GEOGRAPHIC ANALYSIS OF THERMAL EQUILIBRIA A BIOENERGETIC MODEL FOR PREDICTING THERMAL RESPONSE OF AQUATIC INSECT COMMUNITIES

Progress Report
for Period July 1, 1979-June 30, 1980

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Table of Contents

Geographic Analysis of Thermal Equilibria: A bioenergetic model for predicting thermal response of aquatic insect communities

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for

Continuing Research Grant (DE-AC02-79EV10259)

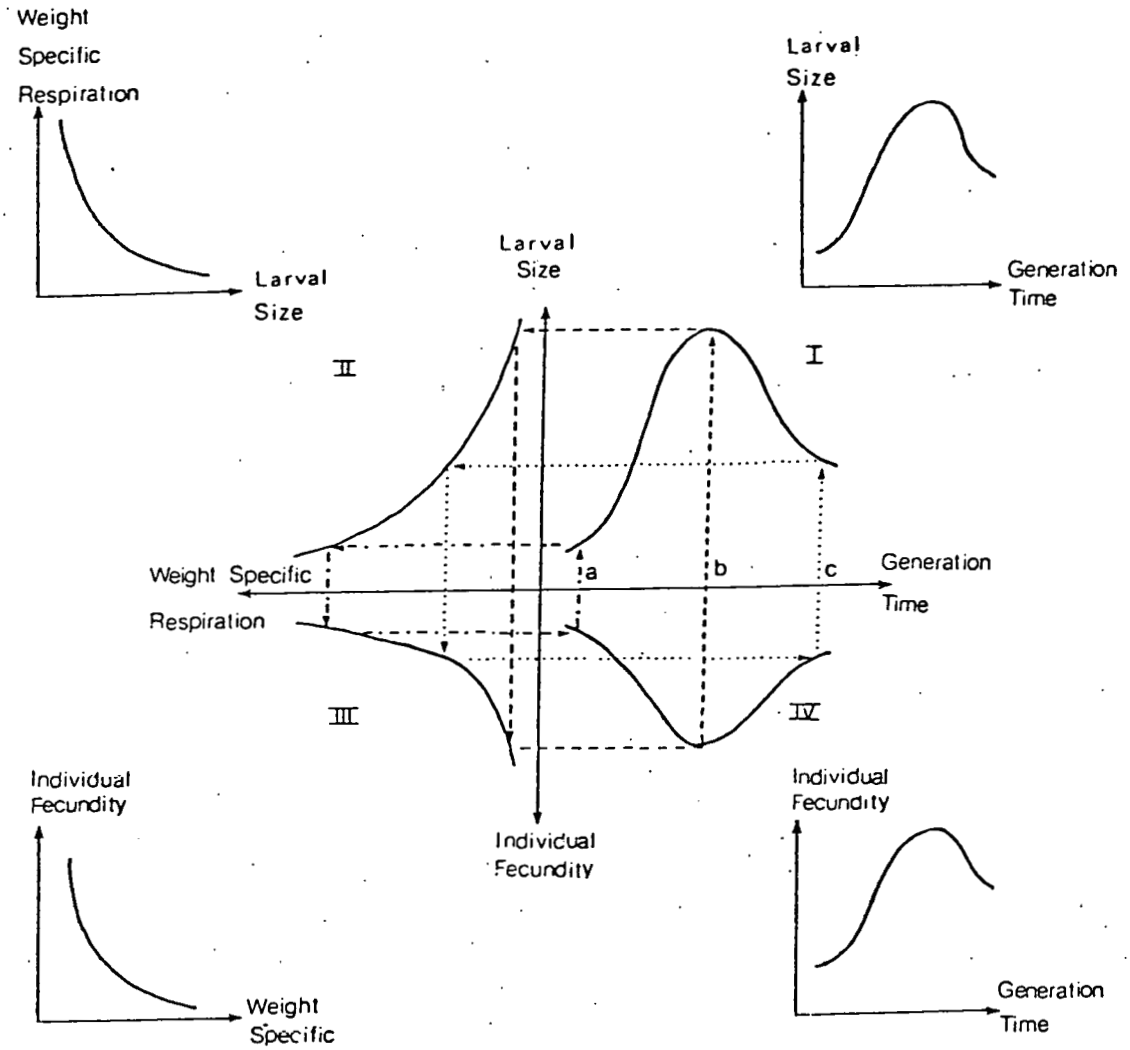
Introduction

From a series of bioenergetic and developmental studies of aquatic insect communities in White Clay Creek, Pennsylvania, we developed a thermal equilibria model (Sweeney and Vannote 1978; Vannote and Sweeney 1080) to describe the effects of natural and altered temperature regimes on the size and fecundity of hemimetabolous insects. Furthermore, we suggested that thermal heterogeneity (spatially and temporally) of streams and its predictable quality are important ecosystem attributes leading to the development and maintenance of a highly structured community of aquatic invertebrates.

Our central hypothesis is that the stability (ability of a subpopulation to recover from serious reduction in numbers by environmental perturbations or fluctuations) of a subpopulation within the geographic range of many stream insect species reflects mainly a dynamic equilibrium between temperature and individual growth, metabolism, reproductive potential, and generation time (Fig. 1). A thermal regime is viewed as optimum when an individuals body weight and fecundity is maximized (e.g. Fig. 1, pathway b). We hypothesize that an equilibrium location, where individual weight and fecundity is maximized, coincides closely with the location of greatest subpopulation biomass. Geographic range extension away from an optimum area (e.g. Fig. 1, pathway a or c) is associated with temperature induced changes in the rate and efficiency of energy use, developmental processes, and generation time.

According to our hypothesis, subpopulations in non-optimal habitats are characterized by low population density and small

Figure 1: A thermal equilibrium model, based on experimental data for White Clay Creek, indicating the population interactions between bioenergetic (growth and metabolic rate) and developmental (fecundity and generation time) parameters for insects reared in optimum and nonoptimum thermal regimes. The individual components of the model are described at the periphery of each quadrant (e.g. the inverse relationship between weight specific respiration and larval size; quadrant II). Pathway b (an optimum thermal regime) shows that maximum adult size is associated with an intermediate generation time, low weight-specific respiration, and high adult fecundity. Larval size and adult fecundity are intermediate in cold, nonoptimal regimes (pathway c). Generation time is shortest in warm regimes (pathway a), but high respiration cost and accelerated development of adult tissues (wing pads, reproductive system) results in small larval and reduced adult fecundity.


Weight
Specific
Respiration
Larval
Size
Larval
Size
Generation
Time
Larval
Size
II
I
Weight Specific
Respiration
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Time
III
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Individual
Fecundity
Individual
Fecundity
Individual
Fecundity
Weight
Specific
Individual
Fecundity
Generation
Time

individuals with reduced fecundity. The ability of these subpopulations to control and/or exploit ecosystem resources is reduced by both the small size and lower density with respect to total community. The competitive position of these species in the community hierarchy is lowered and the probability of competitive extinction due to environmental fluctuations (natural or induced) is increased. The local extinction of a subpopulation occurs theoretically where individual fecundity approaches zero. A species in nature is probably eliminated wherever recruitment falls below the critical threshold needed to maintain the competitiveness of the subpopulation (e.g. wherever reduced fecundity is not compensated for by concomitant changes in other critical life history parameters).

This report summarizes the first 9 months of field and laboratory work to test our central hypothesis. Five river systems were selected for intensive studies on insect growth, metabolism, and fecundity as well as determination of community structure for distinct assemblages of insect species exploiting various trophic and habitat resources. Laboratory studies were initiated to test the relative importance of temperature and food quality on growth, size, and fecundity of insects.

Project Goals, River Site Selection, Data Acquisition

Our project is intended to test the hypothesis that population stability, within the geographic range of many stream species, reflects largely a dynamic equilibrium between temperature and individual growth, metabolism, reproductive potential, and generation time. We propose to delineate the significance of natural thermal variation by quantifying the bioenergetics, developmental dynamics, and spatial distribution of major representative groups of stream insects throughout their geographic range.

During the summer of 1979, larval collections taken from 56 river stations were analyzed to select rivers best suited for study during the 1979 - 1980 sampling year (Table 1). Species lists for the most promising sites were assembled and compared prior to finalizing the selection of the five study rivers. A diverse and productive benthic fauna was an important consideration, but each river drainage selected for study also had to meet the following criteria: (1) an Atlantic piedmont drainage having 1st through 5th order tributaries that were accessible and below 500 m elevation; (2) an intact and fairly natural riparian vegetation bordering most of the length of both major and minor tributaries; (3) a thermal regime, annual discharge pattern, and water quality determined largely by natural processes (i.e. little or no industrialization or urban development, no thermal discharge from a electric power plant, no major

Table 1: List of streams visited and collected during the 1979 site selection process. Asterisks (*) indicate sites chosen for study.

Vermont

*Battenkill River
Green River

New York

Fishing Creek
Little Loyalsock River
Mohawk River
St. Regis River

Pennsylvania

Butler Creek
Doe Run
Fishing Creek
Lick Creek
Little Fishing Creek
Lower Pine Creek
Mehoopany Creek
*Meshoppen Creek
Painters Run
*Pickering Creek
Pigeon Run
Starrucca Creek
Susquehanna River
Tunkhannock Creek
*White Clay Creek
Wildcat Run
Wyalusing Creek

Maryland

Big Elk Creek
Potomac River

Virginia

*Big Otter River
Bearwallow Creek
Boyles Brook
Craig Creek
Doyles Run
Gunstock Creek
Hemp Mill Creek
Hittles Mill Creek
Holiday Creek
*Jordan River
Little River
Little Stoney Creek
Mill Creek
Moormans Run
North Fork Back Creek
North Fork Piney Creek
North Fork Roanoke River
North Fork Thorton River
Over Street Creek
Rappahannock River
Reed Creek
Sheeps Creek
Sinking Creek
Slate River
Smith River
South Fork Piney Creek
Spruce Pine Brook
Stoney Creek
Thorton River
Thumb Creek
Tye River

dams or other impoundments); (4) an underlying geology conducive to moderate or high productivity (e.g. sedimentary or metamorphic bedrock as opposed to streams developed on a granitic batholith structure).

Five river systems were chosen for study during the 1979-1980 sampling year (September 1979 to September 1980). Five sampling stations, approximating 1st through about 5th order streams, were selected in each drainage system. Table 2 briefly characterizes the stream reaches selected for study within each of the five major river drainages. Sites within a major drainage were about 1.5° latitude north and/or south of reaches in any other study drainage. All study reaches satisfied the criteria outlined above. Thermographs were installed and operating at all sites by late October, 1979. Thermograph recording charts are checked monthly (for operation and calibration), and charts are changed every three months.

For each study reach (a total of 24 reaches for 1979-1980) we intend to select 20-25 insect species for intensive study. Data acquisition for each species will usually include: (1) weight distribution of individuals from large (> 50 individuals for each species) collections of larvae at several times during larval development period to characterize larval growth rates and maximum size at maturity; (2) estimation of larval metabolism by measuring respiration rates on a differential respirometer; (3) determination of adult emergence time and the duration of the adult emergence period; (4) quantify individual male and female adult size (i.e. wing length and weight) and fecundity throughout the emergence period. On some species we may attempt to determine the onset and duration of the pupal stage and the weight loss associated with delayed pupation (e.g. spring and summer diapause for many Trichoptera larvae).

In addition to the species specific data described above, we are also determining community structure at each study reach (e.g. species composition within major functional groups). The data will be used to assess how species associations within communities change over broad thermal gradients both within single drainage systems and between systems separated geographically.

Program Modification: Field Studies

Many of the above criteria for station selection are best evaluated in late winter or early spring prior to the emergence period of many aquatic insects. Since the project started in late spring, the selection of study rivers was very difficult because many key species were either too small to identify or still in the egg stage. We are avoiding this problem by starting site selection in early March 1980 for the 1980-1981

Table 2 - List of streams chosen for study during 1979-1980 sampling year. Distinguishing characteristics are given for each site as estimated from U.S.G.S. topographical maps, county road maps, or field observations.

Master River	Reach Name	Study Code	State	Latitude	Longitude	Altitude (m)	Stream Width (m)
Hudson R.	Goodman Bk.	BAT 1	VT	43°13'47"N	73°07'11"W.	432	0.5-1.0
	Gilbert Bk.	BAT 2	VT	43°14'29"N	73°06'29"W	335	1.5-3.0
	W.Br, Battenkill R.	BAT 3	VT	43°13'10"N	73°04'18"W	267	2.0-4.0
	Battenkill R.	BAT 4	VT	43°05'52"N	73°08'31"W	201	8.0-10.0
	Battenkill R.	BAT 5	VT	43°06'04"N	73°14'31"W	164	15.0-25.0
Susquehanna R.	Nine Partners Ck.	MES 1	PA	41°45'27"N	75°44'46"W	414	0.5-1.0
	Hibbard Bk.	MES 2	PA	41°49'11"N	75°56'00"W	371	1.5-3.0
	Mad Dog Run	MES 3	PA	41°44'13"N	75°51'36"W	323	1.5-3.5
	Meshoppen Ck.	MES 4	PA	41°43'02"N	75°52'17"W	310	7.0-9.0
	Meshoppen Ck.	MES 5	PA	41°36'45"N	76°00'58"W	219	12.9-18.0
Delaware R.	Ledyards Ck.	WCC 1	PA	39°52'50"N	75°47'30"W	121	1.0-2.0
	Choates Ck.	WCC 2	PA	39°52'25"N	75°47'30"W	115	2.0-3.5
	White Clay Ck.	WCC 3	PA	39°15'50"N	75°47'16"W	106	4.0-6.0
	Pickering Ck.	WCC 4	PA	40°06'00"N	75°38'36"W		8.0-14.0
Rappahannock R.	Hittles Mill Ck.	JOR 1	VA	38°46'45"N	78°08'24"W	222	0.5-1.5
	Bearwallow Ck.	JOR 2	VA	38°47'07"N	78°08'54"W	280	4.0-7.0
	Hittles Mill Ck.	JOR 3	VA	38°47'38"N	78°07'04"W	225	6.0-10.0
	Jordan R.	JOR 4	VA	38°45'51"N	78°02'04"W	131	12.0-15.0
	Rappahannock R.	JOR 5	VA	38°41'05"N	77°54'15"W	94	20.0-25.1
Roanoke R.	Hemp Mill Ck.	BIG 1	VA	37°24'08"N	79°39'02"W	481	1.0-2.0
	Sheep Ck.	BIG 2	VA	37°24'58"N	79°38'46"W	381	2.0-3.0
	Sheep Ck.	BIG 3	VA	37°25'21"N	79°38'24"W	377	3.0-4.0
	Big Otter Ck.	BIG 4	VA	37°23'22"N	79°33'05"W	260	8.0-12.0
	Big Otter Ck.	BIG 5	VA	37°22'14"N	79°25'14"W	198	15.0-20.0

sampling year. Site selection is decidedly more time consuming and expensive than we had initially estimated. Streams in the southeastern piedmont have been highly impacted by several centuries of intense land use, and locating streams in this region with a reasonably intact fauna is time consuming. We have, however, been able to reduce overall travel costs by purchasing tents and having personnel camp and cook their own meals during most field trips that do not involve using travel trailers (e.g. river site selection, special short-term collecting trips to study sites, etc.).

Our sampling strategy for obtaining data on the emergence time, adult size, and fecundity of study species has also been altered. These measurements are more critical to the success of our project than other study parameters and we have modified our work plan accordingly by: (1) reducing the intensity of the overall sampling effort (i.e. reduce number of trips to each site) during the October to March period while increasing the effort during the period of larval maturation and maximum adult emergence (March through June); (2) emphasizing laboratory rearing as opposed to field rearing of adults as we initially proposed; (3) deploying light traps, malaise nets, and drift nets, (i.e. traps designed to collect adult insects emerging from streams) at all sites to assure the collection of an adequate amount of adult insects.

To accommodate the new work plan, we have increased the insect rearing facilities at the Stroud Center so we can now rear animals collected from each study reach under thermal conditions within 1.5^{o}C of the native environment. Larval specimens for rearing are kept in polypropylene "stream" trays (48 x 27 x 20 cm) and fed both detritus collected from their original stream habitat and diatom communities cultured on plates exposed in the White Clay Creek, Pennsylvania.

The revised work plan is as follows for each of the five major river systems: one field biologist is assigned a particular river system with five stations and spends every other week from March through June collecting and rearing at the study sites. During this field week, each study site is visited daily to collect adults from malaise nets, sweep net for adults, etc. The biologist also spends about six hours at each site collecting larvae for use in weight structures, rearing, respiration, and taxonomy. The biologist brings back to the laboratory larvae of species that are emerging in the field during his field sampling week as well as larvae of species that have not yet emerged but appear near emergence (i.e. have well developed and darkened wingpads). At the end of a given week in the field, the biologist will also take random collections of larvae at each study reach and return the collection to the Stroud Center for further picking, sorting, and rearing under approximately natural thermal and trophic conditions. Thus, alternate weeks will be spent at

the Stroud Center rearing new adult material and processing (dry weights, egg counts, length measurements) material gathered in the field during the previous week. A technician at the Stroud Center will oversee the laboratory rearing during the week the biologist revisits his field stations. All larvae in the rearing trays are sacrificed when the biologist brings fresh populations back from the study sites (e.g. larvae are never kept for more than 13 days in the laboratory).

The above sampling program yields adult material from several sources. First, newly emerged adults are collected from malaise nets, drift nets, and vegetation sweep-samples every other week and at each site. Second, terminal instar larvae are reared to the adult stage continuously in the laboratory, with fresh specimens for rearing being provided every two weeks. Although the intensity of this sampling program creates several logistical problems (e.g. overseeing rearing trays during weekends, transport and storage of extensive field gear) and personal sacrifice (e.g. six day work weeks, odd hour work days to sample early morning and late evening adult emergences), we feel that any reduction in sampling intensity would compromise the quality of required data sets.

We have also altered our workplan with respect to measuring larval respiration. We initially proposed to measure larval respiration in the field by equipping our mobile trailers with differential respirometers. This approach has been abandoned because respiration experiments required continuous attention and severely restricted the mobility of our biologists in the field and made acquisition of other field data more difficult and time consuming. Our biologists now collect larvae for respiration experiments just before returning from the field and perform the experiments at the Stroud Center while simultaneously conducting other duties (sorting, rearing, weighing, etc.). This modification in the work plan avoided adding additional personnel to the field crews or prolonging the field trips to accommodate field measurements on respiration. We have no indication that this work schedule modification will affect the validity of our respiration data sets.

Field Sampling Logistics

Two field teams, each consisting of two biologists and using the Stroud Center as home base, have been assigned data acquisition on the five river systems for the 1979-1980 sampling year. Each field team has two river systems, or a total of 10 sampling reaches, that are distant from the Stroud Center (i.e. > 300 miles north or south). The four study reaches near the laboratory are divided equally between the two field teams. During the fall-winter period, each field crew works as a team when sampling each site. In early spring, however, each field team member is assigned a specific river system for study as described earlier. We have avoided unnecessary duplication of field equipment (e.g. vehicles, trailers,

thermometers, nets, buckets, etc) by alternating field work-weeks among the members of a given team during the spring.

Each study reach was sampled at least once during the fall - early winter period of 1979. The first larval sampling at each reach was more comprehensive, exhaustive, and time consuming than subsequent sampling visits. This resulted largely because most of the insect larvae were at early stages of development and we were unfamiliar with the species composition of these streams. Therefore, in addition to collections for population weight structure, a voucher series for each species or probable species, in cases where positive identification could not be made, was obtained and kept in alcohol for later verification. Also, in the fall, we could not finalize the selection of 20-25 key species for each river until all five river systems had been sampled at least once and a probable species lists compared. Our objective is to maximize the number of species for which we get vital data at several points in their geographic range. Thus, for the first sampling period, specimens for weight structures and vouchers were collected for about twice as many species as will be taken in subsequent sampling efforts.

Program Modification: Trophic Analysis

Cooperative funding by NSF and DOE has permitted expansion of both laboratory and field studies to include the interaction of nutrition and temperature in determining rates of larval growth and developmental processes in aquatic insects. Field studies include experiments designed to assess the trophic equivalence of our study reaches - i.e. develop a simple trophic index for comparing in situ algal production, epiphytic biomass, and particulate detritus at study sites both within and between our river drainages. Concurrent laboratory study emphasize the relative importance of temperature and food quality on larval growth, the timing and duration of adult emergence, and adult size and fecundity. These experiments are discussed in greater detail later in this report.

Summary of Progress and Results

Field Analysis: Temperature

Thermographs have been deployed at all sites since October or November, 1979. The maximum, minimum, and average daily temperature for each of the 24 sites is presently stored on our computer for the months of October, November, and December. We have recently collected the second 3-month recording tape from all the thermographs and the January-February-March data will be on file shortly. After we accumulate a 6 month data file, we can begin to analyze for geographic patterns of temperature for the five river systems. Preliminary observations

indicate that the rivers selected will yield a well defined gradient of temperatures (i.e. both comparing low order versus high order tributaries within a drainage and comparing similar other tributaries at different latitudes). For example, a comparison of mean temperatures at the largest stream sites for the month of November, a poor month for detecting thermal differences between streams, showed about a 4°C difference between our most northern river (Battenkill 5; mean = 7.0°C) and our most southern river (Big Otter 5; mean = 10.8°C). In a geographic comparison, winter months reveal minimal temperature differences, however, these differences will be magnified substantially during the spring-summer period.

Field Analysis: Larval growth and community structure

Insect larvae from all sites were collected at least once during the October-December, 1979, sampling period. Insect collections were partitioned in the field to either species or "tentative" species (i.e. those that appear distinct but were too samll to accurately identify) and about 50 to 200 specimens of each type were killed, dried, and weighed to the nearest microgram. Tables 3, 4, and 5 list the genera for which we have weight structures for at least one species (in most cases 2-6 species per genus) and the collection locations of the weighed specimens. A total of 246 weight structures have been completed as of February, 1980. Future weight structures will be more selective because we will emphasize species that occur in two or more locations within a drainage system and/or between drainage systems (all insect weight data has been entered on our computer file). Weight structures will be used to compare larval growth rates and estimate maximum size for a species at different points in its geographic range.

Presently we have too few data sets (only October through February) on any one species to analyze for geographic patterns. The autumn weight structures did, however, yield some promising patterns for several species. For example, considerable variation in mean larval weight for the stonefly, Taeniopteryx maura, was observed both within a drainage basin (see Jordan River sites 2, 3, 4 in Fig. 2) and between drainage basins for November samples. T. maura grows and emerges largely during cold water periods (i.e. < 10°C) and it appears that larval growth begins earlier in the northern part of its geographic range relative to more southern sites. A more complete interpretation of these and other results must wait additional data on larval growth, timing of adult emergence, adult size, and field data on the seasonal temperature patterns and trophic structure of each study site.

EPHEMEROPTERA (MAYFLIES)	SITE CODE (RIVER & STATION)																									
	BAT1	BAT2	BAT3	BAT4	BAT5	MES1	MES2	MES3	MES4	MES5	JOR1	JOR2	JOR3	JOR4	JOR5	BIG1	BIG2	BIG3	BIG4	BIG5	WCC1	WCC2	WCC3	WCC4	WCC5
GENUS																									
LITOBRANCHA			X																						
EPHEMERA			X	X	X					X							X	X					X		
TRICORYTHODES			X																						
EPHEMERELLA	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	
BAETISCA				X														X								
HABROPHLEBIODES											X															
LEPTOPHLEBIA			X	X			X	X	X	X											X	X	X			
PARALEPTOPHLEBIA	X		X		X	X	X	X	X	X		X				X							X			
BAETIS		X				X			X			X					X	X	X		X					
PSEUDOCLEON													X					X								
EPEORUS	X	X			X	X	X	X	X			X				X	X	X			X					
HEPTAGENIA						X	X	X		X																
RHITHROGENA					X																					
STENONEMA			X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	
STENACRON						X		X	X	X		X														
ISONYCHIA					X				X	X					X					X			X	X	
AMELETUS	X	X				X	X	X								X	X	X			X	X				
SIPHLOPLECTON				X																						

Table 3: The distribution of mayfly genera at the five river sites. BAT = Battenkill, VT; MES = Meshoppen Ck, PA; JOR = Jordan River, VA; BIG = Big Otter Ck, VA; WCC = White Clay Creek, PA.

TRICHOPTERA (CADDISFLIES)	SITE CODE (RIVER & STATION)																								
GENUS	BAT1	BAT2	BAT3	BAT4	BAT5	MES1	MES2	MES3	MES4	MES5	JOR1	JOR2	JOR3	JOR4	JOR5	BIG1	BIG2	BIG3	BIG4	BIG5	WCC1	WCC2	WCC3	WCC4	WCC5
GLOSSOSOMA		X	X		X								X							X	X	X	X		
CHIMARRA								X	X	X			X								X	X	X	X	
DOLOPHILUS	X		X			X	X	X			X	X	X			X	X	X		X	X				
WORMALDIA																X									
PSYCHOMYIA						X																			
CHEUMATOPSYCHE				X	X	X	X	X	X	X		X						X	X	X				X	
HYDROPSYCHE	X		X	X	X	X	X	X	X	X			X			X		X		X	X	X	X	X	
PARAPSYCHE	X	X																							
DIPLECTRONA						X	X	X			X	X				X	X	X			X	X	X		
PTILOSTOMIS											X														
APATANIA	X				X																				
GOERA						X	X																		
HYDATOPHYLAX			X	X							X	X	X										X		
NEOPHYLAX	X	X				X	X	X									X				X		X		
PYCNOPSYCHE	X	X	X	X	X						X										X				
MOLANNA	X										X														
LEPIDOSTOMA	X	X			X											X									
BRACHYCENTRUS			X							X					X										
PSILOTRETA	X										X														
RHYACOPHILA	X	X	X	X							X	X	X			X	X	X	X		X	X			

Table 4: The distribution of caddisfly genera at the five river sites. BAT = Battenkill, VT; MES = Meshoppen Ck, PA; JOR = Jordan River, VA; BIG = Big Otter Ck, VA; WCC = White Clay Creek, PA.

Table 5: The distribution of stonefly, dragonfly, damselfly, and dobsonfly genera at the five river sites.

PLECOPTERA (STONEFLIES)

GENUS	SITE CODE (RIVER & STATION)																								
	BAT1	BAT2	BAT3	BAT4	BAT5	MES1	MES2	MES3	MES4	MES5	JOR1	JOR2	JOR3	JOR4	JOR5	BIG1	BIG2	BIG3	BIG4	BIG5	WCC1	WCC2	WCC3	WCC4	WCC5
PTERONARCYS	X											X													
ALLONARCYS					X		X	X					X			X	X	X	X						
PELTOPERLA	X												X			X	X					X	X		
STROPHOPTERYX																								X	
TAENIOPTERYX			X	X	X	X	X	X	X	X		X	X	X	X		X	X	X	X			X	X		
BRACHYPTERA	X											X				X	X		X	X					
SOYEDINA																X							X		
ALLOCAPNIA																							X		
PARACAPNIA											X	X	X	X	X		X	X	X	X					
ACRONEURIA		X				X	X	X	X	X		X					X	X						X	
NEOPERLA										X															
PHASGANOPHORA		X			X	X																			
PARAGNETINA		X								X			X		X									X	
ISOPERLA		X	X	X							X	X	X			X		X	X	X					
ISOGENOIDES				X																					

ODONATA (DRAGONFLIES AND DAMSELFLIES)

GENUS	SITE CODE (RIVER & STATION)																								
	BAT1	BAT2	BAT3	BAT4	BAT5	MES1	MES2	MES3	MES4	MES5	JOR1	JOR2	JOR3	JOR4	JOR5	BIG1	BIG2	BIG3	BIG4	BIG5	WCC1	WCC2	WCC3	WCC4	WCC5
CORDULEGASTER			X																						
BOYERIA				X											X										
CALOPTERYX																								X	

NEUROPTERA (DOBSONFLIES)

GENUS	SITE CODE (RIVER & STATION)																								
	BAT1	BAT2	BAT3	BAT4	BAT5	MES1	MES2	MES3	MES4	MES5	JOR1	JOR2	JOR3	JOR4	JOR5	BIG1	BIG2	BIG3	BIG4	BIG5	WCC1	WCC2	WCC3	WCC4	WCC5
CORYDALUS																				X				X	
PIGRONIA				X																					

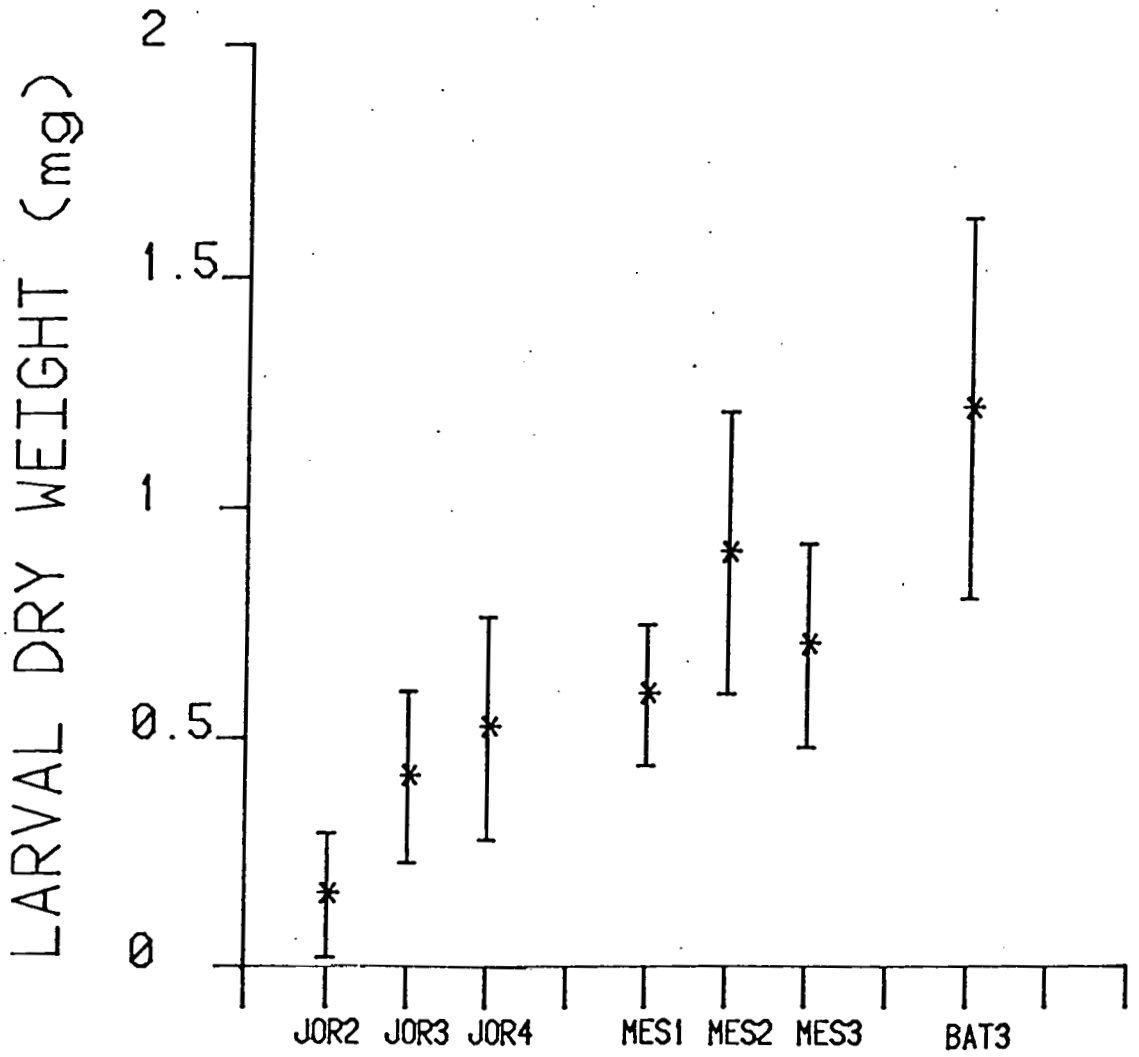

Figure 2: The mean dry weight and standard deviation of *Taeniopteryx maura* larvae from tributaries of the Jordan River, Virginia, the Meshoppen Creek, Pennsylvania, and the Battenkill, Vermont, during November, 1979.

Field Analysis: Trophic structure of river sites

A simple trophic index has been devised which involves monitoring the levels of chlorophyll, ATP, and phospholipids over time on artificial substrates (64 x 134 mm PVC plates held vertically in a rack) placed in riffle areas at each site. The relative abundance and species diversity of the diatom community will also be measured periodically on these plates. To evaluate nutrient equivalence, six artificial substrates will be placed at each site by field crews and two substrate plates collected for analysis every two weeks for the subsequent six week period. At that time, another set of six plates will be exposed at each stream site.

The quality of leaf litter available in the stream channel is also being evaluated seasonally at each site by estimating species distribution and relating leaf species to known growth responses by insects. We decided that quantitative studies to estimate the standing crop of detritus throughout the year are too time consuming and spatially variable to be useful for rapid evaluation of available food resources.

Laboratory Analyses: Relative effects of temperature and food quality on larval growth and adult reproductive potential of aquatic insects.

A large experiment (3 temperatures, 5 diets, 4 species, 2 replications) was initiated in October, 1979, for assessing the relative importance of temperature and food quality to the developmental dynamics of aquatic insect larvae. Four insect species were chosen for study: Leptophlebia intermedia, Peltoperla maria, Tipula abdominalis, and Soyedina carolinensis. The experimental design included rearing early instar larvae of the above leaf eating species to the adult stage on five distinct diets (viz. American beech, chestnut oak, hickory, white ash, and red oak) while being kept at three distinct temperature regimes (viz. ambient White Clay Creek (WCC) temperatures, warming ambient White Clay water $4^{o}C$ (WCC + $4^{o}C$), and warming ambient White Clay water by $8^{o}C$ (WCC + $8^{o}C$)). Two replicate sets of animals (the exact number of individuals per replicate varied with each species) were exposed to each combination of temperature and food type. The growth of experimental animals was also followed in the natural stream. Respiration rates of experimental animals were determined at 1, 5, 10, $15^{o}C$ for use in constructing partial energy budgets for the period of larval growth.

To aid in interpreting results, we also characterized, at various points throughout the experiment, the ATP levels of each leaf species and its associated microflora. For each ATP assay, ten leaf cores (1.3 cm diameter) were extracted for

each treatment (temperature-food type). ATP was also monitored on leaf packs constructed for each species and exposed in natural streams.

The amount of data presently available from this experiment varies considerably from species to species because of basic differences in growth responses to temperature and food quality. For example, many L. intermedia larvae reared on certain diets have already completed growth and emerged as adults in the two warmer thermal regimes (i.e. WCC + 8° and WCC + 4°C). Adult emergence on white ash and hickory diets began about 7 days earlier in the WCC + 8°C regime relative to the WCC + 4°C regime. Emergence has been rather sporadic and delayed on other diets for both WCC + 4 and WCC +8°C. For the white ash and hickory experiments already started, adult size progressively decreased throughout the laboratory emergence period at WCC + 8°C (Fig. 3) although variability was high for white ash. These data alsoshow a substantial difference in female size (Fig. 3) and fecundity (Fig. 4) for adults emerging from the two diets. A comparison of adult size as a function of temperature for each diet is not possible at this time because adults are still emerging from the WCC + 4°C regime and should begin to emerge shortly from the ambient WCC regime.

Our preliminary data on the mayfly, L. intermedia, indicate that larval growth and development appears to be correlated positively with temperature. Larvae grew best on white ash, followed by hickory, and not well at all on the remaining leaf species. The acceleration of larval growth by increasing temperature correlates well with the data for L. intermedia concerning the response of larval respiration rates to increases in temperature. We did not attempt to measure the effect of food quality on larval respiration.

Our ATP analysis on the leaf substrates suggests that in general ATP levels for all leaf species were correlated positively with temperature (Table 6). Among the five leaf species studied, white ash had the highest ATP content which corresponds well with observed growth patterns. However, larvae also grew well on hickory which had the lowest ATP levels of any leaf type. Although these results are incomplete and preliminary, they suggest that the interaction of temperature and food quality may be more complex than was initially estimated and certainly requires additional experimentation.

Preliminary experimental results for the winter stonefly, Soyedina carolinensis also shows that elevated winter temperatures diminished adult size (Table 7) under all diets for which we presently have emergence data. The highest temperature regime (WCC + 8°C) permitted larval growth but energy reserves were insufficient to complete adult emergence and most larvae died while attempting metamorphosis.

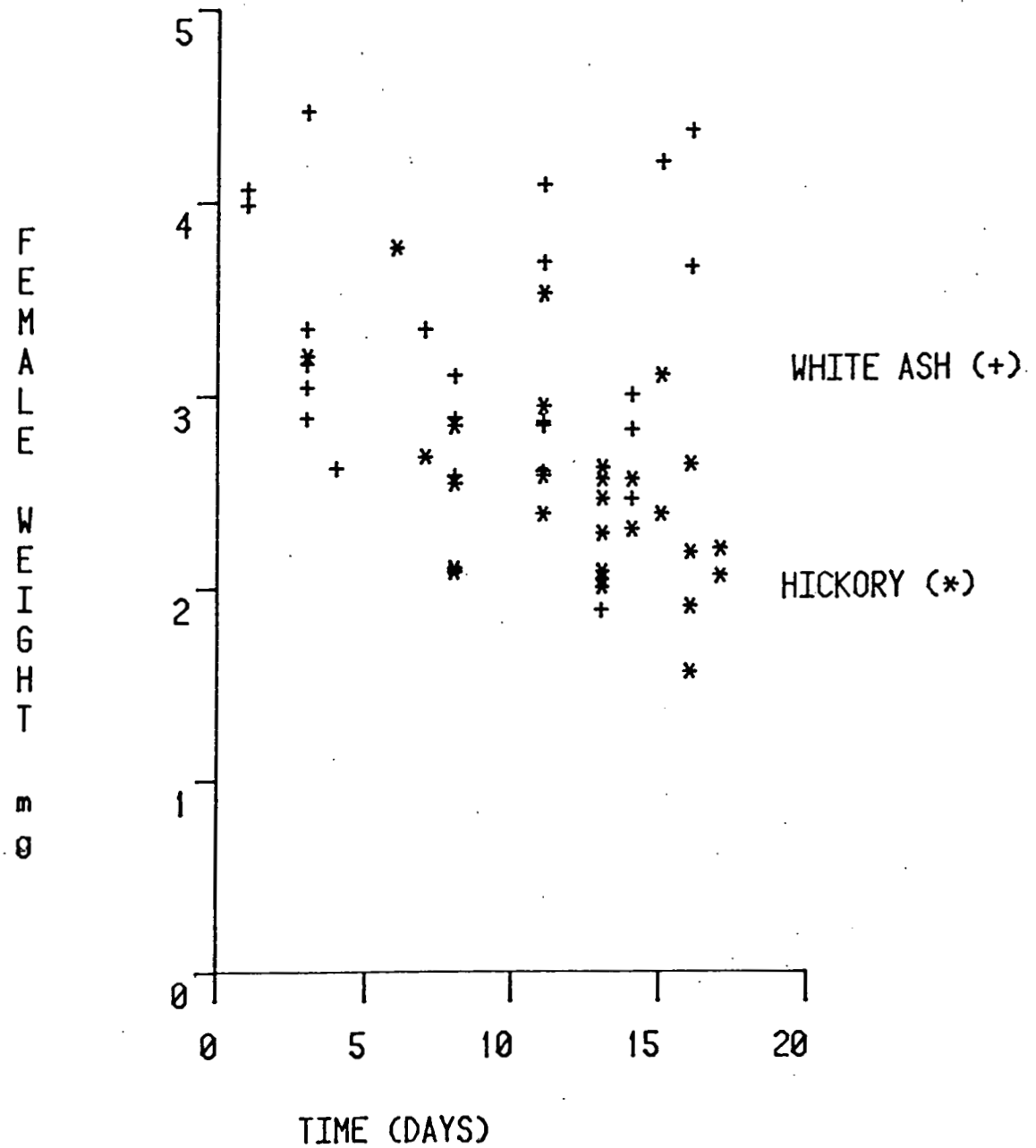

Figure 3. The change in dry weight of adult *Leptophlebia intermedia* during the emergence period for larvae reared on white ash and hickory leaf litter in laboratory microcosm streams.

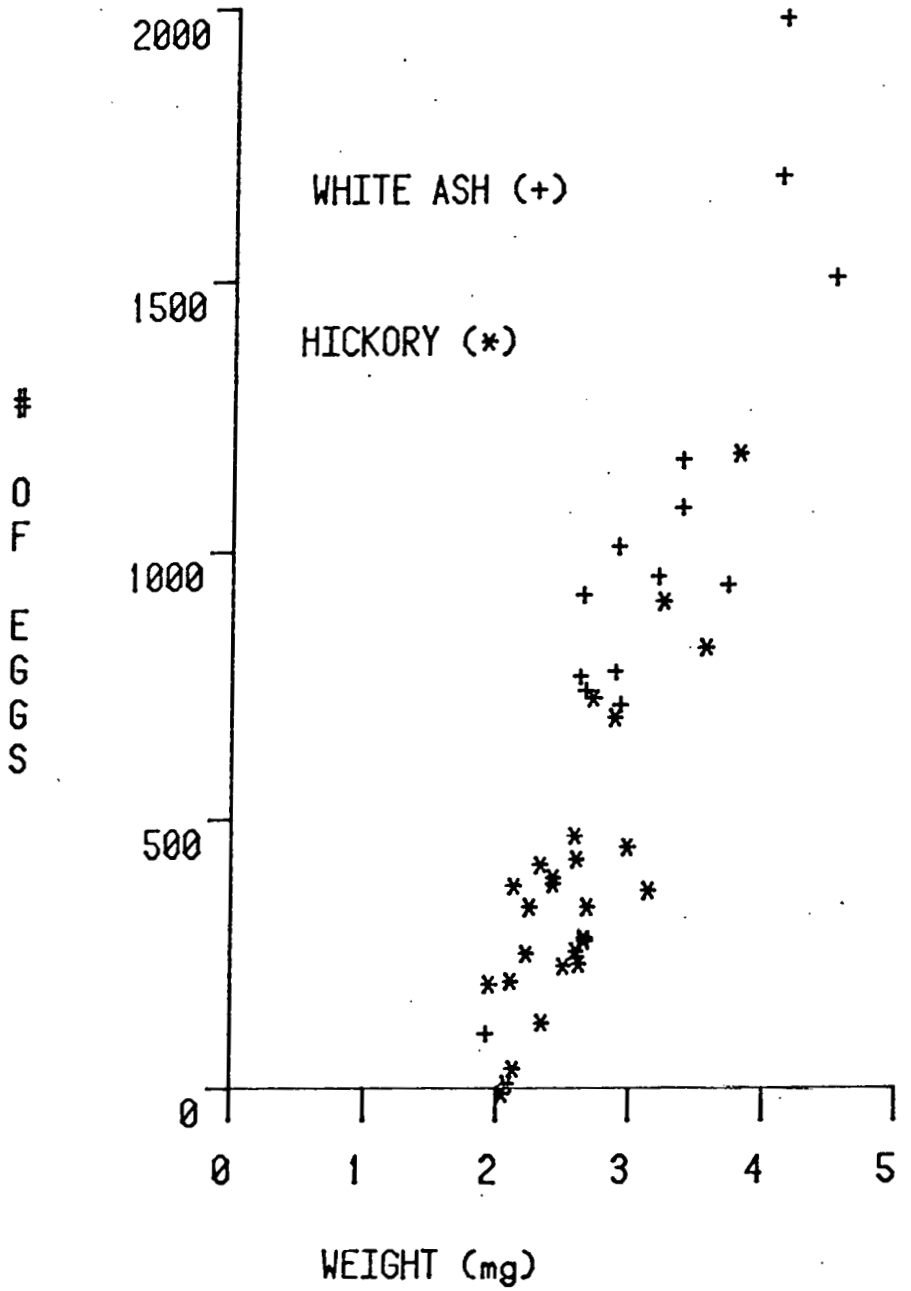

Figure 4. The relationship between fecundity and adult dry weight for the mayfly *Leptophlebia intermedia* reared experimentally on white ash and hickory leaf litter.

Table 6: ATP content (mg/ml) of leaves kept for 6 weeks in experimental rearing trays.

Thermal Regime	White Ash mean ± s.d.	American Beech mean ± s.d.	Chestnut Oak mean ± s.d.	Red Oak mean ± s.d.	Hickory mean ± s.d.
WCC*	76.1 ± 1.5	22.2 ± 1.6	24.2 ± 0.7	25.0 ± 0.6	13.8 ± 0.3
WCC + 4°C	54.7 ± 4.5	32.1 ± 2.3	34.3 ± 0.9	33.3 ± 2.1	12.2 ± 1.9
WCC + 8°C	98.6 ± 4.4	67.2 ± 3.9	50.3 ± 2.7	35.0 ± 1.2	18.7 ± 0.1

*WCC = White Clay Creek, Pennsylvania

Table 7: Mean adult weight for females of *Soyedina carolinensis* reared under varying conditions of temperature and diet.

Thermal Regime	Hickory mean ± s.d.	Red Oak mean ± s.d.	American Beech mean ± s.d.
WCC	1.992 ± .128	1.997 ± .323	1.373 ± .041
WCC + 4°C	1.564 ± .223	1.619 ± .181	1.189 ± .301
WCC + 8°C	* --	* --	* --

*High mortality of larvae and low emergence success.

Experimental results for Tipula abdominalis (cranefly), although incomplete, are similar to results for both L. intermedia and S. carolinensis in that: (1) larval growth was correlated inversely with temperature for most of the five food types; and (2) within a given temperature regime, larval growth was consistently best on hickory and white ash and substantially poorer on chestnut oak, red oak, and american beech (Table 8). The data show that both temperature and food quality have a significant effect on larval growth over the range of variables studied.

Data Management

All field and laboratory data for this project (i.e. temperature records, insect weight structures, adult fecundities, species list, species distribution, etc) are stored both on data cassettes at the Stroud Center and on magnetic tape at the West Chester State College computer facility. The Stroud Center rents a computer port from West Chester State College. The college's computer is a Xerox 560 computer and offers SPSS and BMD statistical packages. All data storage, retrieval, and analysis can be done from our remote terminal at the Stroud Center. Data are coded and stored using widely accepted numbering or coding systems whenever possible. For example, all insect species included in this study have been assigned the number code used by EPA in their Biostoret System. The capacity for data analysis and presentation at the Stroud Center has been greatly enhanced with the recent purchase of a Tektronics 4052 Graphics Terminal and 4662 Digital Plotter.

Proposed Research for 1980 - 1981

River site selection: Southeast states

Five river systems must be selected in the southeastern United States for study by the field teams beginning in October 1980. The rivers and specific study reaches (25) require identification before the spring-summer emergence period to insure the streams support species similar to those studied in the mid-atlantic states. Because emergence begins in February and March in the more southern states, we have already completed one inspection survey in Georgia, South Carolina, and North Carolina. Additional field study will be required throughout the spring and early summer before site selection is finalized.

Southern piedmont streams are highly impacted by sedimentation and it is very time consuming to locate an array of stream sites in relative proximity to each other. Higher elevation streams support increased diversity and more complex community structure, however, water temperature rapidly decreases with elevation. To date, we have identified one promising drainage located on the Duke University forest.

Table 8 - Mean wet weight for Tipula abdominalis larvae after four months growth on various leaf types at three different temperature regimes. Larvae were divided into two size classes at the start of the experiment and reared separately - small (range: 42-123 mg) and large (127-275 mg). Standard deviations of means are given in parentheses.

	Large Size Class					Small Size Class				
	Hickory	White Ash	Chestnut Oak	Red Oak	American Beech	Hickory	White Ash	Chestnut Oak	Red Oak	American Beech
WCC	1222 (30C)	986 (268)	1012 (232)	1177 (231)	981 (187)	1405 (337)	1101 (321)	973 (228)	1050 (221)	924 (233)
WCC + 4°C	1172 (232)	*	820 (162)	1052 (338)	704 (186)	1185 (241)	1048 (269)	796 (210)	799 (168)	845 (155)
WCC + 8°C	1136 (260)	993 (129)	962 (199)	897 (131)	666 (179)	1040 (121)	1088 (226)	761 (185)	691 (134)	745 (194)

* All larvae died two weeks prior to sample due to inadequate circulation within the rearing tray

Completion of field studies on the five mid atlantic streams

Field teams will be deployed to the 5 river systems (Table 2) presently under study at two week intervals for the remainder of the spring emergence period. During the summer months, sampling intensity may be reduced as the number of species in the emergence diminish. The field crews will collect material and develop data on individual biomass prior to and during emergence, emergence duration, fecundity, and larval population structure. To insure adequate characterization of adult weights and fecundity, large scale rearing will be conducted at the Stroud Center utilizing insect samples brought from the field sites at two-week intervals. We anticipate completion of field work on the mid atlantic sites by late September. During October 1981, the field teams will relocate to southeastern states to begin similar field studies.

Effects of food quality on insect size and fecundity

Studies will continue to explore the interactive effects of temperature variation and food quality on growth and fecundity of aquatic insects. To date, these studies have emphasized detrital food resources using insects that grow primarily in the winter. The next series of experiments will focus on growth responses of insects reared on diets of varying proportions of diatoms and fine particulate detritus. These studies will be conducted under various temperature regimes in microcosm streams at the Stroud Center.

Field studies will be conducted to evaluate the relative trophic status (nutrient equivalence) of the five river systems presently under study. The trophic studies will involve estimating the rate of periphyton production on artificial substrates and seasonal estimates of the principal components of particulate detritus. Since the streams selected for study all have riparian forests, at least bordering the river, quality differences in detrital food value among streams will be due largely to species composition and density of the riparian vegetation and the physical retension capacity of the channel.

Data Processing and Analysis

The temperature and weight structure data collected to date have been entered on the computer and are presently stored on magnetic tape. The time interval between data aquisition and computer entry is short. The slowest process has been measuring the dry weight of individual insects, however, this "bottle neck" will be eliminated before the intense spring sampling because we are purchasing an automatic balance with output directly to the computer.

Analysis of relationships between thermal regimes and population parameters for growth, size, and fecundity will begin immediately following data processing for the spring emergence. By mid winter, analysis of the first years data sets should be complete.

Time Allocation: Principal Investigator

The principal investigators, Robin L. Vannote and Bernard W. Sweeney, have devoted approximately 10% of their time to the project during the period July 1, 1979 to March 31, 1980 and plan to devote about 10% during the remainder of the current term which expires June 30, 1980.

PROPOSED BUDGET

2ND Year of Continuing Grant (DE-AC02-79EV10259)

From July 1, 1980 to June 30, 1981	Budget	
	DOE	Institutional
A. Salaries and Wages		
R. L. Vannote (25%)	8,491	
B. W. Sweeney (30%)	5,380	
C. A. Staub (31%)	4,698	
Assistant Data Analyst (100%)	12,331	
2 Field Biologists (100%)	24,140	
1 Entomologist (25%)	2,822	
2 Biological Technicians (100%)	21,682	
Mechanic (15%)	1,897	
Secretary (20%)	2,057	
Part-time Technician (400 hr @$4.50/hr)	1,800	
B. Total Salaries	85,298	-0-
C. Fringe Benefits (17.5% of Salary)	14,927	-0-
Total Salaries & Benefits	100,225	-0-
D. Equipment		
Insect Rearing Units	1,060	1,940
Electrobalance, Cahn 4700 + printer and Computer Interface	10,000	
Computer Terminal	1,600	
Miscellaneous Equipment	3,000	
Total Equipment	15,660	1,940
E. Materials and Supplies	2,000	
F. Domestic Travel	20,300	
G. Foreign Travel	-0-	
H. Publication Costs	800	
I. Computer Costs	2,500	
J. Consultants	7,500*	
K. Other Direct Costs		
Telephone communications with field teams and central administration	900	

PROPOSED BUDGET

2ND Year of Continuing Grant (DE-AC02-79EV10259)

	Budget	
	DOE	Institutional
L. Total Direct Costs	149,885	1,940
M. Indirect Costs	42,216	
56.2% of salaries for site work 24.6% for off site work 0.562 x 67,193 = 37,762 0.246 x 18,105 = 4,454		
	42,216	
N. Total Direct and Indirect Costs	192,101	1,940
Total Project Costs:		194,041
DOE Share	192,101	
Institutional Cost Sharing (1% of total)	1,940	
	194,041	

* $6,500 of the consultant fee is for a graduate research assistant