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Bioenergetic and developmental response of a mayfly to thermal variation[1]

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Abstract

Egg development, growth, and emergence of *Isonychia bicolor* were observed in White Clay Creek (Pennsylvania) at ambient temperatures and in fluctuating experimental regimes with diel minima ranging from 12°–12.9°C and maxima between 12° and 20.1°C. Development rate of both eggs and nymphs was correlated positively with increased magnitude of the diel temperature pulse. Adult metamorphosis was most successful in regimes with diel maxima >16°C.

Subimago body size and fecundity for winter generation females were about double those for the summer generation. Reducing spring and summer water temperatures lowered the fecundity of winter and summer subimagoes.

Weight-specific respiration rates of nymphs measured at 14 constant temperatures (range, 1°–21°C) increased with temperature but were inversely related to body size at a given temperature. Metabolic response to short term (1 h) changes in temperature was immediate; thermal acclimation or compensation was not observed.

Energy budgets were calculated for male and female nymphs reared in various thermal regimes. Growth rates, net growth efficiencies, and production:respiration ratios of female nymphs were about twice those of males at all temperatures. Overall net growth efficiencies for *I. bicolor* averaged 44.16% and P:R ratios 0.84 for the combined sexes.

Freshwater biologists have long recognized the importance of a river's thermal condition in affecting the distribution and well being of aquatic fauna (e.g. Ricker 1934; Ide 1935; Reid 1961). Although alteration of natural thermal regimes can have serious ecological consequences, our ability to predict and interpret the results of altered temperature patterns are poor despite a large "thermal effect" literature. Our usual evaluation of biological response at constant temperatures may be inappropriate for application to streams with ectothermic species that exhibit diel and seasonal temperature fluctuations (Macan 1958; Edington 1966; Crisp and LeCren 1970; Smith 1972).

Fluctuating temperatures are important in the growth and reproduction of stream invertebrates, with their effects mediated through both the magnitude and pattern of thermal variation (Sweeney 1976*a*). I here report the effects of diel and seasonal changes in natural and experimental temperature regimes on egg development, nymphal growth and respiration, and adult fecundity of the mayfly *Isonychia bicolor* (Walker).

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Methods

Study species—*Isonychia bicolor* inhabits riffles of small to medium rivers in eastern North America (Leonard and Leonard 1962). It eats diatoms, filamentous algae, and detritus in White Clay Creek, Chester County (39°53′N, 75°47′W), Pennsylvania (Vannote unpublished). Nymphs gather food from the stream bottom (Clemens 1917) or strain material from the current through setae on each foreleg (Edmunds et al. 1976).

Egg development and nymphal growth—The flow-through system with diel fluctuating temperatures, thermal re-

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gimes, and methods used were described by Sweeney (1976*a*).

Eggs were inseminated artificially for developmental studies. Sperm and eggs from single animals were combined on a culture slide for 5 min and washed into a glass jar (5.5-cm OD × 6.5 cm) with 100 ml of filtered (0.45 μm) stream water. Each jar or "replicate batch" was partially submerged in a particular thermal regime. Six replicates per experimental regime and nine at natural stream temperatures were observed daily for eclosion. Newly hatched nymphs were counted and removed immediately from jars.

Methods for nymphal growth studies in experimental regimes have been described elsewhere (Sweeney 1976*a*). Laboratory experiments at White Clay Creek temperatures were done in a closed, recirculating system consisting of four plastic (PVC) troughs (each 1.5 m × 14.5 cm × 8.5-cm max depth) positioned over a 250-liter reservoir. Water was pumped from the reservoir into the troughs. Substrate, screening, and netting of each trough are similar to those of Sweeney (1976*a*). Temperatures were regulated by pumping reservoir water through glass coils submerged in an indoor stream. Continuous pumping kept temperatures within 1°C of the laboratory stream, which is similar thermally to the creek. Algae and detritus collected from the creek were added to all troughs from a single container. Glass slides (26 × 77 mm) were placed in each trough to study the abundance and diversity of algae. Food quality (algal species, composition of detritus) and quantity were not significantly different among troughs (Sweeney 1976*b*).

Growth studies were started with about 750 small (<1 mg) nymphs in each trough at a specific thermal regime. Average dry weight of nymphs sampled on the first day was compared with later subsamples to measure growth. Since females grew much faster than males, the range of body weights increased during each experiment and the distribution became bimodal. This bimodality was used to determine the sex of nymphs subsampled from experimental populations that appear similar morphologically; extensive rearing studies (unpublished data) have shown this method to be accurate.

Respiration—Oxygen uptake at constant temperatures was measured with a differential respirometer (Gilson 1963). Nymphs were collected from the creek, placed immediately in test vessels with 7 ml of filtered (0.45 μm) stream water, and acclimated to test conditions for 1 h. A cheesecloth strip (2.5 × 2.5 cm) was put in each vessel for nymphs to grasp. Oxygen use was measured at 30-min intervals for 3 h. Carbon dioxide evolved during respiration was absorbed by KOH. The number of animals per vessel varied (1–10) depending on body size and temperature so that measurable quantities of oxygen were consumed in each vessel. Density effects were not significant when vessels with one and more than one animal of similar size were compared at temperatures and with sizes where this was possible.

Respiration during temperature fluctuations was measured with dissolved oxygen (DO) probes (Weston and Stack). Each probe had a thermistor for automatic temperature compensation and a stirrer for circulating water within the respiration chambers (300-ml BOD bottles). A known volume of sterilized substrate (gravel: 1.4–2-mm size) and filtered (0.45 μm) stream water was placed in each chamber. Cheesecloth was not used because it tangled in the stirring device. Before each experiment, chambers and water were heated to the maximum temperature expected during the experiment, aerated to saturation, and then cooled to the lowest experimental (base) temperature. This prevented air bubbles from forming during increases in temperature. Water was always >80% saturated when experiments began.

For DO probe studies, nymphs were collected from the creek at dawn, divided into four–five size categories, and several (5–17 depending on size and temperature) from a given category put into each chamber. One probe per chamber was fit-

Table 1. Summary of egg development experiments for *Isonychia bicolor* in six fluctuating temperature regimes (WCC—White Clay Creek).

	Thermal Regimes					
	1	2	3	4	5	WCC
Avg max (°C)	12.1	14.1	16.1	17.1	19.2	18.1
Avg min (°C)	11.7	12.1	11.8	11.8	12.1	15.1
Avg (°C)	11.8	12.7	13.3	13.5	14.5	17.0
First hatch (d)	47	47	38	35	30	25
Median hatch (d)	50	51	40	43	34	27
Last hatch (d)	78	77	71	70	57	54
First hatch (deg·h > 0°C)	13,992	14,685	13,555	11,658	10,778	10,101
Median hatch (deg·h > 0°C)	14,515	16,598	14,243	14,510	13,665	11,421
No. hatches	608	256	1,721	192	681	1,248

ted and sealed with lanolin. The number of animal chambers (size classes) per experiment varied (1–4) according to the range of weights in the population and the condition of the equipment. Two Winkler oxygen determinations were averaged and used to calibrate probes. Output from the probes was relayed into a switch box and read (or recorded) from one DO meter. One probe-chamber system was kept free of animals and monitored continuously for control. Chambers were put in White Clay Creek water from 0800–1600 hours for studies of natural temperature pulses. Water baths were used to produce "controlled" fluctuating regimes. A typical controlled sequence was: 1 h at base temperature, 2.5 h of gradual rise of 5°C, 1 h at base +5°C, 2.5 h of gradual decrease of 5°C, and 1 h at base temperature. No food was provided during the experiments.

Test animals were killed in hot water, dried at 50°C for 24 h, and weighed on an electrobalance. Temperatures for most experiments were at or near prevailing field conditions.

Fecundity—Subimago females were dried at 50°C for 24 h, weighed, and rewet in 95% ethanol. Eggs were removed from rewetted specimens and counted.

Energy budget—Energy partitioning was expressed as

$$A = G + M + R,$$

Where A is assimilation, G is growth, M is molt skin production, and R is respiration. Assimilation was estimated indirectly as the sum of G, M, and R. Relative growth rates (G) were calculated using the equation of Waldbauer (1968).

The rate of molting was used to estimate the number of molts and body size per molt for an average nymph growing from 0.5 to 13.0 mg. Molt skin weights for each molt were predicted from nymphal body weight by an equation ($MSW = 0.097\ NBW + 0.214$; $n = 31$; $R^2 = 0.82$). Molt skin production was the sum of all predicted skin weights for a given interval and was converted from milligrams dry weight to calories (0.764 $\text{cal}\cdot\text{mg}^{-1}$: Stockner 1971) for the energy budget.

Study animals were not starved initially and were free to move in respiration vessels. Measurements thus include both active and standard metabolism, plus a portion of energy used in the digestion, assimilation, and storage of consumed materials (Warren and Davis 1967). Oxygen consumption ($\mu\text{l}\ O_2\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$) was related to biomass production ($\text{mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$) by a conversion factor of $9.359 \times 10^{-4}\ \text{mg}\cdot\mu\text{l}^{-1}$ of O_2. This factor represents the quotient of the oxycaloric equivalent ($4.825 \times 10^{-3}\text{cal}\cdot\mu\text{l}^{-1}$ of O_2: Brody 1945) divided by the caloric content of an *I. bicolor* nymph (5.155 $\text{cal}\cdot\text{mg}^{-1}$, microbomb calorimeter determination: Vannote unpublished). Respiration in $\text{mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$ was converted to $\text{cal}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$ for the energy budget. Respiration costs for a given period were the sum of hourly values for an average-sized individual. In this way, the effects of both

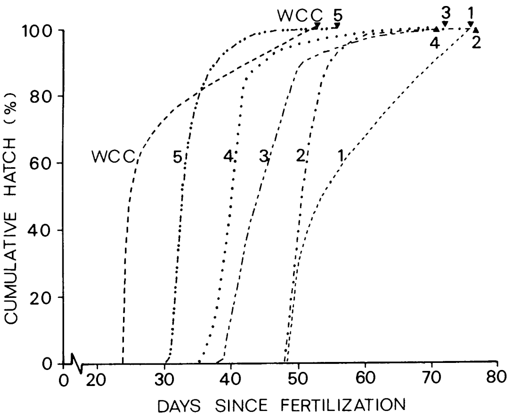

Fig. 1. Temporal distribution of egg hatch for *Isonychia bicolor* at White Clay Creek (WCC) temperatures and in five experimental regimes. Cumulative hatch was calculated at 1-day intervals; lines were visually drawn. (For maximum, minimum, and average temperatures of each regime *see Table 1*.)

short term (1 h) changes in temperature and growth on respiration energy were included.

Results and discussion

Egg development—Developmental time (days to first hatch) and degree-hour (>0°C) accumulations for eclosion were related inversely to maximum diel temperature in regimes pulsing above 14°C (Table 1). Variation in hatching success was not correlated with temperature and may be due largely to problems with artificial insemination.

The small difference between minimum and average temperatures among experimental regimes suggests that the diel maximum may be the best predictor for rate of egg development at fluctuating temperatures. A comparison of egg development in regimes 1–5 and at creek temperatures, however, shows that eclosion occurs sooner in White Clay Creek than would be predicted from the trend of maximum temperatures in experimental regimes, but later with respect to the average temperature trend (Table 1). These data suggest that fluctuating regimes are best characterized for egg hatching by a thermal value lying between average and maximum diel temperatures but more closely aligned with the latter.

Replicate batches of eggs in a given regime usually began hatching on the same day. The temporal distribution of egg hatch, however, was skewed at all temperatures (Fig. 1). Most eggs from a single female would hatch synchronously (e.g. within a week of the first hatch); remaining eggs (≈20%) would hatch after 4–5 weeks. The time between first and last hatch was not correlated with thermal regime. The variation in developmental time within a single clutch may be due largely to differences in eggs with respect to size, nutrient supply, genetic composition, etc. Microenvironmental differences seemed unlikely because eggs were distributed evenly on the jar bottom, siltation and fungal contamination were not a problem, and oxygen concentration was consistently at saturation.

Few workers have studied egg development of lotic macroinvertebrates in fluctuating thermal regimes. Pattée (1975) and Roux (1975) studied the rate of egg development in a planarian and amphipod; Sweeney and Schnack (1977) presented data for an aquatic insect. My results for *I. bicolor* agree with the above studies in that mean temperature appears inadequate to describe egg development in variable regimes, developmental rate increased with increased maximum temperature of the diel regime, and the physiological effect of a given temperature depended on exposure time and the range of diel temperatures associated with it.

Nymphal growth: White Clay Creek temperatures—*Isonychia bicolor* is bivoltine in the creek (Fig. 2). Winter generation adults emerge, mate, and oviposit in early June and eggs hatch in 1–4 weeks. These nymphs metamorphose by early August and egg deposition continues into September. Eggs hatch through autumn and nymphs grow until stream temperatures fall below 15°C. Nymphs collected in late December and divided into four size classes did not grow in laboratory streams when fed algae and detritus and kept at winter stream temper-

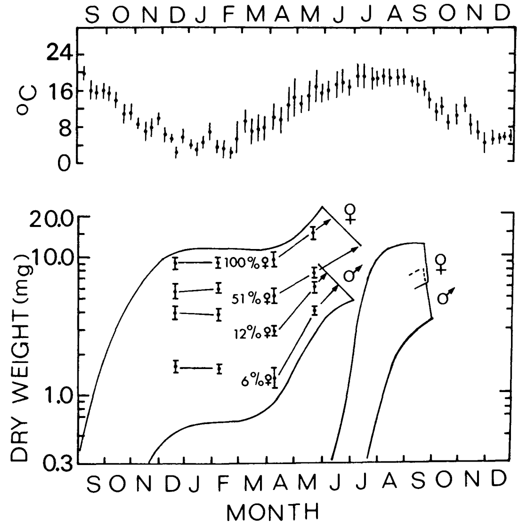

Fig. 2. Population growth of *Isonychia bicolor* in a third-order tributary of White Clay Creek. Solid dots and vertical lines depict diel mean and range of temperature. Upper and lower curved line for each generation shows average of three largest and three smallest nymphs collected from creek (qualitative samples >100 individuals) at 1-week (or less) intervals throughout year. Solid dots and vertical bars indicate mean dry weight and 1 SE for each of four size classes of nymphs reared in laboratory streams at creek temperatures. Arrows show average body size and emergence date of subimagoes from laboratory growth experiments. Sexual composition of four size classes of nymphs collected in early April is indicated.

atures (Fig. 2). Growth resumed in early spring for all four size classes. Figure 2 also shows that male and female nymphs in the creek reach different sizes by midwinter; that the first adults to emerge in June were the largest nymphs of either sex in midwinter (Fig. 2: arrows); that the last cohort to emerge in June of either sex experiences a warmer thermal regime and adults are smaller than earlier cohorts; and that summer generation nymphs grow rapidly but metamorphose at half the size of winter generation adults.

The seasonal variation in adult size of *I. bicolor* agrees with field observations on other polyvoltine species (Thibault 1971; Benech 1972; Fahy 1973; Clifford and Boerger 1974). Few data are available on the quality or quantity of food in streams where seasonal trends in size have been observed. In forested sections of White Clay Creek, net primary production and the concentration of particulate organic matter are greatest in spring and decrease through summer (Bott and Vannote unpublished). Net primary production in open meadow sections exceeds that in wooded reaches and the spring–summer decrease is not as marked. Midsummer levels of both primary production and particulate matter are low but do not appear limiting in this creek. Large quantities of diatoms, detritus, etc. were found in the digestive tract of nymphs throughout summer. Also, the smallest adults to emerge from the winter generation completed nymphal growth during the period of maximum food supply. It appears that food availability is probably not a major factor in the size variation of *I. bicolor* in nature.

Nymphal growth: Experimental regimes—The development of summer generation nymphs was observed at ambient creek temperatures and in five experimental regimes (Fig. 3). The magnitude and rate of growth appeared similar in regimes pulsing above 18°C (regimes 4, 5, and WCC); a slight reduction was observed in regime 3 (diel maximum = 17°C). Temperatures below 15°C attenuated growth and metamorphosis was not observed during either of the two 90-day experiments (regimes 1 and 2). The pattern of growth was similar for both sexes at all temperatures. Female growth rate from hatching to emergence and adult body size were usually about twice those of males.

Maximum stream temperatures in White Clay Creek range from 12°C (first-order tributaries) to 23°C (fourth-order) during summer. Experimental regimes in this study were intended to simulate thermal conditions at points along the creek gradient. The results of growth experiments (Fig. 3) suggest that low-order tributaries might be too cool for *I. bicolor*, and the species does not occur in first- or second-order tributaries of the creek. In addition to temperature, other factors (e.g. qualitative and quantitative

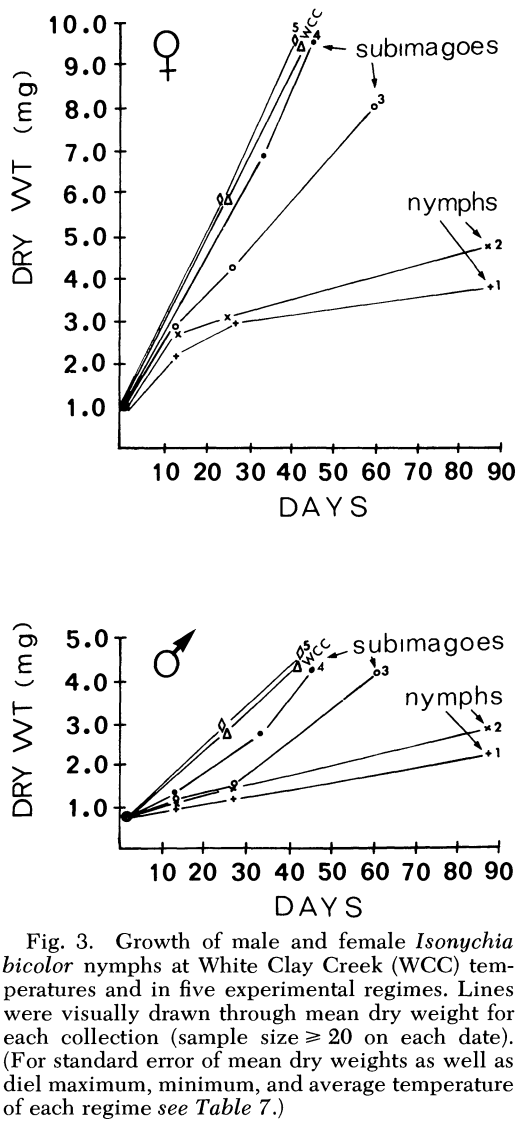

Fig. 3. Growth of male and female *Isonychia bicolor* nymphs at White Clay Creek (WCC) temperatures and in five experimental regimes. Lines were visually drawn through mean dry weight for each collection (sample size ⩾ 20 on each date). (For standard error of mean dry weights as well as diel maximum, minimum, and average temperature of each regime *see Table* 7.)

changes in channel geometry, current structure, and food base) probably affect the ability of *I. bicolor* to colonize and compete successfully in low-order tributaries.

Data from this study and others (Headlee 1940, 1941; Huffaker 1944; Pattée 1975; Sweeney and Schnack 1977) suggest an immediate response to diel changes in temperature. The exact response depends on both the magnitude and pattern of temperature fluctuations. For *I. bicolor*, brief exposure to high temperatures greatly increases the rate of nymphal growth. Studies at constant temperatures usually show the thermal optimum for growth to be higher than a species normally encounters in nature. My data support Howe's (1967) contention that high thermal optima may have resulted from selection of those genotypes growing most rapidly in variable temperatures.

Emergence: *White Clay Creek temperatures*—Winter generation adults emerge from late May through June in the creek, with peak emergence in the first 10 days. Mean body size of subimagoes decreases linearly for both sexes during the emergence period (Fig. 4). Subimagoes collected from 12 and 23 June were used for egg studies and body weights were not determined. A Student-Newman-Keuls (SNK) test (Sokal and Rohlf 1969) showed a significant ($P < 0.05$) reduction of body size for both males and females during emergence. This has been shown qualitatively for other aquatic species (Ide 1940; Benech 1972; Clifford and Boerger 1974).

Summer generation emergence is asynchronous (late July through September) and adult males and females average 4 and 9.5 mg dry wt. Body weights did not decrease significantly for either sex during summer emergence (SNK test: $P < 0.05$). Summer generation adults are similar in size to late emerging adults of the winter generation, perhaps because late winter cohorts are exposed to warm "summerlike" temperatures during growth.

Emergence: Experimental regimes—Female nymphs were collected from the creek in late April when stream temperatures averaged 12.5°C. Fifty nymphs (avg dry wt—10.6 mg) were placed in each of five fluctuating thermal regimes, fed, and reared to maturity. Reduced vernal temperatures delayed emergence, suppressed growth, reduced adult body size, and increased the probability of death during metamorphosis (Table 2). Unsuccessful metamorphosis at low temperatures was indicated by a partial extension of the subimago through the split

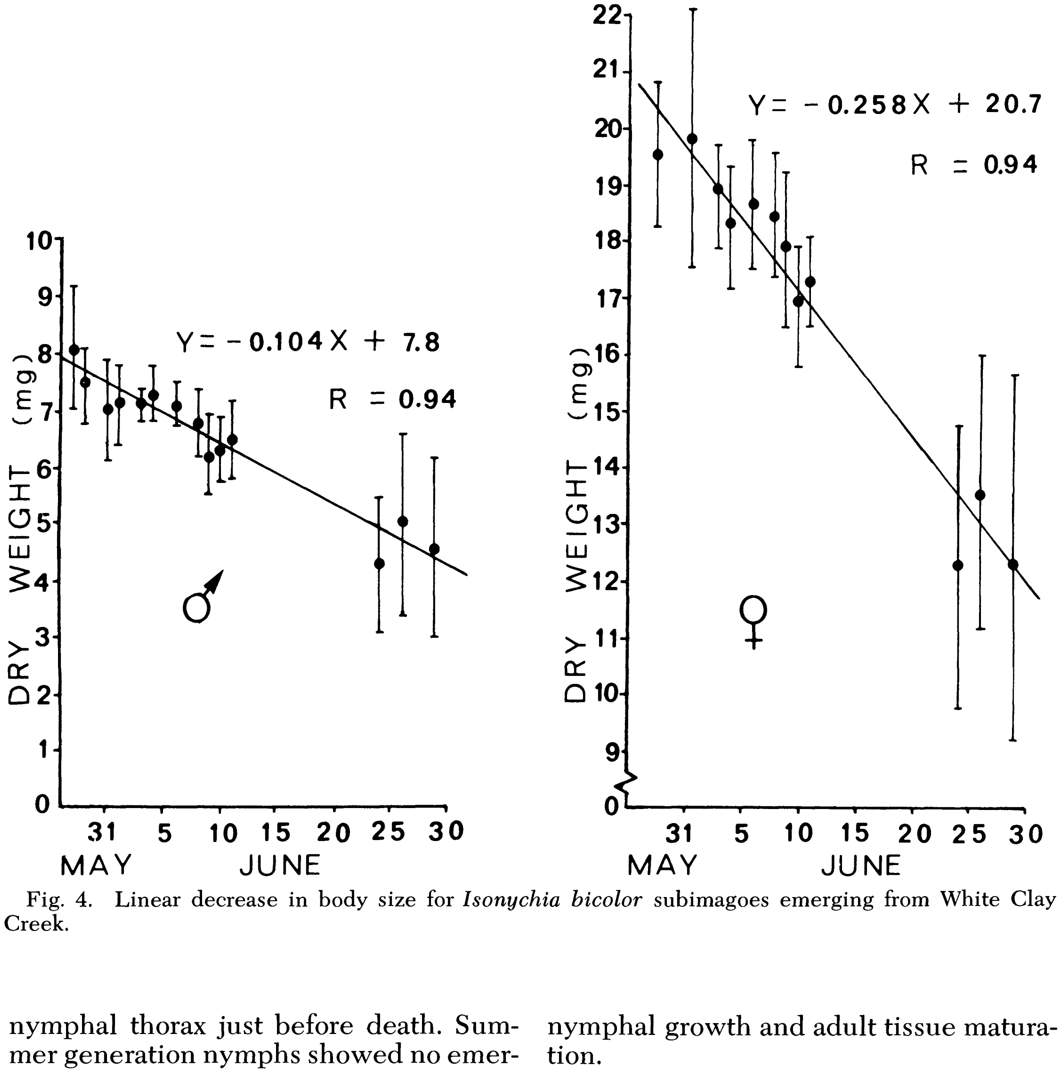

Fig. 4. Linear decrease in body size for *Isonychia bicolor* subimagoes emerging from White Clay Creek.

nymphal thorax just before death. Summer generation nymphs showed no emergence at or below 10°C (Sweeney 1976*b*).

These data suggest that seasonal variation in temperature affects both nymphal tissue growth and the rate of adult tissue maturation in *I. bicolor*. Low temperatures apparently suppress nymphal tissue growth more than adult development and nymphs metamorphose before reaching maximum size. Similarly, adult tissue maturation seems to begin earlier in nymphal development at high temperatures (e.g. summer generation), resulting in small adults. A gradual change from low through intermediate temperatures therefore produces the largest adult by optimizing the relationship between nymphal growth and adult tissue maturation.

Fecundity: Winter generation—Egg production of subimagoes collected the first and last week of emergence from the creek was compared separately (Fig. 5A). Results indicate a gradual shift in weight-specific fecundity, since differences in slope are approaching significance (analysis of covariance, ANCOVA: $F_{1,15} = 3.52$, $0.05 < P < 0.10$). Thus, both female body size (Fig. 4) and weight-specific egg production (Fig. 5A) decrease during spring emergence.

The effect on fecundity of altering vernal water temperatures was studied by placing female nymphs (avg wt = 10.6 mg) in various thermal regimes 30 days

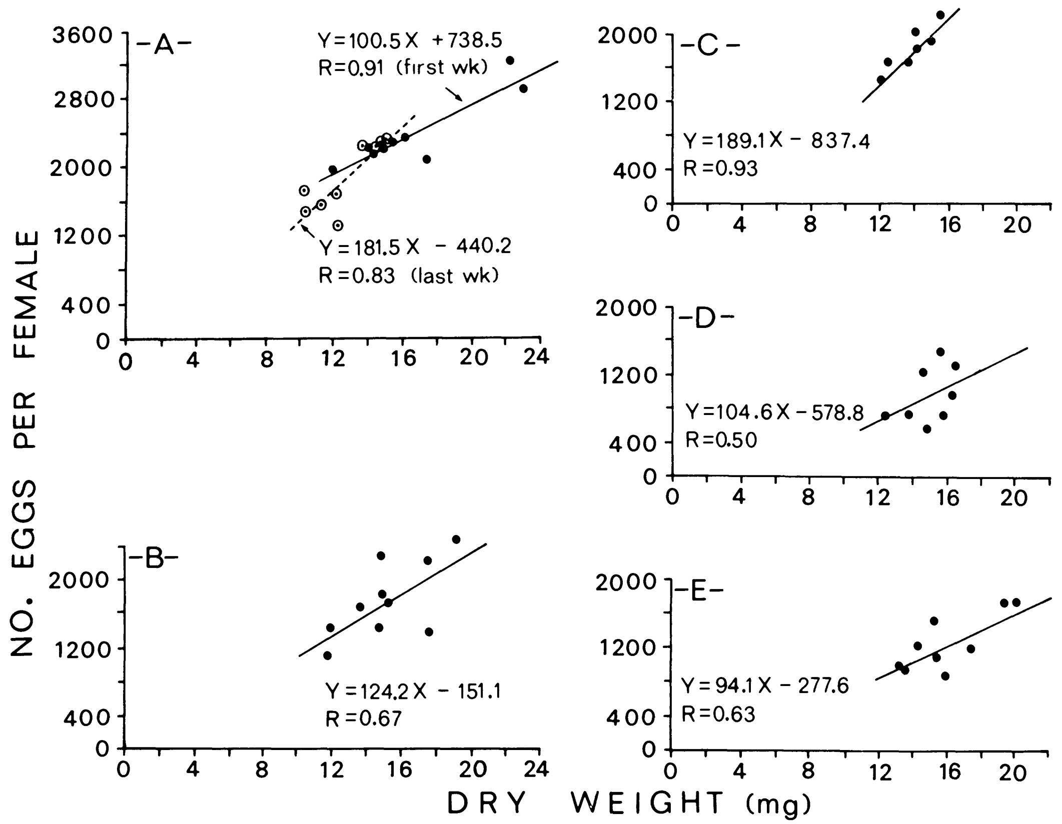

Fig. 5. Weight-specific egg production for *Isonychia bicolor* subimagoes kept at various temperatures during last nymphal instar of winter generation. A—White Clay Creek temperatures; B—regime 4; C—regime 3; D—regime 2; E—regime 1. (For diel maximum, minimum, and average temperatures of each regime *see Table 2.*)

before normal emergence (i.e. subimagoes of Table 2). Egg production in the warmest experimental regime (Fig. 5B; max diel temp, 17.5°C) was similar to results at creek temperatures. Fecundity was depressed in regimes with diel maxima <16.5°C (Fig. 5C,D,E). Large fat bodies were found in subimagoes kept at

Table 2. Adult emergence of *Isonychia bicolor* females kept in five different thermal regimes during last nymphal instar (WCC—White Clay Creek).

	Thermal Regimes				
	1	2	3	4	WCC
Avg max (°C)	12.0	14.2	16.1	17.2	19.0
Avg min (°C)	11.6	12.0	11.9	11.9	13.5
Avg (°C)	11.8	12.9	13.4	14.0	16.1
$\bar{X}_i$*	10.600	10.600	10.600	10.600	10.600
SE $\bar{X}_i$	0.636	0.636	0.636	0.636	0.636
$\bar{X}_f$†	13.976	14.169	14.930	15.582	15.887
SE $\bar{X}_f$	0.376	0.533	1.545	0.044	1.131
First emergence (d)	67	59	55	53	30
Median emergence (d)	71	66	61	54	40
Last emergence (d)	76	78	69	55	51
Emergence success (%)	20.0	28.5	71.4	100.0	100.0

* Avg initial weight (mg) of female nymph.
† Avg final weight of subimago.

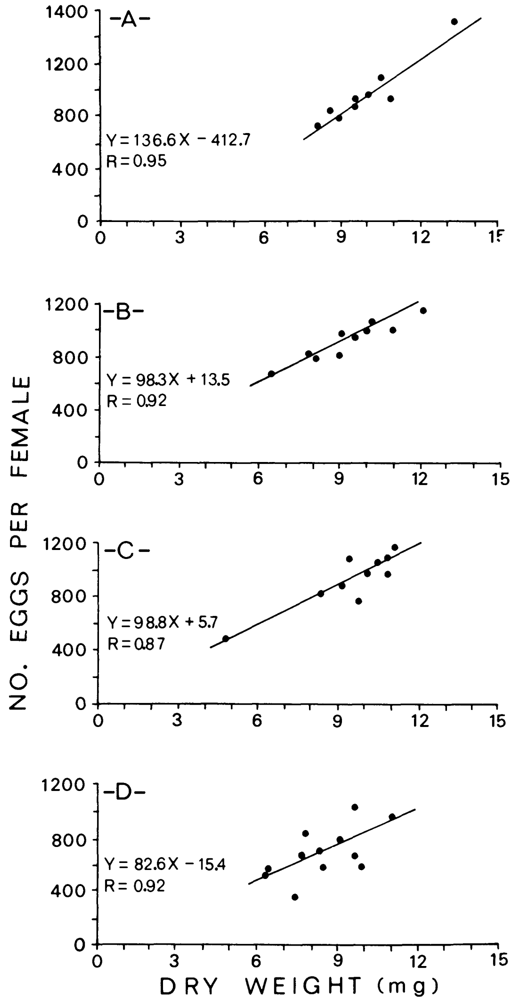

Fig. 6. Weight-specific egg production for *Isonychia bicolor* subimagoes reared in various thermal regimes. A—White Clay Creek temperatures; B—regime 5; C—regime 4; D—regime 3. (For diel maximum, minimum, and average temperatures of each regime *see Table 7*.)

low temperatures (12°–16°C) during late instars; at higher temperatures, fat reserves were depleted during oocyte synthesis. This suggests that reduced temperatures greatly impair the conversion of stored energy into eggs.

Fecundity: Summer generation—Summer generation *I. bicolor* (Fig. 6A) had fewer eggs per individual and per unit weight than the winter generation (Fig. 5A). For example, a 13-mg female contained about 2,050 eggs in the winter generation but only 1,350 eggs in the summer. Although egg size was not studied in detail, egg diameter did not appear to differ significantly among winter and summer generation females. Individual eggs were not weighed.

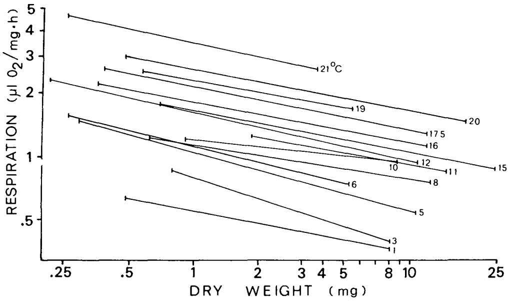

Fig. 7. Weight-specific respiration rates for *Isonychia bicolor* at 14 constant temperatures. Lines are linear regressions on log-transformed data (for regression equation and sample size at each temperature *see Table 3*). Vertical bars at end of each line segment denote size range of nymphs used.

Fecundity of females from the creek (Fig. 6A) was compared statistically with that of animals reared in three experimental regimes with diel maxima of 20°, 18.5°, and 16.9°C (Fig. 6B,C,D). Weight-specific egg production in the 16.9°C regime (Fig. 6C) was significantly lower (ANCOVA: $P < 0.05$) than all other regimes. No difference was observed among the three warmer regimes (Fig. 6A,B,C).

In mayflies, ovulation occurs in the last nymphal instar and eggs are released into oviducts before metamorphosis (Needham et al. 1935). Egg counts on subimagoes are direct estimates of total fecundity and reflect both genetic and phenetic response to the environment during development. Mayfly fecundity has been correlated positively with body length (e.g. Ide 1940; Hunt 1951; Britt 1962; Clifford 1970). Few, if any, data are available on weight-specific fecundity for mayflies. My results indicate that summer adults of *I. bicolor* are smaller and produce fewer eggs per individual and per unit weight than winter adults in White Clay Creek. This suggests a sea-

Table 3. Regression equations (log $Y = b$ log X + log a) for weight-specific metabolism (μl $O_2 \cdot mg^{-1} \cdot h^{-1}$) of *Isonychia bicolor* at 14 constant temperatures.

Temp °C	b_{YX}	S_b	log a	df*	F†	P‡
1.0	−0.201	0.076	−0.265	1,23	6.9	0.025
3.0	−0.338	0.111	−0.104	1,18	9.2	0.010
5.0	−0.267	0.038	+0.013	1,62	48.9	0.001
6.0	−0.276	0.058	+0.044	1,23	22.4	0.001
8.0	−0.182	0.095	+0.058	1,46	3.6	0.100
10.0	−0.101	0.072	+0.075	1,53	1.9	0.250
11.0	−0.201	0.094	+0.151	1,17	4.5	0.050
12.5	−0.241	0.049	+0.211	1,33	23.8	0.001
15.0	−0.179	0.022	+0.202	1,82	62.0	0.001
16.0	−0.183	0.028	+0.253	1,41	40.9	0.001
17.5	−0.222	0.054	+0.334	1,38	16.9	0.001
19.0	−0.177	0.053	+0.351	1, 9	10.9	0.010
20.0	−0.231	0.041	+0.419	1,50	31.3	0.001
21.0	−0.273	0.071	+0.519	1,14	14.6	0.005

* Degrees of freedom.
† Variance ratio.
‡ Level of significance.

sonal response far more complex than simple shifts in body size and egg numbers.

A possible but untested hypothesis is that rearing temperatures affect the number of ovarioles in *I. bicolor*. Increased rearing temperatures reduced both weight and ovariole number in adult *Aedes aegypti* (L.) (Heuvel 1963), but *Culex pipiens* L. reared at lower temperatures had fewer ovarian follicles per unit dry weight (Hosoi 1954). David and Clavel (1967), studying a broader thermal range, found reductions in ovariole numbers both above and below intermediate temperatures for *Drosophila melanogaster* Meigen. Fewer active sites for egg production may explain partially the reduced fecundity at high temperatures (summer vs. winter generation adults) and experimentally low temperatures (both generations).

Respiration: Constant temperatures—Respiration rates were correlated positively with temperature (between 1° and 21°C) but inversely related to body size for any specific temperature (Fig. 7). Regression coefficients of fitted equations seemed to vary considerably over the range of test temperatures (Table 3). But this variation was not significant statistically when all 14 regressions were compared simultaneously (ANCOVA: $F_{13,509} = 0.69$, $P > 0.05$). Significant differences among regression coefficients were obtained when smaller subsets of data were analyzed (e.g. data between 3° and 10°C). These differences were masked statistically in the initial analysis by the total variation and the tendency for coefficients not to vary in one direction with respect to the overall mean coefficient. A shift in regression coefficients over a specific thermal range sug-

Table 4. Multiple linear regression analysis of combined respiration data for *Isonychia bicolor* (log $Y = -0.225 \log X_1 + 0.031 \log X_2 - 0.193$).

Variable	$\bar{X}$	$S_{\bar{X}}$	N	b*	S_b	b'†	b′ ratio
Y (μl O_2/mg/h)	0.068	0.010	537	—	—	—	—
X_1 (mg)	0.449	0.017	537	−0.2253	0.0137	−0.3829	—
X_2 (°C)	11.897	0.245	537	+0.0305	0.0009	+0.7290	1.9

* Partial regression coefficient.
† Standardized partial regression coefficient.

Table 5. Respiration rates ($\mu l\ O_2 \cdot mg^{-1} \cdot h^{-1}$) of *Isonychia bicolor* nymphs during controlled 8-h temperature pulses.

Date	Animals per chamber			8-h Temperature Pulse									Rate (Mh) − rate (Fh)		Avg 8-h rate
		$\overline{X}$*	$s_{\overline{x}}$	First hour (Fh)			Middle hour (Mh)			Last hour (Lh)					
		mg		°C	Obs† rate	Exp‡ rate	°C	Obs rate	Exp rate	°C	Obs rate	Exp rate	Obs	Exp	
6 Dec 74	5	6.505	0.350	2.0	0.336	0.398	7.0	0.930	0.770	2.0	0.509	0.398	2.7	1.9	0.690
	6	4.967	0.240	2.0	—	—	7.0	—	—	2.0	—	—	—	—	0.572
	8	3.301	0.156	2.0	—	—	7.0	—	—	2.0	—	—	—	—	0.698
	10	1.034	0.086	2.0	—	—	7.0	—	—	2.0	—	—	—	—	0.797
11 Dec 74	9	2.742	0.169	3.0	0.552	0.558	8.0	1.129	0.943	3.0	0.836	0.558	2.0	1.7	0.867
	9	1.326	0.125	3.0	—	—	8.0	—	—	3.0	—	—	—	—	1.124
	11	2.005	0.085	3.0	—	—	8.0	—	—	3.0	—	—	—	—	0.797
	7	4.764	0.226	3.0	—	—	8.0	—	—	3.0	—	—	—	—	0.739
14 Feb 75	15	3.099	0.200	3.0	0.647	0.536	8.0	0.961	0.928	3.0	0.462	0.536	1.5	1.7	0.783
	9	6.033	0.401	3.0	—	—	8.0	—	—	3.0	—	—	—	—	0.816
	17	1.614	0.127	3.0	—	—	8.0	—	—	3.0	—	—	—	—	0.821
21 Feb 75	15	3.797	0.762	5.0	0.605	0.721	10.0	1.045	1.038	5.0	0.694	0.721	1.7	1.4	0.903
	10	5.307	0.229	5.0	—	—	10.0	—	—	5.0	—	—	—	—	0.933
	8	7.432	0.419	5.0	—	—	10.0	—	—	5.0	—	—	—	—	0.592
	16	1.755	0.061	5.0	—	—	10.0	—	—	5.0	—	—	—	—	0.977
												0.974			
13 Feb 75	9	6.855	0.321	5.0	0.669	0.616	10.0	0.854	0.974	5.0	0.501	—	1.3	1.6	0.764
	14	2.948	0.151	5.0	—	—	10.0	—	—	5.0	—	—	—	—	1.218
	12	1.179	0.126	5.0	—	—	10.0	—	—	5.0	—	—	—	—	1.002
3 Dec 74	12	2.050	0.163	5.0	0.838	0.851	11.0	1.258	1.232	5.0	0.888	0.851	1.5	1.4	1.098
	8	3.901	0.234	5.0	—	—	11.0	—	—	5.0	—	—	—	—	0.944
15 Nov 74	13	2.279	0.168	6.0	1.044	0.903	11.0	1.509	1.206	6.0	1.161	0.903	1.4	1.3	1.323
28 Feb 75	14	2.920	0.151	6.0	1.073	0.851	11.0	1.682	1.146	6.0	1.172	0.851	1.6	1.3	1.414
	6	7.373	1.082	6.0	—	—	11.0	—	—	6.0	—	—	—	—	1.097
	17	1.369	0.119	6.0	—	—	11.0	—	—	6.0	—	—	—	—	1.668
4 Dec 74	7	6.742	0.301	6.0	0.624	0.696	12.0	1.145	1.026	6.0	0.656	0.696	1.8	1.5	1.049
	12	3.309	0.204	6.0	—	—	12.0	—	—	6.0	—	—	—	—	1.280
19 Nov 74	12	2.403	0.189	7.8	1.194	0.966	14.0	1.827	1.375	7.8	0.907	1.375	1.5	1.4	1.393
20 Nov 74	11	2.271	0.174	10.0	1.032	1.097	15.0	1.377	1.398	10.0	0.836	1.097	1.3	1.3	1.084

* Average weight of a single nymph.

† Observed metabolic rate ($\mu l\ O_2 \cdot mg^{-1} \cdot h^{-1}$).

‡ Expected metabolic rate—calculated from results of metabolic studies at constant temperatures.

Table 6. Respiration rates ($\mu l\ O_2 \cdot mg^{-1} \cdot h^{-1}$) of *Isonychia bicolor* nymphs during White Clay Creek temperature pulses.

				8-h Temperature Pulse				
	Animals per chamber	$\bar{X}$*	$s_{\bar{X}}$	First hour		Last hour		Avg 8-h rate
Date		mg		°C	rate†	°C	rate	
11 Apr 75	11	2.148	0.153	5.0	0.998	12.0	1.825	1.521
14 Apr 75	9	2.780	0.384	5.0	0.856	13.0	1.385	1.219
16 Apr 75	8	3.957	0.406	7.5	1.147	13.0	1.448	1.296
2 Apr 75	8	4.476	0.350	7.0	0.778	14.0	1.152	1.073
28 Apr 75	8	1.323	0.242	9.0	1.286	13.5	1.821	1.483
	8	2.608	0.258	9.0	0.967	13.5	1.205	1.114
17 Apr 75	8	2.742	0.240	8.0	1.029	15.5	1.442	1.261
	5	7.694	0.463	8.0	0.930	15.5	1.273	1.089
8 Aug 75	13	1.711	0.093	12.2	1.542	20.5	3.048	2.360
	13	3.511	0.192	12.2	1.463	20.5	2.987	2.132
9 Aug 75	13	2.061	0.070	12.5	1.502	19.2	2.321	1.932
	7	5.789	0.363	12.5	0.973	19.2	1.473	1.263
10 Aug 75	12	2.029	0.124	12.6	1.436	17.5	1.825	1.603
	9	3.914	0.431	12.6	1.292	17.5	1.595	1.417
12 Aug 75	12	2.500	0.263	13.0	1.468	14.7	1.583	1.508
	10	3.643	0.401	13.0	1.413	14.7	1.526	1.483

* Average weight of a single nymph.
† Metabolic rate ($\mu l\ O_2 \cdot mg^{-1} \cdot h^{-1}$).

gests fundamental differences in the metabolic response of small vs. large nymphs to changes in temperature.

The relative importance of size and temperature in predicting the respiration rate of *I. bicolor* was analyzed by multiple linear regression (Sokal and Rohlf 1969). Partial regression coefficients were standardized and their ratios indicate that temperature is about twice as important as biomass in predicting respiration rate (Table 4). In this analysis, 56% of the variation in respiration rate was explained by temperature alone. Body weight increased the explained variance to 84%.

Respiration: Controlled and naturally fluctuating temperature regimes—Nymphal respiration appears highly sensitive to short term increases and decreases in temperature (Table 5). Only one chamber per 8-h experiment was monitored continuously; average 8-h rates for the remaining chambers were computed from initial and final dissolved oxygen readings. Expected values were derived from regression equations describing respiration at constant temperatures (*see Table* 3). Respiration rate increased rapidly when temperatures were increased (5°–6°C) over a 2.5-h period. Elevated rates returned to original levels when temperatures were lowered back to the initial test temperature. Observed rates were usually close to values predicted from constant temperature studies.

Respiration rates measured during temperature pulses in White Clay Creek also indicate that the metabolism of *I. bicolor* changes diurnally—the amount of change being correlated largely with temperature (Table 6). In the creek, daily water temperatures are usually lowest at 0700 and highest at 1500 hours. It appears that *I. bicolor* metabolism exhibits a similar daily pattern. I do not know if maximum metabolic activity coincides temporally with maximum food ingestion, assimilation, etc. Nymphs collected at 0900 and 1500 always seemed to have their digestive tracts completely filled. The efficiency and rate of processing ingested material, however, may vary considerably over a 24-h cycle.

The metabolism of freshwater gastropods (Berg et al. 1958; Calow 1975) and aquatic insects (Sayle 1928; Pattée 1965; Sweeney 1976*b*) also responds rapidly to diel changes in temperature. I suggest that existing data fail to support Gordon's

Table 7. Partial energy budget and efficiency statistics for *Isonychia bicolor* nymphs reared in six fluctuating thermal regimes of varying magnitudes (WCC—White Clay Creek).

Regime	Sex	Max/ min/ avg (°C)	Days	$\overline{X}_i$* (mg)	$S_{\overline{X}i}$ (mg)	$\overline{X}_f$† (mg)	$S_{\overline{X}f}$ (mg)	G‡ (cal·mg^{-1}·d^{-1})	R (cal·mg^{-1}·d^{-1})	M (cal·mg^{-1}·d^{-1})	A (cal·mg^{-1}·d^{-1})	$G+M/R$§	$G+M/A$ ‖
1	♀	12.6/	1–13	0.707	0.074	2.130	0.867	0.3979	0.1731	0.0062	0.5773	2.33	69.9
		12.0/	13–27	2.130	0.867	2.970	0.262	0.1212	0.1502	0.0028	0.2743	0.82	45.2
		12.3	27–87	2.970	0.262	3.740	0.422	0.0193	0.1406	0.0006	0.1606	0.14	12.4
			1–87	0.707	0.074	3.740	0.422	0.0808	0.1553	0.0017	0.2379	0.53	34.7
	♂		1–13	0.707	0.074	0.840	0.044	0.0682	0.2005	0.0033	0.2720	0.35	26.3
			13–27	0.840	0.044	1.137	0.158	0.1106	0.1889	0.0027	0.3024	0.59	37.5
			27–87	1.137	0.158	2.196	0.438	0.0536	0.1665	0.0009	0.2210	0.32	24.6
			1–87	0.707	0.074	2.196	0.438	0.0607	0.1722	0.0012	0.2343	0.35	26.4
2	♀	14.7/	1–25	0.825	0.046	3.016	0.314	0.2352	0.1621	0.0045	0.4019	1.48	59.7
		12.1/	25–87	3.016	0.314	4.736	0.482	0.0368	0.1382	0.0008	0.1759	0.27	21.4
		13.1	1–87	0.825	0.046	4.736	0.482	0.0833	0.1491	0.0017	0.2342	0.57	36.3
	♂		1–25	0.825	0.046	1.393	0.096	0.1055	0.1837	0.0025	0.2918	0.58	37.0
			25–87	1.393	0.096	2.834	0.246	0.0566	0.1587	0.0011	0.2164	0.36	26.6
			1–87	0.825	0.046	2.834	0.246	0.0650	0.1639	0.0013	0.2304	0.40	28.8
3	♀	16.9/	1–13	0.748	0.045	2.863	0.229	0.4590	0.1704	0.0094	0.6388	2.74	73.3
		12.4/	13–27	2.803	0.229	4.208	0.592	0.1475	0.1467	0.0025	0.2968	1.02	50.5
		13.8	27–60	4.208	0.592	8.092	0.386	0.0986	0.1295	0.0026	0.2308	0.78	43.8
			1–60	0.748	0.045	8.092	0.386	0.1427	0.1393	0.0033	0.2854	1.04	51.1
	♂		1–13	0.748	0.048	1.033	0.094	0.1269	0.1985	0.0028	0.3283	0.65	39.5
			13–27	1.033	0.094	1.297	0.405	0.0834	0.1870	0.0025	0.2729	0.45	31.4
			27–60	1.297	0.405	4.031	0.031	0.1602	0.1558	0.0016	0.3177	1.03	50.9
			1–60	0.748	0.048	4.031	0.031	0.1180	0.1596	0.0023	0.2800	0.75	42.9
4	♀	18.5/	1–13	0.774	0.038	2.752	0.159	0.4448	0.1806	0.0095	0.6350	2.51	71.5
		12.6/	13–34	2.752	0.159	6.892	0.820	0.2107	0.1452	0.0054	0.3613	1.48	59.8
		14.5	34–46	6.896	0.820	9.626	0.542	0.1419	0.1292	0.0024	0.2735	1.11	52.7
			1–46	0.774	0.038	9.626	0.542	0.1907	0.1428	0.0042	0.3377	1.36	57.7
	♂		1–13	0.774	0.038	1.260	0.086	0.1894	0.2035	0.0054	0.3983	0.95	48.9
			13–34	1.260	0.086	2.722	0.188	0.1802	0.1758	0.0034	0.3596	1.04	51.1
			34–46	2.722	0.188	4.215	0.349	0.1849	0.1559	0.0029	0.3438	1.20	54.6
			1–46	0.774	0.038	4.215	0.349	0.1541	0.1675	0.0029	0.3246	0.93	48.4
5	♀	20.1/	1–25	0.743	0.032	5.897	0.653	0.3200	0.1671	0.0069	0.4940	1.95	66.2
		12.9/	25–42	5.897	0.653	9.537	0.560	0.1429	0.1393	0.0032	0.2855	0.87	46.6
		15.4	1–42	0.743	0.032	9.537	0.560	0.2099	0.1521	0.0046	0.3667	1.41	58.5
	♂		1–25	0.743	0.032	2.809	0.299	0.2398	0.1913	0.0049	0.4361	1.27	56.1
			25–42	2.809	0.299	4.511	0.347	0.1409	0.1636	0.0031	0.3078	0.88	46.8
			1–42	0.743	0.032	4.511	0.347	0.1760	0.1758	0.0037	0.3556	1.02	50.5
WCC	♀	20.5/	1–25	0.762	0.041	5.763	0.542	0.3161	0.2030	0.0070	0.5262	1.59	61.4
		16.6/	25–43	5.763	0.542	9.431	0.832	0.1383	0.1709	0.0033	0.3125	0.82	45.3
		18.5	1–43	0.762	0.041	9.431	0.832	0.3039	0.2107	0.0047	0.4192	0.99	49.7
	♂		1–25	0.762	0.041	2.793	0.094	0.2356	0.2336	0.0049	0.4742	1.02	50.7
			25–43	2.793	0.094	4.487	0.396	0.2456	0.2046	0.0036	0.4540	1.21	54.9
			1–43	0.762	0.041	4.487	0.396	0.1701	0.2122	0.0037	0.3862	0.81	45.0

* Avg initial weight of individual nymph for the growth interval.

† Avg final weight of individual nymph for the growth interval.

‡ G = growth, R = respiration, M = molt skin, A = assimilation.

§ Production:Respiration ratio.

‖ Net growth efficiency (NGE).

(1972) proposal of extensive metabolic regulation by aquatic ectotherms during thermal fluctuations.

Insects in general have not shown seasonal compensation or acclimation to environmental temperatures (Lawton 1971; Stockner 1971; Keister and Buck 1974). Data for *I. bicolor* and other stream species (Sweeney 1976*b*) do not show metabolism to be a simple homeostatic process. It is hard to tell whether these animals respond completely to environmental temperatures. For example, metabolism doubles for *I. bicolor* nymphs when temperatures change from 12.2°C to 20.5°C (Table 6). This may represent partial compensation, without which a greater increase would have resulted. It seems that existing data on aquatic species do not support temperature independence but rather temperature-specific stimulation of metabolic processes. "Imperfect" thermal compensation should not necessarily be equated with inefficiency. The overall strategy of aquatic invertebrates may be to keep metabolism within a wide activity range. Diel and seasonal shifts in metabolism may increase the efficiency of resource allocations, energy partitioning, and synthesis or distribution of important cellular compounds.

Energy budget—Table 7 summarizes energy use by *I. bicolor* nymphs during growth in various thermal regimes. Female nymphs had higher assimilation rates and grew faster and more efficiently than males at all temperatures. Net growth efficiencies of both sexes were usually highest when nymphs were small and decreased during growth. Net growth efficiency for the entire growth period was correlated positively with temperature in experimental regimes. Female and male nymphs kept at creek temperatures assimilated 13.4 and 8.1% more energy than animals in regime 5 during development. Growth rates, however, were slightly lower (2.9%—female; 3.3%—male) in the White Clay Creek regime because increased respiration reduced net growth efficiency. High respiration in the creek probably reflects warmer temperatures at night since regime 5 had similar diurnal maxima.

High production to respiration (P:R) ratios were observed for small *I. bicolor* females (range, 1.59–2.74). Average P:R ratios for the entire growth period were 0.71 for males and 0.98 for females. P:R ratios > 0.75 and high net growth efficiencies have been reported for other aquatic macroinvertebrates (*see* Sweeney and Schnack 1977) but both seem higher for *I. bicolor* than in past studies at constant temperatures. Few energy budgets are available for lotic species kept in quasi-natural conditions where temperatures fluctuate diurnally. Edington and Hildrew (1973) and Sweeney and Schnack (1977) studied the energetics of stream insects at fluctuating temperatures and also found that growth rates and efficiencies decreased in summer regimes with reduced diel maxima.

Diel thermal variation affects energy partitioning in *I. bicolor*. Reduced growth efficiency at creek temperatures was attributed to increased respiration at night over that in regime 5. Assimilation was higher in the creek but less energy was available for growth. Stockner (1971) and Sweeney and Schnack (1977) made similar observations for *Hedriodiscus truquii* and *Sigara alternata* respectively in warm thermal regimes. The interpretation for *I. bicolor* assumes that food was not an important experimental variable. This assumption seems justified because: the quality (e.g. particle size, leaf species represented in the mixture, etc.) and quantity of detritus provided during each experiment was similar and did not appear limiting; the rate of algal production per unit area of substrate did not differ significantly among experimental regimes (avg = 0.1 $g \cdot cm^{-2} \cdot d^{-1}$; SE = 0.017); the production of diatom cells was high in each regime (avg = 18.8 cells $\cdot mm^{-2} \cdot d^{-1}$; SE = 2.73); and the dominant algal species (i.e. those representing >90% of total cell numbers) were identical in all regimes (for list of algal species and their relative abundance *see* Sweeney 1976*b*).

Energy lost as shed molt skins during growth represented about 45.6% of total biomass production ($G + M$), 11.4% of total energy produced in calories, but only 5.6% of total assimilated energy ($G + M + R$). Lawton (1971), McCullough (1975), and Sweeney and Schnack (1977) also found low values (range, 1–8.6%) for other aquatic insects.

Synthesis—Streams are often characterized by seasonal and diel temperature fluctuations (Macan 1958; Edington 1966;

Thibault 1971). Annual thermal variance increases with stream order in temperate regions (Smith 1972). Diel variation increases with order up to an intermediate size (order 4–5) but then decreases in larger tributaries (Smith 1972; Vannote unpublished). Climatic changes associated with altitude and latitude also affect the pattern and magnitude of stream temperatures. The potential importance of thermal variation to lotic species has been discussed but largely ignored experimentally. My data show the mayfly *I. bicolor* to be "sensitive" (i.e. responds immediately) to both seasonal and diel changes in temperature. My results agree with the general notion that temperature may be a key factor affecting the distribution, life history, and competitive ability of this species.

The response of *I. bicolor* to short and long term temperature fluctuations indicated little or no tendency to acclimate or compensate metabolically. Animals within a generation (e.g. summer or winter) responded immediately to diel changes in temperature (Tables 5, 6); summer generation animals kept in various temperature regimes (i.e. regimes 2, 3, and 5 of Table 7) did not show significant differences in respiration when measured at a common temperature of 15°C; respiration rates of animals from the winter and summer generation did not differ significantly when compared at temperatures common to both generations (e.g. 12.5° and 15°C). Previous thermal history does not seem to affect significantly the metabolic response of *I. bicolor*, nor of other mayflies (Pattée 1965; Sweeney 1976*b*).

Shifts in energy use when temperature fluctuations were reduced in diel amplitude may reflect changes in the amount of time spent above and below "threshold temperatures." The concept of lower thermal limit, however, is difficult to define absolutely. For *I. bicolor*, the physiological effect of a given temperature appears to be affected by both the length of exposure and the range of temperatures associated with it over a 24-h period.

Energy use by *I. bicolor* seemed optimal when water temperatures pulsed higher than 17°C diurnally while falling below 15°C at night. In general, daily energy flow through insect populations may be pulsed in nature, particularly in small- to intermediate-sized streams. This makes it difficult to estimate any constant temperature that represents adequately, within acceptable confidence limits, a fluctuating regime. Results for *I. bicolor* suggest that the average diel temperature may not be that appropriate temperature.

Temperature sensitivity can be adaptive for *I. bicolor* and other species since reduced temperatures tend to lower energy requirements at times of low food supply (e.g. winter conditions for a grazer) or low intake (e.g. reduced foraging efficiency of visual predators at night, diurnal feeding activity, etc.). Metabolic pathways with different thermal optima could also provide a mechanism for daily (or seasonal) redirection of metabolic flow (e.g. production and use of ATP) and reorganization, without necessitating changes in the relative concentrations of the enzymes of the various pathways (Hochachka and Somero 1973).

In communities of temperature sensitive species, energy flow and rates of short term processes may tend toward uniformity in streams with fluctuating temperatures and high diversity of consumer species. Here the thermal variance maximizes the number of species experiencing an optimum temperature (e.g. maximizes growth and reproduction) each day and distributes their optima over 24 h. Energy flow through populations of various species should increase and decrease at different points in the day, with a net effect approaching uniformity. Many insects, including *I. bicolor*, show maximum population growth (and resource exploitation) during the spring in White Clay Creek when diel changes of 8°–10°C are common (Vannote unpublished production estimates).

The contemporary fauna of temperate streams have evolved within the physical conditions of the lotic system. It seems reasonable that diel fluctuating temperatures would be the norm and perhaps more favorable to these animals than semiconstant regimes. Recent studies have shown significant changes in the invertebrate fauna of streams receiving hypolimnial discharge from large reservoirs (Pearson et al. 1968; Hilsenhoff 1971; Spence and Hynes 1971; Lehmkuhl 1972; Ward 1974). These streams are typically "summer cool" and "winter warm," relative to conditions before dam construction. The reduction of both seasonal and diel thermal variation has been implicated in the disappearance of many aquatic species by the workers cited above. Lehmkuhl (1974) suggested that species may be eliminated by the loss of key "environmental physiological signals," particularly in species with a diapause stage. It seems to me, further, that thermally induced shifts in energy budgeting can disrupt normal growth and emergence patterns and reduce adult body size and fecundity. Reproductive death occurs where recruitment falls below a level critical to successful competition in the community and to population survival in the physical system.

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