To the Graduate Council:

I am submitting herewith a thesis written by Robin Terese Faulk entitled "Oxygen Consumption of Selected Larval Instars of Neophylax consimilis Betten (Trichoptera: Limnephilidae) and Glossosoma nigrior Banks (Trichoptera: Glossosomatidae) in Relation to Temperature and Body Weight." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

David A. Ethier, Major Professor

We have read this thesis and recommend its acceptance:

Accepted for the Council:

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OXYGEN CONSUMPTION OF SELECTED LARVAL INSTARS OF *NEOPHYLAX CONSIMILIS* BETTEN (TRICHOPTERA: LIMNEPHILIDAE) AND *GLOSSOSOMA NIGRIOR* BANKS (TRICHOPTERA: GLOSSOSOMATIDAE) IN RELATION TO TEMPERATURE AND BODY WEIGHT

A Thesis

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ABSTRACT

The respiratory physiological ecology of selected larval instars of two behaviorally and ecologically similar caddisfly larvae, Neophylax consimilis Betten and Glossosoma nigrior Banks, was studied. Larvae were collected from Reed Creek in Blount County, Tennessee, and returned alive to the laboratory. Immature and fifth larval instars of Neophylax and fifth instar Glossosoma larvae were subjected to eight hour respiration studies at experimental temperatures of 5, 10, 15, and 20°C. After each respiration test, experimental organisms were freeze-dried and their weights recorded to the nearest 0.001 milligram.

Statistical analyses of the data revealed a strong inverse relationship between oxygen consumption (respiration) and body weight at all experimental temperatures for immature Neophylax and at temperatures of 10°C and 20°C for fifth instar Neophylax. Fifth instar Glossosoma larvae exhibited weight-dependent respiration at 10, 15, and 20°C. Rates of oxygen consumption at each of the experimental temperatures were not found to vary significantly.

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CHAPTER I

INTRODUCTION

General

The caddisflies, or Trichoptera, are a relatively small order of insects characterized by aquatic immature stages and terrestrial winged adults. To date more than 10,000 species have been described. Their diverse larval forms are found in abundance in many varied freshwater habitats ranging from cold springs to temporary ponds which suggests that they play a significant role in the transfer of energy through the trophic levels of aquatic systems (Wiggins, 1977). In addition, the presence of certain genera and species of Trichoptera in a body of water can be indicative of existing conditions or perturbations within that system, including thermal disturbances (Gaufin and Hern, 1971; Nebeker, 1971; Resh and Unzicker, 1975; Wiggins, 1977).

Since caddisflies comprise a large portion of benthic communities found in fresh waters and are responsible for maintaining at least part of the ecological harmony within these systems, it would appear justifiable that they be given a much higher priority for scientific study than has been accorded them in the past. Much information regarding the general biology of the Trichoptera and other related orders of aquatic insects is now available; nonetheless, there is a

paucity of information concerning respiratory physiological ecology. Oxygen is a basic requirement of all aquatic insects, yet surprisingly few respiration studies have been conducted in North America. Species of Trichoptera have been virtually ignored. The majority of work with immature aquatic forms has been done with European species, primarily with members of the Plecoptera and Ephemeroptera. In consideration of recent innovations in the development of instrumentation for determination of oxygen consumption, present widespread interest in the effects of temperature on aquatic life, and lack of physiological investigative work involving Trichoptera, this research project was thought timely. It was hoped that an insight into respiratory energetics as affected by age, weight, and varying environmental temperatures could be gained.

Experimental Organisms

In order to maximize comparative possibilities two ecologically and behaviorally similar genera living in the same watercourse were selected for respiratory study. They were the caddisfly larvae Neophylax consimilis Betten and Glossosoma nigrior Banks of the families Limnephilidae and Glossosomatidae, respectively. Both are portable case builders commonly found in relatively large numbers in East Tennessee streams and are easily maintained under laboratory conditions.

The Limnephilidae, with some 300 species, represents the largest family of caddisflies in North America. Fifteen species of Neophylax are known in the United States and Canada. Occurring within the area from Newfoundland to Minnesota and southward through Missouri to Georgia are the eastern and central species. Western species are found widely in the mountains from California to British Columbia (Wiggins, 1977).

Larvae of the genus, which may be up to 16.5 mm in length, are confined to running waters where their food is generally fine detrital particles or periphyton. Neophylax builds a tubular larval case constructed of coarse rock fragments with several larger stones on either side serving as ballast. Early instars grow during the late fall and winter months. In early spring, final or fifth instars fasten their cases to rocks, sealing off the entrance and remaining in larval diapause until initiation of metamorphosis. Adults generally emerge during the late summer months (Wiggins, 1977).

Neophylax consimilis Betten was first described in 1934. The mesonotum bears an antero-median notch which is diagnostic of the genus. Larvae of this species have distinctly elongated heads varying from dark brown to black. A pair of ventro-lateral thumb-like projections are present on the first abdominal segment, and the abdomen bears single gill filaments (Flint, 1960).

Representatives of the Glossosomatidae live predominantly in cold streams and rivers with 80 species being found throughout the United States and Canada. Glossosoma nigrior Banks is common in the northeastern part of the North American continent and its range extends westward to Minnesota (Wiggins, 1977). Glossosomatid larvae are typically found on the upper, more exposed surfaces of rocks where they feed primarily on diatoms and organic ooze (Anderson and Bourne, 1974; Kovalak, 1976). Members of this genus build extremely distinctive saddle-shaped cases out of fine rock particles. The structural design of the case, analogous to that of a tortoise shell, enables the head and anal prolegs of the larva to protrude (Ross, 1964).

Larvae of the genus may attain lengths up to 9.5 mm. Of the three thoracic segments only the pronotum is covered with dark, sclerotized plates. All three pairs of thoracic legs are of the same approximate size with the first pair being attached to the pronotum in an extreme antero-lateral position characteristic of the genus. Abdominal gills are generally absent (Wiggins, 1977).

Glossosoma nigrior Banks was first described in 1911. This species exhibits a univoltine life cycle although some bivoltine species have been reported. Glossosomatid larvae grow during the winter months with adults emerging in spring. Unlike Neophylax, fifth instar Glossosoma larvae do

not aestivate but remain active as do previous larval stages (Anderson and Bourne, 1974).

CHAPTER II

LITERATURE REVIEW

Hynes (1970) stated that the study of the ecology of stream insects is still primarily exploratory and descriptive in nature. In recent years refinements in techniques have made evaluation of some of the previously unknown aspects of aquatic ecology possible; however, investigations of trichopteran respiratory physiology have been decidedly few. Mill (1973) presented a comprehensive treatment of the respiration of aquatic insects in which he discussed important morphological and physiological adaptations of the major orders. A similar review was given by Hynes (1970). In the following paragraphs an overview of pertinent contributions to the field of trichopteran larval respiration is presented.

Stream insects have water continuously flowing over their respiratory surfaces. Feldmeth (1968, 1970a) cited Ruttner (1926) as the first to realize the importance of flowing water to the respiration of stream organisms—namely, the prevention of the formation of an enveloping layer that could limit gaseous diffusion into the organism. This enveloping layer is today referred to as the "boundary layer." The rate of oxygen diffusion into the respiratory surfaces of an organism is dependent upon its thickness; it is

therefore not surprising that aquatic animals have evolved mechanisms which serve to effectively reduce the thickness of the boundary layer (van Dam, 1938; Fox and Sidney, 1953; Philipson, 1954; Feldmeth, 1968, 1970a, 1970b; Leader, 1971).

Trichoptera larvae obtain oxygen by cutaneous diffusion, either through the body surface or via tracheal gills. In their studies of aquatic insects Dodds and Hisaw (1925) noted that free-living species were generally found in swiftly flowing waters and were morphologically different from case building forms. Earlier, Dodds and Hisaw (1924) had advanced the idea that the portable case making caddisflies maintained a steady flow of water through their cases by undulatory movements of the abdomen, an idea supported by Milne (1938). This undulation or ventilation by the larva causes water to enter the case through the anterior opening and exit via the posterior opening, thereby bathing abdomen and gills in oxygen rich water and enhancing respiratory efficiency. According to Leader (1971):

> During pumping the anterior part of the body is anchored by means of a dorsal and two lateral protuberances of the first abdominal segment. These are expanded by blood pressure and the lateral protuberances have small terminal hooks or spines which grip the wall of the case. The anal region is fixed rigidly in place by the anal hook, and a wave of sequentially ordered muscular contractions causing dorso-ventral undulations of the abdomen, drives water backwards over the abdominal tracheal gills.

Jaag and Ambühl (1964), working with the limnephilid Anabolia, noted that larvae with cases survived at lower oxygen concentrations than did larvae removed from their cases. Several investigators have shown that ventilatory movements of stream dwelling, tube-case caddisfly larvae are of an increased rate and magnitude in oxygen depleted water and water of increasing temperature (van Dam, 1938; Fox and Sidney, 1953; Philipson, 1954). Leader (1971) observed that frequency of ventilation was related to dissolved oxygen concentration over a small range of oxygen pressure but was inhibited at low oxygen pressures in the marine trichopteran larva, Philanisus plebeius.

> Philanisus however may be regarded as an exceptional member of the Trichoptera in that its environment is one of violent fluctuations. The insects are often left stranded on sheets of coralline as the tide ebbs . . . They may be exposed to very high temperatures or rainfall. Further south in winter they may similarly endure freezing temperatures. Under these conditions the ability to remain quiescent, with a low respiration rate, until the tide flows back again might have selective advantage.

Feldmeth (1968, 1970a, 1970b), working with Pycnopsyche lepida and P. guttifer of the family Limnephilidae, found that as current speed decreased, ventilatory rates increased suggesting that low current speed was compensated for by ventilatory movements in both species. Using the same experimental animals, he determined that respiration rates were increased due to water current. Philipson (1954) demonstrated a similar relationship for Hydropsyche

instabilis, a non-case builder, and Polycentropus flavomaculatus. He observed a decrease in ventilation as current velocity increased.

The functional role of tracheal gills in respiration was first suggested in the eighteenth century. Morgan and O'Neil (1931) and Mill (1973) explained that Reaumur in 1734 believed that tracheal gills of Phryganea larvae served a respiratory function, an interpretation that was later accepted by Dufour in 1847 for a hydropsychid larva and by Houghton in 1868 for several species of caddisflies. However, Sleight (1913) concluded that not all trichopteran larvae were dependent upon tracheal gills as respiratory organs but relied rather on the thin body integument as the chief site of gaseous exchange.

Virtually all case building caddisfly larvae have filamentous gills present on the abdomen as do a few which do not construct cases (Mill, 1973). Dodds and Hisaw (1924) reported an increase in gill filaments with increase in body size for case builders; no such relationship was evident in free-living larvae though these individuals exhibited an inverse relationship between the number of gill filaments and amount of environmental oxygen.

Morgan and O'Neil (1931) experimenting with Macronema zebratum larvae reported that amputation of all tracheal gills did not appreciably affect oxygen consumption. In the

absence of gills larvae apparently depended upon cutaneous respiration through the body surface, implying that tracheal gills, at least in this species, were accessory respiratory organs.

CHAPTER III

MATERIALS AND METHODS

Field Collection

Collection site. Both N. consimilis and G. nigrior larvae were obtained from Reed Creek located approximately two miles above Walland in Blount County, Tennessee. Reed Creek, draining Chilhowee Mountain and emptying into the Little River, supports a rich aquatic fauna, including many representatives of the orders Trichoptera, Plecoptera, Ephemeroptera, and Odonata. Stream substrates vary from fine sand to rock with numerous riffle areas present. The streambed is moderately shaded by stands of Cornus florida (flowering dogwood), Platinus occidentalis (sycamore), Quercus falcata (Southern red oak), and Betula sp. (birch).

Various chemical and physical parameters of the research site were assessed periodically. Water temperature, dissolved oxygen, and pH were monitored over a nine-month period beginning in August 1977 and ending in April 1978. Creek temperatures ranged from a high of 19°C during the late summer to a low of 3°C in the month of February. Dissolved oxygen levels fluctuated from 8.6 to 11.7 mg/liter; pH readings remained virtually unchanged throughout the study, varying between 7.1 and 7.3.

Collection of larvae. Collections of Neophylax and Glossosoma larvae were made by randomly selecting stones from both the riffle and slower moving portions of the stream and randomly removing appropriate organisms with forceps. Larvae were then placed in a flat enamel pan containing stream water, small rocks, and leaf litter. The above container was in turn placed in a styrofoam cooler for transport to the laboratory.

It was observed that the early instars of N. consimilis developed along riffle margins of Reed Creek with the fifth instars being found at the head of riffles. This finding was consistent with that of Sedell (1971) who determined that smaller, immature larvae of N. concinnus and N. oligius developed in riffle margins of clean streams and brooks in Pennsylvania while fifth instars were observed at riffle heads.

Identification of both immature and mature larval instars in the field was based upon sight recognition of characteristic case structure for each genus. Upon arrival in the laboratory a subsequent verification using morphological characters was made.

Laboratory Study

Maintenance of experimental organisms. In the laboratory all larval instars of Neophylax and Glossosoma

were maintained in four Freas 818 incubators at temperatures of 5, 10, 15, and 20°C. Each incubator operated on a photoperiod of 14 hours of light and 10 hours of darkness. All early instar Neophylax were initially placed at 5°C after field collection. Following an acclimation period of three days at 5°C, 60 larvae were transferred to the 10°C incubator. Seventy-two hours later, 40 larvae were then transferred from 10°C to the next higher temperature of 15°C. Of these 40 acclimating at 15°C, half were placed at the highest temperature of 20°C, again after a three-day period. Fifth instar Neophylax and Glossosoma were treated in the same manner described above with a reduction in larval numbers, however. Each group of larvae was acclimated a minimum of three days at each test temperature before being subjected to respiration studies.

At all temperatures experimental larvae were held in flat enamel pans containing water taken from the stream in which they were collected. Vigorous aeration was supplied by means of Hush II and Whisper 600 aquarium pumps. Substrate consisting of small stones and pebbles was provided for larval attachment in each pan. Leaf litter was provided as the only food source; however, animals had access to no food 24 hours prior to respiration tests.

Collection of data. Respiration measurements were made at 5, 10, 15, and 20°C for immature and mature larval

instars of N. consimilis and for mature, fifth instar G. nigrior larvae. All measurements were made employing a Gilson Model GRP 20 differential respirometer. Using a Buchner type funnel, water from Reed Creek was filtered through Whatman #1 filter paper at least two days prior to each test. Streptomycin sulfate was added to the filtered water at a concentration of 25 mg/l and the resulting solution placed in an incubator set at the given test temperature. Organisms were transferred from original holding pans into the filtered, treated water one day prior to each respiration experiment.

Reactive respirometer flasks had a total volume of approximately 9 ml and held roughly 4 ml of test water for the experimental organisms. It was of the utmost importance that the gas volume in the individual reactive flasks equalled that of the individual reference flasks; in order to achieve this objective reference flasks were filled with a 10 mg/l solution of mercuric chloride and then 5 ml of solution were drawn from each. To absorb carbon dioxide the center well of each reactive or test flask was filled with cotton saturated with a 10 percent potassium hydroxide solution.

In order to assure a tight and proper seal, high vacuum silicone stopcock grease was applied to all glassware fittings on the respirometer. Following each respiration

experiment all glassware was boiled for at least two hours in distilled water containing Sparkleen detergent. Glassware was next placed in an acid rinse solution for a minimum of 12 to 24 hours after which it was washed with distilled water and permitted to air dry before being utilized again.

All respiration tests were conducted for 8 hours between the hours of 11:00 a.m. and 7:00 p.m. Eastern Daylight Time with the exception of one experiment. Readings were taken hourly for the duration of the experiments. When testing immature Neophylax larvae, 16 test flasks each containing a single encased larva and 4 control flasks each containing an empty larval case were run at each designated experimental temperature. For each test involving fifth instar N. consimilis and G. nigrior eight test flasks containing one encased larva and two control flasks with a single empty case were run for each genus. Control values were averaged and used to correct oxygen uptake readings of each individual larva. Blank controls (no case) and controls containing a single empty larval case were compared and found to give very similar values, indicating that the case itself was not respiring.

After placing the experimental organisms in reactive flasks and immersing the vessels in the respirometer water bath, the flasks were allowed to equilibrate for at least an hour before sealing the respirometer system. Once sealed,

the system was permitted to equilibrate one additional hour before readings were initiated. This two-hour period prior to evaluation of oxygen consumption was deemed sufficient to allow larvae to recover from handling and adjust to experimental conditions.

After the final hourly reading the respirometer system was opened and test flasks removed from the bath. Individual larvae were removed from their cases by using extremely fine jeweler's forceps and placed in distilled water as a rinse. Specimens were then placed in small stoppered freeze drying vials partially filled with distilled water and immediately frozen in a Frigidaire refrigerator freezer. After filling and freezing approximately 30 flasks, the vials were allowed to sit on slabs of dry ice for 20 minutes before being placed on a Labconco Model 3 freeze dryer. Specimens remained on the freeze dryer for a minimum of 24 hours after which they were removed and weighed on a Cahn Model 4700 automatic electrobalance. Individual weights were recorded to the nearest 0.001 milligram.

Analyses of Data

A series of linear and stepwise multiple regressions were run on the IBM 360/65 computer. Variables included instar group, body weight, oxygen consumption (respiration), and temperature. Oxygen consumption, the dependent variable, and body weight, an independent variable, were transformed

using the logarithm to satisfy the Model I regression assumption of linearity. F-tests were utilized in testing whether the slopes of the individual regression lines were significantly different from a slope of zero. F-tests were also used to determine the model that best explained the variation of the dependent variable after introduction of one or more independent variables in the stepwise multiple regressions and to rank the independent variables according to the amount of variation attributable to each.

In addition to the computer regression programs, Two-way Analyses of Covariance (ANCOVA) were calculated. In each case the ANCOVA was used to ascertain whether instar group and temperature were significantly affecting the regressions and whether these effects were acting independently of one another or interacting. Student's t-Tests were calculated and used to determine regression coefficients which were significantly different from one another. All statistical tests were evaluated at the 5 percent level of significance.

CHAPTER IV

RESULTS AND CONCLUSIONS

Experimental Data

Summaries of respiration data for early and fifth instar Neophylax consimilis and for fifth instar Glossosoma nigrior can be found in Tables A-1 through A-12, Appendix. Adjusted eight-hour readings, microliters O_2/hr, weight of experimental organisms, and microliters O_2/mg wt/hr are presented.

Regressions

The relationship of log. oxygen consumption and log. body weight at each of the four experimental temperatures was analyzed by linear regression for early and fifth larval instars of Neophylax and for fifth instar Glossosoma larvae. A summary of the regression analyses is presented in Table 1. Immature Neophylax are designated as Group 1 with fifth instars of the genus being designated Group 2. Fifth instar Glossosoma represent Group 3.

A significant regression was established between log. oxygen consumption and log. body weight at all temperatures for Group 1; Group 2 showed significant regressions only at 10°C and 20°C. A significant relationship between log. respiration and log. body weight was evident in Group 3 at all temperatures except 5°C.

TABLE 1

SUMMARY OF REGRESSION ANALYSES OF LOG. RESPIRATION AS A FUNCTION OF LOG. WEIGHT

Source	S.S.	D.F.	M.S.	F-Value
	Group 1, Temp. 5°C			
Regression	0.519	1	0.519	4.21*
Error	3.218	26	0.123	
Total	3.737	27		
	Group 1, Temp. 10°C			
Regression	3.447	1	3.447	28.02*
Error	3.454	28	0.123	
Total	6.901	29		
	Group 1, Temp. 15°C			
Regression	4.904	1	4.904	26.08*
Error	5.262	28	0.188	
Total	10.166	29		
	Group 1, Temp. 20°C			
Regression	0.908	1	0.908	11.07*
Error	1.069	13	0.082	
Total	1.977	14		
	Group 2, Temp. 5°C			
Regression	0.375	1	0.375	3.54
Error	1.381	13	0.106	
Total	1.756	14		
	Group 2, Temp. 10°C			
Regression	0.359	1	0.359	4.60*
Error	0.788	10	0.078	
Total	1.147	11		
	Group 2, Temp. 15°C			
Regression	0.138	1	0.138	3.65
Error	0.922	14	0.075	
Total	1.060	15		
	Group 2, Temp. 20°C			
Regression	0.612	1	0.612	7.03*
Error	1.217	14	0.087	
Total	1.829	15		

TABLE 1 (continued)

Source	S.S.	D.F.	M.S.	F-Value
	Group 3, Temp. 5°C			
Regression	0.552	1	0.552	2.13
Error	2.333	9	0.259	
Total	2.885	10		
	Group 3, Temp. 10°C			
Regression	0.860	1	0.860	10.49*
Error	0.820	10	0.082	
Total	1.680	11		
	Group 3, Temp. 15°C			
Regression	1.768	1	1.768	7.69*
Error	2.304	10	0.230	
Total	4.072	11		
	Group 3, Temp. 20°C			
Regression	2.641	1	2.641	20.96*
Error	1.385	11	0.126	
Total	4.026	12		

*Significant at 5 percent level.

Stepwise Multiple Regression

In order to determine whether the independent variables, weight and temperature, were exerting an effect on oxygen consumption and to determine the relative importance of each, stepwise multiple regression was used. Each of the three designated groups of larval instars were analyzed separately and the results presented in Table 2.

Type II Sum of Squares shown in the table is the additional explained variation obtained by adding the independent variable of that step to the regression equation (Log. Oxygen Consumption = $a + b_1W + b_2T$ . . .) already containing the other independent variables. The order in which the independent variables are entered is indicative of the relative amount of variation they explain. The R^2 value signifies the proportion of the total variation explained by the regression equation of each step.

In Group 1 (immature Neophylax instars), a highly significant amount of variation in the dependent variable, log. oxygen consumption, was attributable to the independent variable, log. body weight, entered in step 1. Therefore, log. body weight but not temperature was needed for an adequate model to predict log. oxygen consumption for Group 1.

When, in Group 2 (fifth instar Neophylax), log. body weight was again entered in step 1, it explained a significant

TABLE 2

SUMMARY OF STEPWISE MULTIPLE REGRESSIONS
SHOWING RELATIVE IMPORTANCE OF
INDEPENDENT VARIABLES IN
EXPLAINING VARIATION IN
OXYGEN CONSUMPTION

Depend. Variable	Step No.	Independ. Variable To Enter	S.S.	Type II S.S.	R^2	F-Value
		Group 1				
Log. Oxygen Consumption	1	Log. Weight	8.8409	8.8409	0.3813	63.10*
	2	Temp.	9.1070	0.2661	0.3928	1.89
		Group 2				
Log. Oxygen Consumption	1	Log. Weight	1.9939	1.9939	0.2617	19.11*
	2	Temp.	2.6075	0.6136	0.3422	6.86*
		Group 3				
Log. Oxygen Consumption	1	Log. Weight	6.3304	6.3304	0.4586	38.60*
	2	Temp.	6.7640	0.4335	0.4900	2.77

*Significant at 5 percent level.

amount of variation in log. oxygen consumption. Temperature, entered in step 2, yielded a significant F-value, increased R^2, and therefore served to explain an additional amount of variation in log. oxygen consumption. An adequate model to predict log. oxygen consumption for Group 2 must include both log. body weight and temperature.

Group 3 (fifth instar Glossosoma) exhibited the same trend as that of Group 1. Again log. body weight explained most of the variation in log. oxygen consumption with temperature explaining very little.

Although the results of the stepwise multiple regression analyses indicated a difference between immature and fifth instar Neophylax larvae and between fifth instar Neophylax and fifth instar Glossosoma, they did not explain the nature of the difference. The model for Group 1 and Group 3 included only body weight but yet explained a greater total amount of variation in the dependent variable than did the model for Group 2, containing both body weight and temperature.

Two-way Analysis of Covariance

A Two-way Analysis of Covariance (ANCOVA) was calculated to determine if the relationship of log. oxygen consumption with log. body weight differed for immature and fifth instar Neophylax and whether it differed among temperatures. The results are presented in Table 3. A second ANCOVA was

TABLE 3

TWO-WAY ANALYSIS OF COVARIANCE OF LOG. OXYGEN CONSUMPTION-LOG. WEIGHT RELATIONSHIPS FOR EARLY AND MATURE NEOPHYLAX LARVAL INSTARS

Source	S.S.	D.F.	M.S.	F-Value
Instar	0.2418	2	0.1209	1.02
Temperatures	2.6052	6	0.4342	3.68*
Interaction	0.0614	6	0.0102	0.08
Error	17.3116	146	0.1180	
Total	20.2200	160		

*Significant at 5 percent level.

calculated involving fifth instar Neophylax and fifth instar Glossosoma. The results are given in Table 4.

In both cases, the analyses showed temperature significant when tested at the 5 percent significance level. The study suggested that data from different instar groups could be pooled, but that in each instance, four regression lines, one for each temperature, were the best estimation of the relationship of log. oxygen consumption with log. body weight.

The eight regression lines illustrating log. oxygen consumption as a function of log. body weight are graphed in Figures 1 and 2. The equations for these linear regressions are found in Table 5.

Student's t-Tests

In order to sort regression coefficients differing significantly, Student's t-Tests were made at the 5 percent significance level. Table 6 shows the results of these tests. A significant difference between two regression coefficients would indicate that the two combinations of instar group with temperature which they represent exert a significantly different effect on the rate of change of oxygen consumption with body weight. The results of the analyses indicated that there were no significant differences between the regression coefficients of the four experimental temperatures for either of the pooled groups of larvae.

TABLE 4

TWO-WAY ANALYSIS OF COVARIANCE OF LOG. OXYGEN CONSUMPTION-LOG. WEIGHT RELATIONSHIPS FOR *NEOPHYLAX* AND *GLOSSOSOMA* FIFTH INSTARS

Source	S.S.	D.F.	M.S.	F-Value
Instar	0.4462	2	0.2231	1.83
Temperatures	1.8666	6	0.3111	2.55*
Interaction	0.1124	6	0.0187	0.15
Error	11.1506	91	0.1220	
Total	13.5758	105		

*Significant at 5 percent level.

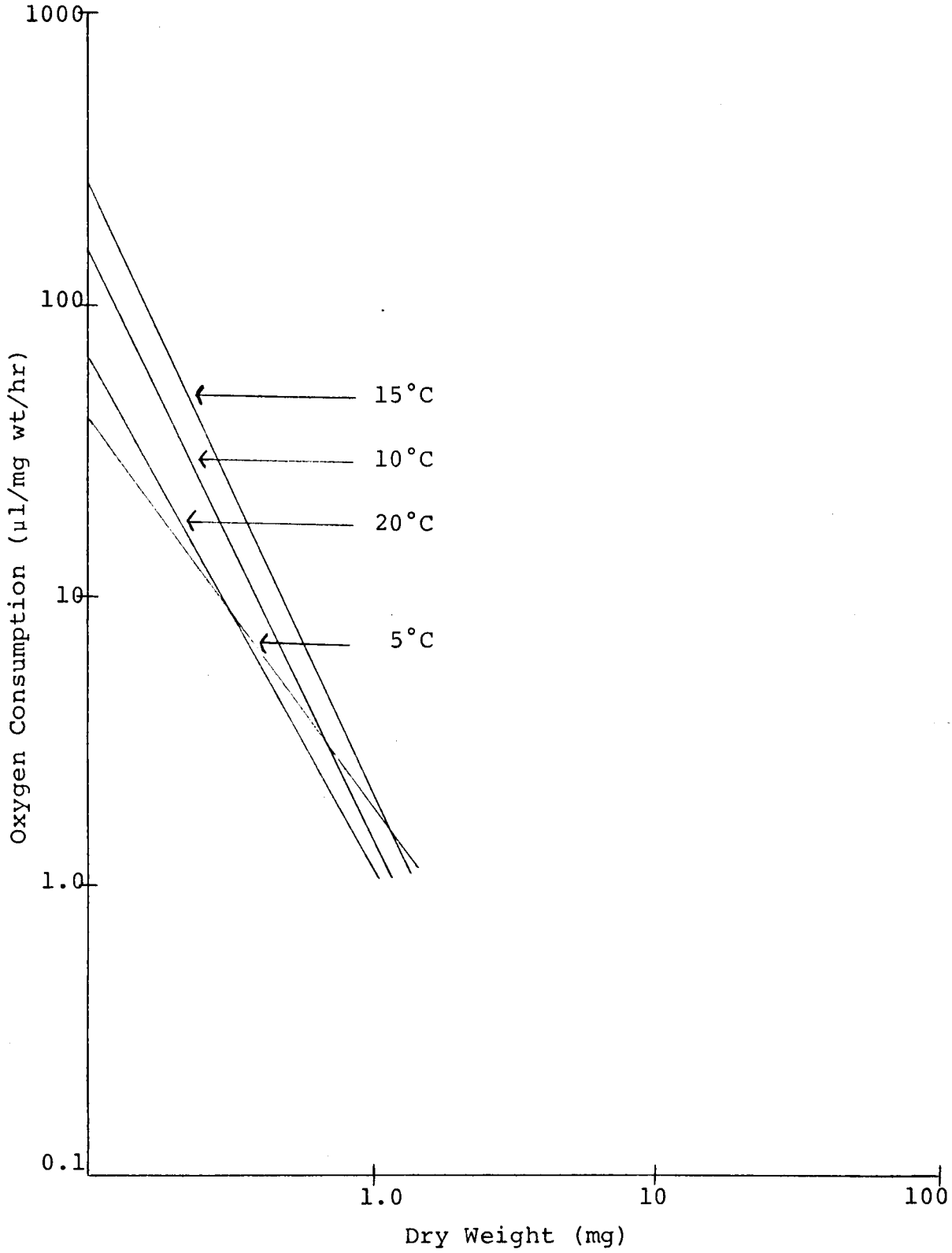


Figure 1. Relationship between log. body weight and log. oxygen consumption for immature and fifth instar Neophylax larvae.

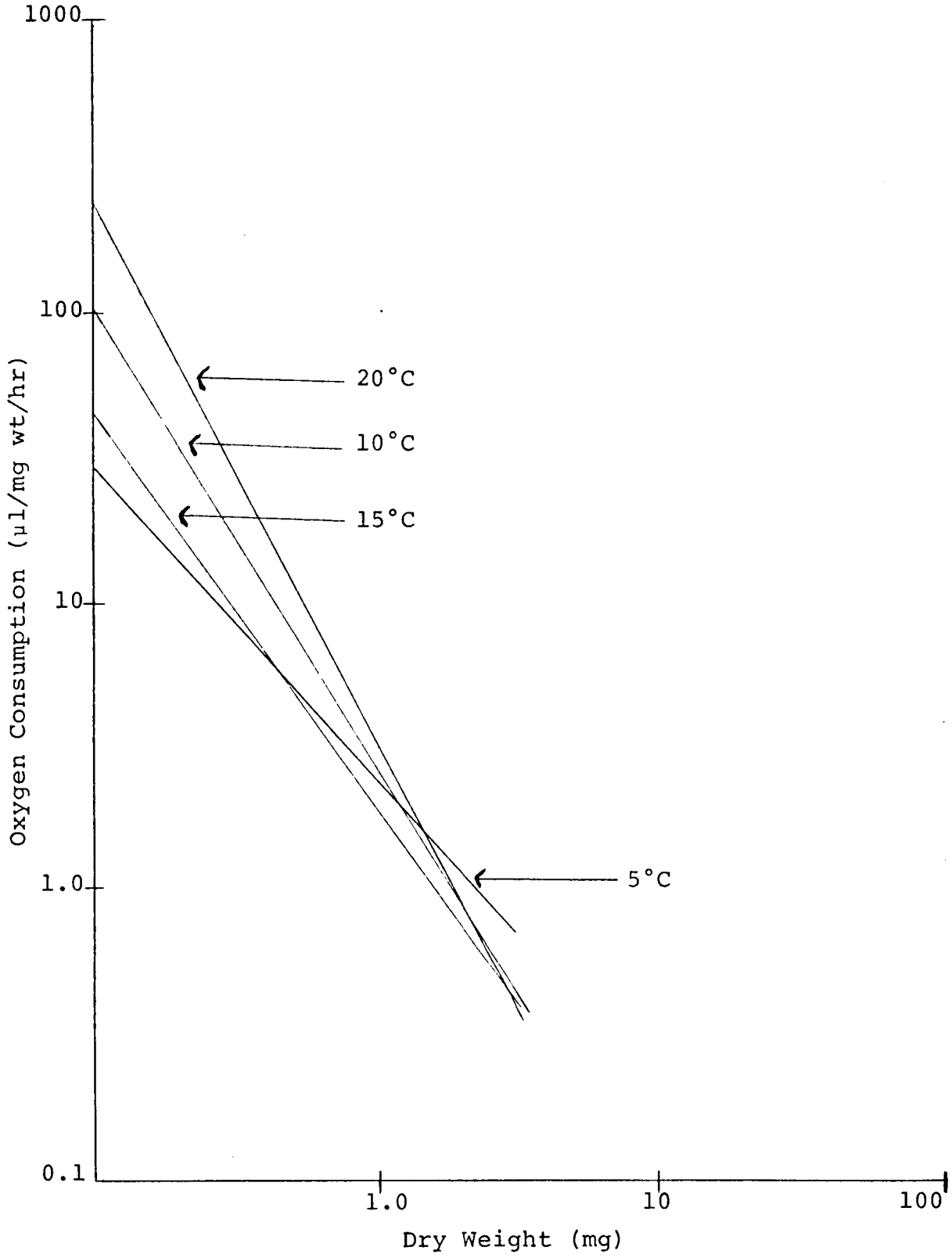


Figure 2. Relationship between log. body weight and log. oxygen consumption for fifth instar Neophylax and Glossosoma larvae.

TABLE 5

REGRESSION EQUATIONS EXPRESSING RELATIONSHIPS OF
LOG. OXYGEN CONSUMPTION AND LOG. WEIGHT

Immature and Fifth Instar *Neophylax*		Fifth Instar *Neophylax* and *Glossosoma*	
5°C:	log Y = 3.705 - 0.839 log X	5°C:	log Y = 3.673 - 0.848 log X
10°C:	log Y = 4.138 - 1.025 log X	10°C:	log Y = 4.409 - 1.137 log X
15°C:	log Y = 4.393 - 1.111 log X	15°C:	log Y = 4.017 - 0.974 log X
20°C:	log Y = 3.600 - 0.734 log X	20°C:	log Y = 4.482 - 1.049 log X

TABLE 6

COMPARISON OF REGRESSION COEFFICIENTS OF LOG. OXYGEN CONSUMPTION TO LOG. BODY WEIGHT USING STUDENT'S T-TEST

Regression Coefficients	t-Value
Immature and Fifth Instar Neophylax	
5°C and 10°C	0.688^{NS}
5°C and 15°C	0.874^{NS}
5°C and 20°C	0.363^{NS}
10°C and 15°C	0.335^{NS}
10°C and 20°C	1.178^{NS}
15°C and 20°C	1.309^{NS}
Fifth Instar Neophylax and Glossosoma	
5°C and 10°C	0.548^{NS}
5°C and 15°C	0.238^{NS}
5°C and 20°C	0.288^{NS}
10°C and 15°C	0.988^{NS}
10°C and 20°C	0.159^{NS}
15°C and 20°C	0.127^{NS}

^{NS}Not significant at 5 percent level.

Conclusions from Statistical Analyses

The results of the analyses indicated that the majority of variation in log. oxygen consumption for early and fifth instar *Neophylax* and fifth instar *Glossosoma* could be attributed to log. body weight. As weight of experimental organisms increased, the oxygen consumption per mg of body weight decreased progressively. The rate of decrease in respiration was independent of temperature, that is to say the rates of oxygen consumption at each of the four experimental temperatures were essentially the same. The data indicated a difference only in the magnitude of the actual oxygen consumption values.

CHAPTER V

DISCUSSION

There is very little information available for comparative purposes on the effects of temperature, body weight, and life stage on the respiration rate of caddisfly larvae. As stated previously, the majority of work in this field has centered on European species; in many instances conditions under which the tests were done make comparisons extremely difficult. Olson and Rueger (1968) explained that in most respiration studies involving aquatic insects, multiple specimens of varying weights were used, a condition which could conceivably alter the average respiration rate because one specimen disturbs another in a confined space or because of an accumulation of toxic waste products. Furthermore, younger and less heavy specimens generally use more oxygen per unit of body weight than do older and heavier individuals.

According to Prosser and Brown (1973) the conditions under which respiration measurements are made are important because the rate of oxygen consumption is influenced by both internal and external variables. The rate of oxygen consumption can be influenced by a host of factors including temperature, activity, nutrition, body size, stage in life

cycle, time of day, previous oxygen experience, and genetic background.

In consideration of these facts, this study emphasized the use of individual insects in both immature and mature larval stages. Every effort was made to hold constant those variables which could affect respiration.

A significant relationship between oxygen consumption (respiration) and body weight has been reported in many aquatic insects. Generally the oxygen consumption per unit of body weight decreases progressively with increasing body weight (Zeuthen, 1955; Knight and Gaufin, 1966; Olson and Rueger, 1968; Kapoor, 1974; Harvey, 1975). However, Kapoor and Griffiths (1975) working with the stonefly nymph, Phasganophora capitata, found oxygen consumption per gram to be independent of body weight as did Petitpren and Knight (1970) experimenting with larvae of the dragonfly, Anax junius. Therefore, it is apparent that the relationship between respiration and body weight does not always follow the same trend in aquatic insect orders.

Immature Neophylax larvae exhibited weight-dependent respiration in the present study at temperatures of 5, 10, 15, and 20°C whereas fifth instars exhibited this relationship only at experimental temperatures of 10°C and 20°C. Fifth instar Glossosoma larvae showed a weight-independent metabolism only at 5°C. The weight-independent metabolism

of both fifth instar Neophylax and Glossosoma might be explained in part by considering the differences between large and small individuals in sensitivity to temperature.

In any consideration of the effects of temperature on respiratory rates of insects, possible modifications due to rate of change in temperature and past temperature history of the insect should be taken into account. Sayle (1928) working with larvae of the dragonfly, Aeschna umbrosa, noted that they responded initially to changes in temperature by either an increase or a decrease in respiratory rate, but after a few days, the rate returned to approximately the original level rather than to the new level characteristic of the experimental temperature.

Neither immature nor fifth instar Neophylax showed an increase in respiratory rate at temperatures ranging from 5°C to 20°C. The same pattern held true for fifth instar Glossosoma. Norris et al. (1964) reported no increase in respiratory rates of the caddisflies, Notiomyia ornata and Chimarra betteni, when temperatures were increased from 21°C to 30°C. Harvey (1975) observed no increase in the respiratory rates of the mayfly, Dolania americana, when subjected to temperatures 2.5, 5, and 10°C above ambient creekwater temperatures.

Keister and Buck (1964) suggested that in such extreme cases where rate of respiration either failed to increase

with temperature or actually decreased over part of the range, a polysystem interaction could be operating. They explained:

> It is not uncommon for a mid-range span of 15°C or 20°C in the respiration-temperature curve to be essentially linear preceding a final prebreak increase in rate. Such an intercalated region of constancy in absolute metabolic increment per degree would be difficult if not impossible to explain in a unitary respiring system. However, in an overall gas exchange contributed to by at least two systems, the straight region could be visualized as the resultant of a temporary progressive slowing of the metabolic rate of system 1 superimposed on continuing increase in the rate of system 2, the final spurt signaling the resumption of activity by system 1 and the eventual break marking the point at which irreversible damage to both systems attains dominance. To make this picture somewhat more concrete (though still speculative), system 1 could be locomotion and system 2 maintenance respiration.

It is the opinion of the author that the acclimation period of three days at each experimental temperature may not have been of sufficient duration to allow the many enzyme systems which undoubtedly contribute to overall respiration to "switch over," thereby resulting in a distorted picture of true respiration rates.

No change in the rate of oxygen consumption at the four experimental temperatures for fifth instar Neophylax may possibly be related to the condition of diapause. For Trichoptera, diapause functions to suspend development until habitat conditions are most favorable and to synchronize adult emergence after periods of dissimilar larval

development (Wiggins, 1977). Diapause then represents a period during which metabolic rate, on a per unit weight basis, is extraordinarily low and stable (Keister and Buck, 1964).

It was expected that non-aestivating fifth instar Glossosoma would show a respiratory rate differing from that of aestivating fifth instar Neophylax. The results of the present study, however, indicated that there was no significant difference between the two. In order to maintain a respiratory rate comparable to that of an active larva, aestivating Neophylax must undoubtedly possess large food (energy) reserves and possibly other compensatory mechanisms not yet known. Fifth instar Neophylax were subjected to respiration tests during the first few weeks after they had sealed off their case entrances and ceased actively feeding. It is possible, therefore, that not enough time had elapsed to allow their metabolic processes to slow sufficiently to lower levels characteristic of diapause; this might serve to explain why an aestivating larva exhibited respiratory rates similar to that of an active, non-aestivating one.

It must be stressed that both Neophylax and Glossosoma are stream dwellers and as such spend their lives exposed to current. Feldmeth (1968, 1970a, 1970b) showed that in the case of Pycnopsyche guttifer and P. lepida, the environmental current velocity to which an organism was subject was

extremely important in determining its behavioral and metabolic responses. One of the major weaknesses, therefore, of the present study would be that the respiration measurements were not made in a flowing system. However, Feldmeth (1968) reported that larvae held for two weeks in zero current showed no respiratory or behavioral changes, indicating that acclimation to current was long term in nature.

Prosser and Brown (1973) stated that even under controlled conditions of temperature, light, and chemical content of the medium, an organism's metabolic rate may fluctuate as a function of time. In view of this fact, in future studies involving the respiration of aquatic insects it would be useful to evaluate possible influence due to diel effects.

It was not possible to monitor the amount of dissolved oxygen in the test or reactive vessels during the actual eight-hour experimental period. As a result it could not be determined whether larval Neophylax and Glossosoma also had an oxygen-dependent respiration. It is the opinion of this investigator that this would in all probability be true. According to Hynes (1970) stream species are usually classified as conformers, meaning that their respiration rates are either increased or decreased in accordance with the dissolved oxygen level. Should this prove to be the case with either of the caddisfly larvae used in the present

research effort, they would be excellent indicator species for reduced oxygen levels in streams caused by large inputs of organic pollutants or by thermal loading.

In conclusion, it is evident that there is a need for careful assessment of the environmental parameters to which an organism is subjected before experimental results are strictly interpreted and set physiological characteristics are given to an organism. Caddisflies, at least from the results of this study, appear to be highly variable organisms and increased effort must be made to better understand their basic physiology.

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APPENDIX

TABLE A-1

RESPIRATION OF IMMATURE NEOPHYLAX CONSIMILIS AT 5°C

Adjusted 8 hr Readings (µl O_2)	µl O_2/hr	Weight of Organism (mg)	µl O_2/mg wt/hr
13.8	1.72500	1.109	1.5554
5.9	0.73750	0.428	1.7231
23.6	2.95000	0.964	3.0602
16.2	2.03125	0.481	4.2230
18.5	2.31250	0.875	2.6429
8.4	1.05625	0.224	4.7154
6.9	0.86250	0.926	0.9314
13.5	1.69375	0.214	7.9147
5.9	0.73750	1.062	0.6944
20.5	2.56250	0.907	2.8252
21.3	2.66250	0.609	4.3719
12.6	1.57500	0.540	2.9167
3.5	0.43750	0.476	0.9191
11.9	1.48750	0.516	2.8827
12.4	1.55000	0.265	5.8490
11.6	1.45000	0.255	5.6863
13.0	1.62500	0.195	8.3333
3.6	0.45000	0.291	1.5464
1.6	0.20000	0.575	0.3478
7.5	0.93750	0.555	1.6892
1.6	0.20000	0.234	0.8547
1.8	0.22500	0.562	0.4003
21.3	2.66250	0.960	2.7734
17.8	2.22500	0.301	0.6697
5.2	0.65000	0.177	3.6723
5.5	0.68750	0.182	3.7775
4.2	0.52500	0.220	2.3864
24.2	3.03125	0.790	3.8370

TABLE A-2

RESPIRATION OF IMMATURE NEOPHYLAX CONSIMILIS AT 10°C

Adjusted 8 hr Readings (µl O_2)	µl O_2/hr	Weight of Organism (mg)	µl O_2/mg wt/hr
4.40	0.55000	0.941	0.5845
3.35	0.41875	0.579	0.7232
10.15	1.26875	0.695	1.8255
11.10	1.38750	1.370	1.0128
28.20	4.52500	0.775	4.5484
36.95	3.61875	0.773	5.9751
5.40	0.67500	3.465	0.1948
12.15	1.51875	0.729	2.0833
11.60	1.45000	0.809	1.7923
12.75	1.59375	0.730	2.1832
8.90	1.11250	0.870	1.2787
36.55	4.56875	3.383	1.3505
9.25	1.15625	0.741	1.5604
14.80	1.85000	0.224	8.2589
25.75	3.21875	0.825	3.9015
5.55	0.69375	0.407	1.7045
10.65	1.33125	0.911	1.4613
23.45	2.93125	0.296	10.0385
5.05	0.63125	0.442	1.4282
21.95	2.74375	0.269	10.1998
1.35	0.16875	0.625	0.2700
13.75	1.71875	0.152	11.3076
19.15	2.39375	1.144	2.0924
15.25	1.90625	3.771	0.5055
2.65	0.33125	0.641	0.5168
8.85	1.10625	0.121	9.1426
17.45	2.18125	0.540	4.0394
12.45	1.55625	0.099	15.7197
2.75	0.34375	0.151	2.2765
13.95	1.74375	1.236	1.4108

TABLE A-3

RESPIRATION OF IMMATURE NEOPHYLAX CONSIMILIS AT 15°C

Adjusted 8 hr Readings (µl O_2)	µl O_2/hr	Weight of Organism (mg)	µl O_2/mg wt/hr
3.45	0.43125	0.687	0.6277
0.25	0.03125	0.600	0.0521
4.45	0.55625	0.697	0.7981
22.35	2.79375	1.107	2.7471
10.05	1.25625	0.883	1.4227
20.15	2.51875	0.908	2.7740
3.95	0.49375	1.226	0.4027
22.95	2.86875	2.012	1.4258
2.65	0.33125	5.918	0.0560
12.45	1.55625	0.944	1.6486
9.95	1.24375	0.244	5.0973
3.25	0.41875	0.623	0.6722
18.60	2.32500	0.205	11.3415
21.55	2.69375	0.889	3.0301
12.95	1.61875	0.735	2.2024
28.20	3.52500	1.216	2.8988
13.10	1.63750	1.065	1.5376
19.60	2.45000	0.742	3.3019
16.40	2.05000	0.727	2.8198
12.20	1.52500	0.465	3.2796
21.40	2.67500	0.809	3.3066
20.60	2.57500	0.449	5.7350
22.90	2.86250	0.832	3.6652
20.90	2.61250	0.781	3.3451
13.90	1.73750	0.463	3.7527
23.50	2.93550	0.331	8.8746
13.00	1.62500	0.432	3.7616
39.70	4.96250	0.200	24.8125
20.10	2.51250	0.605	4.1529
23.20	2.90000	0.156	18.5900

TABLE A-4

RESPIRATION OF IMMATURE NEOPHYLAX CONSIMILIS AT 20°C

Adjusted 8 hr Readings (µl O_2)	µl O_2/hr	Weight of Organism (mg)	µl O_2/mg wt/hr
37.45	4.68125	4.943	0.9470
12.20	1.52500	0.213	7.1596
20.15	2.51875	0.235	10.7181
14.65	1.83125	0.270	6.7824
2.30	0.28750	0.331	0.8686
3.30	0.41250	0.218	1.8922
6.45	0.80625	0.420	1.9196
11.60	1.45000	1.479	0.9804
12.85	1.60625	0.708	2.2687
8.00	1.00000	0.420	2.3809
8.15	1.01875	0.316	3.2239
6.05	0.75625	0.153	4.9428
9.05	1.13125	0.165	6.8561
14.80	1.85000	0.228	8.1140
21.05	2.63125	0.326	8.0713

TABLE A-5

RESPIRATION OF FIFTH INSTAR NEOPHYLAX AT 5°C

Adjusted 8 hr Readings (µl O_2)	µl O_2/hr	Weight of Organism (mg)	µl O_2/mg wt/hr
10.05	1.25625	8.203	0.1531
15.60	1.95000	7.165	0.2722
14.10	1.76250	10.296	0.1712
22.10	2.76250	3.500	0.7893
8.25	1.03125	6.408	0.1609
14.90	1.86250	4.863	0.3830
35.45	4.30625	4.948	0.8703
12.05	1.50625	8.252	0.1825
3.25	0.40625	4.747	0.0856
17.35	2.16875	4.331	0.5008
2.50	0.31250	5.727	0.0546
4.25	0.53125	5.575	0.0953
14.60	1.82500	5.376	0.3395
16.35	2.04375	10.000	0.2044
7.25	0.90625	9.665	0.0938

TABLE A-6

RESPIRATION OF FIFTH INSTAR NEOPHYLAX AT 10°C

Adjusted 8 hr Readings (µl O_2)	µl O_2/hr	Weight of Organism (mg)	µl O_2/mg wt/hr
16.25	2.03125	4.349	0.4671
9.75	1.21875	11.089	0.1099
6.25	0.78125	7.585	0.1030
6.05	0.75625	6.182	0.1223
9.75	1.21875	5.042	0.2417
23.85	2.98125	8.166	0.3651
4.05	0.50625	7.879	0.0643
3.55	0.44375	5.798	0.0765
13.05	1.63125	5.442	0.2998
17.05	2.13125	4.695	0.4539
3.95	0.49375	6.120	0.0807
6.45	0.80630	9.112	0.0884

TABLE A-7

RESPIRATION OF FIFTH INSTAR NEOPHYLAX AT 15°C

Adjusted 6 hr Readings (µl O_2)	µl O_2/hr	Weight of Organism (mg)	µl O_2/mg wt/hr
15.30	1.91250	10.334	0.1851
7.65	0.95625	6.230	0.1535
7.25	0.90625	5.345	0.1696
6.10	0.76250	4.390	0.1737
11.45	1.43125	7.231	0.1979
19.80	2.47500	9.659	0.2562
13.00	1.62500	4.672	0.3478
15.85	1.98125	5.777	0.3430
2.10	0.26250	5.502	0.0477
9.95	1.24375	11.704	0.1063
17.60	2.20000	3.914	0.5621
12.95	1.61875	9.491	0.1706
6.20	0.77500	4.949	0.1566
21.85	2.73125	6.934	0.3939
12.35	1.54375	5.152	0.2996
7.65	0.95625	10.528	0.0908

TABLE A-8

RESPIRATION OF FIFTH INSTAR NEOPHYLAX AT 20°C

Adjusted 8 hr Readings (µl O_2)	µl O_2/hr	Weight of Organism (mg)	µl O_2/mg wt/hr
38.2	4.7750	3.552	1.3443
26.3	3.2875	5.147	0.6387
30.8	3.8500	5.886	0.6541
19.1	2.3875	6.164	0.3873
31.3	3.9125	5.655	0.6919
29.9	3.7375	6.923	0.5399
19.0	2.3750	4.665	0.5091
33.3	4.1625	4.087	1.0185
6.2	0.7750	4.306	0.1800
20.6	2.5750	6.041	0.4263
8.1	1.0125	4.877	0.2076
31.5	3.9375	4.638	0.8490
21.0	2.6250	4.039	0.6500
29.7	3.7125	11.344	0.3273
4.0	0.5000	10.540	0.0474
35.1	4.3875	6.425	0.6829

TABLE A-9

RESPIRATION OF FIFTH INSTAR GLOSSOSOMA AT 5°C

Adjusted 8 hr Readings (µl O_2)	µl O_2/hr	Weight of Organism (mg)	µl O_2/mg wt/hr
4.20	0.52500	1.289	0.4073
12.00	1.50000	2.741	0.5472
13.55	1.69375	1.303	1.2999
8.75	1.09375	0.806	1.3570
7.55	0.94375	3.448	0.2737
25.20	3.15000	3.190	0.9875
0.40	0.05000	2.900	0.0172
7.65	0.95625	1.818	0.5260
23.85	2.98125	2.429	1.2274
7.45	0.93125	1.315	0.7082
9.20	1.15000	1.448	0.7942

TABLE A-10

RESPIRATION OF FIFTH INSTAR GLOSSOSOMA AT 10°C

Adjusted 8 hr Readings (µl O_2)	µl O_2/hr	Weight of Organism (mg)	µl O_2/mg wt/hr
5.55	0.69375	3.407	0.2036
9.95	1.24375	3.540	0.3513
27.90	3.48750	2.910	1.1985
13.55	1.69375	0.879	1.9269
16.10	2.01250	1.668	1.2065
14.75	1.84375	0.560	3.2924
10.95	1.36875	1.863	0.7347
7.10	0.88750	2.690	0.3300
6.95	0.86875	9.112	0.0953
3.90	0.48750	7.879	0.0619
8.50	1.06250	1.846	0.5756
36.55	4.56875	7.035	0.6494
2.65	0.33125	1.201	0.2758
8.25	1.03125	0.640	1.6113
20.75	2.59375	1.384	1.8741

TABLE A-11

RESPIRATION OF FIFTH INSTAR GLOSSOSOMA AT 15°C

Adjusted 8 hr Readings (µl O_2)	µl O_2/hr	Weight of Organism (mg)	µl O_2/mg wt/hr
17.15	2.858300	2.411	1.1855
15.85	2.641700	1.057	2.4992
23.55	3.925000	3.586	1.0945
16.25	2.031250	1.333	1.5238
11.95	1.991700	1.522	1.3086
2.95	0.491700	0.980	0.5017
15.95	2.658300	2.311	1.1503
6.15	1.025000	4.905	0.2090
8.55	1.425000	0.333	4.2793
1.25	0.208300	1.508	0.1381
3.55	0.597000	3.907	0.1482
0.95	0.158300	4.240	0.0373

TABLE A-12

RESPIRATION OF FIFTH INSTAR GLOSSOSOMA AT 20°C

Adjusted 8 hr Readings (µl O_2)	µl O_2/hr	Weight of Organism (mg)	µl O_2/mg wt/hr
7.6	0.9500	1.358	0.6996
2.7	0.3375	3.156	0.1069
7.4	0.9250	1.788	0.5173
33.1	4.1375	3.586	1.1538
5.5	0.6875	3.029	0.2270
25.6	3.2000	1.659	1.9288
30.0	3.7500	0.320	11.7187
29.5	3.6875	1.289	2.8607
30.8	3.8500	0.802	4.8005
23.7	2.9625	1.557	1.9027
25.7	3.2125	0.444	7.2354
11.6	1.4500	1.621	0.8945
30.8	3.8500	4.889	0.7875

VITA

Robin Terese Faulk was born in Perry, Georgia, on August 6, 1954. She attended elementary school in Jeffersonville, Georgia, and following her junior year of high school, was admitted to Georgia College, Milledgeville, Georgia, in September 1972. She received a Bachelor of Arts degree in Biology, Magna Cum Laude, from that institution in June 1975. In the fall of 1975 she accepted a teaching assistantship at The University of Tennessee and began study towards a Master of Science degree in Ecology which was awarded in August 1978.