taxonomists (Spieth 1941, Traver 1931, 1935, Burks 1953) to distinguish subspecies of *H. limbata* are summarized along with their relationships to the above groupings in Table 12. Similarly, characters used for *S. interpunctatum* subspecies (Spieth 1947) and their relationships are given in Table 13. Although the sources of the temperature independent variations were not studied, these appear to be caused by individual genetic variability within the test population. As discussed previously, the reported differences in genitalia of *H. limbata* apparently do not exist.

A subspecies is an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of the species (Mayr 1965). A sufficient degree of morphological difference between subspecies resulting from geographical isolation should exist, although there is no general agreement as to how different two subspecies must be. Genetically based subgroups are

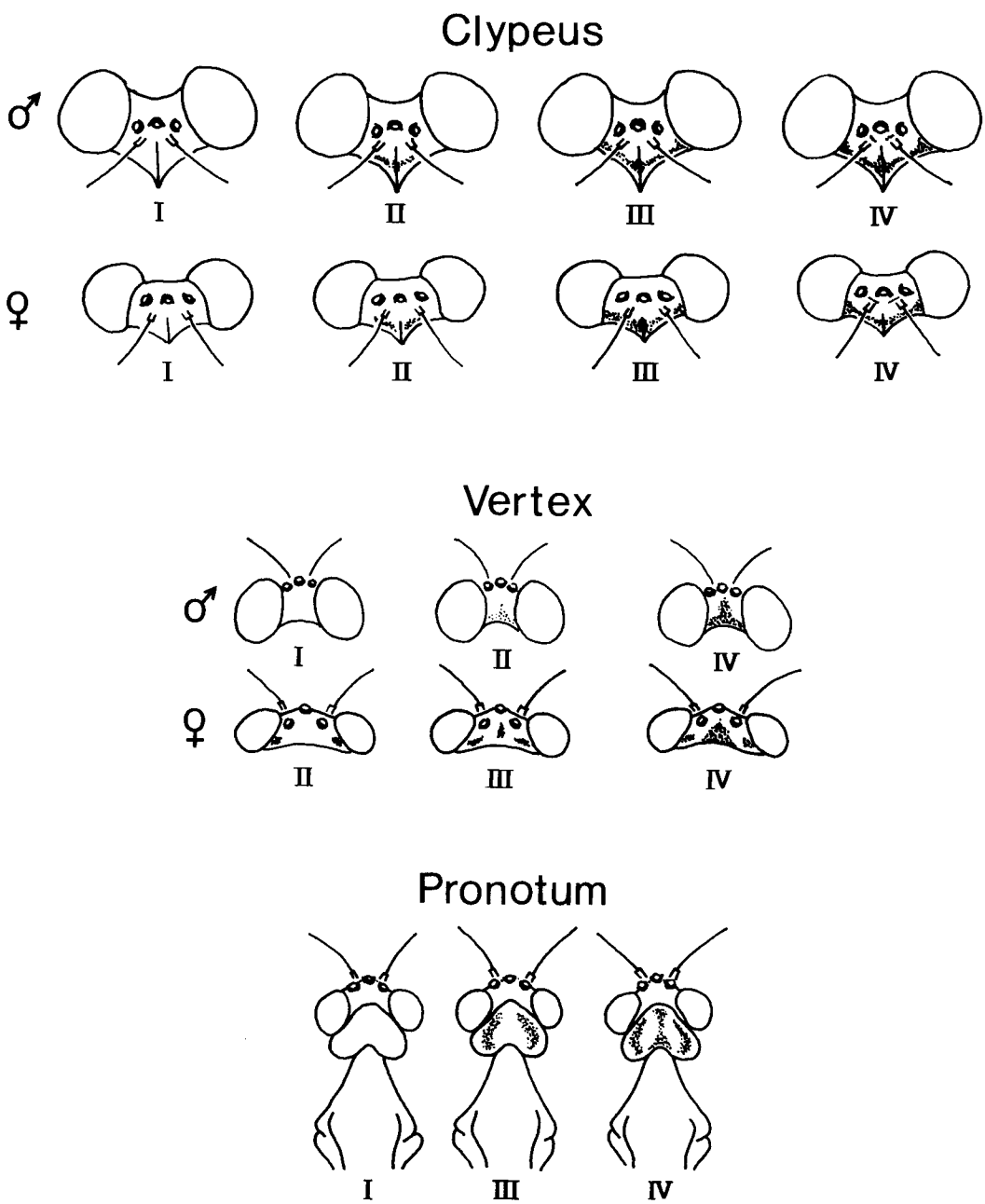

Fig. 10. Head and pronotal maculation of *S. interpunctatum* adults reared from different thermal regimes (I, not maculated; II, slightly maculated; III, moderately maculated; IV, heavily maculated).

implicit in this concept of geographic subspecies. The nominal subspecies described for *H. limbata* and *S. interpunctatum* do not meet these criteria. There are no clear geographic isolates, and variants of these mayflies appear to be for the most part the result of developmental responses to thermal conditions that can be no more sharply delineated than their spatially and temporally variable causative factors.

Populations of a species that differ phenotypically as a response to different environmental conditions they are subjected to during embryological or postembryological development are considered to be ecophenotypes (Ross 1974) (ecomorphs of some authors). Differences between ecophenotypes are not genetically based; however, controlling conditions can act in concert with normal genetic variation. Thus, it is often the distribution of

Table 11. Percent frequency of clypeus, vertex, and pronotum maculation patterns observed in *S. interpunctatum* adults reared from different thermal regimes

	Thermal regime			
	A	B	C	D
Clypeus				
Not maculated	15	24	53	23
Slightly maculated	16	22	36	35
Moderately maculated	16	43	0	18
Heavily maculated	53	11	11	25
Vertex				
Not/slightly maculated	24	28	62	71
Moderately maculated	71	56	21	22
Heavily maculated	5	16	17	8
Pronotum				
Not maculated	4	12	15	28
Moderately maculated	26	68	85	68
Heavily maculated	70	20	0	4

variation that is distinctly differentiated from one ecophenotype to another. Ecophenotypic variation of insect species with complex life cycles may be particularly complex when temperature is the controlling condition because seasonal cohorts as well as spatial populations are affected. This situation has caused considerable confusion in butterfly taxonomy (Shapiro 1980) and has been observed in aquatic insects species as well (Vepsalainen 1971, 1973, 1974, Anderson 1973, Stock 1980).

Our results indicate that several phenotypic differences previously thought to be taxonomically significant for *H. limbata* and *S. interpunctatum* can be generated in individuals (presumably from the same genetic stock) by rearing them in different thermal regimes. Evidently the degree of phenotypic difference is manifested within the phenotypic plasticity of the genome as a result of temperature related environmental factors acting on the larvae during postembryonic development. Because both species have relatively large distributional ranges (so that on a geographic scale many thermal regimes may be experienced) and because it has been shown here and by others that both species have complex life cycles related to seasonality (so that temporally many thermal regimes may be experienced), the complex phenotypic variability contributing to the historical taxonomic difficulty of these species can be explained. What have been considered subspecies (or species) and their intergrades are explicable as ecophenotypes. Other intraspecific differences that were temperature independent are also invalidated as taxonomic characters, because they varied considerably among individuals, and because their frequencies within the distributional ranges of the species do not clearly demark geographic populations.

Although our data do not entirely preclude the possible existence of subspecies in range extremes, we cannot support the retention of a subspecific nomenclature that neither reflects defensible concepts of evolving populations nor provides a useful or even usable classification. Our conclusions may suggest possible explanations for other polymorphic species (or so-called species complexes) that

Table 12. Relationship of historical taxonomic characters of *H. limbata* adults to developmental thermal regimes

Character	Temperature dependent	Temperature independent	
	(Variable)	(Variable)	(Constant)
BL	+		
FWL		+	
F:tb		+	
Tb:t		+	
3t:2t		+	
FL:BL	+		
Penes shape			+
Base body coloration	+		
Dorsal and ventral abdominal mac.	+		
Fore wing coloration	+		
Hind wing infuscation		+	
Leg color		+	
Cerci		+	
Compound eye		+	
Pro-, meso-, and metathorax color		+	

BL, Body length; FWL, fore wing length; F:tb, fore femur to tibia ratio; Tb:t, fore tibia to first tarsi ratio; 3t:2t, 3rd to 2nd fore tarsus ratio; FL:BL, fore leg to body length ratio.

Table 13. Relationship of historical taxonomic characters of *S. interpunctatum* adults to developmental thermal regimes

Character	Temperature dependent	Temperature independent	
	(Variable)	(Variable)	(Constant)
FWL		+	
FWL:1t	+		
2t:1t	+		
Base body coloration	+		
Abdominal maculation	+		
Stigmal spots	+		
Wing coloration		+	
Marginal veins, bulla		+	
Hind leg middle band		+	
Cerci		+	
Clypeal maculation	+		
Vertex maculation	+		
Pronotum color	+		
Meso- and metathorax color	+		

FWL, Fore wing length; FWL:1t, fore wing length to 1st fore tarsus ratio; 2t:1t, 2nd to 1st fore tarsus ratio.

have broad geographic ranges, complex life cycles, demonstrate either intergradation geographically or seasonally, and have thus been difficult to manage taxonomically. Furthermore, many specific and subspecific characters of coloration and size, in particular, might now be viewed with considerably more caution. We hope this study will lead to a more precise taxonomy and clearer understanding of species and populations. More studies of variability and its causative factors will undoubtedly be of great value to the taxonomist.

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Received for publication 18 April 1983; accepted 3 October 1983.