

Life History and Growth of Three Populations of
Glossosoma nigrion (Trichoptera: Glossosomatidae)
from Three Thermally Distinct Locations

by

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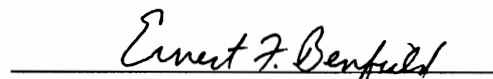
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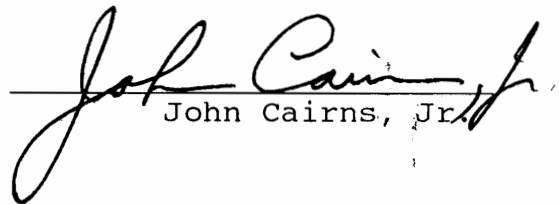
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Introduction

In general, insects demonstrate little ability to acclimate to, or compensate for changes in temperature (Lawton 1971, Kiestler and Buck 1974). When exposed to new thermal regimes, the metabolic response of these poikilothermic animals is immediate and in the direction of the temperature change. Temperature-induced changes in an aquatic insect's metabolism are of fundamental importance because such changes determine its metabolic maintenance costs. The cost of maintenance will determine how much assimilated energy can be devoted to the production of eggs, tissue, or metabolic storage products (e.g. fats and oils). The end result of these interconnected processes is reflected in the final size attained by the organisms as well as their fecundity and success of emergence. These three population features are relatively easy to enumerate and have frequently been used to define fitness. In addition to these parameters, several authors (e.g. Dingle and Hegmann 1982, Istock 1982) regard a species' life history as a major fitness phenotype. The degree of genetic flexibility or plasticity in fecundity, final size, life history, etc. determines not only the success of a species within a given habitat but its ability to expand its geographic distribution.

The majority of studies examining the influence of

temperature on aquatic species have either been confined to the laboratory or to field observations. Few studies have documented the life histories and growth of populations located at sites that differed primarily in temperature regime. Preliminary field observations identified three larval populations of the caddisfly, Glossosoma nigrrior, that apparently differed not only in voltinism but also in the size and growth rates. These initial observations were somewhat unexpected, given the relative proximity of the three locations.

It was hypothesized that the observed differences in life history could be attributed to differences in stream temperature at each location. The primary objectives of this study were: (1) to characterize the thermal regimes at each station; (2) describe the life history of each population; (3) and examine the growth rates of the various cohorts, both between and within seasons (e.g. winter versus summer cohorts) at the three stations.

Literature Review

It is necessary to distinguish between the terms "life cycle" and "life history". The life cycle of an organism has been defined as the "cycle of events which enables the products of reproduction themselves to reproduce" (Callow 1978) and as "the sequence of morphological stages and physiological processes that link one generation to the next" (Butler 1984). Perhaps the most descriptive definition is that provided by Buikema and Benfield (1979) which defines a life cycle as a "series of stages in form and function through which an organism passes between the successive recurrences of a specified primary stage (e.g. egg to egg)". On the other hand, most definitions of the term "life history" incorporate not only those features listed above for the life cycle but also include many other biological variables, including reproductive success, rate and pattern of growth, fecundity, longevity, behavior, response to environmental factors, competition, prey-predator interactions, etc. (Oliver 1979, Waters 1979a, Buikema and Benfield 1979). The expansiveness of such definitions can make quantifying a species' life history difficult. The approach taken by Butler (1984) helps to simplify this process. Butler suggests that the components of a life cycle (e.g. egg, five instars, pre-pupa, pupa, and adults) will be the same for each member of a particular species.

Each population of that species can, however, exhibit qualitative and quantitative differences in the events comprising the life cycle; these differences make up the "life history" of the population. Thus, according to Butler (1984), a particular mayfly population with a bivoltine life history could exhibit asynchronous egg hatch, parthenogenic reproduction, and complete two life cycles within a year.

Although the field of aquatic ecology, particularly that concerned with aquatic insects, has long been dominated by treatises describing the natural history of a species, studies detailing fundamental life history characteristics of many species have yet to be completed. Such information is critical in the application of more recently developed ecological methodologies (Rosenberg 1979, Butler 1984). Rosenberg (1979) felt that this type of information was crucial to studies of community level processes. Resh (1979) pointed out that knowledge of population life histories would facilitate the development of appropriate sampling strategies so that the stated objectives of benthic research could be attained. Life history information is required not only for realistic experimental design and interpretation of data generated by toxicity studies involving macroinvertebrates, but also in extrapolating laboratory derived data to field conditions (Buikema and Benefield 1979).

Much also remains to be learned about those environ-

mental parameters that influence the life history of a population. The three most important environmental factors include photoperiod (Beck 1980, Sweeney 1984), nutrition (Anderson and Cummins 1979, Scriber and Slansky 1981, Sweeney 1984, Sweeney and Vannote 1984), and temperature (Ward and Stanford 1982; Sweeney and Vannote 1981, Sweeney 1984). Of these, the influence of temperature on aquatic insects is perhaps the most thoroughly studied. Despite the extent of research in this area, little information exists concerning the responses of insects to thermal variation. Furthermore, while many studies have been conducted that involve the influence of temperature on ephemeropteran and dipteran life histories, little is known concerning the thermal response of various life history characteristics of several groups, including the Trichoptera (Sweeney 1984).

Finally, most studies involving temperature and aquatic insects have been conducted in the laboratory rather than in the field. Those studies conducted under field conditions have usually been confined to the correlation of life history patterns to seasonal temperature changes at a single location; few have attempted to compare populations at two or more thermally different habitats. Until such research is conducted, it remains "unknown whether aquatic insect populations along natural thermal gradients exhibit as much intraspecific variation in life history characteristics as might be predicted a priori based on laboratory or field

studies of one local populations."(Sweeney 1984).

Some insect orders apparently demonstrate greater flexibility in voltinism than do others. Plecoptera typically exhibit life cycles longer than one year although univoltinism is not uncommon; bivoltinism is rare (Waters 1979b). The Ephemeroptera are much more variable in their life cycles, with some species exhibiting semivoltinism as well as uni-, bi-, and even multivoltinism (Edmunds et al. 1976). The aquatic dipteran family, Chironomidae, is perhaps the most variable in terms of voltinism, with many species demonstrating multivoltinism (Oliver 1971) while numerous Arctic species may require several years to complete a life cycle (Butler 1980). Although most studies have indicated that Trichoptera are univoltine, multivoltinism has been documented (Wiggins 1977, MacKay and Wiggins 1979). Parker and Voshell (1982) reported that Hydropsyche sparna exhibited life histories that ranged from univoltinism to trivoltinism. Cuffney and Minshall (1981) found that an Idaho population of Arctopsyche grandis was univoltine while studies conducted in California indicated that this same species was bivoltine. A population of the limnephilid Dicosmoecus atripes in Alberta, Canada required two years to complete a life cycle while one in Oregon was univoltine (Gotceitas and Clifford 1983). In each of the examples discussed above, temperature was mentioned as the factor primarily responsible for observed differences in

voltinism.

Temperature is regarded as the most important factor affecting the ecology and distribution of organisms (e.g. Lemhkuhl 1979, Ward and Stanford 1982, Hutchinson 1976, Brittain 1976, Vannote and Sweeney 1980, Brittain 1983, Sweeney 1984, Sweeney et al. 1986). Although temperature is typically used to define the heat content of a body, it may best be regarded as the average kinetic energy of atoms and molecules comprising a system. Thus it is a measure of a system's heat intensity, rather than its total heat (Hochachka and Somero 1973). Because temperature is correlated with molecular activity, changes in environmental temperature can directly affect (both positively and negatively) various internal chemical reactions of organisms.

Organisms can avoid potentially adverse temperature changes by employing behavioral, physiological, or anatomical means to maintain a constant internal temperature. Homeotherms are defined as those organisms that are capable of maintaining a relatively constant internal body temperature while poikilotherms are those organisms whose internal body temperature varies in the same direction as that of the environment (Hochachka and Somero 1973). Organisms may also be categorized by the primary source of their internal body heat. The major source of endothermic body heat is internal (i.e. metabolic) while that of ectotherms is derived from the environment (Prosser 1973). Al-

though the internal bodytemperature of ectotherms seldom exceeds ambient levels, they can maintain relatively constant body temperatures, generally by behavioral compensation. Kavaliers (1980a) reported that the gastropod Heliosoma trivolis exhibited behavioral thermoregulation and found that the crane fly Tipula plutonis actively selected preferred temperatures when placed in a horizontal thermal gradient (Kavaliers 1980b). Other studies have documented diel variations in temperature selection by the crayfish Oreonectes immunis (Crawshaw 1974) as well as a number of fish (Reynolds and Casterlin 1979). Several studies have shown that large bodied insects such as sphinx moths and African dung beetles are capable of endothermy (Bartholomew and Heinrich 1978). However, endothermy among insects is usually a simple by-product of sustained muscle activity and the body temperature does not remain constant. Some species reduce metabolic demands during thermally adverse periods by becoming quiescent (Pohl 1976). Most insects, however, exhibit minimal (if any) capability to regulate their internal body temperatures and thus rely on metabolic compensation to maintain relatively constant activity rates (Prosser 1973, Hochachka 1973, Hochachka and Somero 1973).

Metabolic compensation by poikilotherms is accomplished by employing an array of complex molecular mechanisms. Among the most fundamental way in which metabolic reactions

may be regulated is by controlling the concentration of substrate required for a metabolic reaction or pathway (Hochachka and Somero 1973, Lehninger 1975, Hochachka 1973). In addition, substrate affinity of many ectothermic enzymes is directly correlated with temperature. For instance, as temperature decreases, affinity for a substrate increases and the rate of the reaction thus remains unchanged (Hochachka and Somero 1973, Prosser 1973). Changes in the membrane structure of cells and organelles have also been associated with controlling substrate concentrations. Kalapur et al. (1982) found that temperature induced changes in the phospholipid composition of mitochondrial membranes of locusts (Schistocera gregaria) that had been raised at two different temperatures. Changes in these lipids produced changes in membrane fluidity. Such changes would affect not only the Arrhenius activation energy of membrane bound enzymes (and thus the rates of the biochemical reactions catalyzed by these enzymes) but also the transport of substrates across the altered membranes.

The other major category of metabolic compensation employed by poikilotherms involve enzymes. Although not as extreme as the changes experienced by terrestrial insects, aquatic insects such as G. nigrior do experience some diurnal thermal fluctuation and must be able to adjust immediately to such changes. These organisms must rely on phenotypic changes, employing genetic products already con-

tained within their cells or that can be generated by enzyme induction (Hochachka and Somero 1973). Although limited, poikilothermic organisms can employ a number of different processes to provide enzymes with the proper enzyme-substrate affinities to accomplish both immediate temperature compensation and seasonal acclimation (Hochachka and Somero 1973). Enzymes undergoing such changes are typically those involved with energy liberation rather than with protein synthesis (Prosser 1973). One means of metabolic compensation involving enzymes includes the synthesis of seasonally specific isozymes such that winter and summer acclimated organisms would possess distinctly different isozymes. Seasonal differences in isozymes have been demonstrated for fish and would be expected in long-lived aquatic invertebrates such as Corydalis sp. and Orconectes sp. It is also possible that winter and summer populations of G. nigrrior would possess different isozymes.

Other strategies of immediate metabolic compensation include the maintenance of an array of isozymes, certain forms of which would be better suited for a given temperature range than others. Schott and Bruvsen (1980) used electrophoretic techniques to examine the enzymatic properties of a damselfly (Argia vivida) that inhabited a natural geothermal gradient. The authors found that the nymphs acclimated to a wide range of temperatures (15 - 40°C) by alternating the structure of certain enzymes (qualita-

tive changes) and by increasing the cellular concentration of others (quantitative changes). Rather than altering the actual amino acid sequence to produce an isozyme, poikilotherms may possess lipoprotein enzymes in which the protein remains unchanged but the lipid content varies; variation in the lipid would result in functional changes in the enzyme (Hochachka and Somero 1973).

Glossosoma nigrior

The order Trichoptera represents one of the few almost exclusively aquatic insect orders. It is also one of the largest orders of aquatic insects, second in numbers only to the Diptera (Wiggins 1978, Mackay and Wiggins 1979). The ancestral trichopteran is thought to have arisen from an organism with net-like wing venation, similar in appearance to modern Megalopterans. Although the exact relationship remains unclear, the Lepidoptera are also believed to have evolved from the ancestral line leading to the Trichoptera (Ross 1956). Lepidopteran and trichopteran adults of each order resemble each other at least superficially in that both have wings covered with hair or scales. Additionally, immature forms of both groups produce and utilize silk during some portion of larval development.

According to Ross (1956), ancestral Trichopterans first entered the aquatic environment in cool, lotic habitats. The group diversified under these conditions, filling available

niches and exploiting new habitats. The Rhyacophilidae, Philopotamidae, and the Glossosomatidae are generally considered the three most primitive families in the order (Ross 1956).

The Glossosomatidae are saddle-case makers. Larval cases resemble the pupal cases constructed by the Rhyacophilidae (Ross 1956). Glossosomatid cases are constructed of fine sand grains held together by silk secretions. Openings between sand grains allow free circulation of water over the larva, facilitating respiration (Wiggins 1977). Rather than enlarge their cases from one molt to the next, Glossosomatid larvae build completely new cases (Anderson and Bourne 1974). The case protects the larvae, allowing them to move about freely during the day, camouflaged from vertebrate predators (Mackay and Wiggins 1979). Larvae seldom abandon their cases but will enter the drift in response to catastrophic events such as heavy siltation (Waters 1962), high temperature, or reduced current velocity (Anderson and Bourne 1974).

Members of the family Glossosomatidae are typically cool-adapted, although some specialized forms have been found in tropical regions (Wiggins 1977). Members of this genus are commonly the dominant saddle-case makers encountered in cold mountain streams (Ross 1951). The genus Glossosoma belongs to the subfamily Glossosomatinae and the tribe Glossosomatina (Ross 1956). Approximately 25 species

have been reported in North America; all but three are confined to western montane regions (Wiggins 1977). The three eastern species (G. nigrrior, G. intermedium, and G. lividum) belong to the subgenus Eomystra. Neubauer and Robertson (1985) recently developed a key to the larvae of these three glossosomatid species.

Glossosomatid larvae are categorized as scrapers (Cummins 1978) and possess blade-like, toothless mandibles (Mackay and Wiggins 1979) that enable them to feed on periphytic algae (Badcock 1949, Jones 1950, Anderson and Bourne 1974). Cummins (1973) suggested that the diet of some Glossosoma sp. populations was dominated by detrital material. Shapas and Hilsenhoff (1976) reported that the gut contents of some Wisconsin species of Glossosoma consisted of equal portions of diatoms and detritus while Oregon populations consumed not only diatoms but also fragments of moss and liverworts (Chapman and Demory 1963).

While it is apparent that algal material (e.g. diatoms) represents a major constituent of the diet, it remains unclear whether Glossosoma sp. preferentially grazes on certain algae or are simply opportunistic feeders. Tisdale and Kovalak (1979) examined the gut contents of G. nigrrior larvae (instars II-V) and concluded that no significant differences existed in the diatom size distribution consumed by the four instars examined in the study. The authors con-

cluded that G. nigrrior is a non-selective feeder. However, more extensive studies by Oemke (1984a, 1984b) contradicted these findings and indicated that Glossosoma sp. does not feed randomly but actively selects certain algal species for consumption. G. nigrrior larvae are typically found grazing on rock surfaces, exposed directly to the water current (Chapman and Demory 1963, Hynes 1970, Kovalak 1976). Kovalak (1976, 1978, 1979, 1980) suggested that the positioning of G. nigrrior on various rock surfaces is due not so much to food availability but the need to satisfy respiratory requirements. Larger individuals with a smaller surface-to-volume ratio tend to be located in areas of higher current velocity (and higher dissolved oxygen concentrations) but which were less desirable as feeding sites.

Cummins (1975), Kovalak (1978), Vannote and Sweeney (1980), and Georgian and Wallace (1983) all indicate that G. nigrrior has a bivoltine life history pattern. Production studies completed by Tebo and Hassler (1961) also support a bivoltine pattern for this species. The western species, G. penitum, also produces two generations per year (Anderson and Wold 1972, Anderson and Bourne 1974).

Site Description

Big Stony and Sinking Creeks flow through Giles County, Virginia (Figure 1) and are tributaries of the New River. Giles County lies within the Valley and Ridge physiographic province and is thus part of the folded Appalachians. Much of this region is composed of deformed sedimentary rocks of the Paleozoic age (Lesure et al. 1978).

Big Stony Creek

Big Stony Creek is a mountain stream whose headwaters arise in Monroe County, West Virginia at an elevation of 975 m. The stream flows in a southwesterly direction through Giles County and empties into the New River. The change in elevation over this distance is 475 m. Its length from headwaters to mouth is approximately 24 km. The steep, heavily wooded watershed of Big Stony Creek lies in the Jefferson National Forest. Much of this area is heavily forested with second or third growth hardwoods. Small isolated stands of mature hemlock (Tsuga caroliniana Englem.) are preserved on Peters Mountain; the stream flows along the southeastern slope of the mountain. Thick stands of rhododendron (Rhododendron maximum L.) and mountain laurel (Kalmia latifolia L.) are frequently encountered throughout the area (Lesure et al. 1978).

Although geological studies dealing specifically with the Big Stony Creek watershed have not been conducted,

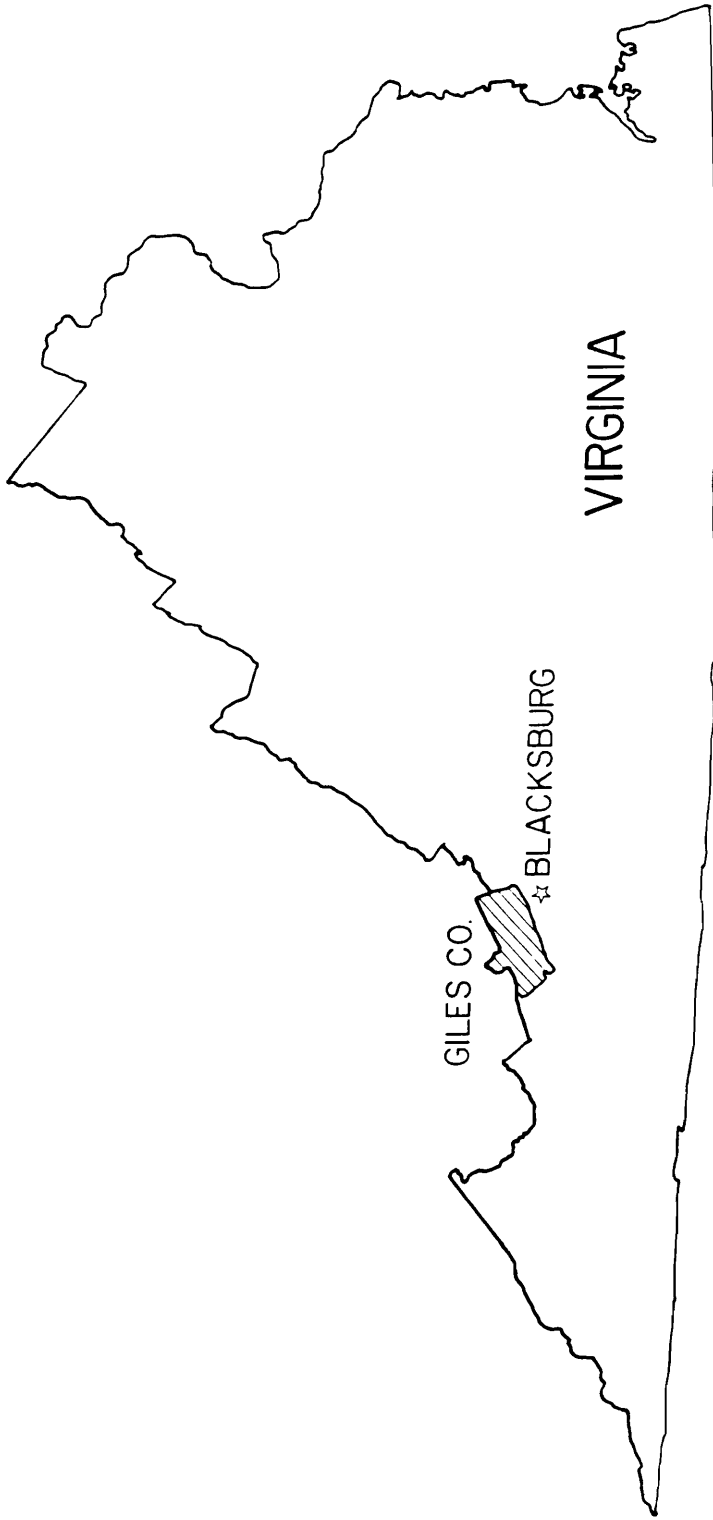


Figure 1. Giles County, Virginia.

surveys of locations adjacent to and/or forming part of the creek's drainage basin provide sufficient information about its geological characteristics. The immediate drainage area is composed of exposed sedimentary rocks from the Ordavician, Silurian, and Devonian ages. The youngest geological formations are located along the major streams in the region and are composed of small deposits of alluvial clay, sand, and gravel of Quaternary age. Dominant sedimentary rock types are both marine and non-marine in origin and include sandstones, shales, and some white quartzite. Small tributary streams near the village of Interior have been found to contain relatively high concentrations (>70 mg/L) of zinc. The source of the zinc is limonite, a prevalent rock type in the area (Lesure et al. 1978).

Station 1 was located on Big Stony Creek (37° 26'N, 80° 31'W) above the confluence with White Rocks Branch, just outside the White Rocks Recreational Area (Figure 2). The average width, depth, and current velocities recorded at this station are listed in Table 1. Using the classification scheme of Strahler (1957), Big Stony Creek may be categorized as a second order stream at this site. The mixed hardwood canopy is dense and shading is essentially 100% during the summer. Mountain laurel and rhododendron are abundant in the area. The substrate consists primarily of gravel and cobble interspersed with many large rocks.

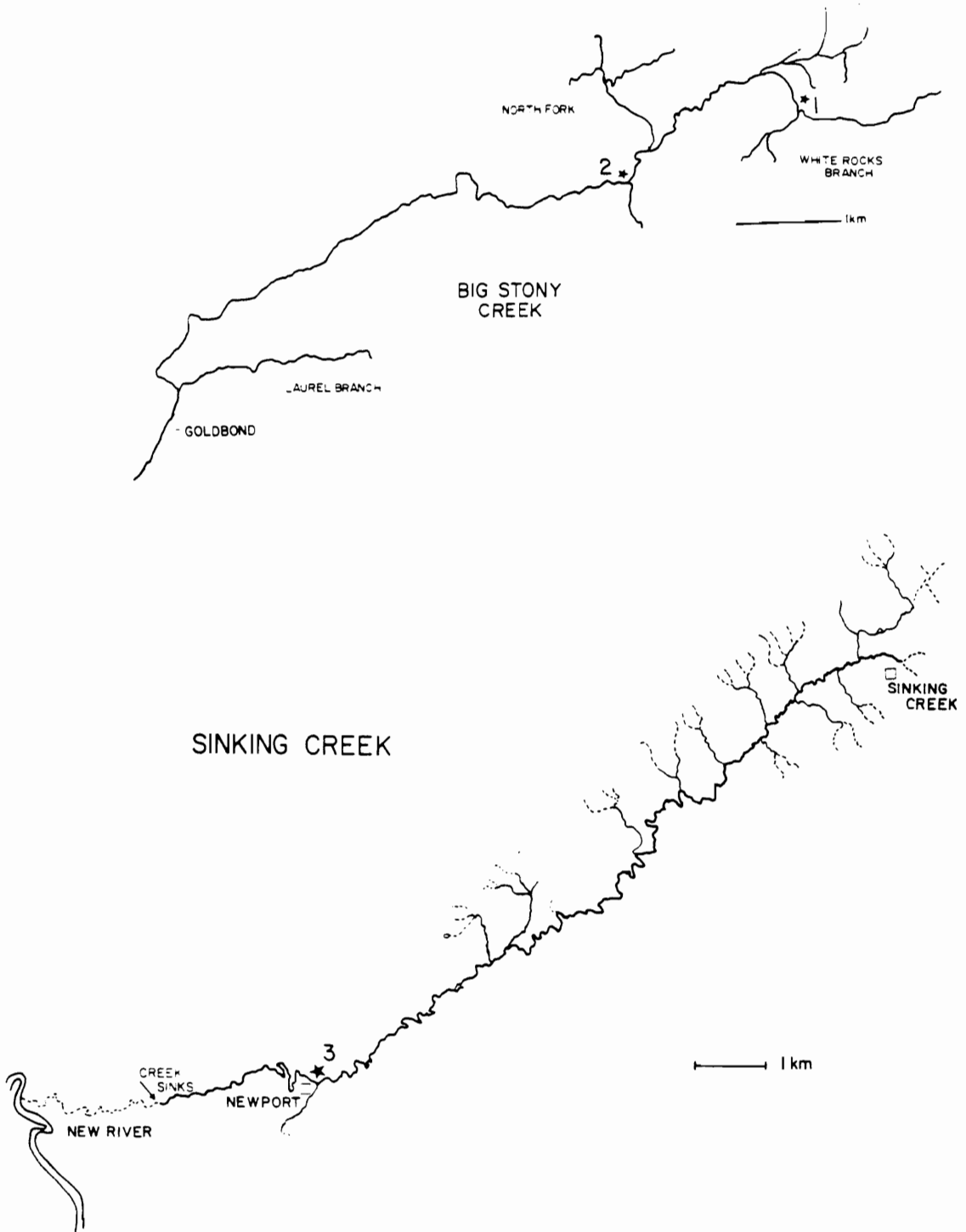


Figure 2. Location of Stations 1, 2, and 3 on Big Stony and Sinking Creeks.

Table 1. Mean physical parameters measured at Stations 1, 2, and 3.

Station	\bar{x} depth (m)	\bar{x} current velocity (cm/sec)	range (cm/sec)	\bar{x} width (m)
1	0.5	57.2	31.3- 89.7	6.0
2	0.6	42.8	23.3-100.8	13.4
3	0.7	79.9	36.5-108.9	15.2

This section of Big Stony Creek is characterized by long riffles and short pools.

Station 2 was located on the main branch of Big Stony Creek (37°25'N, 80° 33'W) approximately 5.3 km downstream from the first station (Figure 2). The drop in elevation was 49 m from Station 1 to Station 2. This diminished gradient allows the stream to meander through open fields and areas of reduced canopy. Big Stony Creek is a third order stream at this location. The canopy at Station 2 is also dominated by mixed hardwoods with rhododendron, mountain laurel, and hemlock being well represented. Approximately 40% of the stream is shaded during the summer. The aquatic macrophyte Justicia americana (L.) grows along an island located at this site. The substrate is dominated by gravel, stones, and small rocks. Long shallow riffles followed by relatively long shallow pools typify stream morphology at Station 2. Additional information concerning the physical characteristics of this station is listed in Table 1.

Sinking Creek

The headwaters of Sinking Creek are formed by the convergence of small springs in western Craig County, Va. (elevation 760 m). The majority of the stream flows in a southwesterly direction through Giles County, Va. and empties into the New River. Sinking Creek is 65 km long from headwaters to mouth. The change in elevation over this

distance is 244 m. Most of the drainage basin is dominated by agricultural land and the canopy is reduced to non-existent for almost all of the stream's length. During summer droughts, the portion of the stream located west of the State Route 625 bridge is known to sink underground (Hobbs 1975).

Hobbs (1953) conducted a geological analysis of the Sinking Creek drainage basin. This study indicated that marine sedimentary rock of the Upper Cambrian and Lower Devonian dominates much of the strata. The lower two thirds of strata is composed of dolomite ($MgCO_3$) and limestone ($CaCO_3$) while the upper third contains sandstone, siltstone, and various shales.

Station 3 was located on Sinking Creek upstream from the village of Newport, Va. ($37^{\circ}18'N$, $80^{\circ}20'W$), approximately 500 m downstream from the State Route 42 bridge (Figure 2). The stream is a third order stream at this site. The substrate is dominated by gravel and small cobble although larger stones are occasionally encountered. There was no canopy at this station. Stream morphology can be characterized by very long pool-like sections followed by relatively shallow riffles. Other physical characteristics are listed in Table 1.

Methods and Materials

Macroinvertebrate Samples

Sampling sites at each station were located in riffle sections of the streams. Sampling was confined to a transect established across each riffle. A stratified random sampling design was followed in which both the gravel/pebble and rock/cobble habitats were searched at random within defined transects. Despite a clumped distribution, G. nigrilor larvae were collected to adequately represent the population structure present at each station. On a given sampling date, 100 larvae were removed from each riffle, or if numbers were low, a maximum of 1 hr was spent searching for individuals. Larvae were hand-picked from rocks from the stream bed and were placed in small plastic buckets containing stream water. During summer, containers were placed on ice in styrofoam coolers and aerated using portable aerators. Samples were then returned to the laboratory.

Larvae were collected biweekly at Station 1, beginning in September 1981. When it became apparent from the samples that the population structure was not changing, collections were taken monthly until June 1982. At this time, biweekly collections were resumed until January 1983. Larvae were collected biweekly at Stations 2 and 3 from October 1981 to May 1983 and July 1983, respectively.

Larvae were killed with hot water, blotted, and head

capsule widths measured to determine the instar of a given individual. The widest section of the capsule was measured to the nearest 0.01 mm with an ocular micrometer. Larvae were then placed on clean glass cover slips, dried in an oven at 55° C for 24 hr, and removed from the oven and placed in a desiccator prior to weighing. Dried material remained in the desiccator at least 4 hr prior to weighing. Larvae were individually weighed to the nearest 0.001 mg using a Cahn Electrobalance (Model 4700).

With few exceptions, most species of Trichoptera have five larval instars (Wiggins 1977, Mackay and Wiggins 1979). It is frequently difficult to distinguish between the various instars, particularly the smaller ones. Mackay (1978) was able to use head capsule width to identify the various instars of several hydropsychid species by employing Dyar's Law. Dyar's Law states that successive instars of holometabolus insects usually exhibit an increase in size in a regular geometric progression (Dyar 1890). The method that Mackay adapted from Dyar's work was used to distinguish between the five larval instars of G. nigrrior. Similarly sized larvaewere selected and arbitrarily assigned to an instar group (i.e. instar II, III, V, etc.). Head capsule widths of each larva within a group were then recorded and regressionanalysis used to establish the relationship between headcapsule width and instar. The resultant regression equation was:

$$\log_{10} \text{ head capsule width} = 0.151(\text{head capsule width}) + 2.0173$$

The following equation was used to predict head capsule width:

$$W_n = 1/f W_{n+1}$$

where W is the mean value of the head capsule width, n is the instar number, and f is the factor of increase (Mackay 1978). For these populations of G. nigrrior, $f = 1.42$. Once this relationship was determined, larvae could be assigned to the correct instar and the life history pattern of each population could be established.

To further aid in establishing life history patterns of G. nigrrior at each station, attempts to collect adults were made. Techniques employed included sweep-netting, light-trapping (Coleman lanterns and UV lights), and laboratory rearing of pupae.

Physical Parameters

Physical data were collected approximately every three months. Depth and width of each study riffle were recorded. A General Oceanics Digital flow meter was used to record velocity at the center of each riffle at a depth of approximately 10 cm. Current velocities were recorded over a 60 sec period. Three readings were taken at each station. These readings were averaged and used to determine the current velocity in cm/sec for each station.

Stream temperature was measured by two different

methods. Submersible continuously recording thermographs (Ryan Instruments, Kirkland, Washington) were used to provide a record of the thermal regime at each station. The thermographs were placed inside 0.6 m long sections of 15 cm diameter well-casing. The well-casing was then anchored to large boulders or cement-filled cinder blocks using steel chain. Temperature readings were begun in February 1982 and continued through January 1983. In addition, temperature readings were taken approximately weekly at each station using a thermometer. Thermal regimes were characterized in a number of ways including temperature-time accumulations (degree-days). A stream averaging one degree Celsius for one day represents a degree-day. Classically, threshold temperatures (temperatures below which biological development ceases) are defined empirically. In this study, 0° C was arbitrarily chosen as the threshold temperature (see Sweeney 1976).

Chemical Parameters

Water chemistry data were also gathered every three months at each station. One liter samples were collected in polyethylene containers, placed on ice, and returned to the laboratory. Total alkalinity, CaCO₃ hardness, pH, and conductivity were measured immediately upon return. Samples were refrigerated at 4° C until the rest of the analyses could be completed. Analyses were completed within 24 hr of

collection. Chemical parameters were determined by methods described in Standard Methods (APHA 1981). A YSI Conductivity meter (Model 32) was used to determine conductivity while pH readings were taken with an Orion Research Ionalyzer meter (Model 399A). All cations concentrations were measured using a Perkin Elmer Model 460 Atomic Absorption Spectrophotometer.

Data Analyses

Graphical analyses were used to establish whether mean dry weights and pattern of biomass accumulation differed among the three G. nigrilor populations. Comparisons were made within seasons (i.e., mean dry weights of each population were examined for the winter and summer generations) as well as between seasons (e.g., dry weights of summer and winter generations at Station 2 were compared). Mean total dry weights of larvae collected at a given station were plotted against both time and temperature. Time was defined as the "generation time" with Day 1 equal to the first day 1st instar larvae were observed in the samples. Generation time was determined to have been completed when a preponderance of prepupae and pupae were detected in the populations. Therefore the term "generation time" actually reflects the period of maximum larval growth rather than the end of a given generation. Frequently, generation time actually extended far beyond the period of

maximum growth (e.g., the winter generation). The thermal regime at each station was expressed in terms of degree days. For these analyses, degree day calculations spanned the period two weeks prior to Day 1 of a given generation to the last week of that generation. The two week period prior to Day 1 represents the average time required for egg incubation in most species of Trichoptera (Roback 1974, Mackay and Wiggins 1979).

In an effort to reduce variability in the dry weight data, a "cohort" was arbitrarily identified at each station. In this manner, late-hatching individuals or individuals from a previous generation were not considered to belong to a cohort and were thus excluded from analysis.

Statistical analyses were employed to examine differences in the dry weights of the three populations. The goal of these analyses was to determine if temperature could have contributed to the difference in larval weights indicated by graphical analyses. The same set of comparisons examined graphically were also examined statistically. A $\log_{10}(\text{dry weight} + 1)$ transformation was performed. This transformation is often recommended for field data and has an advantage over other $\log X$ transformations in that it is a better transformation for small values (Green 1979, Allan 1984).

A mixed model regression was used to statistically analyze the transformed ($\log_{10} X + 1$) dry weight data. The

SAS procedure for general linear models (GLM) was employed (SAS 1982). It was conceded a priori that time would significantly influence the dry weight variable. To account for time in the statistical model, it was assigned a dummy variable. A "dummy variable" is any arbitrarily assigned finite value that allows different categories to be distinguished (Kleinbaum and Kupper 1976, Draper and Smith 1981). Dummy variables were also used to account for the deterministic effect station location might have on larval dry weights.

To further facilitate the adjustments necessary to account for the influence of time on dry weight data, a covariance approach was employed. By assigning "time" the role of covariant, an attempt was made to "artificially equate" the different time periods of growth by treating the populations from each station (or for a given generation) as if they had all undergone development during the same time period, the best estimate of which was X (adjusted mean time). Thus the use of the adjusted mean time in effect removes the influence of time on the comparison of the mean dry weights for a given population by considering what the mean dry weight would be for each population if all the populations had undergone development during the same period of time.

Examination of the plots of the residuals of initial regression models indicated that the variances of the dry

weight data were not homogenous. In order to reduce the heteroscedascity of the data, the populations at each station were divided into two size classes. Instars I-IV comprised Group I while Group II included instar V and prepupae. Grouping the instars into these two main size categories was consistent with observed patterns of growth and increases in biomass; a major weight increase was observed between instars IV and V. Thus in terms of dry weight, instars I-IV were more similar to one another than to the fifth instars and prepupae. It was recognized that dividing the data into two groups would reduce the value of the regression coefficient but this particular statistic was not of major importance in the evaluation of this data. As mentioned above, these statistical analyses were conducted not to determine a predictive relationship between temperature and larval dry weights but rather, were performed only to determine if temperature differences contributed significantly to dry weight differences indicated in the graphical analyses. Thus the overall significance of the model was of greater importance than the value of the regression coefficient. If the model was able to account for a large portion of variability in the data, statistical significance was indicated and the contribution of temperature to the model could then be evaluated.

The main effects examined in the mixed regression models were time, generation (season), station, and

temperature (degree days). Interaction effects were incorporated into some of the models to improve the fit of that model to a particular data set. These interaction effects included time*temperature, time*generation and time*station. The Type I sums of squares was used to determine the contribution of a particular variable in the order of its appearance in the model. The overall importance and contribution of a given variable was evaluated by the Type III sums of squares.

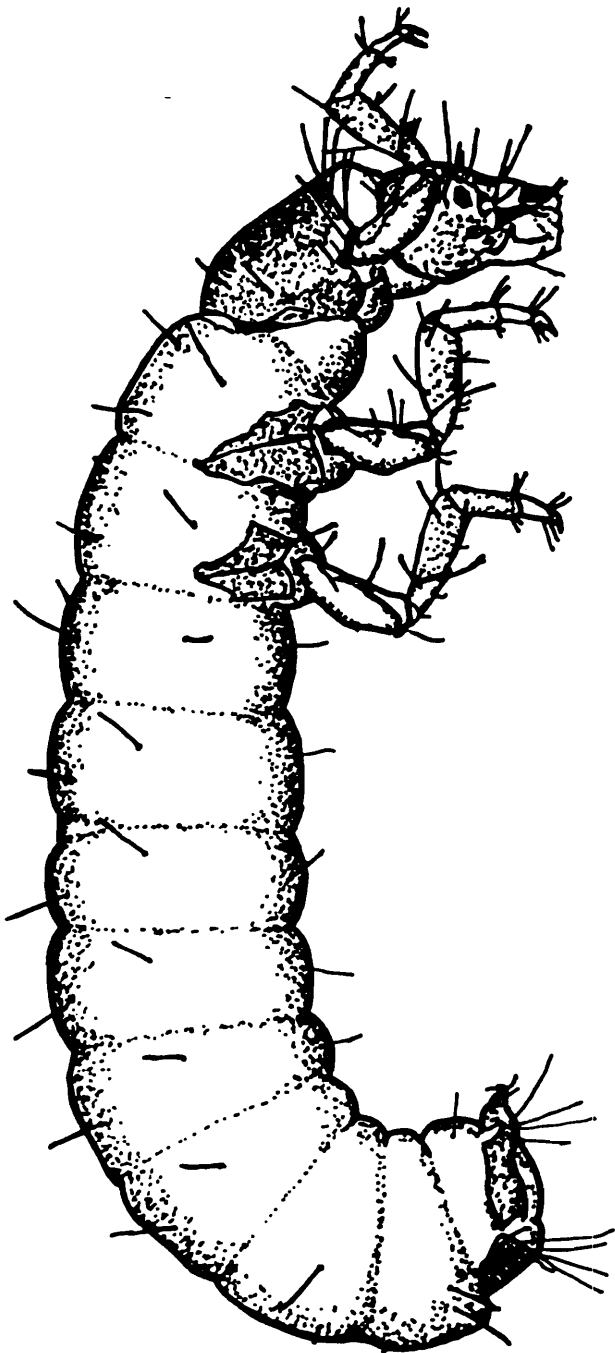
Results

General Observations

First and second instar larvae (Figure 3) were most often encountered on gravel substrates, usually in areas of reduced current. Larger individuals tended to be located on larger substrates (rock) and were generally exposed to swifter current velocities. However, the above habitats were not mutually exclusive; various instars were often found on the same substrate. Frequently large numbers of individuals were found on a given rock. It was not uncommon to remove in excess of 100 small larvae from a fist-sized rock. This gregarious behavior was exhibited by all instars and would tend to indicate that intraspecific competition for food and/or suitable substrate locations was at a minimum.

Larvae were usually found on rocks that were colonized by diatoms. Random microscopic observations of G. nigrrior gut contents confirmed that larvae grazed on diatoms. What often appeared to be amorphous detritus was actually identified as very small diatom species when examined under higher magnification (100 X).

Glossosoma nigrrior individuals appear to possess a remarkable ability to remain affixed to rocks in relatively swift currents. Unlike trichopterans such as Goera sp., Glossosoma nigrrior larvae remain attached to rocks removed from the stream bed. Occasionally live specimens were



G. nigrrior

25X

Figure 3. Larva of Glossosoma nigrrior.

returned to the laboratory in glass vials. When these individuals were observed microscopically, they were often found to have covered the glass with a netting of silk, thus enhancing their ability to move about the vial. It is likely that this type of netting was also secreted on rock surfaces, in a manner similar to the netting secreted by members of the Simuliidae. Ross (1956) also observed that free-living predaceous Rhyacophilid larvae also maintain their "footing" in swift water by clinging to silken threads spun over rock surfaces. The use of silk in this manner would permit G. nigrrior larvae to graze on diatoms growing on rocks located in swift current, permitting these larvae to exploit habitats unavailable to many other grazers.

The majority of larval growth (> 90%) occurred in the fifth instar. Just prior to the prepupal stage, G. nigrrior takes on a very robust appearance: the body "fills out" due to the accumulation of oils and fatty deposits. These deposits are easily observed through the almost transparent body wall and represent energy reserves needed during the pupal period. Pupal cases were usually found on the under surface or downstream side of rocks. Pupae are apparently vulnerable to predation as it was not uncommon to find chironomids along with pupal remains in the empty cases.

Both sweep-netting and light trapping were employed to obtain adult G. nigrrior. These methods proved less than successful perhaps due to the fact that these efforts were

initiated at dusk and continued throughout the evening. There are indications that G. nigrrior adults are more active during the day than at night (J. Weaver, pers. comm.).

Life Histories

The G. nigrrior larval instars present on each collection date at each station is presented in Figure 4. It is clear from that the population at Station 1 was univoltine. This contrasted with the situation at Stations 2 and 3; these populations were bivoltine. Reports from the literature also indicate that G. nigrrior is bivoltine.

A summary of the life histories of the G. nigrrior populations present at each station is illustrated in Figure 5. The absence of individuals at Station 1 from March through late May, coupled with the sudden appearance of first instar larvae in early June suggests that eggs hatch at this location from late May through June. Larval growth is rapid, and pupation, followed by emergence, occurred from August into September. Eggs laid during this period overwinter and do not hatch until the following spring. Individuals failing to emerge in fall remain in the pupal form throughout the winter. Few, if any, emerge the following spring.

Eggs at Station 2 also hatch from mid-May to early June (Figure 5); larvae also exhibit accelerated growth

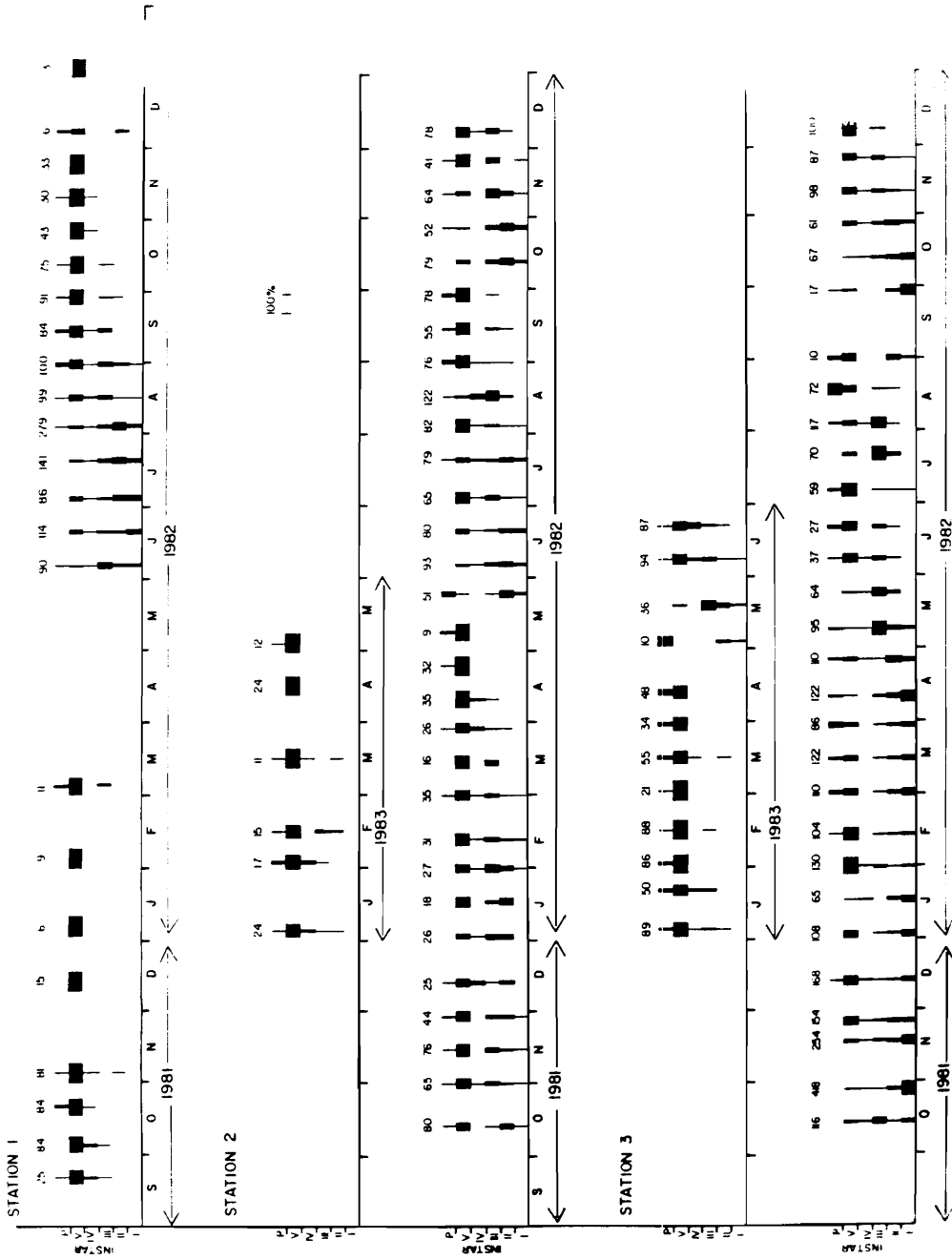


Figure 4. Larval instar distributions of three populations of *G. nigrrior*.

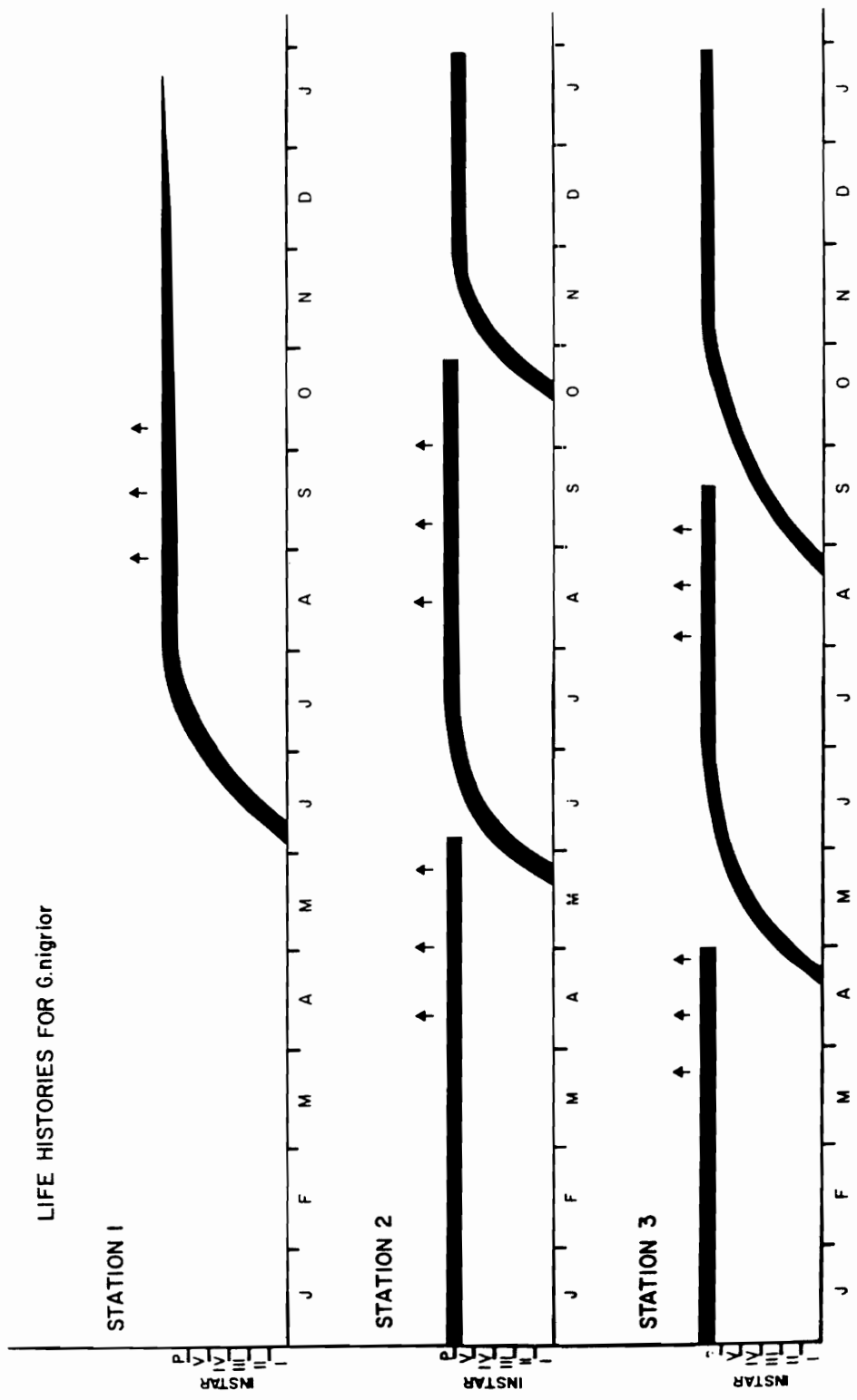


Figure 5. Summarization of life histories of *G. nigrrior* at three study sites.

throughout the summer and reach the pupal stage by mid-August. Emergence and oviposition take place from September through October. The resultant eggs hatch throughout the month of October. As indicated in Figure 5, some overlap exists between the winter and summer generations, at least until early December. Members of the winter generation at Station 2 grow throughout the winter period. Pupation and emergence take place during the months of April and May. The eggs oviposited during this period form the summer generation.

Egg eclosion at Station 3 begins in mid-April and continues through mid-May (Figure 5). The resultant larvae represent the summer generation. Like the two populations on Big Stony Creek, the G. nigrior larvae in Sinking Creek grow rapidly throughout the summer. Pupation, followed by emergence, begins in late July and continues into September. Larvae representing the winter generation hatch from eggs laid during these months. Winter generation larvae exhibit some growth throughout the entire winter period although the majority of the population reached the fifth instar by December. Pupation and emergence begins in mid-March and continues through April (Figure 5).

Temperature

Thermograph recordings allowed the following parameters

to be calculated for all months except February; mean daily temperature, maximum daily temperature, mean daily temperature pulse, maximum daily temperature pulse and monthly degree day accumulations (Tables 2 and 3). Due to the temperature sampling sequence, it was impossible to obtain an accurate record of the February 1983 thermal regime at the three stations. However, biweekly stream temperatures were recorded with a field thermometer, permitting mean monthly temperatures to be estimated for this month (Table 3).

As can be seen in Table 3, the thermal regimes at each station differed from one another. For most of the year, Station 1 was the coolest of the three stations while Station 3 was the warmest. However, for a brief period in the spring (February and March), Station 1 had higher mean daily temperatures than did Station 2. The warmest month at each of the three stations was July. During this month, the warmest mean daily, as well as mean maximum daily, temperature was attained (Table 3). January was the coolest month at Stations 1 and 3 while Station 2 exhibited its lowest mean daily temperatures during the month of February.

The diel temperature variation at each station was expressed in terms of temperature "pulses". A temperature pulse represents the number of degrees the temperature rises from the minimum to the maximum temperature during a given day. The mean as well as the maximum daily temperature

Table 2. Thermal parameters measured at Stations 1, 2, and 3.

Station	Total Degree Days	Range in Annual Temperature
1	3172.4	-0.5 to 18°C
2	3545.5	-0.5 to 23°C
3	4317.6	0 to 26°C

Table 3. Monthly temperature parameters characterizing the thermal regimes at Stations 1, 2, and 3.

	1982												1983	
	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.		
Station 1														
\bar{x} Daily Temp.	6.1	7.3	11.7	13.2	15.1	14.3	12.1	9.4	6.8	5.9	1.9	3.1		
\bar{x} Max. Daily Temp.	7.0	8.3	12.6	13.8	15.9	15.4	12.6	10.1	7.7	5.4	2.6	-		
\bar{x} Daily Pulse	1.7	1.9	1.5	1.4	2.3	2.3	1.1	1.6	1.7	1.1	1.0	-		
Max. Daily Temp. Pulse	3.3	3.2	2.8	2.6	4.0	2.6	2.6	2.7	2.3	1.3	0.8	-		
Station 2														
\bar{x} Daily Temp.	4.9	8.8	14.3	14.6	17.8	17.0	13.5	10.4	6.5	6.4	2.5	2.1		
\bar{x} Max. Daily Temp.	6.9	10.4	15.8	15.8	18.9	18.3	14.7	11.4	7.6	7.0	2.9	-		
\bar{x} Daily Pulse	3.0	3.3	3.0	2.3	2.9	2.7	2.5	2.1	1.9	1.2	0.9	-		
Max. Daily Temp. Pulse	4.0	3.9	4.0	3.2	4.9	3.2	3.1	3.0	2.6	1.4	1.3	-		
Station 3														
\bar{x} Daily Temp.	8.6	10.9	15.4	16.5	19.4	18.6	16.2	13.6	10.9	7.0	3.7	5.8		
\bar{x} Max. Daily Temp.	9.8	11.0	16.2	17.6	20.4	19.9	17.1	14.3	11.5	7.6	4.1	-		
\bar{x} Daily Pulse	2.3	3.1	2.9	2.2	2.7	2.7	1.5	1.6	1.3	1.3	0.9	-		
Max. Daily Temp. Pulse	4.3	5.2	3.8	3.8	4.6	3.0	2.1	2.3	2.0	1.5	1.4	-		

pulse was calculated for each station (Table 3). Aside from December and January, Station 2 exhibited the greatest thermal variability of the three stations. In terms of the mean daily pulse, Station 3 proved to be the most thermally variable station during the month of December while Station 1 was found to be the most variable during January. With the exception of the months of November and January, Station 1 was the least thermally variable of the study locations. During October, both Stations 1 and 3 exhibited only a 1.6° C temperature pulse between the average daily minimum and maximum temperature while Station 2 and 3 exhibited the same average diel temperature fluctuation (0.9° C) for the month of January. Stations 2 and 3 exhibited their greatest mean daily temperature fluctuations in April while the month of July represented the period of greatest thermal variability at Station 1.

The thermal regime at each station was also described in terms of degree days (Table 2). For most of the year, Station 1 was again found to be the coolest of the three stations while Station 3 was the warmest (Table 2 and Figure 6). However, for a brief period during early spring (March and April), Station 1 was warmer than Station 2 (Figure 6). This was also indicated by the mean daily temperatures for these months (Table 3). Following this two month period, both Stations 2 and 3 exhibited increases in heat accumulation. Because of its larger size and reduced canopy,

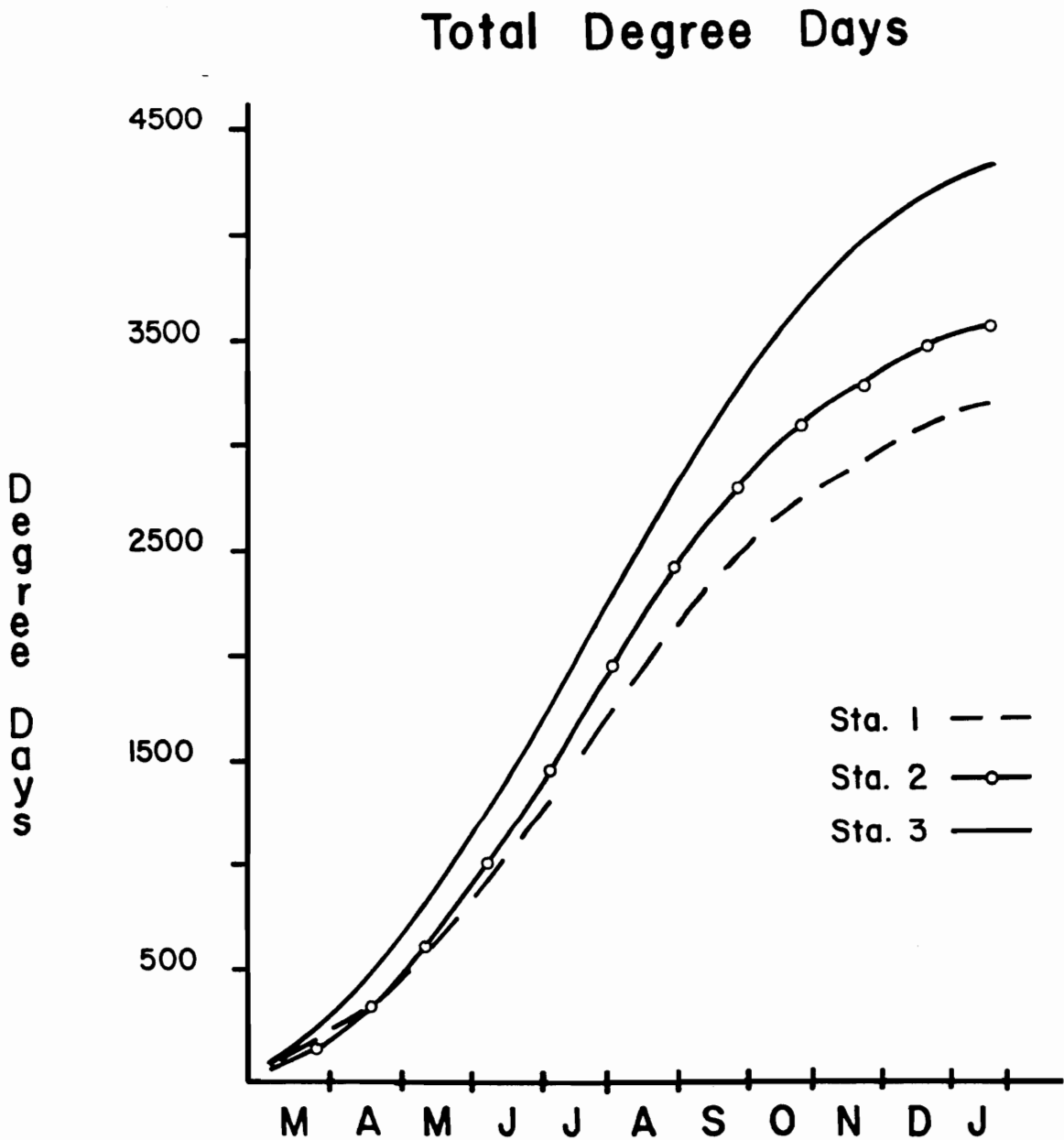


Figure 6. Comparison of degree days accumulated during the completion of the summer and winter generations of *G. nigrivor* at three study sites.

Sinking Creek (Station 3) absorbed and retained more heat than did Stations 1 and 2. Although cooler than Station 3, Station 2 was found to accrue more degree days than Station 1. The accumulation of more heat at Station 2 than at Station 1 is reflected in its greater thermal variability. This thermal variability is due to the partial shading that exists at this location, its distance from ground-water sources, and the fact that the stream flows slowly through areas of reduced canopy. On an annual basis, Station 1 accumulates the least amount of heat; this may be explained by its proximity to groundwater sources and its heavily shaded watershed. This in turn is reflected in the relative lack of thermal variability recorded at this station.

Relationships between Temperature and Growth

Graphical analyses were used to determine if the observed differences in voltinism and degree days accumulated at each station were reflected in the growth patterns of each of the three populations examined.

The most obvious differences in the degree day accumulations are those that occur between the summer and winter seasons at a given station. During the summer generation (period of maximum larval growth) at Station 2, a total of 2290.4 degree days was accumulated while only 894.6 degree days were accrued during the winter generation at this station (Figure 7). Despite this difference, the number

of days from egg hatch to the appearance of large numbers of prepupae and pupae in the samples of the summer and winter populations was approximately the same (i.e., 129 and 125 days, respectively; Figure 8). The transformed mean total dry weights of *G. nigrior* larvae collected during each generation at Station 2 were also plotted against the number of degree days required to complete a generation (Figure 8). The winter generation responded more quickly to the accumulated heat and attained a higher final mean dry weight than members of the summer cohort (2.50 vs. 1.43 mg, respectively) despite the fact that fewer degree days accumulated during this generation than that of the summer.

A similar pattern was noted when the summer and winter generations were compared at Station 3. As was the case at Station 2, the number of degree days accumulated during the summer generation exceeded the total number of degree days to which the winter cohort was exposed (2225.3 vs 1314.6 degree days, respectively; Figure 7). The total mean dry weights of each cohort were plotted against the number of days required to complete the respective generations (Figure 9). It was found that while a slightly longer period was required for completion of the winter generation, its members attained a much higher final dry weight than did their summer counterparts (2.56 vs 0.89 mg). Although slightly more time was necessary to complete growth during the winter, it appears that members of the winter generation

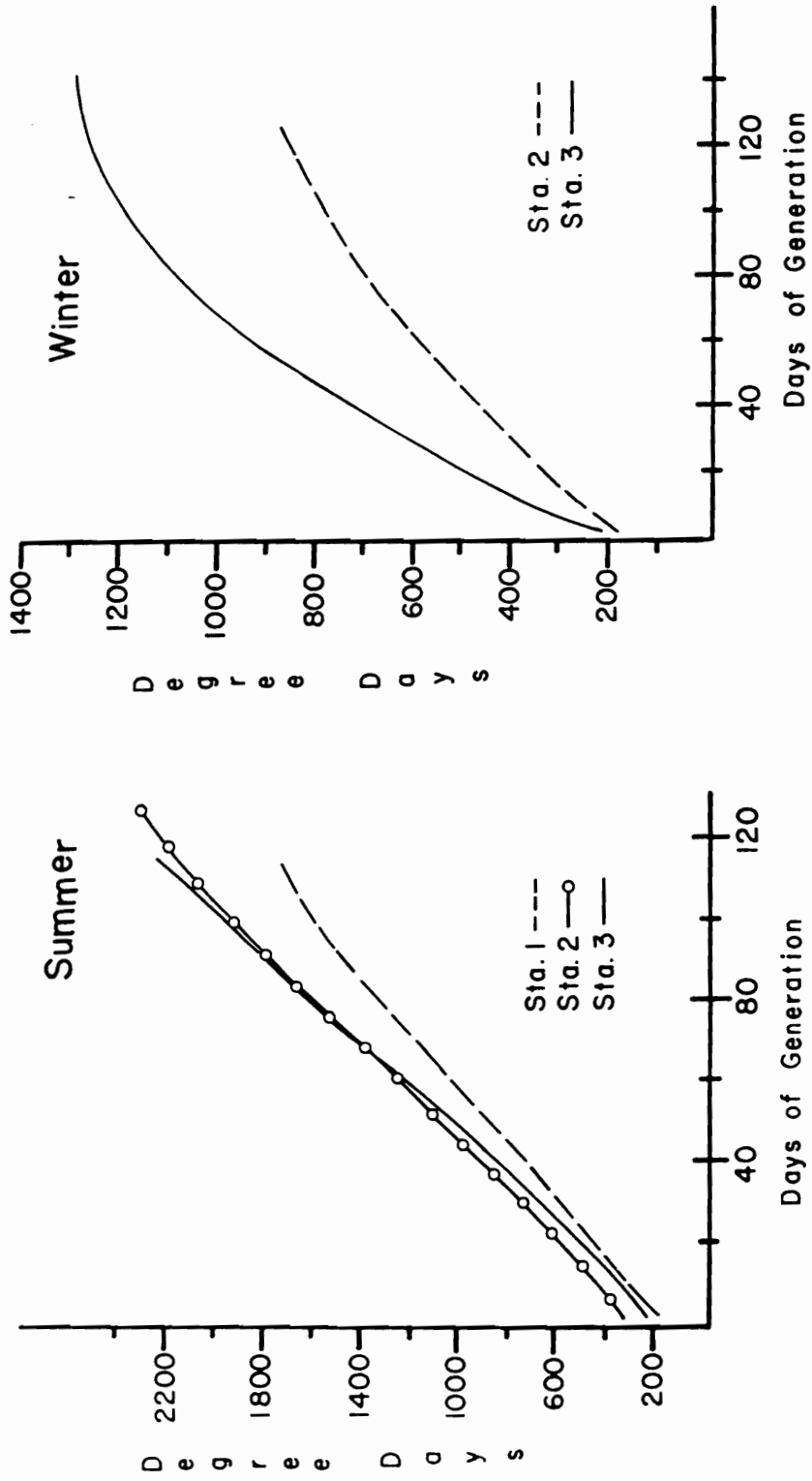


Figure 7. Degree days accumulated during the summer and winter generations at three stations.

Population Growth - Station 2

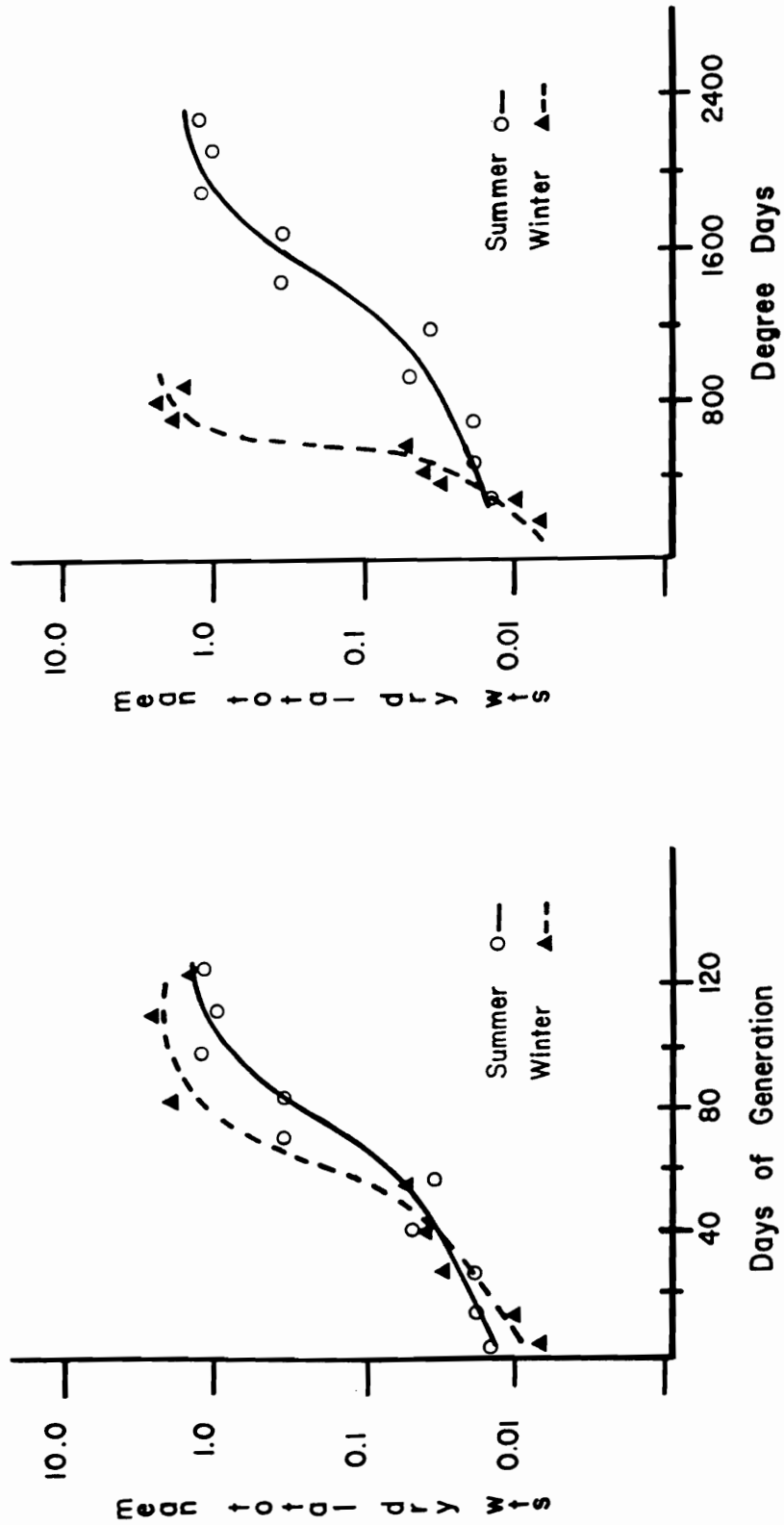


Figure 8. Growth rates of the summer and winter generations of *G. nigrivorax* at Station 2.

Population Growth - Station 3

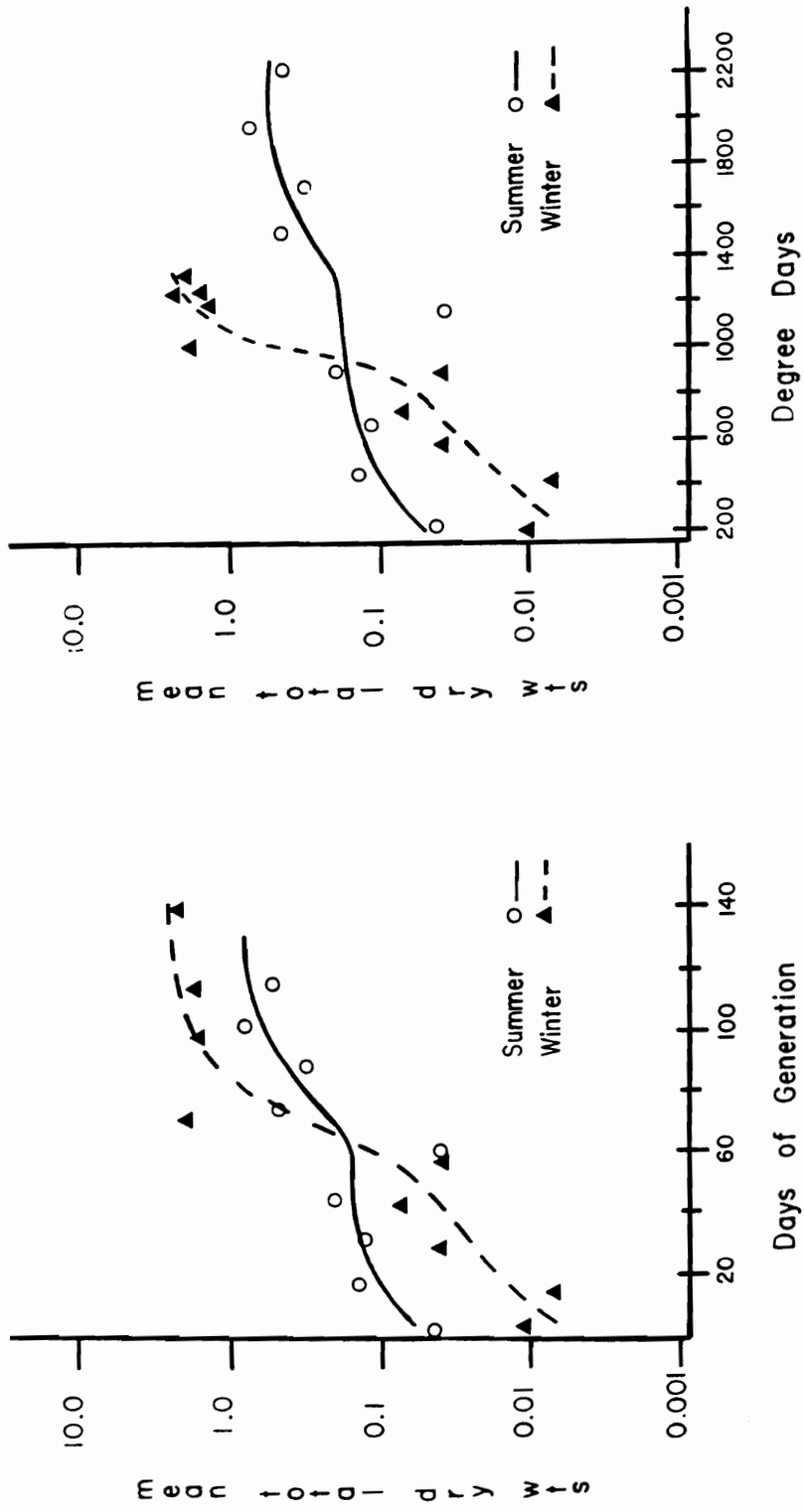


Figure 9. Growth rates of the summer and winter generations of G. nigrior at Station 3.

responded more rapidly to the accrual of heat than did larvae in the summer generation (Figure 9). As was the case at Station 2, when evaluated in terms of degree days, larvae of the winter cohort were able to grow more rapidly and achieve greater final dry weights than were the G. nigrrior larvae of the summer generation.

As previously discussed, the number of degree days accumulated at each station on an annual basis differed (Figure 6). This inequity in heat accrual was also observed on a seasonal basis (Figure 7). During the summer generation, Station 1 was the coolest of the stations (1722 degree days) while Stations 2 and 3 were somewhat warmer (2290.4 and 2225.3 degree days, respectively). The winter generation at Station 2 was exposed to a total of 894.6 degree days while that at Station 3 was exposed to 1314.6 degree days (Figure 7).

For a given season, it was possible to compare the growth patterns of the G. nigrrior populations present at the three stations. The dry weights of the larvae from each station were plotted against the number of days required to complete the summer generation (Figure 10). It was found that larvae from Station 3 completed their growth in a somewhat shorter time period than did larvae at the other locations. However, though larvae at Station 3 had higher initial weights than did those at Stations 1 and 2, those larvae at Station 1 achieved higher final dry weights than did their

Growth of Summer Generations

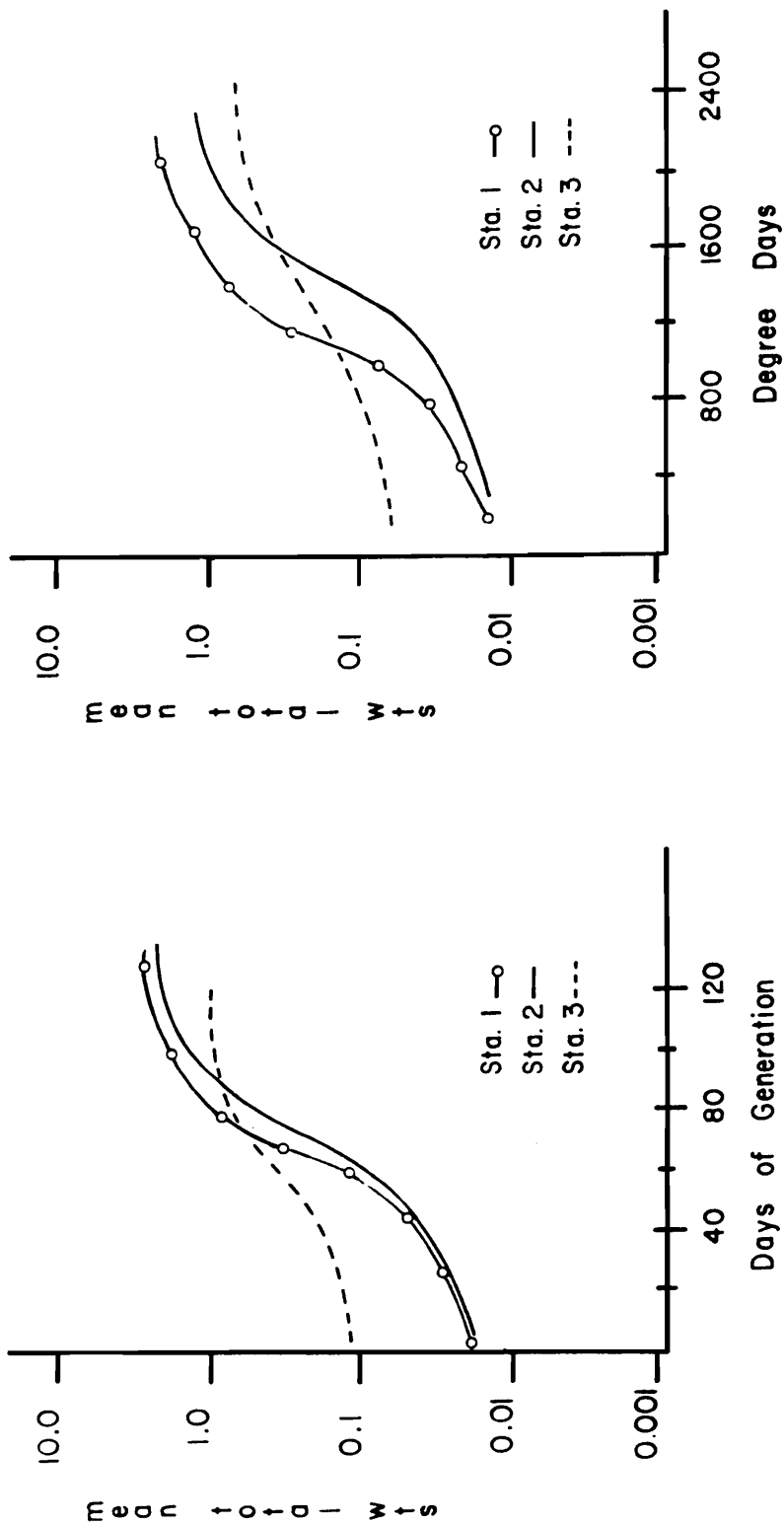


Figure 10. Growth rates of the summer generations of *G. nigrilor* at Stations 1, 2, and 3.

Station 3 counterparts (1.71 mg vs 0.89 mg, respectively) and were substantially heavier than the larvae at Station 2 (see Figure 10).

The same dry weight values were plotted against the total number of degree days accumulated at each station during the summer generation (Figure 10). As demonstrated in this figure, the larvae at Station 1 exhibited the greatest increase in biomass per unit of accrued heat. A similar trend was noted at Station 2. Thus it appears that the fewer the number of degree days to which G. nigrrior larvae are exposed, the faster they grow and the higher their final mean dry weights; reduced maintenance costs result in higher final dry weights.

Comparisons between winter generation at Stations 2 and 3 were made to determine if the trends noted for the summer generations were evident during the winter. The number of degree days accumulated at Station 3 during this generation exceeded that attained at Station 2 (1314.6 vs 894.6 degree days, respectively; Figure 11). When the dry weights of the larvae at each station were plotted against the accumulated degree days, it was clear that the population at Station 2 grew much more rapidly than that at Station 3. This difference in growth rate is not as evident when the dry weight data is plotted against the number of days required to complete the winter generation at each station (Figure 11). Chronologically, the larvae at Station 3 appeared to

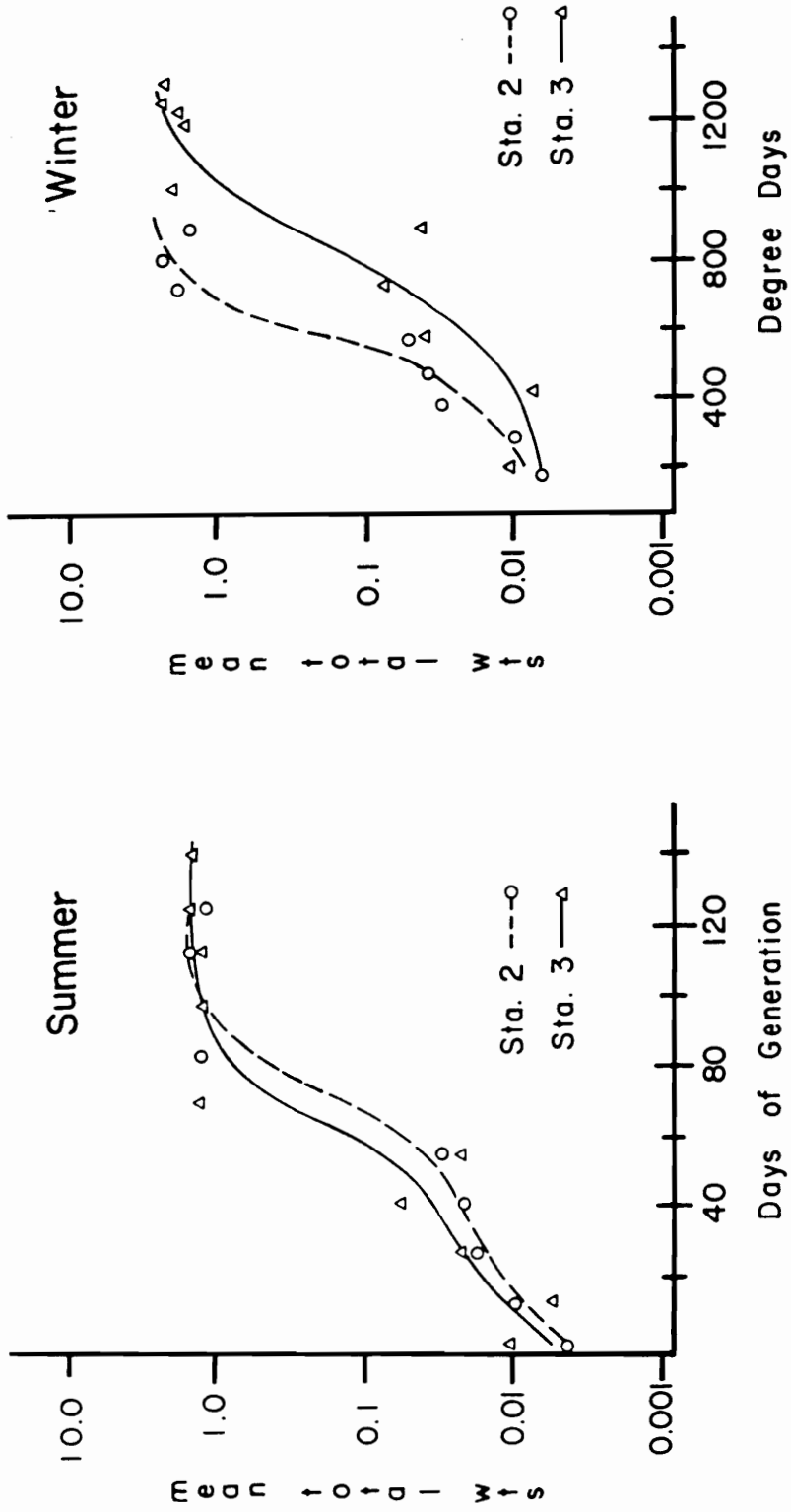


Figure 11. The summer and winter generations of *G. nigrrior* at Stations 2 and 3.

grow somewhat more rapidly than those at Station 2. Nonetheless, the accelerated growth rate among larvae exposed to fewer degree days noted at Stations 1 and 2 were also observed during the winter generations at Station 3. Larvae exposed to fewer degree days grow more rapidly and achieve higher final dry weights. This inverse relationship indicates that *G. nigrior* larvae are apparently better adapted for growth at lower temperatures. As evidenced by the above graphical analyses, growth is less efficient or perhaps suppressed at higher temperatures, thus resulting in slower rates of growth and lower final dry weights.

The results of mixed model regression analyses were used to determine if temperature contributed significantly to the patterns of larval growth indicated by the graphical analyses. Larval dry weight data were examined both within seasons and between stations.

Differences in larval dry weights were examined on a seasonal basis. Comparisons were made among weights of larvae collected at Stations 1, 2 and 3 during the summer and at Stations 2 and 3 during the winter. Within each season, dry weight data were further subdivided into one of two instar groups. Group I represented larvae instars I through IV, while instar V and prepupae comprised Group II. Equation 1 was written for Group I larvae collected during the summer season;

$$Y = \mu + \alpha + \beta_0 + \beta_1X + \beta_2Z + \beta_3W + \beta_4(W*Z) + \epsilon$$

where Y represents mean larval dry weights, X equals the covariant time (expressed as the number of days required to complete the summer generation), Z equals the dummy variables representing Stations 1, 2 and 3, and W represents the thermal regime expressed as degree days accumulated during this generation. This model fits the data very well ($p < 0.0001$) and temperature was found to contribute significantly ($p = 0.036$) toward explaining the dry weight differences observed among Group I larvae during the summer season. The interaction effect (temperature*station) was also highly significant ($p = 0.0001$), indicating that temperature not only influenced the smaller larvae directly but also acted indirectly by influencing some unmeasured factor at each station.

Comparisons were also made among the larger larvae (Group II) collected during the summer at Stations 1, 2 and 3. Equation 2 fit the data well and accounted for a significant portion ($p = 0.0001$) of the variation observed in the data set:

$$Y = \mu + \alpha + \beta_0 + \beta_1X + \beta_2Z + \beta_3W + \epsilon$$

where Y = mean larval dry weights, X represents the covariant time, Z is the dummy variable representing the three stations, and the degree day temperature is represented by W. As was the case for the smaller larvae, the thermal regime (degree days accumulated during the summer generation) contributed significantly ($p = 0.0003$) toward explaining the

dry weights differences observed among the Group II larvae.

Only the dry weights of larvae collected at Stations 2 and 3 could be compared during the winter season. Equation 1 also fit the dry weight data for the winter population of Group I larvae and accounted for a significant ($p = 0.0001$) portion of the variation in the dry weight data for this larval size; the degree day variable contributed significantly ($p = 0.0001$) to the model. Like the model used to fit data collected during the summer season, the interaction term temperature*station also made a significant contribution ($p = 0.0001$) to this model.

Dry weight data of the larger larvae (Group II) collected during the winter at Stations 2 and 3 was also fitted by a mixed regression model. The test statistic (F value) indicated that the model fit the data well ($p = 0.0001$). However, the very low value of the regression coefficient ($R^2 = 0.0252$) indicated that this was actually a weak model; the overall indication of significance was more a function of the relatively large n value ($n = 369$) rather than the contribution of the various parameters included in the model. Based on this analysis, there was no evidence to suggest that either the degree days or station variables differed enough to account for the observed differences in the weight of the older instars found at Stations 2 and 3 during the winter season.

In summary, mixed model regression models determined

that temperature, expressed as degree-days, accounted for a significant portion of the variation exhibited by the larval dry weights. This was true for all comparisons with the exception of the comparisons made between Group II larvae collected during the winter at Stations 2 and 3. Although the F statistic suggested that the model fit the data ($p = 0.001$), the exceptionally low R^2 value indicated that the model was actually weak and that the highly significant F statistic was more than likely a result of the relatively large sample size. These analyses supported the results of the graphical analyses which indicated that differences existed in the dry weights of the larvae and suggested that temperature significantly influenced the growth of G.nigrior larvae at the three study sites.

Discussion

Relatively few studies have examined the complex interacting physical factors which dictate the thermal regime of an aquatic environment (Smith and Lavis 1975). Among the more extensive studies of the geomorphological parameters that help influence lotic thermal regimes are those by Leopold and Maddock (1953), Smith (1972), and Smith and Lavis (1975). Smith and Lavis (1975) reported that large scale topographic features determine altitude and aspect of drainage basins while the amount of solar radiation reaching the water surface is regulated by microtopographic features such as bankside vegetation, angle of the stream bank, and channel depth (Smith and Lavis 1975). Large scale- and micro-topographical features were found to influence the thermal regimes of all three stations included in this study. The differences in the thermal regimes of Big Stony and Sinking Creeks are attributable to the distance of each station from the headwaters of the two creeks and the extent to which each station was shielded from solar radiation.

Station 1 accumulated the fewest degree days (3172 degree days) of the three stations studied and can be characterized as being "summer-cool" and "winter-warm". The amount of thermal variation exhibited by Big Stony Creek at this location was relatively small when compared to the variation recorded at Stations 2 and 3. This thermal

stability was the result of the close proximity of Station 1 to the stream's headwaters and the closed canopy that dominates the drainage basin from the headwaters to Station 1. The steep angle of the bank also helped minimize thermal fluctuations at Station 1 by shading large segments of the stream.

The temperature of the ground water at any given latitude tends to remain stable, varying little on a seasonal basis (Vannote and Sweeney 1980). Groundwater temperatures in western Virginia average 13.8° C annually (Collins 1925). Organisms inhabiting the upper reaches of streams are in close proximity to groundwater sources and therefore experience relatively narrow ranges of temperature. Although Station 1 was located 5.3 km downstream from the headwaters of Big Stony Creek, the physical features of this location (e.g., dense canopy, steep stream banks) helped decrease the amount of solar radiation reaching the surface of the water.

The higher number of degree days accumulated at Station 2 as compared to those at Station 1 can be attributed to: a) the greater distance between Station 2 and the headwaters; b) a decrease in stream gradient between Stations 1 and 2; and c) a reduction in the canopy at Station 2. The reduction in stream gradient between Stations 1 and 2 contributed to the higher heat accumulation at Station 2 as follows: although Big Stony Creek descends approximately 30.5 m/km from

its headwaters to Station 1, the stream only descends 9.3 m/km between Stations 1 and 2. This gradient reduction resulted in a concomitant decrease in current velocity, permitting Big Stony Creek to meander slowly between Stations 1 and 2 through areas with reduced to non-existent canopy. The reduced current increases the amount of time the stream travels through unshaded areas, resulting in greater exposure to solar radiation, and subsequently increases the heat accumulated by the stream when it reaches Station 2. Local "microtopographic" characteristics such as stream width and riparian vegetation further contribute to the addition of heat from solar radiation. The stream was much wider at Station 2 than at Station 1, reducing the percentage of the stream surface shaded by banks and riparian vegetation. Although portions of the stream were shaded during the day, relatively large sections of Big Stony Creek remained open to direct solar insolation at this location.

Station 3 on Sinking Creek was the warmest of the three study sites, accumulating 4317 degree days between February 1982 and January 1983. The increased heat accumulation at this third order location was also a result of its greater distance from its headwaters, a reduction in gradient at this location, and the comparatively greater distance between its banks. Although large patches of riparian vegetation still exist along the banks of the stream, most of the drainage basin was used for grazing or cultivation and

riparian vegetation had been removed from an extensive portion of the stream. Consequently, solar radiation had a major impact on the thermal regime at Station 3.

While it is evident that both seasonal and diel temperature fluctuations are inherent characteristics of stream ecosystems, long term studies of a small creek in Pennsylvania have indicated that stream thermal regimes exhibit what has been termed "predictable variability" (Sweeney and Schnack 1977). Studies on the Pennsylvania creek have demonstrated that certain thermal events occur annually within ± 5 days due to a high correlation between seasonal changes in the photoperiod and the development of the riparian vegetation (Sweeney and Schnack, 1977). Although the thermal regimes at Stations 1, 2 and 3 were characterized for only one year, they can probably be regarded as typical of the thermal conditions present at each location for any given year.

As previously discussed, the results of the present study established that differences did exist in the number of degree days accumulated and the pattern of diel thermal variability among stations (Table 3). However, while the difference in the total number of degree days accumulated at Stations 1 and 3 was substantial (3172 versus 4317 or 26.5% more degree days), the number of degree days accrued at Stations 1 and 2 was similar (3172 and 3545, respectively), with Station 2 accumulating only 11% more heat than did

Station 1. Although apparently insignificant, Brittain (1976) indicated that small differences in heat accrual (e.g., 11%) can influence populations of aquatic macro-invertebrates. In studies of the distribution of two lake-inhabiting mayflies, Brittain found that an 8% difference existed between the degree hours accumulated in two lakes during the summer. He equated this difference to a permanent average temperature difference of 0.83° C or, alternatively, a time period of 3-4 weeks (Brittain 1976). Brittain suggested that this difference in degree hours may have contributed to excluding the two mayfly species from one of the lakes he studied. While similar calculations were not completed for the present study, it was apparent that this 11% difference in degree days between Stations 1 and 2 could be physiologically important and account for the differences observed in the life histories in the populations of G. nigrior at each station.

Although relatively easy to calculate and capable of producing reasonably correct predictions of insect growth rates, expressing thermal regimes in terms of accumulated degree days has some limitations in application (Baskerville and Emin 1969, and Wagner et al. 1984). These limitations include the fact that degree day calculations can obscure important variations in the diel thermal component (Crisp and LeCren, 1970). For instance, daily temperature pulses can be extremely important to ectothermic organisms, sti-

mulating growth and development. Diel temperatures may rise above a critical threshold long enough to initiate metabolic activities that may, at a minimum, satisfy the maintenance requirements of organisms (Sweeney 1977). In addition, many authors have suggested that seasonal temperatures are of primary importance in affecting the competitive success and thus the ability of aquatic insects to expand their geographic range (e.g., Macan 1961; Reid 1961; Eddington 1965; Smith and Lavis 1975; Brittain 1976; Vannote and Sweeney 1980). Most aquatic insect species have evolved within this milieu of changing temperatures. However, despite its importance, detailed examinations regarding the influence of thermal regimes on the ecology and evolution of aquatic insects are recent and few in number (Ward and Stanford 1982). A complete understanding of temperature in influencing aquatic insects awaits further investigation. Nonetheless, it is apparent that in order for an aquatic insect species to successfully compete in a given location, it must have evolved temperature sensitive biochemical responses, the results of which are subsequently manifested in growth, fecundity and life history patterns.

This study indicated that despite the geographic proximity of these three G. nigrrior populations, marked differences existed in their voltinism (Trapp and Hendricks 1984). The population at Station 1 was clearly univoltine while those at Stations 2 and 3 were bivoltine. Voltinism

may be defined as the "number of life cycles an individual and its progeny can complete in one year." (Butler 1984). In large part, voltinism depends on the length of the life cycle which in turn is governed by factors affecting growth and the development rate. While it is likely that fundamental genetic constraints influence growth and development, evidence in the literature strongly suggests that much flexibility exists in the number of life cycles a given species can complete at a particular locale. In most cases, variability in voltinism is the product of environmental influences on the rate of growth and development (Wallace and Merritt 1980). Temperature (Sweeney 1977; Sweeney and Vannote 1978, 1981; Vannote and Sweeney 1980) and temperature and nutrition (Anderson and Cummins 1979; Ward and Stanford 1982; Sweeney 1984; Sweeney and Vannote 1984) are most commonly cited as the major contributors to geographic variation in the voltinism of a species. Harper (1973) and Brittain (1974, 1978) found species of Plecoptera that alternated between semi- and univoltinism in response to differences in thermal regime. Mackay (1979, 1984) found thermal regime influenced the growth rates and thus the number of generations produced per year by Hydropsyche sparna inhabiting a Canadian river. Mackay's studies of H. sparna indicated that this species was univoltine at colder stations and bivoltine, with some members exhibiting trivoltinism, at warmer stations (Mackay 1979, 1984). Based

on the life history patterns exhibited by each of the G. nigrrior populations examined in the present study, it appears that differences in stream temperatures also influenced the voltinism of this species (Trapp and Hendricks 1984).

Although members of the summer generation at each location laid eggs during the fall, only eggs at Station 1 failed to hatch until the following spring. This suggests that the months of August, September, and October are "thermally critical" to these three G. nigrrior populations (Trapp and Hendricks 1984). When the mean and maximum diurnal temperatures at Stations 1 and 2 were examined for these months (Table 3), it was found that they were similar, especially for the latter two months. Temperatures at Station 3 were somewhat higher for this period. However, when the mean diel temperatures were considered in conjunction with mean diel temperature pulses, it was apparent that the maximum daily temperatures reached at Station 1 were lower than those reached at Stations 2 and 3.

In addition, temperatures were lower during the spring at Station 1 than they were in the fall. Yet eggs hatched in the fall at Stations 2 and 3 but failed to hatch at Station 1. If temperatures were not sufficiently high enough to stimulate egg eclosion at Station 1 during the fall, what factors initiated spring embryonic development and subsequent hatching at this location when temperatures were

lower? The answer may lie in the length of time eggs were exposed to a particular temperature as well as the range of diel temperatures associated with it. Sweeney and Schnack (1977) and Sweeney (1977) reported that egg development of many aquatic insects living in fluctuating thermal environments depends largely on the magnitude of the diel temperature pulse. These authors thought that the warm portion of the diel temperature cycle was crucial in stimulating embryonic development. Corbet (1964) developed a hypothesis to explain the synchronization of "summer" species of odonates that overwinter in a variety of instars. Synchronization of final instar development occurs in response to a series of rising temperature thresholds and development would only occur when temperatures were rising. Lutz (1968, 1974) and Paulson and Jenner (1971) found that Corbet's hypothesis explains developmental patterns in several species of odonates. A similar scenario could explain why G. nigrrior eggs hatched in the spring of the year at Station 1 but not during the fall. Despite the low mean spring temperatures, the diel fluctuations associated with these temperatures, coupled with the rising vernal temperatures, may have been sufficient to elicit egg eclosion. During other (i.e., warmer) periods of the year, similar temperature pulses would have no effect on G. nigrrior eggs. Unlike the population at Station 1, the G. nigrrior populations at Stations 2 and 3 were bivoltine. As

previously mentioned, the maximum daily temperatures at these two locations during August, September, and October were higher than those attained at Station 1. These maximum daily temperatures were sufficiently high enough to initiate egg eclosion, resulting in bivoltine rather than univoltine populations at Stations 2 and 3.

The three G. nigrrior populations differed not only in terms of voltinism but also in their rates of growth. Results suggest that each G. nigrrior population exhibited a unique growth rate within a given season and that for a given station, the growth of the winter generation differed from that of the summer. When examined on a chronological basis, the differences in the rates of growth were relatively minor.

The similarity in growth rates between the winter and summer generations was somewhat unexpected. Most studies have found aquatic invertebrate growth rates to be highest in the summer and lowest in the winter (McDiffet 1970; Heiman and Knight 1975; Svensson 1977; Siegfried and Knight 1978) although Brittain et al. (1984) found that the stone fly, Capnia atra had an inherent ability to grow faster at colder temperatures. However, when the patterns of growth were examined in terms of physiological time, significant differences in growth were noted. In this instance, physiological time was expressed in terms of degree-days. According to Taylor (1981), the rate at which time passed for a

developing ectotherm is a function of its genetically controlled, temperature-dependent developmental curve and the thermal regime in which it lives. The developmental rate curve acts as a filter, emphasizing certain temperatures by translating temperature into insect growth and development. The relative positions of the filter and the temperature regime along the temperature scale determine the rate of growth and development. The relative positions of the filter and the temperature regime along the temperature scale determine the rate of growth and development; the more development that occurs between Points A and B, the faster physiological time passes for a developing insect (Taylor 1981). Populations of G.nigrrior living under colder thermal regimes accumulated larval biomass at a more accelerated pace per unit heat (e.g., degree-days) than did their counterparts living in warmer locations. Physiological time therefore passes more rapidly for G.nigrrior larvae living in cooler locales.

According to Calow and Townsend (1981), rapid development, shortened generation time, greater reproductive output and increased individual survivalship are all positively correlated with fitness. It would appear that G. nigrrior individuals living at cooler locations or members of the winter generation would represent the "fittest" condition based on their reduced generation time and more rapid rate of growth. The capacity of G. nigrrior to grow faster at

cooler temperatures most likely reflects their ancestral condition; Glossosmatidae evolved in cold mountain streams (Ross 1956). Members of this family subsequently expanded their geographic distribution to include warmer lotic habitats. The ability of G. nigrrior to grow and reproduce in both warm and cold habitats as well as shift between uni- and bivoltinism indicates that this species exhibits sufficient genetic flexibility to attain optimal phenotypic strategies in a variety of habitats. Butterfield (1976) similarly found that Tipula subonodicornis exhibited enough metabolic flexibility to decrease its temperature coefficient during larval development, allowing this species to grow until late autumn at the northern end of its range. The reduction in temperature coefficient also restricted the developmental rate of more southern members of the T. subonodicornis population; the overall effect of the flexibility in the temperature coefficient was to expand the potential geographic range of this species (Butterfield 1976).

Tauber and Tauber (1978) also found that the temperature threshold for the development of the green lacewing (Chrysopa carnea) decreased with increasing latitude (and decreasing temperature). This species was therefore able to exist in far more habitats than if it had not been capable of maximizing its development at various temperatures. The results of the present study suggest that

these three populations of G. nigrrior exhibited the same phenomenon. Not only did growth and development occur under cool thermal regimes (e.g. the population at Station 1 and the winter generations at Stations 2 and 3) but significant growth took place at the warmer summer temperatures recorded at both Station 2 and Station 3. Although the ability to grow and complete development at extremes in water temperature was demonstrated in the closely spaced G. nigrrior populations, this inherent capability accounts for the relatively wide geographic distribution of this species in eastern North America.

In addition to voltinism and growth patterns, larval weights were also found to differ between stations for a particular season as well as between seasons for each station. Larvae living under the coolest thermal regimes consistently exhibited the greatest larval biomass. Members of the summer generation at Stations 2 and 3 were significantly smaller than the population at Station 1 while members of the winter generation at Stations 2 attained much higher final larval weights than did their summer counterparts. Other authors have also documented higher winter than summer weights for this and other species. Members of the winter generation of a Georgia, USA, population of G. nigrrior were found to exhibit a final ash-free dry weight 1.5 X greater than that of summer generation members (Georgian and Wallace 1983). Sweeney and Vannote (1981)

reported a 50% reduction in the size of a summer cohort of G. nigrrior as compared to that of the winter. Brittian et al. (1984) found that Capnia atra nymphs grew larger at low temperatures. These authors concluded that large size may be a selective advantage for C. atra populations that experience rigorous winter conditions during nymphal life. The greater weights attained by G. nigrrior larvae exposed to cooler temperatures suggest that this species is most metabolically efficient at cooler temperatures and is best able to convert assimilated energy into tissue at lower rather than higher temperatures. Invertebrates living at lower temperatures lose less assimilated energy via respiration. Under these conditions, more energy can be directed towards tissue elaboration rather than to maintenance. The end result is the production of larger individuals. Large size is an advantageous feature in that larger individuals have lower weight-specific respiration rates. More assimilated energy can therefore be devoted to the production of reproductive tissue (e.g. gonadal and egg material). A number of authors have documented a positive correlation between increased fecundity and large non-feeding adult females (Colbo and Porter 1981, Ratte 1985, Sweeney and Vannote 1981). Based on these and similar studies, it may be concluded that the large larvae of the winter generation at Stations 2 and 3, as well as those from the population at Station 1 produced larger and perhaps more

fecund females than did larvae exposed to warmer thermal regimes.

The high summer temperatures apparently retarded the growth of the summer generation individuals at Stations 2 and 3. In terms of physiological time (degree-days; Taylor 1981), members of the summer generation grew slower and achieved lower final larval weights than did their winter counterparts. The lower final weight of the summer cohort was the result of higher maintenance costs associated with warmer temperatures. Because maintenance costs were higher, less assimilated energy could be allocated for tissue elaboration. The final weight attained by summer cohort larvae was diminished not only by increased maintenance costs but also by the likelihood that the higher temperatures initiated early development of adult tissue in smaller larvae. Early organization of adult tissues would also act to reduce the length of the larval growth period. The increased maintenance costs combined with the early formation of adult tissues would result in smaller summer cohort females and a probable decrease in fecundity (e.g., number of eggs) per individual.

Although temperature fluctuations and patterns of heat accrual were most likely to have had the greatest influence on the larval weights, growth rates and voltinism of the three G. nigrrior populations, the influence of nutrition on these organisms can not be ignored. G. nigrrior are scrapers

and like most scrapers, are heavily dependant on primary producers (algae) as a source of food. A number of studies have indicated that the distribution of scrapers is closely associated with the patterns of primary productivity. The river continuum concept (Vannote et al. 1980) predicts that scraper production is most likely to be maximum in unshaded, intermediately sized streams where autochthonous production is greatest. This prediction was supported by the results of a study by Hawkins and Sedell (1981) who found a relatively high correlation between scraper abundance and high autochthonous production along the length of a western stream. According to the model developed by McIntire and Colby (1978) for a small Oregon stream, periphyton productivity was closely correlated with both light and temperature. In most habitats, both of these factors would normally attain their maximum values in the summer but high primary productivity would shift to spring and fall in small streams with closed canopies. This pattern of primary production should be paralleled by peaks in grazer abundance. However, studies of the seasonal production dynamics of a guild of six grazing insects indicated patterns of peak macroinvertebrate biomass that differed from those predicted by the model developed by McIntire and Colby (Georgian and Wallace 1983). Georgian and Wallace found that rather than exhibit predicted autumnal and vernal peaks in biomass production, the grazer production in

an Appalachian stream was approximately equal in the spring and summer, lower in winter, and lowest in fall. They attributed the high summer production to the lack of canopy at their study site while reduced fall grazer production was the result of reduced fall periphyton productivity apparently typical of small streams in the eastern deciduous biome. Hornick et al. (1981) studied net primary productivity in Guys Run, a small Appalachian stream physically similar to Station 1 on Big Stony Creek. The results of this study indicated that primary production in the fall was actually lower than that in the winter, despite the fact that Guys Run was ice-covered in January and February. It is possible that a similar scenario occurred at Station 1 on Big Stony Creek; inadequate autumnal primary productivity could provide the selection pressure to eliminate a second generation at Station 1. During the summer, both temperature and light conditions supported algal primary productivity that was sufficient to sustain a population of G. nigror at all three stations. The period of emergence and egg-laying at Station 1 during the fall would correspond to the decline in primary productivity observed in Guys Run (and similar small Appalachian streams; Hornick et al. 1981). If eggs were to hatch during this period at Station 1, food supplies would be inadequate to sustain the resultant first instar larvae through winter. Baker (1982) found that the impact of poor diets might be greater on young rather than

older individuals of the odonate species Coengrian resolutum. If fall food supplies were inadequate or limiting at Station 1, it would be more advantageous for G. nigrior to remain dormant in the egg form and hatch the following spring when algal productivity would be increasing.

Sweeney et al. (1986) conducted a series of experiments on the mayfly, Leptophlebia intermedia to determine if adult size and fecundity were influenced more by thermal regime than by food quality. Although the results could not conclusively determine which factor had the greatest influence on the developmental stages of L. intermedia, it was concluded that temperature was the principal factor determining how long nymphs grew and that nymphal (and adult size) ultimately depends on how fast and efficiently an individual grows within a given period of time. The authors also concluded that diet (food quality) can influence the magnitude of larval growth (Sweeney et al. 1986). Sweeney and Vannote (1986) also completed a study on the stonefly Soyenua carolinesis. The results of this two year study determined that while diet exerted some influence on the seasonal pattern and magnitude of larval growth and adult size, seasonal patterns and magnitudes in temperature had the highest correlation with larval growth and adult size. The results of these experiments support those of the present study. However, all three studies indicate that

further research is still necessary to fully determine the effects of temperature on aquatic insect growth.

The plasticity observed in the larval weights, growth rates, and voltinism of the three populations of G. nigrrior contributes to the ability of this species to expand in geographic range. The environmental conditions at Station 1 more closely resemble those under which ancestral G. nigrrior populations are thought to have evolved than do the conditions at Stations 2 and 3. The cool water temperatures, particularly during the fall, may either suppress algal production and/or reduce winter densities of those algal species preferred or required in the diet of G. nigrrior. Studies conducted by Oemke (1984a,b) provide evidence of the close relationship between G. nigrrior and algal productivity. He compared diatoms found in the guts of G. nigrrior larvae collected from a first and a third order stream in southern Michigan to periphyton collected from natural substrates in these two streams. Not only were there remarkable similarities in the diatom species found in the guts of the larvae collected from the two streams but the results indicated that G. nigrrior was a discriminating feeder, and did not feed on periphyton at random or ingest diatom species based strictly on their availability (Oemke, 1984a). Comparisons of larval gut volumes indicated that diatoms were an important food source for all G. nigrrior

instars inhabiting the first order stream and for smaller larvae living in the third order stream (Oemke 1984b). Calculations determined that G. nigrrior larvae inhabiting the first order stream consumed 3.6% of the daily spring and fall diatom standing crops and ingested up to 20% of the winter standing crop per day. These data suggest that G. nigrrior inhabiting a second order stream such as Station 1 on Big Stony Creek could have a significant impact on the annual algal productivity of the stream. It would be difficult to sustain a winter generation and it would be more advantageous if eggs laid in the late summer or early fall remained dormant until spring when rising vernal temperatures stimulated both egg eclosion and algal productivity.

The bivoltinism exhibited by the populations at Stations 2 and 3 indicated that under appropriate thermal conditions, eggs laid by members of the summer generation will hatch to produce a winter generation. Fall water temperatures were warmer for a longer period and initiated egg eclosion at these locations. The resultant larvae were sustained during their early critical growth periods by the relatively abundant supplies of algae at these locations; algal production remained high through the early fall due to the warmer water temperatures and increasing light penetration associated with leaf abscission.

Based on the results of this study, the winter thermal

regime at Stations 2 and 3 can be considered the more optimal for members of this species inhabiting most temperature locations. If an organism's metabolic efficiency is evaluated in terms of how well energy is catalyzed into genetic information (Callow 1977), then the winter generations of G. nigrrior can be regarded as more metabolically efficient. Maintenance costs are reduced and more assimilated energy is devoted to tissue elaboration. The resultant large individuals are capable of producing a greater number of eggs. This higher fecundity exhibited by the winter generation would suggest that this generation represents the fitter condition; evolutionary fitness is closely linked to fecundity (Butler 1984).

By virtue of their larger size, larvae in the winter generation are potentially more fecund than their summer counterparts. However, the winter generation is composed of fewer individuals. The reduced larval densities may reflect lower winter algal productivity forcing individuals to compete for more limited food sources. On the other hand, algal productivity is higher, food resources more abundant, and greater numbers of G. nigrrior may be supported during the summer months. These advantageous conditions are offset by the fact that summer temperatures represent suboptimal thermal conditions for this species. The lower dry weights of summer generation larvae suggest that G. nigrrior is less metabolically efficient at higher

temperatures. Maintenance costs are greater and less assimilated energy can be channeled toward growth. These combined factors may explain why summer generations of G. nigrrior are comprised of small individuals that rapidly reach maturity. The resultant small adults produce may produce fewer eggs per individual. However, despite the potentially reduced individual fecundity, the greater number of individuals comprising the summer generation means that the total number of eggs that can be laid by this generation is significant.

It could be argued that the production of one rather than two generations per year would readily permit G. nigrrior to invade areas with suboptimal summer thermal regimes. But as previously discussed, these trichopterans evolved in and are best adapted to cooler thermal regimes. The likelihood that this species could successfully invade warmer areas already inhabited by species adapted to these thermal regimes is reduced without the production of a winter generation. Because of its greater metabolic efficiency at low temperatures, G. nigrrior has a competitive edge during the winter at most locations. By producing a winter generation, genetic recombination occurs twice rather than once a year. In addition, the winter generation acts as a reservoir for the summer cohort, supplying it with both genetic material as well as individuals. These factors combine to increase the chances

of G. nigrion successfully invading warmer habitats. Without this flexibility in its life history, it is likely that the distribution of G. nigrion would have remained restricted to cold mountain streams.

Summary

This study was undertaken to document the life histories of three field populations of G. nigrrior. Each population was located at a site that differed from the other sites primarily in terms of thermal regime. This study represents one of the few field studies that have examined the impact of differences in thermal regime on aquatic insects; the majority of such studies have been confined to the laboratory or restricted to observations of the effect seasonal temperature changes may have on a population at a given location. The objectives of this study were threefold: 1) to characterize the thermal regimes at each station, 2) to describe the life histories of each G. nigrrior population and, 3) to examine patterns of growth of the winter and summer cohorts at each station and to compare the larval growth patterns at each station for a given season.

Temperatures recorded by continuously recording thermographs established that each station differed not only in the total number of degree days accrued annually, but also in seasonal and daily patterns of temperature change. Aside from a brief period (March and April), Station 1 was the coolest of the stations while Station 3 was the warmest. These temperature differences were attributed to the influences of local physiography and riparian vegetation.

The results of this study determined that the population

at Station 1 was univoltine while those at Stations 2 and 3 were bivoltine. This differs from previous studies that have always reported that G. nigrior was bivoltine. The univoltinism of the population at Station 1 suggests that this species exhibits some plasticity in its life history pattern. Furthermore, the differences in life history were correlated primarily to differences in the thermal regime and pattern of diurnal temperature change observed at each station during certain periods of the year.

Comparisons between the winter and summer cohorts at a given station (e.g. Stations 2 and 3) produced interesting results. In each instance, winter populations were composed of larger individuals that were likely to have exhibited lower metabolic costs and better assimilation efficiency than their summer counterparts. Larvae forming the summer cohort were exposed to rising summer temperatures. These higher temperatures led to higher maintenance costs, leaving less energy for tissue elaboration. The end result was the production of smaller summer cohort individuals.

These comparisons also indicated that the number of days required to complete a winter and summer generation at a station was approximately equal. However, far more degree-days were required to complete the summer generation. These results suggest that G. nigrior is better adapted to metabolize during the cooler winter months and that the pattern of heat accrual during the summer may suppress larval

growth.

The effect of temperature on the winter and summer cohorts at a given location was also observed when larvae from different stations were compared for a given season. When the summer cohorts from populations at Stations 1, 2, and 3 were compared, it was found that larval size was inversely correlated with thermal regime; larger larvae were found at cooler locations. Also, fewer degree-days were required to complete a generation exposed to cooler temperatures. Similar growth patterns were also observed between the winter populations at Stations 2 and 3.

The observed plasticity in the life history is believed to have contributed to the ability of G. nigrrior to invade and compete in habitats exhibiting relatively warm thermal regimes. Because of better metabolic efficiency, members of the winter generation are able to invade areas in which the summer cohort would not normally be able to compete with established species. Upon entry into a new area, the winter generation acts as a reservoir for the summer cohort, producing eggs that form this cohort. In this manner, G. nigrrior is capable of expanding its geographic distribution and is not restricted to living in cold mountain streams.

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Appendix

Appendix Table 1. Results of mixed model regression analysis of the dry weights of the summer generation at Stations 1, 2, and 3; Group I larvae.

Source	d.f.	Sums of Squares	Mean S. S.	F value	PR > F	R ²
Model	1	0.46472659	0.07745443	161.08	0.0001	0.475
Error	1067	0.51304641	0.00048083			
Corrected Total	1073	0.97777300				
		Type I S.S.				
Time	1	0.08936514		185.86	0.0001	
Station	2	0.36262063		337.08	0.0001	
Cumm. Degree Day	1	0.00205523		4.27	0.0389	
Cumm.* Station	2	0.01068560		11.11	0.0001	
		Type III S.S				
Time	1	0.00271575		5.65	0.0177	
Station	2	0.02810340		29.22	0.0001	
Cumm. Degree Day	1	0.00211437		4.40	0.362	
Cumm.* Station	2	0.01068560		11.11	0.001	
		Log(Dry + 1) \bar{x}	n	C.V.		
		0.02099519	1074	104.44		

Appendix Table 2. Results of mixed model regression analysis of the dry weights of the summer generation at Stations 1, 2, and 3; Group II larvae.

Source	d.f.	Sums of Squares	Mean S. S.	F value	PR > F	R ²
Model	4	2.34892548	0.58723137	17.64	0.0001	0.105
Error	598	19.90669733	0.03328879			
Corrected Total	602	22.25562280				
		Type I S.S.				
Time	1	1.84683290		55.48	0.0001	
Station	2	0.20640169		3.10	0.0458	
Cumm. Degree Day	1	0.29569140		8.88	0.0030	
		Type III S.S				
Time	1	0.46909457		14.09	0.0002	
Station	2	0.45936781		6.90	0.0011	
Cumm. Degree Day	1	0.29569140		8.80	0.003	
		Log(Dry + 1) \bar{x}	n	C.V.		
		0.25393608	603	71.85		

Appendix Table 3. Results of mixed model regression analysis of the dry weights of the winter generation at Stations 1, 2, and 3; Group I larvae.

Source	d.f.	Sums of Squares	Mean S. S.	F value	PR > F	R ²
Model	4	0.08311154	0.02077789	42.17	0.0001	0.352
Error	310	0.15274178	0.00049272			
Corrected Total	314	0.23585332				
		Type I S.S.				
Time	1	0.06611145		134.18	0.0001	
Station	1	0.00062833		1.28	0.2597	
Cumm. Degree Day	1	0.00077286		1.57	0.2114	
Cumm.* Station	1	0.01559890		31.66	0.0001	
		Type III S.S				
Time	1	0.02275618		46.19	0.0001	
Station	1	0.00164849		3.35	0.0683	
Cumm. Degree Day	1	0.01329905		26.99	0.0010	
Cumm.* Station	1	0.01449890		31.66	0.0001	
		Log(Dry + 1) \bar{x}	n	C.V.		
		0.01599911	315	138.74		

Appendix Table 4. Results of mixed model regression analysis of dry weights of members of the winter generation at Stations 1, 2, and 3; Group II larvae.

Source	d.f.	Sums of Squares	Mean S. S.	F value	PR > F	R ²
Model	3	0.60331924	0.20110641	3.15	0.0250	0.025
Error	365	23.33885300	0.06394206			
Corrected Total	368	23.94217220				
		Type I S.S.				
Time	1	0.05394696		0.84	0.3590	
Station	1	0.00014862		0.04	0.09616	
Cumm. Degree Day	1	0.54922366		8.50	0.0036	
		Type III S.S.				
Time	1	0.59811351		9.35	0.0024	
Station	1	0.52366887		8.19	0.0045	
Cumm. Degree Day	1	0.54922366		8.59	0.0036	
		Log(Dry + 1) \bar{X}	n	C.V.		
		0.45626762	369	55.42		

Appendix Table 5. Results of mixed model regression analysis of the dry weights of the winter and summer generation at Station 2; Group I larvae.

Source	d. f.	Sums of Squares	Mean S. S.	F value	PR > F	R ²
Model	4	0.01478025	0.00369506	13.37	0.0001	0.109
Error	437	0.12080984	0.00027645			
Corrected Total	441	0.13559009				
		Type I S.S.				
Time	1	0.00998464		36.12	0.0001	
Generation	1	0.00019679		0.71	0.3998	
Cumm. Degree Day	1	0.00451974		16.35	0.0001	
Time * Cumm.	1	0.00007948		0.29	0.5921	
		Type III S.S				
Time	1	0.00707680		25.60	0.0017	
Generation	1	0.00167116		6.05	0.0143	
Cumm. Degree Day	1	0.00063831		2.31	0.129	
Time * Cumm.	1	0.00007948		0.291	0.592	
		Log(Dry + 1) \bar{x}	n	C.V.		
		0.01482431	442	112.16		

Appendix Table 6. Results of mixed model regression analysis of the dry weights of the winter and summer generation at Station 3; Group I larvae.

Source	d.f.	Sums of Squares	Mean S. S.	F value	PR > F	R ²
Model	4	2.03263941	0.50815985	15.58	0.0001	0.179
Error	286	9.33029521	0.03262341			
Corrected Total	290	11.36293460				
		Type I S.S.				
Time	1	0.73711891		22.59	0.0001	
Generation	1	0.76080931		23.32	0.0001	
Cumm. Degree Day	1	0.44468240		13.63	0.0003	
Time * Cumm.	1	0.09002879		2.76	0.0978	
		Type III S.S				
Time	1	0.05029999		1.54	0.2154	
Generation	1	0.71889730		22.04	0.0001	
Cumm. Degree Day	1	0.34800639		10.67	0.0012	
Time * Cumm.	1	0.09002879		2.76	0.0978	
		Log(Dry + 1) \bar{x}	n	C.V.		
		0.30576017	291	59.07		

Appendix Table 7. Results of mixed model regression analysis of the dry weights of the winter and summer generation at Station 3; Group II larvae.

Source	d.f.	Sums of Squares	Mean S. S.	F value	PR > F	R ²
Model	4	0.26146176	0.06536544	48.90	0.0001	0.319
Error	418	0.55873023	0.00133668			
Corrected Total	422	0.82019990				
		Type I S.S.				
Time	1	0.11777735		88.11	0.0001	
Generation	1	0.11618761		86.92	0.0001	
Cumm. Degree Day	1	0.02316820		17.33	0.0001	
Time * Cumm.	1	0.00432854		3.24	0.0727	
		Type III S.S				
Time	1	0.04876581		36.48	0.0001	
Generation	1	0.13623386		101.92	0.0001	
Cumm. Degree Day	1	0.00633096		4.74	0.030	
Time * Cumm.	1	0.00432854		3.24	0.030	
		Log(Dry + 1)X	n	C.V.		
		0.04483272	423	81.55		

Appendix Table 8. Results of mixed model regression analysis of the dry weights of the summer generation at Stations 1,2, and 3; Group I larvae.

Source	d.f.	Sums of Squares	Mean S. S.	F value	PR > F	R ²
Model	4	5.823222657	1.45580664	25.34	0.0001	0.182
Error	457	26.25399760	0.05744857			
Corrected Total	461	32.07722420				
		Type I S.S.				
Time	1	0.33676641		5.86	0.0159	
Generation	1	4.45229264		77.50	0.0001	
Cumm. Degree Day	1	0.71301125		12.41	0.0005	
Time * Cumm.	1	0.32115628		5.59	0.0185	
		Type III S.S				
Time	1	0.14593784		2.54	0.1117	
Generation	1	0.41155519		7.16	0.0077	
Cumm. Degree Day	1	0.58258394		10.14	0.0015	
Time * Cumm.	1	0.32115628		5.59	0.0185	
		Log(Dry + 1) \bar{x}	n	C.V.		
		0.02099519	1074	104.44		

Vita

Kathleen Trapp was born December 30, 1953 in Berlin, West Germany. After several moves, her family settled in Xenia, OH. She graduated from Beaver Creek Highschool in 1972. She attended Miami University in Oxford, OH and received a B. A. in Zoology in June 1976. Kathleen then attended the University of Wisconsin at La Crosse where she earned a Master of Science degree in Biology in 1979. Her research project involved a study of the macroinvertebrate population of a lake located on the Upper Mississippi River. During this time, she also worked as a biological technician for the U. S. Fish and Wildlife Service.

Kathleen began a study for a Ph. D. degree in Zoology at Virginia Polytechnic Institute and State University in September 1979. During this period, she taught undergraduate courses in general biology and aquatic biology and participated in a research project designed to assess the environmental impact of discharge from an industrial plant located on the Shenandoah River. In 1984, she left VPI & SU to take a position as an aquatic toxicologist and macroinvertebrate specialist with Environmental and Chemical Sciences, Inc. in Aiken, SC. In November 1985, she joined the staff of the University of South Carolina at Aiken as an adjunct professor. She defended her dissertation in June 1986.

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LIFE HISTORY AND GROWTH OF THREE POPULATIONS OF
Glossosoma nigrrior (Trichoptera: Glossosomatidae)
FROM THREE THERMALLY DISTINCT LOCATIONS

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(ABSTRACT)

Three populations of Glossosoma nigrrior Banks (Trichoptera: Glossosomatidae) were compared to determine how differences in thermal regime might affect their life history as well as the growth of individuals within each population. Two populations were located in Big Stony Creek (Stations 1 and 2) while the third was located in Sinking Creek (Station 3).

The thermal regimes at each station differed in their seasonal patterns of temperature change and the amount of heat accumulated annually. Aside from a brief period during the spring, Station 1 was the coolest, Station 2 was intermediate, and Station 3 (Sinking Creek) was the warmest of the three sites.

Populations of G. nigrrior at Stations 2 and 3 ex-

hibited typical bivoltine life histories. However, the population at Station 1 was univoltine with larvae present only during the summer. Comparisons among the three summer cohorts present at each station indicated that individuals growing under cooler thermal regimes were larger and grew more rapidly than did individuals exposed to warmer temperatures. A similar pattern was observed between the winter and summer cohorts located at Stations 2 and 3; members of the winter cohort at each station attained higher final dry weights and entered the prepupal stage more rapidly than did their summer cohort counterparts.

The larger body size attained by G. nigrrior living under cooler thermal regimes suggests that this trichopteran is metabolically more efficient at cooler temperatures. With less of its metabolized energy being allocated for maintenance costs, a large individual may channel more energy towards reproductive efforts.

The flexibility in voltinism and differing body size (and thus reproductive capacity) of each cohort are advantageous life history features that have allowed G. nigrrior to inhabit areas that may be only thermally suitable for this species during certain periods of the year. This ability to adjust its life history strategy to thermal conditions of a given habitat has allowed G. nigrrior to expand its geographic distribution from cool mountain streams to warm water lotic habitats.