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KING, ROBERT HOWARD
NATURAL HISTORY AND ECOLOGY OF STICTOCHIRONOMUS ANNULICRUS (TOWNES) (DIPTERA: CHIRONOMIDAE), AUGUSTA CREEK, KALAMAZOO COUNTY, MICHIGAN.

MICHIGAN STATE UNIVERSITY, PH.D., 1979

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NATURAL HISTORY AND ECOLOGY OF STICTOCHIRONOMUS ANNULICRUS (TOWNES) (DIPTERA: CHIRONOMIDAE), AUGUSTA CREEK, KALAMAZOO COUNTY, MICHIGAN

By
Robert Howard King

A DISSERTATION

Submitted to
Michigan State University
In partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

W. K. Kellogg Biological Station
Department of Entomology

1978

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The natural history and ecology of *Stictochironomus annulicrus* (Townes) was conducted in Augusta Creek, Kalamazoo County, Michigan. *S. annulicrus* had two generations per year with a spring emergence, beginning in mid to late April, and a summer emergence, beginning in late August. Oviposition sites were localized and used by females of succeeding generations. Linear egg masses containing 100 to 800 eggs each were laid just beneath the water's surface on vegetation. The incubation period for eggs was temperature dependent, increasing with lower temperatures, but development rate and temperature were not directly proportional. Newly hatched larvae displayed a planktonic behavior for 20 to 30 minutes before constructing a tube of detritus. Larvae remain tubiculous during all instars and obtain food by collecting fine particulate detritus and associated constituents at the end of the larval tube. Instars were easily distinguished by measuring either the width of the head at the eye spots, width of labial plate, or the distance from the lower edge of the labial plate to the occipital foramen. The ratio of increase (r) did not conform to Dyar's rule.

Winter form larvae were larger than summer form larvae with this size difference also apparent in pupal and adult stages. Sexual dimorphism was also apparent in pupal and adult stages with females being larger.

Larvae were found in depositional areas and had a contagious distribution. Densities varied between sites and seasonally at a given site. Density estimates at Kellogg Forest site on 1 August 1974 were $161/m^2$ (n = 6) and on 10 April 1974 were $338/m^2$ (n = 20). At Nagel site, density estimates were $2115/m^2$ (n = 9) on 9 July 1974 and $1325/m^2$ (n = 26) on 26 April 1974.

Larval growth rates decreased with successive instars and each instar had increased growth rates with increases in temperature. Larval growth rates, monitored in the laboratory, varied according to levels of food quality. Highest growth rates were on ground ash (*Fraxinus nigra*) leaves, intermediate rates were on *Tipula* feces, and lowest rates were on natural stream detritus.

A poor relationship existed between carbon and nitrogen values of foods and larval growth rates, while a good relationship was found for ATP, respiration, and percent ash values of foods and larval growth rates.

ACKNOWLEDGEMENTS

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INTRODUCTION

"In the brooks the slight grating sound of small cakes of ice, floating with various speed, is full of content and promise, and where the water gurgles under a natural bridge, you may hear these hasty rafts hold conversation in an undertone. Every rill is a channel for the juices of the meadow. Last year's grasses and flower-stalks have been steeped in rain and snow, and now the brooks flow with meadow tea...."

Henry David Thoreau
8 March 1890

Aquatic midges (Diptera: Chironomidae) are a diverse and ubiquitous group of insects with a worldwide distribution. Less than one-half (~4,000) of the existing species (10,000 to 15,000) have been described. Midge larvae are often the dominant organisms comprising the benthic fauna of ponds, lakes, streams, and man-made impoundments and are an important source of food for other animals. The non-biting adults often create a serious nuisance when excessive numbers emerge during the spring and summer months. Midges have been used as "indicators" of natural water quality because of their ecological differentiation and Thienemann (1922), Brundin (1958), and Deevey (1941) have used midges to classify lakes according to different trophic statuses.

While this important group has attracted the attention of many scientists, relatively little is known about the ecology and natural history of individual species. References to some of the significant contributions to the ecology and natural history of chironomids are found in Thienemann (1954), Darby (1962), Oliver (1971), and Fittkau, *et al*. (1976).

Stictochironomus annulicrus (Townes) (Chironomidae: Chironomini) was described by H. K. Townes (1945), at that time *Stictochironomus* was used as a subgenus of the genus *Tanytarsus*. The type specimen was collected in New York with paratypes from New York and Ontario. These specimens were collected in the months of May, August and September. Roback (1966) described the immature stages from specimens collected in a constant temperature spring (~16 C) near Oak Ridge, Tennessee. Roback noted only a slight difference between the larval forms of *S*. *annulicrus* and *Tanytarsus* (*Stictochironomus*) *sp. 1* which he previously described in 1957 and suggested that the difference may be only local variation. Curry (personal communication) and Roback (1966) have indicated that the immature forms which Johannsen (1937) described under the name *flavicingula* Walk. may be synonyms of *annulicrus*.

Wilhm (1970a) studied some of the ecological aspects of benthic macroinvertebrate populations in a constant-temperature spring. *Stictochironomus* larvae were especially abundant in areas of detritus accumulation where they comprised over 50% of the invertebrates and 70% of the total animal biomass. Wilhm (1970b) also used _S. annulicrus_ in a laboratory study involving the transfer of radioisotopes between detritus and benthic macroinvertebrates.

In Augusta Creek the larval forms of _S. annulicrus_ are commonly found in areas of detrital deposition such as mud banks and pools, and high larval densities often occur in springs adjacent to the main channels. Specimens were also found in other southern Michigan streams.

Stictochironomus annulicrus larvae, found in Augusta Creek, have a detritivorous mode of nutrition, feeding on fine organic particles (< 1 mm), throughout all larval instars.

In a study in which Meitz (1976) characterized the microflora associated with the intestinal tracts of several aquatic insects, dense populations of filamentous bacteria were found associated with the wall of the hind gut of _S. annulicrus_ larvae and trichomycetes, an obscure group of fungi, were commonly attached by means of holdfasts to the inside of the peritrophic membrane. Rod and spiral shaped bacteria were found in the lumen of the larval midgut. Such microflorae have been shown to be generally representative of detritivore feeding macroinvertebrates.

A number of studies on the ecology of Augusta Creek have been conducted. Chemical changes in leaves during processing were investigated by Suberkropp, _et al_. (1976) and the microflora associated with decomposing leaves was characterized by Suberkropp and Klug (1974, 1976). Quantitative assessments of allochthonous inputs and studies of processing rates were made by Petersen and Cummins (1974). Their study included responses of invertebrates to differences in leaf species. Growth rates of selected coarse and fine particle-feeding detritivores, fed whole hickory (Carya glabra) leaves, were investigated by Cummins et al. (1973). The growth rates of detritivores were shown to be dependent upon culture temperature and animal density and combinations of animal species (shredders and collectors) within a feeding chamber. The life history and ecology of one of the dominant insect predators in Augusta Creek, Nigronia serricornis (Say), (Megaloptera: Corydalidae), was studied by Petersen (1974). This study included population dynamics and an annual energy budget for the species. Howard (1975) investigated the life history and ecology of three species of Pycnopsyche (Trichoptera: Limnephilidae) which are large particle feeding detritivores (shredders) common in Augusta Creek. The ecology and natural history of Paratendipes albimanus (Diptera: Chironomidae) was studied by Ward (1977). Also, a general summary of land use patterns in the Augusta Creek Watershed has been prepared by Mahan and Cummins (1978).

The purpose of the present study was to obtain information on the natural history and ecology of a lotic detritivore feeding on fine particulate organic matter (FPOM). The larval forms of S. annulicrus are detritivorous, common in the stream system, and of a size range allowing for laboratory manipulation. The life cycle of the insect, including the behavior and duration of each life stage under natural conditions, was investigated. Larval growth rates were determined at various temperatures and on selected foods. Detrital food was characterized by carbon, nitrogen, total organic and adenosine tri-phosphate (ATP) content, and by respiration of associated microbial biomass.

DESCRIPTION OF STUDY AREA

Augusta Creek is a third order stream system (Strahler, 1957) located in Barry and Kalamazoo counties, Michigan (Figure 1). The gentle rolling topography is the result of the Wisconsin Ice Age, the last ice advancement of the Pleistocene Epoch approximately 11,000 years before present (Dunbar, 1962). The Augusta Creek watershed is located within the Gray-Brown Podzolic soil region of Michigan with soils characterized by diverse types ranging from mucks and peats to sands and gravel, but loamy sand and sandy loams are dominant. Most of the soils originated from limy parent material and are moderately productive agriculturally (Whiteside, et al. 1959).

The stream system drains an area of approximately 68 Km^2 and has a slope of 2.03 m/Km (Manny and Wetzel, 1973). An average annual discharge for a six year period of 1.06 m^3/sec. (37.4 ft^3/sec.) was recorded at the United States Geological Survey gaging station located at the lower end of the watershed

Figure 1. Augusta Creek watershed showing B Avenue, Nagel and Kellogg Forest study sites.

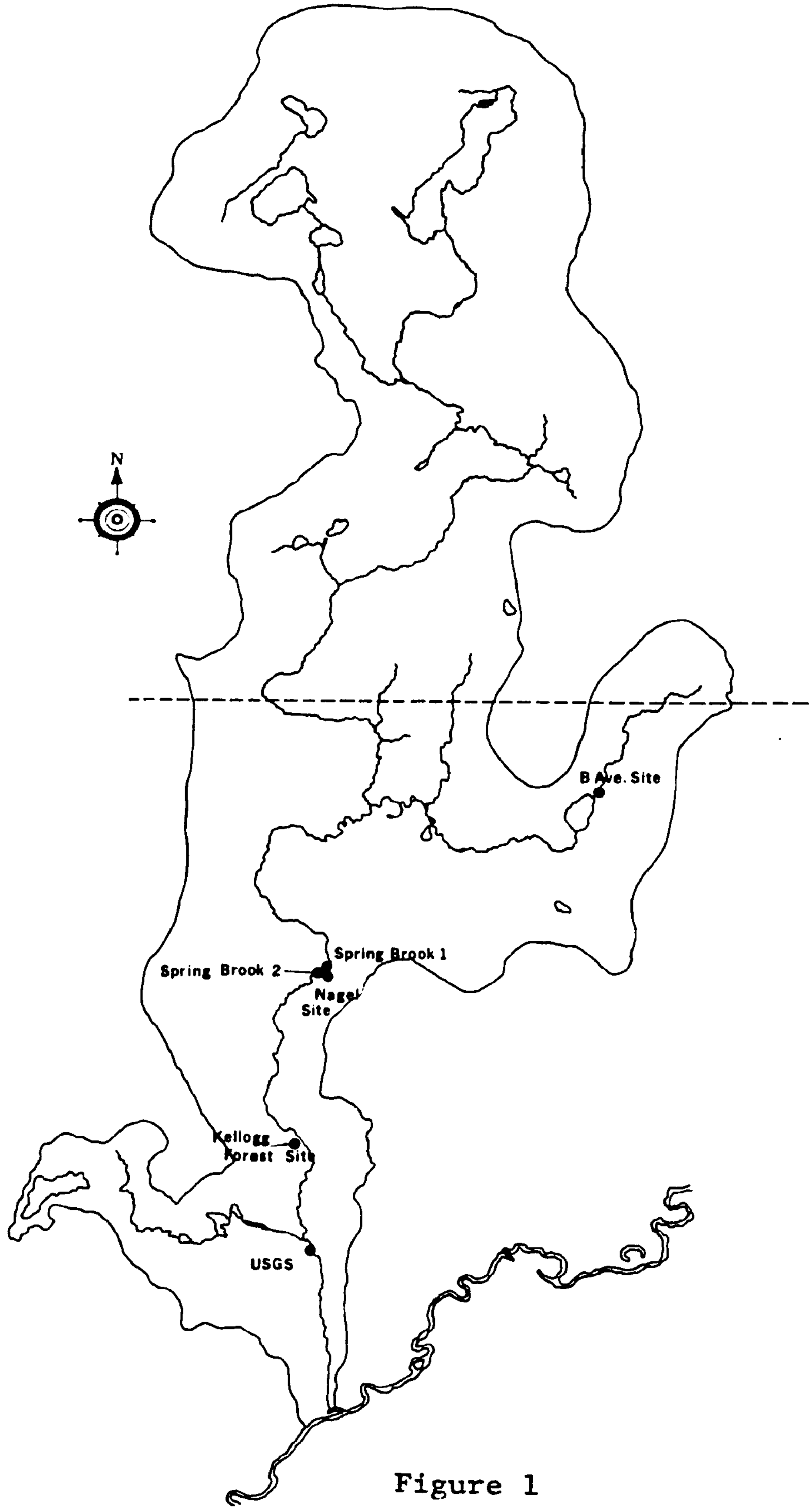

N
B Ave. Site
Spring Brook 1
Spring Brook 2
Nagel Site
Kellogg Forest Site
USGS

Figure 1

(U.S.G.S., 1965-1968; Figure 1). The landscape of the watershed is about 50% agricultural (pasture and row crops) and 50% hardwood forests and marshlands. The stream is shaded along most of its course by riparian shrubs and/or mixed deciduous trees which contribute a large portion of the annual carbon input (Cummins, 1972, 1973).

Salmo trutta L., brown trout, are present in the lower sections of the stream with Salvalinus fontinalis (Mitchell), brook trout, common in some of the small headwater tributaries. Total alkalinity as $CaCO_3$ ranges from 160 to 210 mg/l and pH values range from 7.5 to 8.7.

A major portion of the natural history, ecological field data, and laboratory study materials were collected at the B Avenue, Nagel, and Kellogg Forest study sites of Augusta Creek (Figure 1).

Methods

Discharge was monitored at B Avenue, Nagel and the Kellogg Forest sites approximately weekly starting June, October, and November 1973 respectively through January 1975. Mean velocities (n = 3 or >) were measured with a Beauvert Midget Current Meter (Nerpic Corporation, Genoble, France), and cross-sectional areas were determined for each site to enable discharge calculation according to Hynes (1970). Velocity and discharge data are recorded for B Avenue, Nagel and Kellogg Forest sites in Appendix A, and maximum, minimum and mean discharge is summarized in Table 1.

Temperature was monitored weekly with Bristol continuous temperature recording instruments (Model 636. Bristol Corporation, Waterbury, Conn.) at the three study sites. Taylor maximum-minimum Celsius thermometers were used to obtain records from the spring brook sites (Figure 1). Temperature data are recorded in Appendix B, and maximum, minimum, and mean annual temperatures for each site are given in Table 1.

B Avenue

The B Avenue site is a first order headwater tributary of Augusta Creek. It drains a large swamp which is densely covered with mixed deciduous vegetation, then flows for approximately 200 m through an open marsh of mixed grasses and sedges. At the lower end of the marsh the stream passes through a culvert under B Avenue and flows into a densely wooded area for approximately 58 m and into a small marl lake (Figure 1). The stream has one to two meter wide riffle sections and pools up to four meters in width. A mean discharge of 0.07 m^3/sec. (2.6 ft^3/sec.) was recorded for a 12 month period extending from 1 December 1973 to 1 December 1974 (Table 1). The maximum and minimum discharge values were measured on 16 May 1974 and 13 August and 10 September 1973 respectively, during a period extending from 22 June 1973 to 1 January 1975 (Appendix A,

Table 1. Summary of temperature and discharge values from sites on Augusta Creek, 1973-1974.

Site	$\bar{x}$ Annual Temperature C	S.D.*	Maximum Temperature C	Minimum Temperature C	$\bar{x}$ Annual Discharge m^3/sec	$\bar{x}$ Annual Discharge ft^3/sec**	Max. Discharge m^3/sec	Min. Discharge m^3/sec
B Avenue	8.7	5.7	20.0	0.0	0.07	2.6	0.4	0.03
Nagel	9.8	6.9	26.0	0.0	1.3	44.8	2.3	0.5
Spring Brook No. 1	9.3	1.8	14.0	1.5	0.005	0.177	---	---
Spring Brook No. 2	11.4	3.0	20.0	3.0	0.004	0.141	---	---
Kellogg Forest	10.5	7.0	26.0	0.0	1.4	50.2	2.8	0.5

* S.D. = Standard Deviation

** ft^3/sec for other discharge data found in Appendix A.

Table A-1). The maximum water temperature recorded at B Avenue for the period 1 October 1971 to 15 May 1975 was 20.0 C (Table 1, Appendix B, Tables B-1, B-2, and B-3). Frazil ice occurs occasionally during the winter months throughout Augusta Creek and anchor ice was observed only in a riffle section at the B Avenue site for a short period (2-3 days) during February, 1972.

A population of S. annulicrus, located in a pool at the lower portion of the marsh, was the focal point for most of the studies at this site. The pool was 4 meters wide, 5.4 meters long and had a maximum water depth of 0.5 meters. The bottom sediments were 55 to 65% organic matter by weight. The surrounding vegetation consisted of a mixture of grasses and sedges with Nasturtium officinale R.Br. (water cress) bordering much of the pool.

Nagel Site

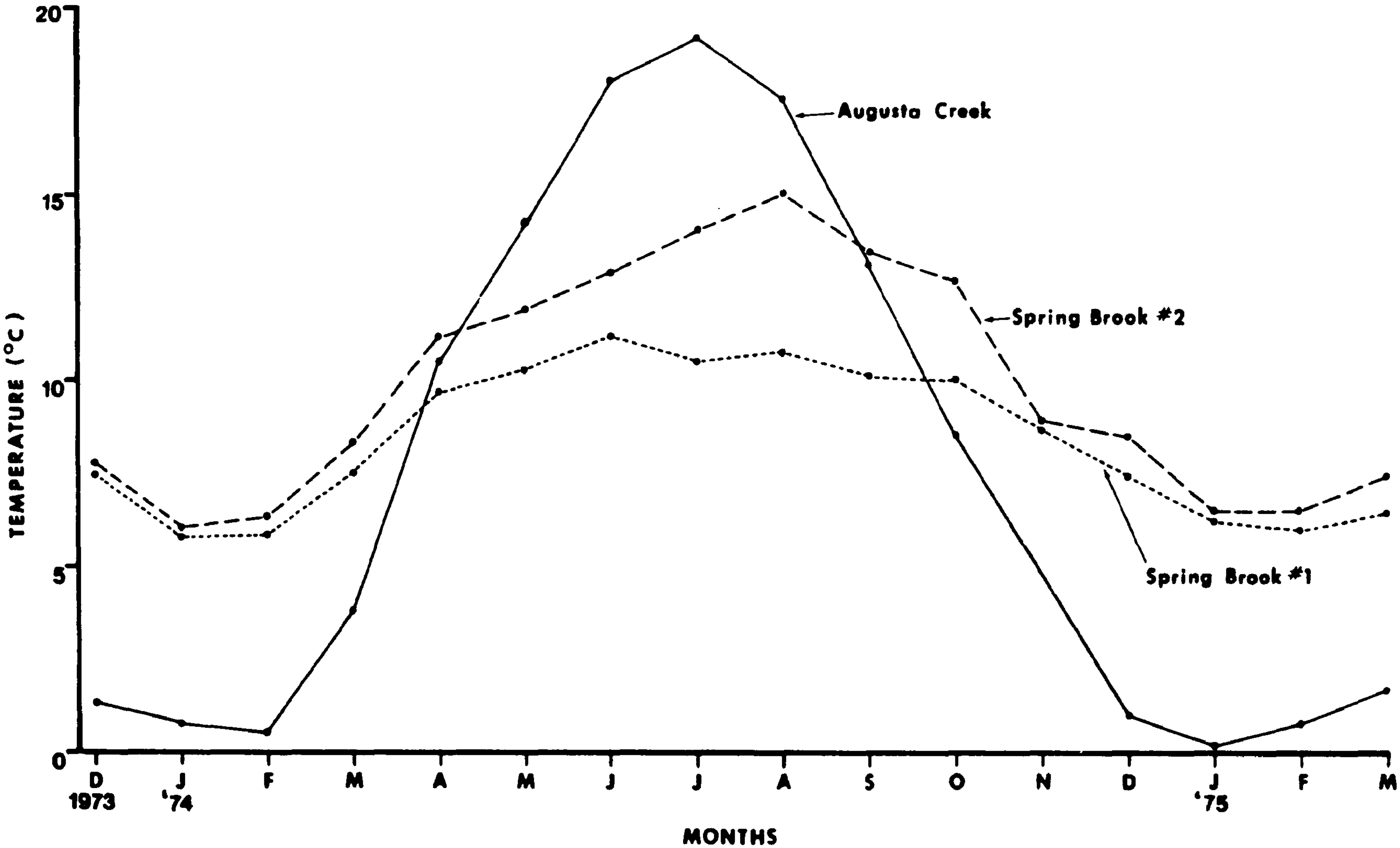
The stream at the Nagel site was three to six meters in width and had a mean annual discharge of 1.3 m^3/sec. during 1973 (Table 1, Appendix A, Table A-2). Water temperatures commonly reached 22-23 C in the summer months and a maximum of 26 C was recorded during the study period (Table 1, Appendix B, Table B-4, B-5). The riparian vegetation consisted of grasses, sedges, and shrubs (primarily Rosa, Salix, and Cornus), which do not form a canopy over the stream. Beds of rooted macrophytes, including Potamogeton pectinatus L., P. nodosus Poir., and Sagittaria sp., were commonly found during the summer months. Numerous springs, with mean temperatures of 10-11 C, are located adjacent to the main channel. The brooks arising from the springs flow in an almost perpendicular direction towards the main channel. The springs and their brooks are commonly choked with N. officinale.

The majority of the studies on S. annulicrus at the Nagel site were conducted in two of the spring brooks (Figure 1). Spring Brook No. 1 was chosen because of its relatively constant temperatures, reflecting the reduced influence by air temperatures, which is characteristic of a majority of the spring brooks at this site. Spring Brook No. 2 was influenced to a greater extent by air temperatures, but did not fluctuate as much as the main channel (Table 1, Figure 2). The mean water temperature entering Spring No. 2 was 11.4 C annually, which was two degrees higher than most of the springs in the area.

Spring Brook No. 1

The study section of Spring Brook No. 1 was a pool located approximately three meters above the confluence with the main channel. This pool was one meter wide, four meters long, with a maximum water depth of 0.2 meters. The mean annual temperature was 9.3 C $\pm$ 1.8 C and discharge was 0.005 m^3/sec (0.177 ft^3/sec), remaining almost constant annually (Table 1). It was an area of detrital deposition with sediments ranging from 55 to 65% organic content by weight. The area around the pool consisted of mixed grasses

Figure 2. Mean monthly temperatures at Nagel Site, 1973-1975.



Augusta Creek
Spring Brook #2
Spring Brook #1
TEMPERATURE (°C)
20
15
10
5
0
D
1973
J
'74
F
M
A
M
J
J
A
S
O
N
D
J
'75
F
M
MONTHS

Figure 2

and sedges and clumps of _N_. _officinale_ were scattered throughout the pool.

Spring Brook No. 2

The lower portion of the pool in Spring Brook No. 2 joined the main stream channel and was influenced by its flow characteristics. During periods of medium to high discharge, the pool was approximately two meters wide, six meters long with a maximum water depth of 0.15 meters. During periods of low flow, it was reduced to about one meter wide, five meters long with a maximum depth of 0.1 meter. The discharge from this spring was almost constant annually (approximately 0.004 m^3/sec), while the mean annual temperature was 11.4 C $\pm$ 3.0 C (Table 1). The pool sediments were 55 to 65% organic and the surrounding vegetation consisted of mixed grasses and shrubs.

Kellogg Forest

The Kellogg Forest site is a third order stream, similar to the Nagel site, located approximately 2 Km above the confluence of Augusta Creek with the Kalamazoo River. This is a wooded area of mixed deciduous trees providing a partially closed canopy over the stream during the leaved season. The average discharge for 1973 was 1.4 m^3/sec (50.2 ft^3/sec)(Table 1, Appendix A-Table A-3). The maximum temperature recorded during the study period was 26 C (Table 1, Appendix B-Table B-8, B-9).

LIFE HISTORY

Methods

Dry weights for each life stage were obtained by oven drying specimens at 50 C to a constant weight and weighing to the nearest 1 μg on a Cahn R. G. Electrobalance (Ventron Instruments Corp., Paramont, Calif.). Due to their small size eggs and newly hatched larvae were weighed on pre-weighed aluminum pans in groups of 10 to 50 specimens per pan. Late first and second through fourth instar larvae, pupae, and adults were weighed individually.

Number of eggs per mass, egg development, larval behavioral observations, and lengths of first and second instars were determined using a Wild M5 dissecting microscope (50x magnification). Body lengths for third and fourth instar larvae were determined by placing larvae, killed in hot water, on a straight edge graduated in mm units.

Larval head width at the eyespots, width of the labial plate, and distance from the lower edge of the labial plate to the occipital foramen were measured for instar differentiation using an ocular micrometer in a Wild M20 compound microscope at 200 or 400x magnification. Larval head capsules were mounted ventral side up in Hoyer's mounting medium (Ward's Natural Science Establishment, Inc.) on a one by three inch glass slide and covered with a No. 2 coverslip.

The summation of temperature expressed as degree-days has been used very effectively by terrestrial entomologists in predicting the emergence of various insects (Andrewartha and Birch, (1954). Miller (1941), Mundie (1954), Konstantinov (1958a), Palmen (1962), and Koskinen (1968a) have demonstrated that the onset of emergence in chironomids is correlated with the summation of degree-days. In this study degree-days were calculated as follows:

$$\text{degree-days} = t(x-a)$$

where t is time in days, x is temperature at which the measurements were made, and a is the "developmental zero" temperature. The result is an estimate of the "effective" temperature. The "developmental zero" for *S. annulicrus* is not known, but is probably between 0.0 and 1.0 C. A "developmental zero" of 0.0 C was assumed in this investigation. Summer generation chironomids from Augusta Creek and the summer and winter generation chironomids from the cold springs, and most of the spring brooks were never exposed to temperatures at or below "developmental zero."

Eggs and Incubation

Eggs are laid within a mass consisting of a single gelatinous string which is cream colored when laid, but becomes a dark brown due to adhering detrital particles. Each string consists of a double row of eggs placed obliquely to one another along the central axis of the mass (Figure 3). This type of egg mass is unusual among

Figure 3. Eggs, chorion, and larva of *S. annulicrus*. A = egg 5 hours old at 20 C; B= egg 45 hours old at 20 C; C = chorion; D = newly hatched larva.

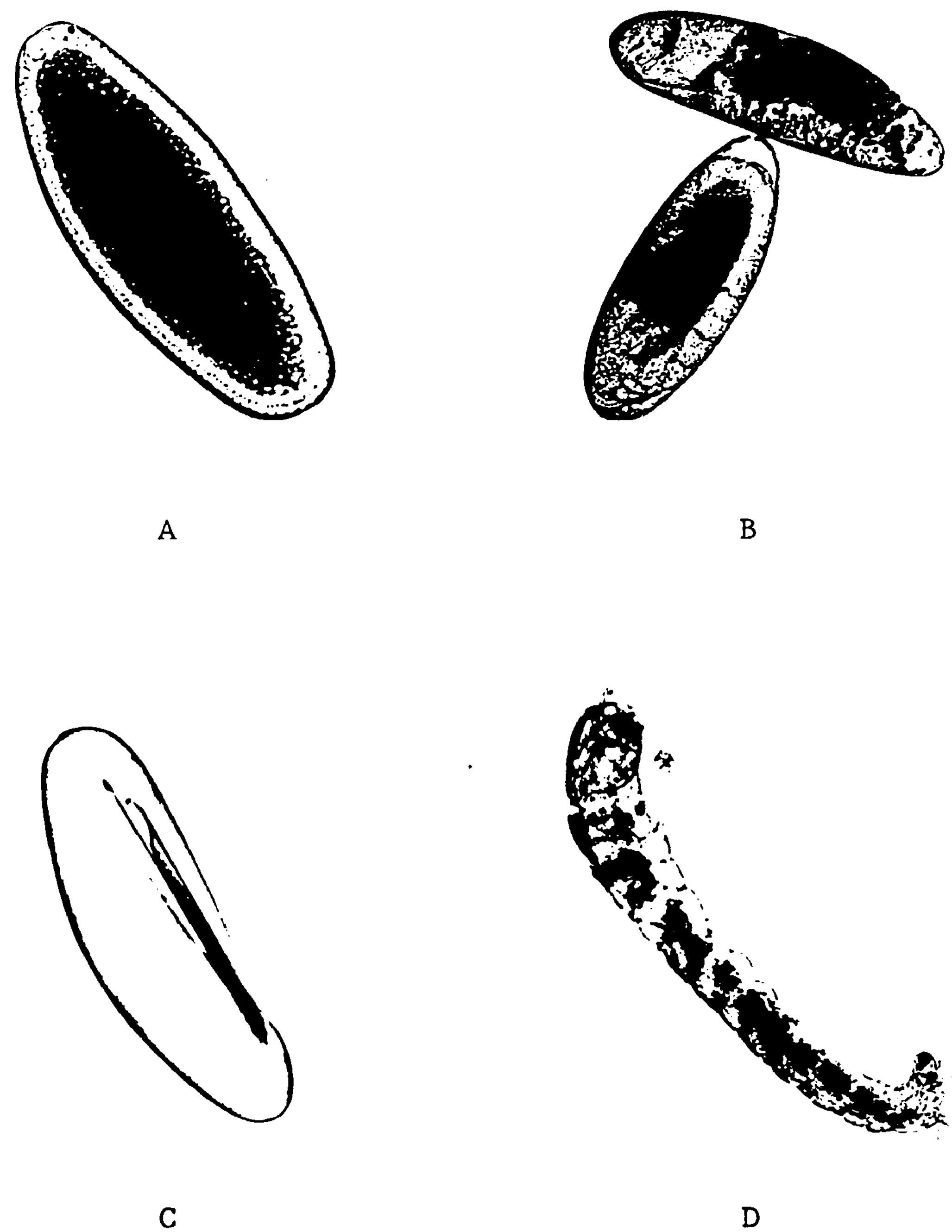


Figure 3

members of the Chironominae. As Oliver (1971) has indicated, this linear type of egg mass is characteristic of Orthocladiinae and Diamesinae, while a spherical mass is characteristic of Chironominae.

Egg masses of spring emerging adults (winter generation) are longer and contain a greater number of eggs per mass than those of the summer emerging (summer generation) adults. The eggs of both generations weigh approximately 5.3×10^{-4} mg dry weight each. Egg masses of winter generation adults range from 5.0 to 13 cm in length and eggs per mass range from 120 to 840 with a mean of 521 eggs per mass (n = 15). Summer generation egg masses range from 2.5 to 6.0 cm in length and eggs per mass range from 100 to 600 with a mean of 368 eggs per mass (n = 25). Olander and Palmen (1968) found a similar pattern for a marine chironomid, Clunio marinus Halid. A population from the northern Baltic Sea oviposited egg masses which ranged from 90 to 120 eggs each, while a population from warmer waters of the Atlantic oviposited masses which ranged from 40 to 80 eggs each.

The incubation period for eggs of S. annulicrus is temperature dependent, increasing with lower temperatures, but development rate and temperature are not directly proportional (Table 2). Egg masses less than two hours old, kept at constant temperatures of 20, 15, and 10 C began hatching in 55, 98, and 146 hours respectively. The temperature accumulated by the beginning of eclosion at 15 C and 10 C were approximately the same, but less accumulation of temperature was required at 20 C for egg maturation. Hatching within an egg mass is not synchronous and the duration of eclosion is also temperature dependent (Table 2).

Table 2. Time and temperature requirements for eclosion of *S. annulicrus* eggs.

Temperature C	Onset of Eclosion Hours	Onset of Eclosion Degree-hours	Duration of Eclosion Hours	Duration of Eclosion Degree-hours
20	55	1100	44	880
15	98	1470	48	720
10	146	1460	120	1200

Prolarvae begin to contract and extend their entire bodies prior to hatching with the frequency of body movements increasing as hatching nears. Upon eclosion, the chorion splits longitudinally along the flattened side of the egg (Figure 3).

Larvae

Newly hatched larvae, approximately 0.62 mm in length, are cream colored with two pairs of red eye spots. They crawl back and forth through the mass and eventually leave through exits produced by previous mechanical breakage or larval activity. Larvae were observed to remain within intact masses for eight hours before producing an opening to the external environment.

Upon leaving the egg mass, larvae display a planktonic behavior, beating or flailing the body segments and remaining suspended in the water. This type of behavior of first instar lentic species has been reported by Mordukhai-Boltovskay and Shilova (1955), Hilsenhoff (1966), Kellák (1968) and Oliver (1971), but has not been reported for lotic species. Hilsenhoff (1966) reported a strong positive phototaxis in first instar larvae of *Chironomus plumosus* (L.) and suggested that these larvae were dispersed by water currents in Lake Winnebago.

Newly hatched *S. annulicrus* larvae observed in the laboratory continued a planktonic behavior for 20 to 30 minutes even though a substrate of detritus had been provided. There was no evidence of feeding during this period. According to Oliver (1971), Alekseyev (1965) reported feeding by some planktonic first instar chironomid larvae on suspended algae and detritus. Larvae of *Chironomus dorsalis* (Meigen) did not seize particles directly from the water, but fed on detritus which adhered to the anal brush and claws of the posterior prolegs which are sticky at this stage (Oliver, 1971).

After this brief planktonic existence *S. annulicrus* larvae often construct a tube of detritus only to abandon it and construct a new one. This activity is repeated several times. Larvae remain tubiculous during all four instars and obtain food directly from the substrate at the end of the tube with the aid of the mouthparts. Food consists primarily of detritus and associated constituents. There is no indication that S. annulicrus larvae are capable of filter feeding even in the first instar.

Cream colored first instar larvae develop a rusty tinge before moulting. The paired eyespots, which are red on hatching, turn black during the first stadium. Early second instar larvae are pink, becoming light red prior to moulting. Third and fourth instars are a bright red with late fourth instars becoming crimson in color. Terminal instar larvae enter a prepupal stage which is distinguished by a swelling and change in color from red to white of the thoracic segments. Larvae do not ingest food during this stage.

Instar Differentiation

It is believed that most of the Chironomidae have four instars (Thienemann, 1954; Ford, 1959; Oliver, 1971; and McCauley, 1974). The head capsule is not subject to growth during a stadium making it possible to distinguish instars by various measurements such as head length or width, width of labial plate, length of mandibles, and antennal length. In this study instars were distinguished by measuring the width of the head at the eye spots, width of labial plate, and distance from the lower edge of the labial plate to the occipital foramen. Because accurate measurements of the labial plate and head widths could be obtained only if the ventral surface of the head capsules were parallel to the flat surface of the glass slide, measurements of the labial plate to occipital foramen were therefore the easiest to obtain accurately. Figure 4 illustrates the range of these three measurements for each of the four instars of S. annulicrus and gives the ratio of increase (r) between successive instars for each structure. The ratio of increase, calculated from mean values for each structure, did not increase at a constant rate for any structure measured (Figure 4), and thus does not conform to Dyar's rule (Imms, 1934). Although Ford (1959) reports that the species of chironomids he investigated generally conformed to Dyar's rule, Berg (1950) found that the values of r (1.62, 1.52, 1.43) calculated from mean lengths of head capsules for successive instars of Cricotopus elegans Joh. did not conform.

Table 3 summarizes dry weights and body lengths for the four larval instars. These can be used as estimates of instar grouping, but caution is required when specimens fall in the regions of overlap between instars (Table 3).

Table 3. Maximum and minimum dry weight and length ranges for each instar of S. annulicrus.

Instar	Dry Weight (mg)	Length (mm)
I	0.0005 - 0.001 [1.]	0.47 - 2.0 [2.]
II	0.0009 - 0.022	1.8 - 4.2
III	0.015 - 0.269	3.2 - 7.5
IV	0.212 - 2.385	7.2 -14.0

1. Newly hatched larvae, 22 to 62 larvae/15 replications < 24 hours old. $\bar{x}$ = 0.00047 mg.
2. Newly hatched larvae < 24 hours old. N=10, $\bar{x}$=0.62.

Figure 4. Instar differentiation and size increase ratios for *S. annulicrus*. A = lower edge labial plate to foramen magnum; B = width of labial plate; C = head width at eyes.

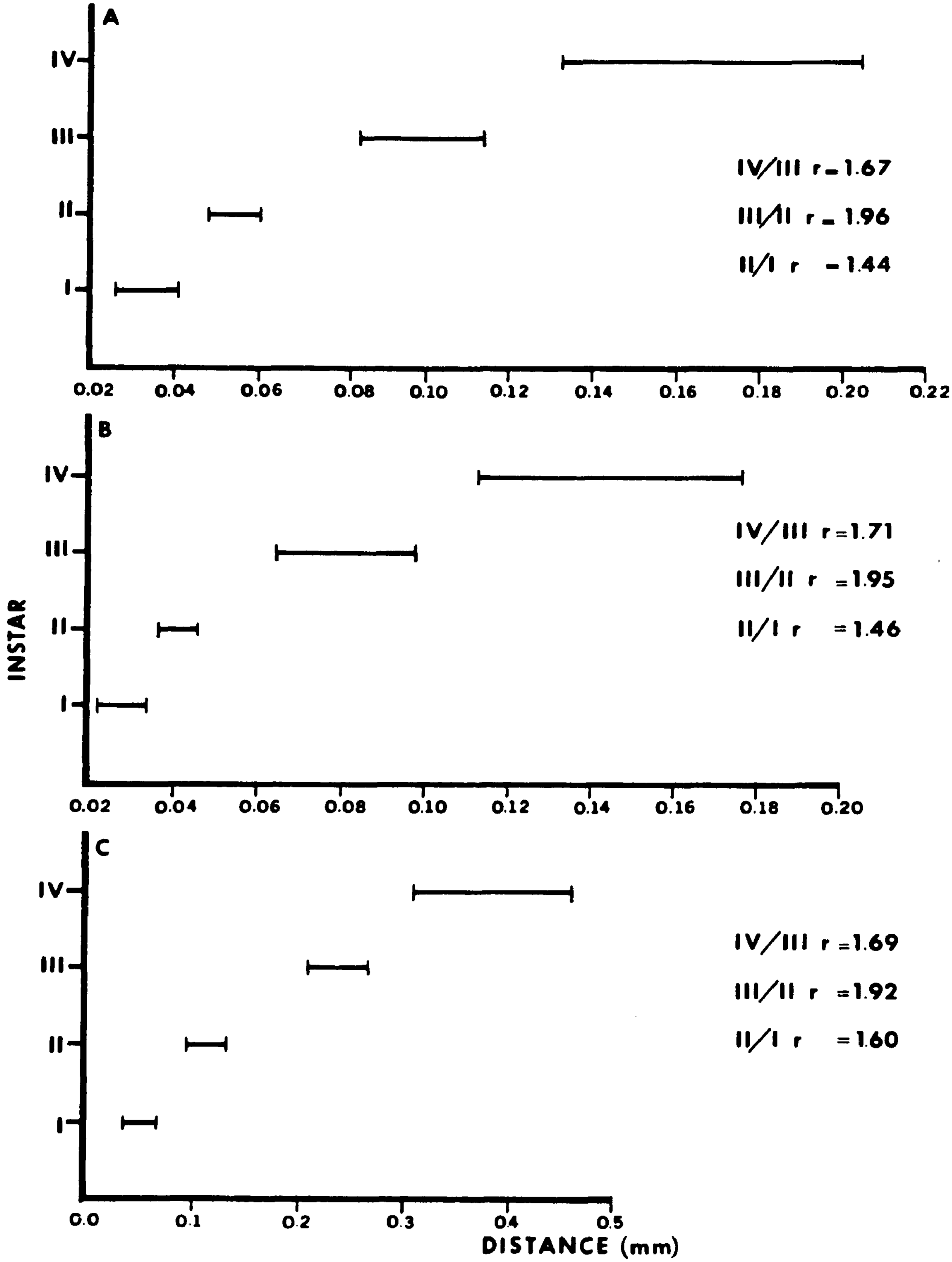

A
IV
III
II
I
IV/III r = 1.67
III/II r = 1.96
II/I r = 1.44
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
0.18
0.20
0.22
B
IV
III
II
I
INSTAR
IV/III r = 1.71
III/II r = 1.95
II/I r = 1.46
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
0.18
0.20
C
IV
III
II
I
IV/III r = 1.69
III/II r = 1.92
II/I r = 1.60
0.0
0.1
0.2
0.3
0.4
0.5
DISTANCE (mm)

Figure 4

Pupae

Newly moulted pupae are red with a few scattered areas of dark pigment, becoming very dark upon maturation. Summer generation pupal exuviae measured from the anterior portion of the pronotal tubercle to the posterior end of the anal lobes, ranged from 8.1 to 9.6 mm in length. Sexual dimorphism is apparent as female exuviae averaged 9.6 mm (n = 25, S.D. = 0.35), while male exuviae averaged 8.7 mm (n = 44, S.D. = 0.41); but separation of sexes based on length is impossible due to a partial overlap of size ranges. Pupation takes place in the detrital tubes of terminal instar larvae where they generally remain until their emergence. On 22 and 23 August 1973 pupae were observed at Spring Brook No. 2 (Figure 1) with the anterior half of the body exposed above the sediment. These pupae were in a vertical position with their bodies slowly oscillating. Corixidae grasped exposed pupae, pulled them from the sediments and fed on them. This exposed behavior of the pupae and predaceous activity of corixids, which are often considered to be herbivorous, was observed only during this two day period and is probably not common.

The duration of the pupal stage is controlled by temperature and photoperiod. Hilsenhoff (1966) reported pupal stages of <u>Chironomus</u> <u>plumosus</u> (L.) lasting one day at 24 C and six to eight days at 10 C. In the laboratory under natural day length conditions and at a temperature of 22 C ($\pm$ 2 C) pupal stages of *S. annulicrus* ranged from 15 to 48 hours. Laboratory observations have indicated that the lower temperature threshold for pupation is between 5 C and 8 C with a slightly lower emergence threshold. Pupation will not take place at 5 C, but adults will emerge at 5 C. *Stictochironomus annulicrus* has a marked diel pattern of early morning emergence. Pupae which do not ecdyse during the early morning on a given day, probably, will not ecdyse until the following morning.

Adults

Emergence and Adult Activity

Ecdysis takes place as soon as the pupae reach the surface of the water. Adults generally remain on the surface for a short period (one to three seconds) before flying to nearby vegetation. The length of time the adult remains on the surface is apparently temperature dependent. Adults observed emerging when air temperatures were 10 C or above remained on the water for only one to three seconds before flying to nearby trees and lighting 10 to 12 meters above the ground. Adults observed emerging on 1 September 1974, when the air temperature was 7 C remained on the water for 30 to 60 seconds before flying to short grasses and shrubs bordering the stream. Approximately two hours later, when air temperatures had reached 10 C, the adults began flying from the grasses and landing in trees approximately 10 to 12 meters above the ground level. It has been shown that the selection of the resting site for many species of chironomids is related to temperature, wind, and humidity (Oliver, 1971). While elaborate mating swarms are typical for many species of chironomids (Oliver, 1971), swarming or mating was never observed for S. annulicrus in the natural environment or laboratory even after many periods of vigilance (~ 40 hours of observation).

Larvae and pupae were collected in Augusta Creek and placed in emergence cages and continuously circulating experimental stream channels (Cummins, 1972) for purposes of obtaining life history data of the adult stage. Most laboratory emergence experiments were conducted at times paralleling emergence in Augusta Creek, which aided in simulating natural light, humidity, and temperature conditions. Emergence cages were 66 cm on a side, 114 cm high, and covered with 0.2 mm mesh nylon screen. Each cage was equipped with a plastic tray (50 cm on a side by 10 cm deep) containing natural stream detritus and water which was aerated continuously. Emergence cages were placed adjacent to a window in the laboratory, in a greenhouse, and out of doors in an attempt to utilize various light, humidity, and temperature conditions.

Large numbers of adults emerged in the cages over three to five week periods providing various life history data, but swarming or mating did not occur. Adults also emerged from the experimental stream channels, enclosed in screen to the ceiling height of approximately five meters, but swarming and mating were not observed. Within the emergence cages oviposition occurred, but no development of eggs took place. In order to obtain longevity and oviposition data, adults of known age were removed from the emergence cages and placed in five and ten dram vials and 60 x 20 mm plastic petri dishes containing water. Male to female numbers per container were: one to one, two to one, or two to two. Seventeen females (total = 55) oviposited, but no egg development occurred.

Both males and females lived as long as 10 days in the laboratory, but the average life-span for both sexes was 5.5 days. Oviposition of virgin females took place approximately four days after emergence. In the laboratory oviposition commonly began at about sunrise and would continue for a period of about four hours. Females would alight on the surface of the water and deposit an egg mass in one to three minutes. Most females would deposit only one egg mass, but two of the 50 females observed laid a large mass which was immediately followed by a second smaller mass.

Oviposition

Oviposition sites were localized and used by females of succeeding generations. These sites were typically open areas of the stream where riparian vegetation consisted of grasses, sedges or shrubs. Gelatinous strings of eggs were attached to emergent structures such as aquatic macrophytes and grasses or on the upper surface of floating algal mats. Oviposition sites were typically areas such as pools, stream margins, or springs where current velocities were generally less than 4 cm/sec. Most masses were laid just under and parallel to the surface of the water, but masses have been found with one end attached at the water's surface and the other end attached as far as five cm beneath the surface. Due to declining water levels, egg masses were occasionally exposed to the air resulting in desiccation and eventually total egg mortality.

During the 1974 fall egg-laying season (28 August - 1 October) a total of 353 egg masses were removed from the pool area at the B Avenue site (Figure 1). No egg masses were found in the 80 meter section between the pool and Hamilton Lake during this period. This contagious pattern of egg-laying and reuse of specific oviposition sites was observed at locations throughout the Augusta Creek drainage. It is apparent that alterations of the terrestrial habitat adjacent to the stream as well as alterations in channel morphology could result in changes in the distribution and density of populations of *S. annulicrus*.

Phenology

Table 4 summarizes the duration of summer and winter generations for selected sites and years with degree-days accumulated were available. In these examples a generation is considered to be the time from newly hatched larvae to emerging adults. Emergence dates are based on field observations of adults or the presence of pupal exuviae at the beginning of an emergence period. Dates for newly hatched larvae are based on field observations of hatching in the first egg masses deposited by the preceding generation. If hatching egg masses were not observed, the presence of first instar larvae was estimated at 12 days from the appearance of the first adults. This was based on observations that a substantial number of females follow the emergence of the first males by about four days, females in the laboratory oviposited in about four days, and four days were allowed for hatching.

Summer generations at the study sites investigated (Table 4) ranged from 96 days at B Avenue in 1974 to 131 days at Spring Brook No. 1 in 1973. Winter generations were longer, ranging from 207 days at Spring Brook No. 1 for the 1973-74 generation to 219 days at Spring Brook No. 2 for the 1974-75 generation. Synchrony of emergence from Augusta Creek, based on observations at these sites, was more evident for winter generations with a spread of only 12 days, while an emergence period of 35 days was indicated for summer generations. Similar observations were made by Hilsenhoff (1966) for Chironomus plumosus in Lake Winnebago in which the spring emergence was over a shorter period than the fall. The degree of synchronization tends to increase with increasing latitude, with arctic species being highly synchronous (Oliver, 1971). This phenomenon

Table 4. Duration of generations for *S. annulicrus* at three study sites.

SITE	GENERATION	DURATION	DAYS	$\bar{x}$ TEMPERATURE C	DEGREE-DAYS
B Avenue	Summer	5 May 1972 to 20 Aug. 1972	105	14.9	1566
B Avenue	Summer	22 Apr. 1974 to 14 Aug. 1974	96	16.8	1611
B Avenue	Winter	4 Aug. 1973 to 10 Apr. 1974	218	7.8	1695
Spring Brook #1	Summer	24 Apr. 1973 (No Fall Emergence)	--	--	--
Spring Brook #1	Summer	24 Apr. 1973 to 4 Sept. 1973	131	--	--
Spring Brook #1	Winter	16 Sept. 1973 to 12 Apr. 1974	207	7.7	1599

Table 4. (continued)

SITE	GENERATION	DURATION	DAYS	$\bar{x}$ TEMPERATURE C	DEGREE-DAYS
Spring Brook #2	Summer	25 Apr. 1973 to 22 Aug. 1973	117	--	--
Spring Brook #2	Summer	21 Apr. 1974 to 28 Aug. 1974	127	13.5	1711
Spring Brook #2	Winter	3 Aug. 1973 to 9 Apr. 1974	217	9.0	1952
Spring Brook #2	Winter	9 Sept. 1974 to 17 Apr. 1975	219	9.1	1993

is probably due to the large variation in larval growth rates within the same environment. These variations are not as evident in winter generations because of the longer growing season at temperatures below pupation thresholds, resulting in a "surplus" of degree-days. Larval growth rates decrease with successive instars and growth rates of late fourth instar larvae were lower than those of early fourth instars given the same environmental conditions. This decrease in growth rate with age results in a relationship between size and maturity.

The variations in the number of days required for the completion of a generation are lower when considering a specific habitat or study site. The 1973 summer generation at Spring Brook No. 2 began emerging after 117 days and the 1974 summer generation after 127 days. The time required for winter generations are even closer. The 1973-74 winter generation began emerging at 217 days while emergence of the 1974-75 winter generation began at 219 days (Table 4).

Degree-days accumulated for summer generations ranged from 1566 at B Avenue to 1711 at Spring Brook No. 2, while for winter generations the range was from 1599 at Spring Brook No. 1 to 1993 at Spring Brook No. 2. These data indicate that the minimal accumulative temperature requirement for a generation in Augusta Creek would be approximately 1550 to 1650 degree-days. This is a conservative estimate based on cognizance of the errors in determining generation times and temperature accumulations.

A seven day error in generation time estimate during a period when the mean daily temperature was 15 C results in an error of 105 degree-days. Biological factors such as food quality influence larval growth rates and it is probable that food quality differences do exist between habitats and between seasons at the same habitat.

Summer generation adults began emerging from Spring Brook No. 1 on 9 June 1973, 13 days after emergence had begun at Spring Brook No. 2. Unfortunately temperature data are not available for this period, but records for the same dates in 1974 (25 April - 22 August) indicate that Spring Brook No. 2 accumulated 1590 degree-days while Spring Brook No. 1 accumulated only 1408 degree-days. These data are useful in illustrating the temperature differences of the two study sites, differences which probably exist each year. Figure 2 illustrates the annual temperature patterns for these two spring brooks and the main channel at the Nagel site.

Emergence began in Spring Brook No. 2 on 28 August 1974 after 1711 degree-days had accumulated. Only three adults were known to have emerged from Spring Brook No. 1 during the fall of 1974 and there were no egg masses found at the site during that fall emergence period. Two male exuviae were found on 6 September 1974 and one on 25 September 1974. This site reached 1600 degree-days on 3 September 1974 and did not accumulate 1700 degree-days until 10 October 1974, later than the normal fall emergence period. The last evidence of adult activity for the 1974 season at any of the Augusta Creek study sites was 1 October. The mean daily temperature for the period from 1 October to 18 October 1974 was 9.5 C which is above the pupation temperature threshold for S. annulicrus. Since prevailing water temperatures did not explain the absence of adults during the period, the duration of a generation is not solely temperature dependent. It is possible that conditions for growth such as a low food quality did not allow for emergence at 1550 to 1700 degree-days.

Adults of the winter generation were larger than those of the summer generation (Table 5). Mature larvae were collected during the emergence periods of both summer and winter generations and placed in emergence cages to obtain adult weights. Table 5 presents dry weights of males and females for summer and winter generations from Spring Brook No. 2. Dry weights of both males and females of the winter form were significantly larger at the 95% confidence level (t test, Snedacore, 1956) than the dry weights of summer form males and females.

Koskinen (1968a) reported that larval populations of Chironomus salinarius Kieff. which had been exposed to low temperatures produced adults with longer wings than those exposed to warmer temperatures. Growth and development rates of 12 species of larval Chironomidae from the River Thames were monitored at 10, 15, and 20 C (Mackey, 1977) and all species attained larger terminal instar weights at the

Table 5. Summer and winter form adult weights of *S. annulicrus* from Spring Brook No. 2 (S.D. = standard deviation).

GENERATION	TIME OF EMERGENCE	MALES (mg dry wt.)	FEMALES (mg dry wt.)
Winter	Spring-1974	$\bar{x}$ 0.7357 S.D. 0.1430 n 34	$\bar{x}$ 1.1479 S.D. 0.3087 n 43
Winter	Spring-1975	$\bar{x}$ 0.6902 S.D. 0.1647 n 39	$\bar{x}$ 1.1196 S.D. 0.2240 n 55
Summer	Fall-1974	$\bar{x}$ 0.4911 S.D. 0.0841 n 150	$\bar{x}$ 0.6598 S.D. 0.1338 n 150
Summer	*Spring-1975	$\bar{x}$ 0.5736 S.D. 0.1037 n 105	$\bar{x}$ 0.9049 S.D. 0.1826 n 103

* Larvae collected 1 August 1974 prior to fall emergence and held at below pupation temperature threshold level until Spring 1975.

lower temperatures. Olander and Palmen (1968) reported that adult forms of *Clunio marinus* Halid. were larger in colder environments than warmer ones. According to Hashimoto (1968) adult body length of the chironomid *Clunio tsushimenus* Tokunaga is determined by the length of the growing period, with longer growing periods resulting in an increase in body length. Konstantinov (1958a) found that the weight of pupating larvae of *Chironomus dorsalis* (Meigen) raised at 15 C was 11.1 mg while larvae raised at 30 C weighed 5.6 mg. His explanation of this size difference phenomenon was: "as the temperature raised (up to a given point), the tempo of larval growth and of their development speeds up, with the latter process being influenced to a greater extent than the former." Sweeney and Vannote (1978) have demonstrated that adult body size and fecundity of a number of aquatic insects depend largely on thermal conditions during the immature period. They suggest that an optimum temperature regime for growth is one that permits an insect to achieve maximum adult weight and fecundity and that rearing insects at temperatures above or below the optimum results in lower adult weight and fecundity. Four summer species of mayflies and one summer hemipteran species were reared under various temperature regimes with those at the coolest temperatures resulting in smaller adults.

Hall *et al*. (1970) have shown that the size of adult *Chironomus tentans* Fabricius was related to nutrient level.

Laboratory cultures of varying food levels were maintained at 23 C. Adults which emerged from cultures of low food levels averaged 6.5 mm in length while adults reared at high food levels averaged 8.5 mm. None of the adult C. tentans collected in the natural environment were as small as those produced at the low food levels (Hall et al., 1970). It is probable that the smaller adults obtained from the low food level cultures were in response to a lack of food and not to a low food quality. In the natural environment fine particle feeders such as C. tentans are exposed to foods of varying quality, but are probably only rarely limited by food quantity.

The "holdovers" listed in Table 5 are adults which would normally have emerged during the 1974 fall emergence, but were collected as terminal instar larvae and placed at a temperature below the pupation threshold in an attempt to produce a winter form. On 1 August 1974, 250 fourth instar larvae were collected at Spring Brook No. 2 and placed in an aquarium with natural stream detritus and water which was continuously aerated and maintained at 8 C in a Living Stream (Frigid Units, Model LS 700). This brook had accumulated 1307 degree-days on 1 August and emergence began on 28 August 1974 after 1711 degree-days had accumulated (Figure 5). The larvae in the laboratory aquarium began emerging on 23 September 1974 after 1723 degree-days had accumulated (Figure 5). At this time, the temperature of the laboratory culture was reduced over a three day period to 5.0 C where it was maintained until 27 February 1975. Fifteen adults emerged during the three day period that the temperature was decreasing. The number of adults emerging was reduced at 5 C, but seven adults emerged over a 26 day period before emergence ceased. On 27 February 1975 the aquarium containing the remaining larvae was removed from the Living Stream and placed in an emergence cage located in a greenhouse experimental facility. Emergence began on 1 March 1975 and continued until 22 March 1975, while the aquarium water temperature ranged from 10 C to 16 C. The adults were collected on the dates indicated in Figure 5 and weighed. The dry weights of the adults emerging during the period from 1 to 22 March 1975 are listed in Table 5 under the heading Summer Generation "Holdovers." The dry weights of these adults did not equal the weights of winter forms, but were found to be significantly larger than the summer form adults belonging to the same progeny. These results differ from those reported by Sweeney and Vannote (1978) in which three species of winter-spring mayfly naiads were transferred to low temperatures. These transferral experiments resulted in small adults with reduced fecundity for each species relative to animals reared at natural temperatures.

A total of 224 adults emerged from a culture of 250 larvae; a mortality of only 7.1%. As can be seen from Figure 5, the first portion of the emergence was dominated by males, the latter by females. Similar patterns have been

Figure 5. Laboratory emergence records of adults from 1974 summer larvae collected 27 days prior to emergence in natural environment.

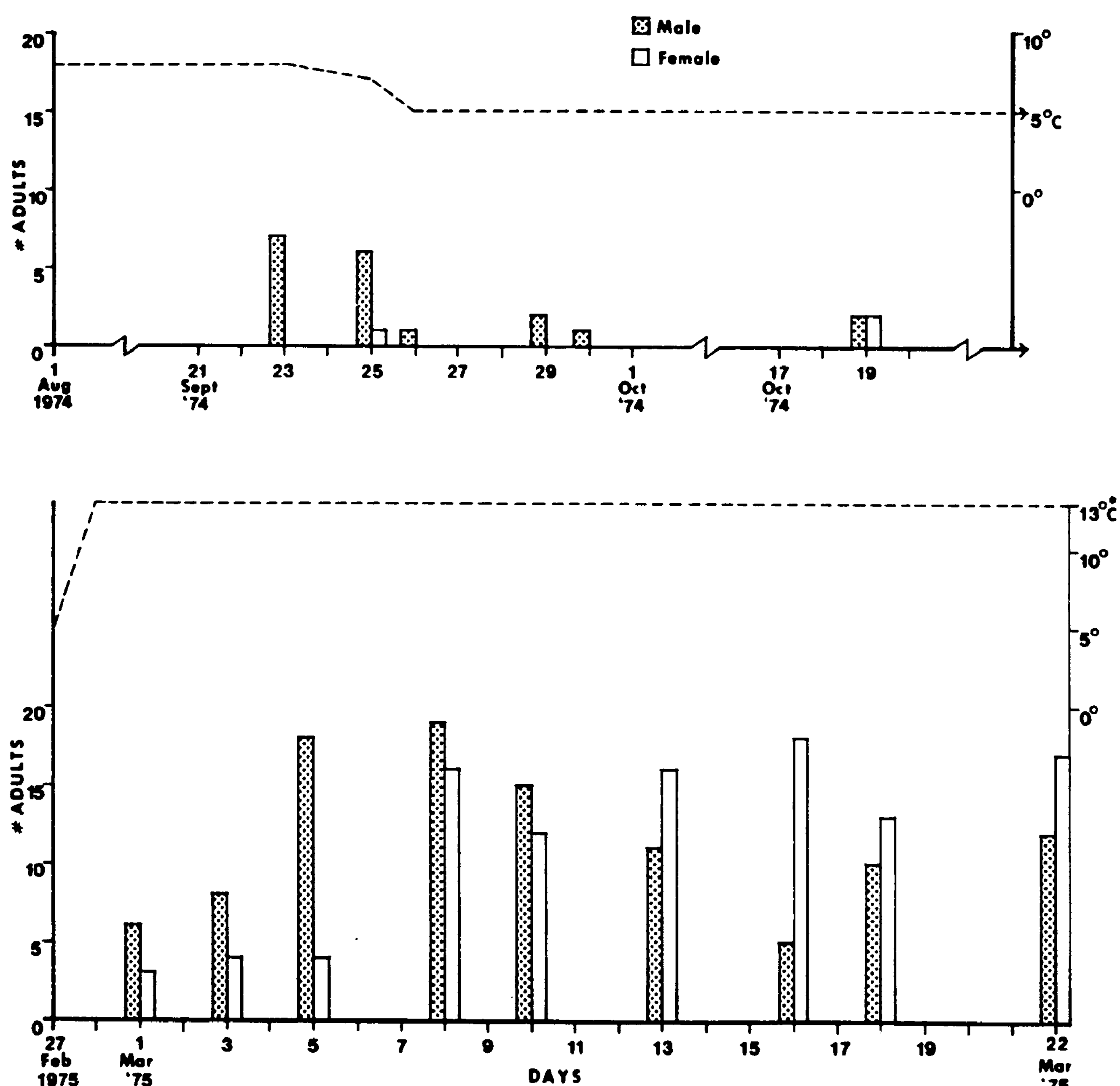

Male
Female
ADULTS
20
15
10
5
0
10°
5°C
0°
1 Aug 1974
21 Sept '74
23
25
27
29
1 Oct '74
17 Oct '74
19
13°C
10°
5°
0°
27 Feb 1975
1 Mar '75
3
5
7
9
11
13
15
17
19
22 Mar '75
DAYS

Figure 5

reported for Clunio marinus Halid. (Caspers, 1951) and Allochironomus crassiforceps K. (Palmen, 1962). Miller (1941) found that the males of several species in Lake Costello had emergence peaks before the females. Tanytarsus dubius Malloch. and T. viridiventris Malloch. had emergence peaks about two days before the females, while the males of Procladius culiciformis L. peaked seven days prior to that of the females and males of Chironomus nigrohalteralis (Malloch) emerged for 10 days before any females appeared (Miller, 1941).

Based on observations made in this study, it appears that temperature summation is of value in predicting the minimal generation times of S. annulicrus under natural food and temperature conditions in Augusta Creek. The reliability of such predictions is dependent on the accuracy of the temperature data and life history observations.

The prediction of winter generation emergences cannot be made by temperature summation records alone because a "surplus" of degree-days typically occurs at the sites studied in Augusta Creek. The data provided in Table 6 indicate that mean daily temperature records can be used to estimate emergences of the winter generation. The mean daily temperatures during the onset of emergence ranged from 9.8 C to 12.0 C which is above the lower temperature threshold level for pupation. Approximately one week of mean daily temperatures above pupation thresholds, determined in the laboratory to be slightly below 8.0 C, resulted in emergence (Table 6). Therefore, temperature summation appears to be of primary importance with temperatures above the pupation threshold necessary for pupal development. Variance from this pattern may be due to parameters such as food quality and availability.

Table 6. Emergence dates of winter generations with emergence and pre-emergence mean daily temperatures.

SITE	ONSET of EMERGENCE	$\bar{x}$ DAILY TEMPERATURE* (C) at onset	one week prior	two weeks prior
B Avenue	5 May 1972	11.3	8.6	4.2
B Avenue	22 Apr. 1974	10.3	8.9	6.3
Spring Brook #1	24 Apr. 1974	9.8	9.5	7.0
Spring Brook #2	21 Apr. 1974	12.0	10.5	7.8

*Mean daily temperature values were calculated from mean weekly values.

POPULATION ECOLOGY

Methods

Pilot studies established that in Augusta Creek *S. annulicrus* larvae are limited in distribution to depositional areas rich in fine particulate organic matter (FPOM: particles in diameter < 1 mm) where currect velocities are generally $\leq$ 4.0 cm/sec. Thus, the quantitative sampling program was designed to include only depositional areas in the study reaches of the Kellogg Forest and the Nagel site Spring Brooks (No. 1 and No. 2). These areas are representative of the habitats in which S. annulicrus larvae are found in the Augusta Creek watershed. An attempt was made to obtain a large number of sample means, each based on a large number of sample units, providing reliable larval density and biomass data for both the summer and winter generations. Sampling dates were chosen at periods when all larvae were (<3.0 mm long) large enough to facilitate the processing of a maximum number of samples.

A random sampling design was employed in which randomly selected transects allowed statistical inferences to be drawn (Weber, 1973). Transects were employed to assure the inclusion of an adequate cross section of each habitat and to maintain relative ease of sampling. The starting point along each transect was randomly chosen with each successive sample unit taken at 50 cm intervals. The placement of each transect was influenced by the size and shape of each sampling site, Larval densities and dispersal patterns were estimated by taking quantitative samples with a circular, 14.4 cm diameter (0.016 m^2) Plexiglas corer. The sampler was forced 8 to 10 cm into the sediments, a plastic cap was inserted under the corer forming a tight seal, and the corer and contents lifted. While in the field, each sample was placed in a large sieve with 400 μm mesh brass screening to wash and remove the finer particles. Stictochironomus larvae were removed from the sediments, counted, and taken to the laboratory for dry weight determinations or for use in laboratory experiments. The sieve was determined to be adequate after preliminary checks were made in which a known number of larvae, which were in the smaller size range sampled (3.0 to 8.0 mm), were placed in the sieve and then retrieved. Prior to retrieval the sieve was submersed and agitated in the water in a manner typical of the sample treatment. In each trial all larvae remained on the sieve.

The spacial dispersion of _S_. _annulicrus_ larvae was evaluated with the aid of mathematical procedures described by Elliott (1971) and Southwood (1966). The relationships between the variance (s^2) and the arithmatic mean ($\bar{x}$) indicated that the populations were either randomly ($s^2 = \bar{x}$) or contagiously distributed ($s^2 > \bar{x}$).

The index of dispersion (I), or variance to mean ratio was obtained by:

$$I = \frac{s^2}{\bar{x}}$$

The Chi-squared test for small samples ($n < 31$) was used for agreement with a Poisson series (random distribution):

$$X^2 = \frac{s^2\ (n-1)}{\bar{x}}$$

Contagious distributions were expressed by the negative binomial involving the calculation of the exponent $\hat{K}$.

The following two methods of estimating $\hat{K}$ were used:

$$1.\quad \hat{K}_1 = \frac{\bar{x}}{s^2 - \bar{x}}$$

$$2.\quad \hat{K}_2 = \frac{x^2 - \frac{s^2}{n}}{s^2 - \bar{x}}$$

The second estimate of K is considered to be the most accurate for small samples ($n \leq 50$) (Elliott, 1971).

The statistics U and/or T were used to test agreement with a negative binomial:

$$U = s^2 - \left(\bar{x} + \frac{\bar{x}^2}{K}\right)$$

$$T = \frac{(\Sigma x^3 - 3 \times \Sigma x^2 + 2 \times \Sigma x)}{n} - s^2\left(\frac{2s^2}{\bar{x}} - 1\right)$$

U and T have expected values of zero indicating perfect agreement with a negative binomial, but agreement is accepted at the 95% probability level ($P > 0.05$) if the value of U or T differ from zero by less than its standard error (Elliott, 1971).

Biomass estimates for Kellogg Forest, Spring Brook No. 1 and Spring Brook No. 2 study sites are based on quantitative samples which were taken prior to the onset of emergence of winter and summer generations. Larval dry weights were obtained by oven drying at 50 C for a minimum of 24 hours prior to weighing individual larvae on a Cahn R.G.

Electrobalance.

Weight of gut contents (food) of fourth instar larvae was determined gravimetrically after gut contents, which were removed by dissection from 10 freshly killed larvae, had been oven dried at 50 C to a constant weight. Larvae were killed with hot water immediately after removal from sediments to prevent egestion of gut contents. Gut contents are expressed as percent of total dry weight.

Ash-free dry weight (AFDW) estimates for larval and adult forms are based on ashing data from Wilhm (1970a) for larval, pupal, pupal exuvial, and adult forms of *S. annulicrus*. He used a drying temperature of 105 C and an ashing temperature of 500 C, however, length of time for ashing and drying were not given.

Dry weights of fourth instar larval and pupal exuviae were determined from exuviae collected from laboratory emergence chambers. Individual dry weights for 34 larval and 106 summer form pupal exuviae were determined.

Dispersion

Analysis of quantitative sampling data indicated that third and fourth instar larvae of *S. annulicrus* were predominantly contagious distributed (Appendix C - Table C-1). The sample variance (s^2) for each of the 24 samples was greater than the arithmetic mean ($\bar{x}$) indicating a contagious distribution, but agreement with Poisson series was accepted ($P > 0.05$) for four of the 24 samples. These random distributions occurred where insect densities were possibly so low that their distribution was effectively random. As an example, at the Kellogg Forest, a random distribution was indicated in Pool No. 2 on 3 July and 1 August 1974 and in Pool No. 1 on August 1974. Eight samples were taken at each site with sample means of 2.5, 2.5, and 2.8 larvae/m^2 respectively with relatively low variance estimates for each mean (Appendix C, Table C-1). Random distributions of sparse populations and contagious distributions of more dense populations of the same species have been observed for several insects (Southwood, 1966). U and/or T indicated agreement with the negative binomial ($P > 0.05$) for the remaining 20 samples (Appendix C, Table C-1). The ranges for values of I, X^2, and $\hat{K}$ are given in Table 7.

Table 7. Parameters indicative of dispersion patterns of *S. annulicrus*.

Number of Sample means *	Distribution	I	X^2	$\hat{K}_2$
4	Random	1.2-2.1	6.9- 14.4	2.1-21.4
20	Contagious	2.6-280.7	8.1-1403.6	0.5- 6.2

* See Appendix C

Insect aggregation is common (Elliott, 1971; Mundie, 1971) and can be due to insect behavior or heterogeneity of the environment. The dispersal mechanism of *S. annulicrus*, away from oviposition, was probably due to a combination of larval activity and water current. Depositional areas, such as pools, appear to be very uniform and yet larval aggregation takes place. Possibly larvae are attracted to each other or to a particular area because of the biological characteristics of the substrate. Brinkhurst and Chua (1969) state that organic matter and microflora available as food for detritus feeders may be more important to their ecology than the physical and chemical factors commonly investigated. Studies with tubificid oligochaetes by Wavre and Brinkhurst (1971) have indicated that the nature of the food available to the worms may be a primary factor in determining the distribution and abundance of species. Hall *et al*. (1970) found that the benthic invertebrates of low nutrient ponds tended to be highly dispersed, while in high nutrient ponds they tended to be densely clumped.

Density

Standing crop estimates were made at the Kellogg Forest, Spring Brook No. 1 and No. 2 study areas for winter and summer generations of *S. annulicrus* (Appendix C, Table C-2). Density differences between the Kellogg Forest and Nagel site (Spring Brooks No. 1 and No. 2) were evident during the study period. Samples taken on 1 August 1974 at the Kellogg Forest indicated a density of 161 larvae/m^2 while samples from 9 July 1974 at the two springs at the Nagel site had a mean of 2115 larvae/m^2 (Table 8). Differences between these two sampling areas are also evident for winter generations, with 338 larvae/m^2 on 10 April 1974 at the Kellogg Forest and a mean of 1325 larvae/m^2 for the two springs at the Nagel site on 26 March 1974. Springs and spring brooks, common at the Nagel site, are often oviposition locations which may account for the higher larval densities at Spring Brook No. 1 and No. 2. The distribution of larvae in much of the main channel of Augusta Creek may be due to the drift of individuals from these oviposition sites, especially during the planktonic stage of the first instar.

Table 8. Standing crop estimates for summer and winter generations at two study sites on Augusta Creek.

Site-Date	n	Number/m^2	S.D.	S.E.	C.V.
Kellogg Forest*					
1 August 1974	16	161.2	122.5	30.6	76.0
10 April 1974	20	337.7	242.8	54.3	71.9
Nagel Site**					
9 July 1974	9	2114.9	2157.1	719.0	102.0
26 April 1974	26	1324.6	1827.1	358.3	137.9

*Combined data from Pool No. 1 and No. 2.
**Combined data from Spring Brook No. 1 and No. 2.

Benthic predators are present in the springs and spring brooks adjacent to, and in the depositional areas of Augusta Creek. Potential predators of *S. annulicrus* larvae, considered to be common, included leeches (Hirundinae), *Sialis sp.* (Sialidae), and dragonfly naiads (Gomphidae and

Corduligasteridae). It was not within the scope of this study to determine the effects of predators on S. annulicrus, but the observations shown in Table 9 indicate that the predation by benthic invertebrates may influence the abundance of this midge. The larval densities for Pool No. 1 on 1 August 1974 and Pool No. 2 on 3 July and 1 August 1974 are the lowest recorded at any site during this study. Of interest is the fact that the highest predator densities recorded were at Pool No. 2 on 3 July 1974 and Pool No. 1 on 1 August 1974. The twelve fold decrease of midge larvae in Pool No. 1 was possibly related to the observed increase in the gomphid population (Table 9).

Table 9. Densities of gomphid naiads and S. annulicrus larvae at the Kellogg Forest, 1974.

Site	Date 1974	n	Gomphidae No./m^2	S.D.	Midge larvae No./m^2	S.D.
Pool 1	3 July	7	0	-	2094	2311
Pool 2	3 July	8	69	39	154	109
Pool 1	1 August	8	38	56	172	113
Pool 2	1 August	8	8	22	154	139

Quantitative samples taken at Spring Brook No. 2 indicated about an eight fold increase in larval density in July 1974 (Table 10). During this time interval the width of the spring brook had decreased from 1.5 to 0.3 m. The larvae apparently migrated with the receding water, and thus were concentrated into a smaller area. Discharge in the main channel had decreased at this site from 0.79 m^3/sec on 10 July 1974 to 0.46 m^3/sec on 31 July 1974, the lowest discharge recorded for the period from 3 October 1973 to 1 January 1975 (Appendix A). The lower water level in the main channel resulted in an increase in the slope of the lower reach of the spring brook. The increased velocity of the spring brook produced a deeper, but narrower channel, resulting in a redistribution of *S. annulicrus* larvae. This redistribution resulted in an increase in larval desities, but the dispersion pattern, and indicated by $\hat{K}_2$, was not changed (Table 10).

Table 10. Larval densities and stream widths for two sampling periods at Spring Brook No. 2, Nagel site.

Date 1974	n	Larvae No./m2	$\hat{K}_2$	Approximate width of sampling area (m)
9 July	6	2,548	0.8	1.5
31 July	6	19,771	1.0	0.3
		Increase = 676%		Decrease = 400%

Wilhm (1970a) recorded larval density of fourth instar *S. annulicrus* prior to the onset of emergence of the summer generation in open areas of a constant temperature spring near Oak Ridge, Tennessee as 17,500/m^2. This density compares to that recorded in Augusta Creek at Spring Brook No. 2 on 31 July 1974. While the larval density reported by Wilhm is high, open areas comprised only 4% of the

93 m^2 spring at the time his data were collected. Approximately 96% of the spring was choked with vegetation (Nasturtium and Spirogyra) and had a density of 250 larvae/ m^2, which is comparable to the densities recorded at the Kellogg Forest site.

Biomass

Gut contents were determined to comprise 12.8% of the total larval dry weight (Table 11). Wilhm (1970a) reported that gut contents of *S. annulicrus* comprised 16.8% of the total weight based on a comparison of larvae dried immediately after collection with those dried after three days of starvation.

Table 11. Estimated gut loads and percent of total larval weight of gut contents for terminal instar larvae.

Number of Larvae	Estimated Gut Load (%)	Percent of Total Larval Weight
10	$\bar{x}$ = 71.3 S.D. = 10.3	$\bar{x}$ = 12.8 S.D. = 7.5
	Range = 62.5-87.5	Range = 3.1-24.7

Exuviae of terminal instar summer form larvae and pupae from Augusta Creek had mean dry weights of 0.032 mg and 0.045 mg respectively (Table 12). Wilhm (1970a) reported that ash comprised 15% of fourth instar larvae, 9% of pupae, 36% of exuviae, and 7% of adults of *S. annulicrus*. Larval dry weights and ash-free dry weights

Table 12. Dry and ash-free dry weights of larval and pupal exuviae.

Fourth Instar Larval Exuviae	Pupal Exuviae
n = 34	Males
Range = 0.027 - 0.040 mg Dry Wt.	n = 59
$\bar{X}$ = 0.032 mg Dry Wt.	Range = 0.029 - 0.057 mg Dry Wt.
$\bar{X}$ = 0.020 mg AFDW	$\bar{X}$ = 0.042 mg Dry Wt.
	$\bar{X}$ = 0.027 mg AFDW
	Females
	n = 27
	Range = 0.030 - 0.666 mg Dry Wt.
	$\bar{X}$ = 0.047 mg Dry Wt.
	$\bar{X}$ = 0.030 mg AFDW

obtained from samples collected during this study from the Kellogg Forest, Spring Brook No. 1, and Spring Brook No. 2 study areas are given in Appendix C (Table C-3). Mean ($\bar{x}$) larval dry weights were converted to an ash-free basis by the subtraction of 12.8% of the dry weight for gut contents and then 9% for ash content. The 9% was determined by Wilhm (1970a) for pupae which would not have had material in their gut tracts.

Table 13 is a summary of biomass estimates for summer and winter generations at the Kellogg Forest and Spring Brook No. 2 study sites. The estimate for Spring Brook No. 1 is based on one generation per year. Mean larval weights are from samples which were taken just prior to the onset of emergence in order to obtain larval density estimates and maximum larval weights. Since females are heavier than males and tend to emerge later, larval weights obtained after the onset of emergence would tend to be higher due to the predominance of females.

Summer form larvae ranged from 0.603 mg AFDW at Spring Brook No. 2 to 0.913 mg AFDW at the Kellogg Forest (Table 13). Winter form larvae ranged from 1.135 mg AFDW at Spring Brook No. 2 to 1.346 mg AFDW at the Kellogg Forest. The largest larvae (1.664 mg AFDW) were recorded prior to the spring emergence at Spring Brook No. 1. The trend of larger larval sizes for winter forms is in accord with the similar trend in adults discussed earlier. Smaller larval specimens were found at the onset of emergence for both the summer and

Table 13. Biomass estimates just prior to emergence of *S. annulicrus*.

SITE	YEAR	GENERATION	NUMBER/m^2	mg AFDW/LARVA	SURVIVING BIOMASS/ m^2/GENERATION	SURVIVING BIOMASS/m^2/yr
Kellogg Forest	1973	Summer	530.1	0.8257	437.7	892.3
	1974	Winter	337.7	1.3462	454.6	
	1974	Summer	161.2	0.9128	147.1	601.8
	1974	Winter	337.7	1.3462	454.6	
Nagel Spring No. 2	1974	Summer	2548.1	0.6033	1537.3	3205.8
	1974	Winter	1470.2	1.1349	1668.5	
Nagel Spring No. 1	1974	One/Year	1335.5	1.6639	2222.1	2222.1

winter generations at Spring Brook No. 2 than from either Spring Brook No. 1 or the Kellogg Forest (Table 13). The size differences between habitats cannot be explained from data collected in this study, but may be related to larval density and/or food quality. The higher larval densities may result in lower microbial densities on detrital particles because of excessive cropping of food. The principle source of detritus for the main channel of Augusta Creek was deciduous leaves (Howard, 1975), while detritus in the spring brooks was derived from terrestrial grasses and herbaceous plants, plus the aquatic macrophyte *Nasturtium officinale*. Thus, the initial allochthonous inputs of spring brooks may be of lower nutritional quality than that of the main channel.

The ratio of larval densities for summer/winter generations was 1.57 at the Kellogg Forest in 1973-74, while the ratio of suviving biomass for summer/winter generations was 0.96. The same trends exist at Spring Brook No. 2 for 1974 (summer/winter density ratio of 1.73 and a summer/winter biomass ratio of 0.92). The similarities in biomass between summer and winter generations at a given site are due to the larger larval size obtained by the winter generation larvae. This trend is not true for the 1974 summer/winter generations at the Kellogg Forest probably because of the low larval densities of the summer generation.

Table 14 consists of both actual and estimated adult weights from Spring Brook No. 2. The actual adult weights, expressed as AFDW, are from reared specimens. Estimated adult weights are from larvae, collected prior to the onset of emergence. The larval weights were expressed as AFDW minus the AFDW of larval and pupal exuviae. The weights of adults are less than the estimated adult weights for both the summer and winter forms. The difference is probably due to metabolic losses of prepupal, pupal and adult stages.

Table 14. Observed and estimated adult weights for summer and winter generations at Spring Brook No. 2, Nagel Site.

Year	Generation	Estimated Adult AFDW (mg)	Observed Adult AFDW (mg)
1974	Summer	0.5543	0.5352
1974	Winter	1.0859	0.8759

LARVAL GROWTH CHARACTERISTICS

Methods and Materials

Most growth experiments were conducted with third or early fourth instar larvae collected from Augusta Creek one to three days prior to the initiation of an experiment. Because of the difficulty of obtaining first instar larvae in the field, early instar growth data were obtained from specimens which hatched from field-collected egg masses.

Growth chambers consisted of continuously aerated 500 ml Erlenmeyer flasks or glass bowls (19.5 cm diameter, 6.0 cm depth) which were placed in Living Streams. These streams served as constant temperature ($\pm$ 1.0 C) water baths and were located near windows where essentially natural light conditions prevailed.

Stream detritus used in growth experiments was collected from depositional areas in Augusta Creek and particles between 0.075 and 1.0 mm were wet sieved in the field and taken to the laboratory and stored frozen. Insect feces were collected approximately every seven days from cultures of Tipula abdominalis (Say). This woodland stream shredder, common in Augusta Creek, was being used in laboratory experiments by other investigators and served as a convenient producer of fine particles. Tipula feces were wet sieved into particles between 0.075 and 1.0 mm and frozen until needed for experiments. Whole Fraxinus nigra Marsh leaves, picked just prior to abscission and air dried, were ground with a Thomas-Wiley F.K.I. Micro Mill (Arthur H, Thomas Co., Philadelphia, Pa.). The particles produced were placed in three liter Erlenmeyer flasks with stream water and aerated vigorously for 10 days at 20 C ($\pm$ 2.0 C). During this time, the water in the flasks was replaced three times with fresh water. This material was then wet sieved and particles retained on a 0.075 mm sieve were frozen.

"Recalcitrant" detritus is a convenient term for stream detritus that had been stock-piled in a large plastic wading pool (approx. 1.5 m in diameter by 0.4 m in depth), which was filled with water and aerated for approximately 6 months (Nov. - May). The pool contained approximately 5 cm of stream detritus and an invertebrate fauna typical of depositional zones in Augusta Creek.

Approximately two cm of food was placed in each 500 ml Erlenmeyer flask amounting to 10 g ($\pm$ 2.0) of dry material. Flasks were filled with stream water and innoculated with a small amount of animal-free fresh stream detritus. The detritus was incubated for variable periods ranging from 7 to 14 days prior to placing pre-weighed animals in the flasks. Larval densities within a flask were based on densities in Augusta Creek. Larvae used in a given experiment were very similar in size and experiments were of short duration (<25 days). In one feeding experiment (Appendix D, Figure 8) the food in each flask was removed 7 days after the onset of the experiment and was replaced with fresh food which had been exposed to larvae.

A mean growth rate per individual per chamber was calculated according to Waldbauer (1968) as follows:

Relative Growth Rate =

$$\text{RGR} = \frac{\text{Weight Gain}}{\text{Median Weight}} \times \frac{1}{\text{Time}}$$

Weight Gain = Final Weight - Initial Weight

$$\text{Median Weight} = \frac{\text{Initial Weight} + \text{Final Weight}}{2}$$

Time = Duration of experiment in days.

Initial weight estimates were obtained by wet-weighing each larva. For each feeding chamber a minimum of 5 wet-weighed larvae were randomly chosen for oven drying at 50 C to a constant weight to obtain a percent water estimate. This value, determined for each chamber, was used to estimate initial dry weight. Upon completion of the experiment larvae were removed from the sediments, killed with hot water, and dried at 50 C to a constant weight. All animal weights were obtained with a Cahn Electrobalance. Adhering water was removed from larvae by blotting with a lint free absorbant tissue just prior to weighing. A wet-weight was determined by taking and average of 5, 10, and 15 second weight readings. Dried specimens were removed from the drying oven and placed in a desiccator containing Drierite (W. A. Hammond Drierite Company, Xenia, Ohio) or Silica Gel (Davison Chemical, Baltimore, Maryland) and allowed to reach room temperature. Desiccant was also placed in the weighing compartment of the Cahn Electrobalance during the weighing of dried specimens.

Respiration rates of microbial populations colonizing foods were obtained using two Model 20 Gilson Differential Respirometers (Gilson, 1963). Approximately 0.5 to 1.5 g (AFDW) of food was placed in each autoclaved reaction vessel with 2 ml of filtered (0.45 μm pore size, membrane filter) stream water. CO_2 was absorbed by 0.4 ml of 20% saturated KOH on filter paper placed in the side arm of each reaction vessel. The water bath temperatures were the same as the feeding temperature of each treatment and respirometers were covered to simulate darkness. Three experimental control vessels containing filtered stream water were used on each respirometer. After respirometers were allowed to equilibrate for one hour, readings were taken every 15 minutes over a three hour period. Upon completion of the experiment the foods in each vessel were dried at 50 C to a constant weight and weighed on a Mettler Model H16 balance (Highstown, N. J.). The calculation of respiration rates were preformed on a Hewlett-Packard 2100A mini computer (a modification of program by Petersen, 1974) and are expressed as $\mu l O_2$/mg dry wt./h. Ash content of foods was determined by combustion of one to four gram (dry weight) subsamples at 550 C in a Thermolyne Model F-41730 muffle oven (Thermolyne Sybron Corp., Dubuque, Iowa) for 24 hours.

Total carbon and nitrogen as percent of total weight of food material were determined on a Model 1104 Carlo Erba Elemental Analyzer.

ATP was extracted using a method described by Suberkropp and Klug (1976). Approximately 4 g wet weight of food material was placed in a 50 ml polypropylene centrifuge tube and 19 ml of 0.6N H_2SO_4 added. Tubes were kept in an ice bath after addition of acid until centrifugation, a time interval of 4 to 5 minutes. Samples were centrifuged at 10,000 g for 15 minutes at 5 C. Four ml of supernatant was decanted and diluted with 4 ml of 0.05 M Hepes (N-2-hydoxyethyl-piperazone-N-2-ethane sulfonic acid)-$MgSO_4$

buffer (pH 7.5). The sample was adjusted to a pH of 7.1 with NaOH and frozen until assayed.

Extracted ATP concentrations were determined according to Suberkropp and Klug (1976) by measuring the light emitted when the sample ATP reacted with a luciferin-luciferase enzyme complex, using a Aminco Chem. Glow^R Photometer coupled to a C.S.I.^{R} - 208 Integrator.

Growth Patterns

Relative Growth Rates (RGR) of S. annulicrus larvae typically decrease with successive instars (Table 15). First instar larvae which fed on Tipula feces at 5 C grew at about 8% body weight per day (RGR = 0.08 mg/mg/day), while fourth instar larvae grew at about 1% body weight per day (RGR = 0.01 mg/mg/day). An increase in temperature resulted in higher growth within an instar, but the pattern of decreasing rate with successive instars remained the same. The percent reduction in growth rate from first instars to fourth instars at 5, 15, and 20 C were 81.5, 61.5 and 81.0 respectively. Decreases in growth rate with age are typical of many animals including insects (Warren, 1971; Winberg, 1971; Chapman, 1971; and Makey, 1977). Konstantinov (1958b) reported growth indices for individual larvae for six species of chironomids (Subfamilies Chironominae and Orthocladiinae) that were fed hydrolyzed yeast cells at constant temperatures (18,22, or 24 C) under what he termed "optimum conditions". RGRs calculated from calculated from Konstantinov's data for comparison purposes, produced rates for the six species which were generally higher than the maximum rates for S. annulicrus, but the rate of decrease with age was similar during the growth phase, ranging from 33.0 to 85/4% ($\bar{x}$ = 66.3%). The species studied by Konstantinov can be characterized as fast maturing species with five species completing the larval phase in 20 days or less. Chironomus plumosus (L.) required 50 days to complete the larval stages and had a first instar RGR of 0.42 mg/mg/day ($\bar{x}$ of 10 individuals) and a fourth instar RGR of 0.04 mg/mg/day ($\bar{x}$ of 10 individuals) which compare with the rates for S. annulicrus at 20 C (Table 15).

Table 15. Relative growth rates for S. annulicrus larvae at various temperatures fed on Tipula feces.

	5 C			15 C			20 C		
Instar	$\bar{x}$ RGR	S.E.	n*	$\bar{x}$ RGR	S.E.	n	$\bar{x}$ RGR	S.E.	n
I	0.08	0.013	3	0.13	0.007	4	0.43	0.006	6
II	0.06	0.022	3	0.09	0.009	4	0.21	0.023	6
III	0.07	0.006	3	0.07	0.013	4	0.11	0.035	10
IV	0.01	0.002	5	0.05	0.004	5	0.09	0.001	6

* n = No. of experimental feeding chambers 18-22 larvae/chamber.

Figure 6 is a semi-log plot of mean individual larval weight gain for early instar larvae. The curves for larvae fed at 5 C on Tipula feces and at 10 C on natural stream

Figure 6. Weight gain of S. annulicrus fed on Tipula feces.

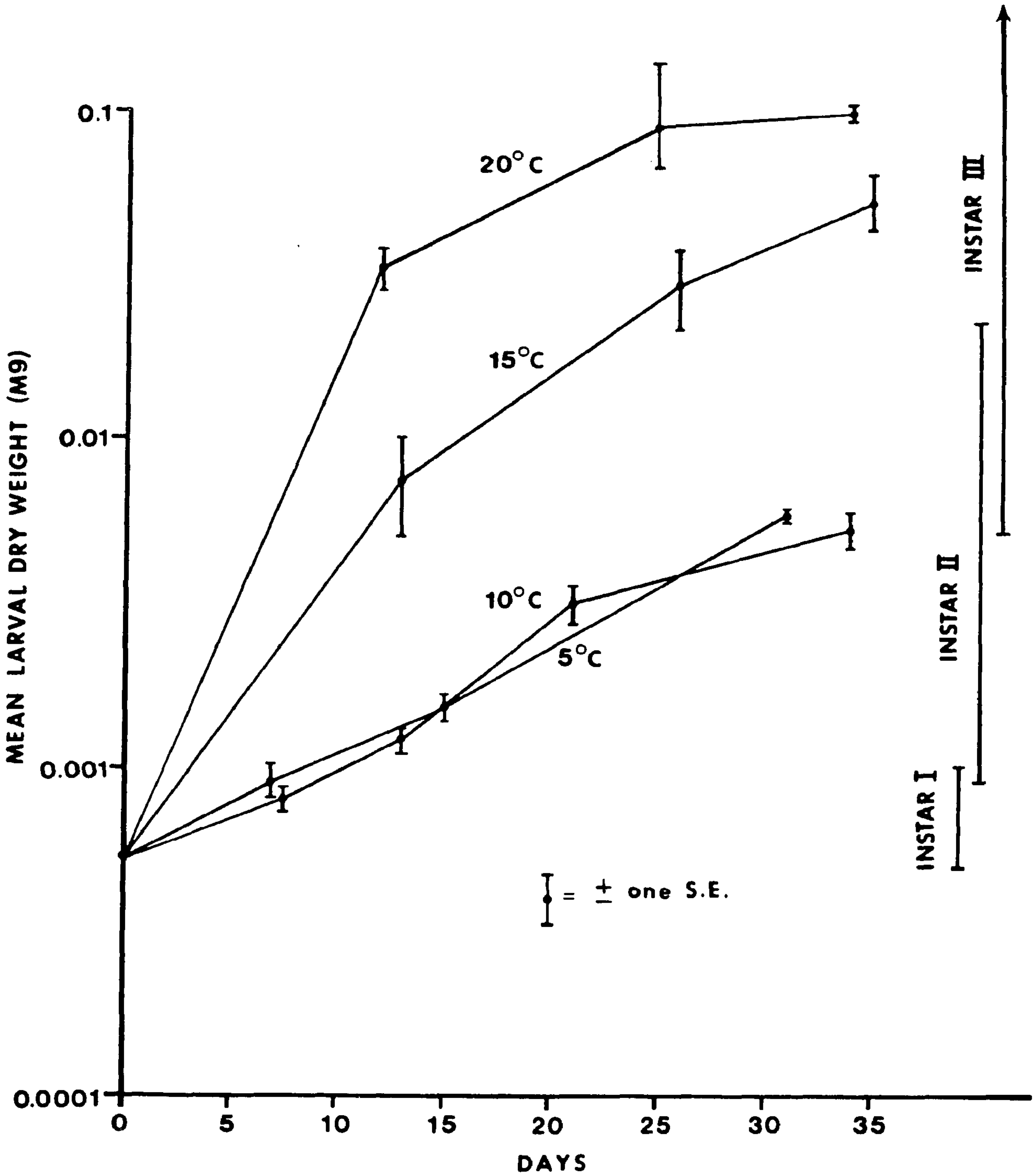

MEAN LARVAL DRY WEIGHT (M9)
0.1
0.01
0.001
0.0001
20°C
15°C
10°C
5°C
= ± one S.E.
INSTAR I
INSTAR II
INSTAR III
0
5
10
15
20
25
30
35
DAYS

Figure 6

detritus are very similar in slope and indicate an exponential rate of increase. Larvae fed at 15 and 20 C on *Tipula* feces indicate higher inital growth rates, but with a definite slowing trend apparent. This decrease in rate at 15 and 20 C was possibly a function of the physiological age of the larvae. A majority of the larvae fed at 5 and 10 C had reached second instar within 31 to 34 days respectively, while larvae fed at 15 and 20 C were third instars in 26 and 12 days respectively.

Recirculating experimental stream channels (Cummins, 1972) were utilized to monitor fourth instar larval growth rates of *S. annulicrus* at two temperatures (Table 16). The RGRs for the larval populations in each stream were very similar ranging from 0.012 to 0.009 mg/mg/day in Stream I (~5C) and from 0.015 to 0.003 mg/mg/day in Stream II (~10 C). A gradual decline in growth rate occurred at approximately the same rate in each stream. This growth pattern is probably characteristic of individual larvae with increases continuing throughout the growth phase, altered only by periodic molts.

The coefficients of variation (%) for larval dry weights decline conspicuously in both stream channels at approximately the same date (Table 16). These declines indicate a reduction of growth rate with physiological age, the younger larvae "catching up", which may have contributed to the degree of synchrony in the development of the individuals. The initial coefficients of variation were

Table 16. Growth rates of fourth instar S. annulicrus larvae in the two recirculating stream channels.

	Date	$\bar{x}$ Temperature °C	n	$\bar{x}$ Dry weight mg	S.D.	C.V.%	% Gain/Day	RGR mg/mg/day
Stream Channel I	12/20/73	5.4	76	0.478	0.340	71.1	---	---
	1/22/74	5.4	56	0.715	0.378	52.9	1.5	0.012
	3/1/74	5.4	118	1.033	0.390	37.7	1.2	0.010
	4/8/74	5.4	90	1.446	0.426	29.4	1.1	0.009
Stream Channel II	12/20/73	10.3	90	0.559	0.399	71.4	---	---
	1/22/74	10.4	92	0.921	0.424	46.1	2.0	0.015
	2/28/74	10.4	145	1.257	0.358	28.5	1.0	0.008
	4/8/74	10.4	80	1.433	0.388	27.1	0.4	0.003

* --- = Initial sample weights-no growth calculated.

very high for the dry weights obtained in both channels, probably the result of collecting a wide size range of individuals for stocking purposes. Coefficients of variation for samples collected at a fiven sampling site in Augusta Creek range from 20.0 to 50.0% for both summer and winter generations.

Reasons for a decrease in growth rate with age are not clear, but are probably the result of complex and interrelated ractors including physiological and behavioral aspects of maturation of the larvae. Factors such as rate of consumption, digestibility and efficiency of conversion of food to energy, and metabolic rate may be involved. Waldbauer (1968) states that the approximate digestibility (A.D.) and the efficiency of conversion (E.C.I.) do not remain constant, but decline with age during the growth period of the insect. He reports A.D.s for four species of leaf-eating insects and suggests that the decline with age may be due to an increase in particle size of food ingested by older insects. This increase in particle size results in a reduction of surface area of the food particles exposed to digestive enzymes (Walbauer, 1968). Fenchel (1970) working with marine detritus and Hargrave (1972) working with freshwater detritus have both demonstrated an increase in microbial densities and respiration rates with decreasing particle size. Boling et al. (1975) point out that the assumption of an inverse relationship between detritus particle size and microbial respiration may be overly simplistic and factors such as particle shape and quality influence the degree of microbial colonization.

The results of a larval feeding esperiment in which early fourth instar larvae (groups of 16-24/flask) were fed either stream detritus, _Tipula_ feces, or ground ash leaves (_Fraxinus nigra_) at 5 and 15 C are found in Appendix D, Table D-2. Table 17 is a summary of Appendix D, Table D-2 and illustrates the influence of food types on growth rates of _S. annulicrus_. A comparison, based on larval RGRs and percent gain/day, of the three food types places natural detritus as the lowest, _Tipula_ feces intermediate, and ground ash (_Fraxinus nigra_) as the highest quality food for _S. annulicrus_. This comparison holds true for animals fed at both 5 and 15 C. Larvae fed at 5 C on ground ash had an increase in body weight per day of 1.3%, while no gain (-0.3% gain per day) was recorded for larvae which fed on natural stream detritus. This weight gain on ground ash is similar to maximum weight gains reported by Cummins _et al_. (1973) for the shredder _Tipula_ (% gain = 1.5) and the collector _Stenonema_ (%gain = 1.8), both of which were fed at 5 C. The _S. annulicrus_ larvae which fed on ground ash at 15 C had an increase in body weight per day of 16.2% which was 13.1% higher than the percent gain per day for larvae which fed on natural detritus. The loss in weight by the animals fed at 5 C on natural detritus incubated for 14 days prior to feeding was undoubtedly related to insufficient food quality. Growth experiments have indicated that fourth

Table 17. Growth rates of fourth instar *S. annulicrus* larvae on various foods and at two temperatures.

Food	Temperature C	Replications	$\bar{x}$ RGR mg/mg/day	S.E.	$\bar{x}$ % Gain	S.E.
Stream detritus (no incubation)	5	5	-0.006	0.001	-0.6	0.2
Stream detritus	5	5	-0.004	0.001	-0.3	0.2
Tipula feces	5	5	0.010	0.002	1.1	0.3
Ground ash leaves	5	5	0.012	0.0002	1.3	0.02
"Recalcitrant" Stream detritus	15	3	-0.009	0.002	-0.8	0.2
Stream detritus	15	5	0.025	0.002	3.1	0.4
Tipula feces	15	5	0.047	0.004	7.9	1.3
Ground ash leaves	15	5	0.065	0.006	16.2	4.6

instar larvae do gain weight when fed natural detritus at 5 C. Larval growth rates in stream channel I at 5.4 C (Table 16) ranged from 0.009 to 0.012 mg/mg/day. The data in Table 18 are the results from feeding experiments in which larvae were fed natural detritus at 5 C, but the 14 day food incubation period for the first set was 5 C while the second set was 15 C. Growth rates of larvae fed at 5 C on 5 C incubated food were all negative (Table 18), while those larvae fed at 5 C on food incubated at 15 C showed positive growth rates in three of the five chambers. The implication being that the natural detritus incubated at the higher temperature was of a higher food quality, possibly resulting from a greater microbial density.

Negative growth rates were also obtained by larvae which fed on nonincubated stream detritus at 5 C (RGR = -0.006 mg/mg/day) and "recalcitrant" detritus at 15 C (RGR = -0.009 mg/mg/day) (Table 17).

An experiment was conducted to determine if larval growth rates would be reduced if a natural food was diluted with a food of apparent lower quality. This would indicate if these organisms are capable of selecting one food over another. An insulation material comprised of pulverized wood was used as the low quality food. This material consisted primarily of cellulose with total nitrogen ranging from 0.06 to 0.1% at the end of a 21 day feeding experiment. This material was of a physical nature very similar to stream detritus, making it practical as a dilutant. Both

Table 18. Fourth instar *S. annulicrus* larvae fed on stream detritus at $5^{o}C$.

Food Incubation Period Time days	Temperature C	Initial Animal Density		% Mortality	RGR mg/mg/day	% Gain/day
14	5	16		6.3	-0.003	-0.3
14	5	18		0.0	-0.001	-0.1
14	5	22		9.1	-0.001	-0.1
14	5	18		0.0	-0.012	-1.1
14	5	18		11.1	-0.002	-0.2
			$\bar{x}$	5.3	-0.004	-0.3
			S.E.	2.3	0.001	0.2
			C.V.%	96.8	85.4	119.9
14	15	17		0.0	0.003	0.4
14	15	16		18.8	0.0004	0.04
14	15	18		11.1	0.004	0.4
14	15	17		11.8	-0.004	-0.4
14	15	17		11.8	-0.004	-0.4
			$\bar{x}$	10.7	-0.0006	0.04
			S.E.	3.0	0.001	0.2
			C.V.%	63.2	31.6	100.5

food types consisted of particles whthin a 0.120 mm to 1.0 mm size range. Table 19 includes the treatments and a summary of the results of this 21 day feeding experiment. The fastest growth rates were for larvae which fed on 100% stream detritus, with complete mortality in the feeding chambers which were 100% cellulose wood fiber. It is likely that this mortality can be attributed to starvation. Ten terminal instar larvae were placed in each of three chambers consisting of 100% cellulose wood fiber for 21 days with only 76.7% mortality. It is probable that these physiologically older larvae were able to metabolize stored body fat reserves and/or had lower metabolic rates. The food mixtures (ex. 10g detritus and 4.5 g wood fiber) were 1:1 ratios on an ash-free dry weight basis. The mean growth rates for Treatments #1 and #2 are very similar and rates for Treatments #3 and #4 are also very similar (Table 19). Larvae in feeding chambers with diluted food were able to maintain growth rates sililar to larvae fed non-diluted detritus. Observation of larval gut contents indicated that the larvae in diluted food chambers were ingesting both detritus and wood fiber. This would imply that these animals were not selective in feeding behavior, but were maintaining growth rates by some other means. For example, the food may not have been of a lower quality, as assumed, or the larvae were able to regulate food intake. As cited by Cummins (1973), House (1965) and Gordon (1968) have demonstrated that feeding rates of some terrestrial insects

Table 19. Growth responses of third instar *S. annulicrus* larvae at 7.0 C fed under various food conditions with an initial larval density of 15 per chamber.

Treatment Number	Treatment (Food Type)	Number of Chambers	Mortality %	RGR* mg/mg/day	S.E.
1	10 g Detritus	4	58	0.0034	0.0011
2	10 g Detritus 4.5 g Insulation	4	75	0.0031	0.0007
3	5 g Detritus	4	45	0.0019	0.0003
4	5 g Detritus 2.25 g Insulation	4	57	0.0013	0.0003
5	5 g Insulation	3	100	-	-

* RGR = Relative Growth Rate

can be regulated on the basis of nutrient content of the food. It is possible that the wood fiber when mixed and incubated with stream detritus was colonized by microbes from the detritus and stream water, which was added to the feeding chambers. This stream detritus and water could have served as a nitrogen source. Further studies are necessary before questions concerning feeding rate regulation with aquatic insects such as S. annulicrus can be answered satisfactorily.

The difference in mean growth rates for Treatments #1 and #3 indicate that the larvae in chambers containing only 5 g of detritus were food limited. Larval densities of 15 per 5 g may have resulted in excessive "cropping" of detritus associated microbes. Kajak et al. (1968) and Kajak and Warda (1968) concluded that reduced chironomid growth under crowded conditions was the result of a decline in ingestion rates, but Hargrave (1970b) demonstrated that increased densities of the amphipod Hyalella azteca (Saussure) resulted in effectively reducing sediment microfloral populations.

Food Quality

Growth rates of S. annulicrus fed on reasonably natural foods in short term experiments can be used as a means of rating food quality (i.e. poor, good, etc.). These ratings can be applied to aquatic invertebrate species which have the same digestive capabilities and nutritional requirements.

Several studies have shown that many invertebrate detritivores (both terrestrial and aquatic) attain nutrition from the microflora associated with food particles and not from the plant material itself. It is assumed that S. annulicrus attains its nutrition in a similar manner. Studies by Newell (1965) and Fenchel (1969) have demonstrated that microorganisms constitute the food source for marine detritus consumers. The amphipod Parhyalella whelpleyi Shoem feeds on detritus including its own fecal pellets, utilizing only the associated microorganisms which Fenchel (1970) describes as the "real food". The freshwater detritivore Hyalella azteca digests algae and bacteria from ingested food (Hargrave, 1970a; 1970b). Dependence of lotic insect detritivores on leaf colonizing microflora for nutrition has been demonstrated (Kaushik and Hynes, 1968; Wallace et al,1970; Barlocher and Kendrick 1973a,1973b; Cummins,1973) and Cummins (1977) used the analogy of the microbes as "peanut butter" and leaves as "crackers". "In order to obtain 'peanut butter', crackers must be ingested." Food quality to many aquatic invertebrate detritivores is dependent, therefore, upon quality and quantity of microflora which is in turn influenced by chemical and physical characteristics of a given food and the environment. In an attempt to further characterize food quality, carbon, nitrogen, inorganic ash, oxygen consumption, and ATP values were determined for foods used in feeding experiments involving S. annulicrus.

Carbon - Nitrogen

Soil microbiologists have used carbon and nitrogen values as an index of decomposition rate of materials of plant orgin. Hodkinson (1975) states that lower C:N values result in increased rates of decomposition with values > 25.0 resulting in nitrogen limitations. Soil detritus with low C:N values are labile and have higher microbial populations than more refractory materials characteristic of detritus with high C:N values (Whitkamp, 1966; Anderson, 1973).

Percent nitrogen and carbon as percent of total dry weight in the foods used in larval growth experiments at 5 and 15 C are given in Table 20. The means are estimates of nitrogen and carbon present during the feeding period. Nitrogen and carbon in the various forms of stream detritus at both temperatures are very similar with values for nitrogen ranging from 1.74% for "recalcitrant" detritus to 1.89% for 5 C non-incubated detritus. Carbon values ranged from 32.45% for "recalcitrant" detritus to 33.49% for stream detritus at 15 C. The lowest nitrogen values were for Tipula feces ranging from 1.20% at 5 C to 1.16% at 15 C. Standard errors indicate that these values are significantly lower than the nitrogen values for any of the forms of stream detritus. The total nitrogen in feces of the shredder Pteronarcys, fed a diet of mixed deciduous leaf species, was 1.6% (n=2) which was also lower than the values for natural detritus. Carbon values for Tipula feces ranged from 45.46% at 5 C to 44.87% at 15 C and were very

Table 20. Percent total nitrogen and carbon in foods during fourth instar _S. annulicrus_ feeding experiment.

Food Type	n*	% Nitrogen	S.E.	% Carbon	S.E.	C:N
5 C						
Stream detritus (no incubation	6	1.89	0.08	33.15	1.17	17.5
Stream detritus	12	1.76	0.06	33.43	0.56	19.1
Tipula sp. feces	6	1.20	0.01	45.46	0.91	37.9
Ground ash leaves	6	2.58	0.06	46.23	0.40	17.9
15 C						
"Recalcitrant" Stream detritus	6	1.74	0.06	32.45	2.70	18.7
Stream detritus	12	1.87	0.03	33.49	0.61	17.9
Tipula sp. feces	6	1.16	0.04	44.87	0.83	38.7
Ground ash leaves	6	3.10	0.15	47.38	0.77	15.3

* n = number of replicates each composed of two subsamples for carbon and nitrogen data.

similar to the carbon values for ground ash leaves, which ranged from 46.23% at 5 C to 47.38% at 15 C. Those higher values are probably due to the fact that gound ash leaves and *Tipula* feces had not been exposed to breakdown processes as long as stream detritus. The highest nitrogen vlaues were in ground ash leaves ranging from 2.59% at 5 C to 3.10% at 15 C. The higher amount of total nitrogen at 15 C was probably due to a greater amount of microbial biomass and/or a greater amount of leaching of non-nitrogenous constituents at this higher temperature. Kaushik and Hynes (1968, 1971), Anderson (1973), Triska *et al*. (1975), and Suberkropp *et al*. (1976) have shown increases in absolute nitrogen due to increases in microbial biomass in leaves. An absolute increase in protein in leaves placed in a New Zealand stream was reported by Davis and Winterbourn (1977) and Barlocher and Kendrick (1973b) attributed increases in protein on leaves to hyphomycete fungi.

A leaching experiment with *Fraxinus nigra* leaves from the same source as those used in the larval feeding experiments has shown increases in percent nitrogen for leaves that had leached in sterile stream water for 24 hours at 20-22 C (Table 21). Non leached leaves contained 1.81% nitrogen which increased to 2.85% in leaves which were in water for 24 hours. Absolute nitrogen did not increase during the leaching experiment indicating that the increase in percent nitrogen was actually due to more rapid losses on non-nitrogenous leaf constituents while the weight

Table 21. Percent and absolute nitrogen and C:N values in sterile *Fraxinus nigra* leaves placed in sterile filtered stream water.

Control leaves (no water)	Hours Leached 24	48	120
	Percent Total Nitrogen		
n = 6	9	9	9
$\bar{x}$ = 1.81*	2.85	2.88	2.70
S.D. = 0.27	0.29	0.42	0.25
S.E. = 0.11	0.10	0.14	0.08
C.V.% =15.0	10.0	14.7	9.3
	Absolute Nitrogen (mg)		
n = 9	3	3	3
$\bar{x}$ =18.26**	18.67	18.10	17.33
S.D. = 0.15	1.04	0.56	0.21
S.E. = 0.05	0.60	0.32	0.12
C.V.% = 0.8	5.6	3.1	1.2
	C:N		
23.13	15.78	15.48	16.26

* = % total nitrogen on a dry weight basis
** = Mg. Nitrogen/g of leaf on a dry weight basis

of nitrogen remained relatively constant.

The forms of stream detritus used in this experiment (Table 20) had C:N values ranging from 17.5 to 19.1 which are similar to the values for a salt marsh studied by Christian, *et al*. (1975) which ranged from 13.9 to 19.1. Sediments from Lakes Ontario, Erie and Huron were lower with values of 9.1, 9.5, and 7.8 respectively (Kemp and Mudrochova, 1973). Non-leached ash leaves had an initial C:N of 23.13 which dropped to 15.78 after 24 hours in sterile stream water (Table 21). Ground ash leaves used in this feeding experiment had C:N values of 15.3 in 15 C flasks and 17.9 in 5 C flasks (Table 20). C:N values for ash which had been leached for 24 hours or ash which had been ground, leached, and fed to *S. annulicrus* were very similar to values for natural stream detritus. Implications are that C:N values decline rapidly after plant materials enter the water due to leaching of non-nitrogenous substances and then stabilize as decomposition continues. This is supported by Christian *et al*. (1975) and Godshalk (1977) who have shown that C:N ratios of decomposing aquatic macrophytes decrease during early stages of decomposition.

Percent Ash Content

The organic content (or inorganic) of foods may likely influence food quality. Many fine particle feeders do not distinguish between food quality, but ingest particles within an appropriate size range (Cummins, 1973; 1977). Gut contents of *S. annulicrus* collected from Augusta Creek contain non-nutritional components such as silt and sand as well as detritus. Inorganic materials may actually dilute detritus, lowering food quality.

The percent ash for each food type used in the fourth instar feeding experiments, prior to incubation, is given in Table 22. The ash content for stream detritus and "recalcitrant" detritus is very similar and was the highest of all food types measured. *Tipula* feces were intermediate with 16.0% ash and ground ash leaves were lowest with 9.8% ash. Also recorded in Table 22 are the percent ash in these three food types after a 14 day incubation period and approximately a seven day feeding period. The most conspicuous change in percent ash occurred in ground *Fraxinus nigra* leaves which decreased during the experiment. This is apparently due to the leaching of inorganics from the leaves. A similar reduction occurred in whole *F. nigra* leaves which had been placed in sterile stream water (Table 23). The percent ash content had decreased from 10.9% to 8.4% after leaching 24 hours. Nykvist (1959) reported that inorganics such as potassium, phosphorus, and calcium are readily leached from *Fraxinus excelsior* leaf litter. It would appear as though the percent ash of natural stream detritus, derived from leaf litter, actually goes through a short "reduction" phase and then begins to gradually increase as processing continues.

Table 22. Percent ash in foods used in fourth instar *S. annulicrus* feeding experiments.

	Stream detritus	"Recalcitrant" detritus	*Tipula* feces	Ground ash leaves
Prior to incubation				
n	5	5	5	5
$\bar{x}$ % ash	34.88	35.02	15.96	9.82
S.D.	1.32	1.05	0.91	1.11
S.E.	0.59	0.47	0.41	0.50
C.V. as %	3.78	3.00	5.68	11.28
Termination of Feeding experiment				
5°C				
n	5	---*	5	5
$\bar{x}$ % ash	34.24	---	14.48	7.60
S.D.	0.87	---	0.78	0.16
S.E.	0.39	---	0.35	0.07
C.V. as %	2.54	---	5.36	2.08
15°C				
n	5	---	5	5
$\bar{x}$	34.86	---	16.28	8.18
S.D.	1.34	---	0.70	0.15
S.E.	0.60	---	0.31	0.07
C.V. as %	3.84	---	4.29	1.83

* --- = no data available

Table 23. Percent ash in sterile *Fraxinus nigra* leaves placed in sterile stream water.

	Sterile Whole Ash Leaves	After Leaching in Sterile Stream Water 24 hours	48 hours	120 hours
n =	5	3	3	3
$\bar{x}$ =	10.88%	8.4%	8.5%	8.4%
S.D.=	0.769	0.100	0.304	0.230
S.E.=	0.344	0.057	0.175	0.132
C.V.%=	7.1	1.1	3.5	2.7

Figure 7 summarizes growth rates and some characteristics of foods fed to *S. annulicrus* at 5 and 15 C. No growth was obtained for larvae fed non-incubated and incubated natural stream detritus at 5 C and "recalcitrant" stream detritus at 15 C. These foods also contained the highest percent ash and the lowest percent carbon of any food type with the exception of natural stream detritus at 15 C. The highest animal growth rates were on ground ash leaves at both temperatures. This food type consisted of the highest percent carbon and nitrogen and also the lowest percent ash. Good growth rates were also obtained on *Tipula* feces at both temperatures (Table 17). As illustrated in Table 20, *Tipula* feces had the lowest percent nitrogen and the highest C:N values of any food type. The

Figure 7. Growth and percent carbon, nitrogen and ash for various foods at 5 C and 15 C.

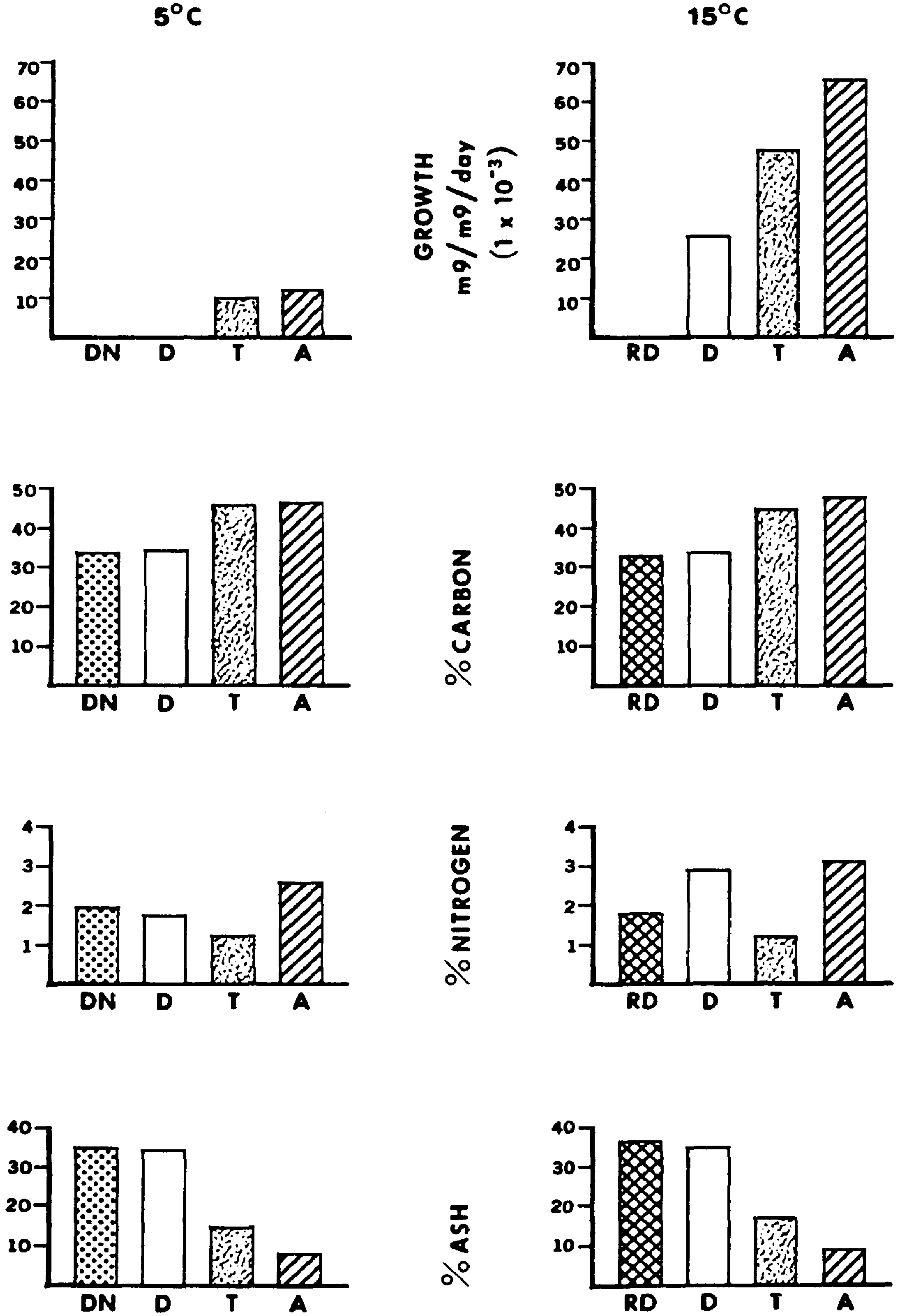

5°C
15°C
70
60
50
40
30
20
10
DN
D
T
A
RD
GROWTH
m9/m9/day
(1 x 10⁻³)
% CARBON
% NITROGEN
% ASH
4
3
2
1

Figure 7

C:N value for this food type was 37.9 at 5 C and 38.7 at 15 C, while the poorer quality foods ranged from 17.5 for non-incubated stream detritus at 5 C to 19.1 for incubated stream detritus at 5 C. This indicates that total nitrogen and carbon values are not a reliable indication of food quality for S. annulicrus. Poor correlation between decomposition rates and percent nitrogen content of terrestrial leaf litter has been reported by Melvin (1930), Daubenmire and Prusso (1963) and Anderson (1973). They suggested other properties which may influence decomposition rates including trace elements, physical structure, and presence of toxic compounds. It has been suggested that polyphenols may influence decomposition (Edwards and Heath, 1963), while Anderson (1973) demonstrated that polyphenol content in two leaf species did not account for differneces observed in decomposition rates. Suberkropp et.al. (1976) state that in lotic systems the availability of notrogen to microorganisms and insects may be greatly reduced by the complexing of proteins with refractory compounds in leaves.

Certainly the availability of nitrogen for use by microbial and invertebrate organisms is important in determining food quality. The forms of nitrogen in the comparatively "old" stream detritus are probably different than the nitrogen in the "young" detritus (Tipula feces and ground ash leaves).

In this experiment an inverse realtionship existed between percent ash in foods and growth rates (Table 22 and

Figure 7). Stream detritus, which is of comparatively poor food quality based on larval growth rates observed in this study, typically ranged from 34-35% ash (Table 22). Ground ash leaves are of high food quality and typically ranged from 7.6 to 9.8% ash. Tipula feces are intermediate in terms of food quality and were also intermediate in ash content, ranging from 14.5 to 16.3% ash. In this study it is evident that the ash content of the foods used is a reasonably good indication of food quality. This relationship probably applies to most foods available to this insect species in its natural environment.

ATP and Respiration

The use of the adenosine tri-phosphate (ATP) assay for microbial biomass estimates as proposed by Holm-Hansen and Booth (1966) has been widely accepted (Hobbie *et al.*, 1972; Holm-Hansen and Pearl, 1972; Holm-Hansen, 1973; Ausmus, 1973; Burnison, 1975; Brezonik *et al.* , 1975; Karl and LaRock, 1975; Christian *et al.*, 1975; Bancroft *et al.*,1976; Suberkropp and Klug, 1976; and Cunningham and Wetzel,1977). The efficiency of ATP recovery from detritus is variable depending on the method of extraction and the nature of the detritus. Karl and LaRock (1975), Suberkropp and Klug(1976), and Cunningham and Wetzel (1977) have found that extracts often contained substances that inhibited light emission in the luciferin-luciferase measurement of ATP. Karl and LaRock (1975) demonstrated that cations such as Ca^{++} and Na^{+} contributed to light emission inhibition. In addition to Ca^{++}, Cunningham and Wetzel (1977) reported that polyphenolic compounds interfere with ATP assays. Because of the differences in food types used in this study it cannot be assumed that efficiency of recovery was constant for all foods.

Respiration rates of sediments and detritus have been used as an estimate of microbial biomass and activity. Witkamp (1966) found that in terrestrial systems respiration rates of leaf litter correlated well with bacterial counts. Increases in respiration rates of leaf litter observed by Iversen (1973) were the result of increases in microbial densities on the leaves.

ATP and respiration values were also determined in this study for foods in an attempt to measure food quality. This was based on the supposition that there is a direct relationship between microbial biomass associated with foods and quality of food to a fine particulate detritivore such as *S. annulicrus*. A positive relationship was found for both ATP and respiration values of foods and larval growth rates (Table 24). Ground ash leaves were of the highest food quality based on growth rates and had the highest ATP and respiration values at both temperatures. The lowest growth rates were on stream detritus which also had the lowest respiration and ATP values.

Table 24. Respiration and ATP values for foods during 5 C and 15 C feeding experiment.

FOOD TYPE	μ 1 O_2/mg/hr*	S.E.	nm ATP/g*	S.E.
5 C				
Stream Detritus	0.007	0.003	0.053	0.027
Tipula feces	0.047	0.006	0.572	0.260
Ground Ash Leaves	0.064	0.010	27.035	6.068
15 C				
Stream Detritus	0.043	0.006	0.036	0.036
Tipula feces	0.091	0.014	0.707	0.392
Ground Ash Leaves	0.187	0.029	14.427	4.970

* See Appendix D, Table A-1 for experimental design.

SUMMARY AND CONCLUSIONS

The fine particulate detritivore, Stictochironomus annulicrus (Townes) (Diptera: Chironomidae), is common to Augusta Creek depositional areas and adjacent spring brooks with two generations per year. A spring emergence occurred over a three to four week period beginning the second or third week of April and a late summer emergence over a four to five week period beginning the third or fourth week of August.

Oviposition sites were localized and used by females of succeeding generations. Egg masses, which consisted of gelatinous strings containing 100 to 800 eggs, were laid just under the water surface on vegetation such as grasses, sedges, or shrubs. The incubation period for eggs was temperature dependent, increasing with lower temperatures, but development rate and temperature were not directly proportional.

Upon leaving the egg mass, larvae display a planktonic behavior for 20 to 30 minutes with no evidence of feeding during this period. This behavior undoubtedly is an important dispersal mechanism for this lotic species. Larvae construct a tube of detritus and remain tubiculous during all four instars obtaining food directly from the substrate at the end of the tube with the aid of the mouth parts. Food consists of fine particulate detritus and associated constituents. Instars were easily distinguished by measuring either the width of the head at the eye spots, width of labial plate, or the distance from the lower edge of the labial plate to the occipital foramen. The ratio (r) of increase did not increase at a constant rate for any structure measured and thus, did not conform to Dyar's rule. The maximum larval length recorded was 14.0 mm and maximum dry weight was 2.385 mg. Summer form larvae were smaller than winter form larvae. The mean ash-free dry weight of 1974 summer form larve just prior to emergence at the Kellogg Forest site was 0.913 mg while the winter form larvae from the same site had a mean of 1.346 mg. Summer form larvae at the Nagel site, Spring No. 2, for the same year had a mean ash-free dry weight of 0.603 mg and winter form larvae had a mean of 1.135 mg. These size differences were also apparent for the pupal and adult stages. Sexual dimorphism was also apparent in pupal and adult stages with females being larger.

Third and fourth instar larvae have a contagious distribution and showed agreement with Poisson series ($P > 0.05$) for most samples. Larval density estimates varied between sites and seasonally at a given site. Larval density estimates at Kellogg Forest site on 1 August 1974 were $161/m^2$ ($n = 16$) and on 10 April 1974 were $338/m^2$ ($n = 20$). At Nagel site, density estimates were $2115/m^2$ ($n = 9$) on

9 July 1974 and $1325/m^2$ (n = 26) on 26 April 1974.

It appears that temperature summation is of value in predicting emergence times of S. annulicrus. Degree-days accumulated for summer generations ranged from 1566 at B Avenue to 1711 at Spring Brook No. 2, while for winter generations the range was from 1599 at Spring Brook No. 1 to 1993 at Spring Brook No. 2. These data indicate that the minimal accumulative temperature requirement for a generation in Augusta Creek would be approximately 1550 to 1650 degree-days. Temperature summation appears to be of primary importance providing water temperatures increase to levels above the pupation threshold (8.0 C). Variance from this pattern may be due to parameters such as food quality and availability.

Laboratory experiments demonstrated that larval growth rates decreased with successive instars and each instar had increased growth rates with increases in temperature. First instar larvae fed Tipula feces at 5 C had a mean RGR of 0.08 mg/mg/day and at 20 C a RGR of 0.43 mg/mg/day. Fourth instar larvae fed Tipula feces at 5 C and at 10 C had RGRs of 0.01 mg/mg/day and 0.09 mg/mg/day respectively.

Larval growth rates varied according to levels of food quality. Highest growth rates were on ground ash (Fraxinus nigra) leaves, intermediate rates were on Tipula feces, and lowest rates were on natural stream detritus. In an attempt to further characterize food quality, carbon, nitrogen, inorganic ash, oxygen consumption and ATP values were determined for foods used in feeding experiments. A poor relationship between carbon and nitrogen values and growth rates existed in this study. Ground ash had the highest percent total nitrogen and the highest animal growth rates, but Tipula feces ranked as intermediate in quality had the lowest nitrogen values (1.16 and 1.20) and the highest C:N values. C:N values were similar for ground ash (15.3 and 17.9) and stream detritus (17.9 and 19.1) with very dissimilar growth rates. It is apparent that the availability of nitrogen for use by microbial and invertebrate organisms is imperative in determining food quality.

In this study an inverse relationship existed between percent ash in foods and growth rates. Ash content of the foods used in this study is a reasonably good indication of food quality. A positive relationship was found for both ATP and respiration values of foods and larval growth rates. The lowest growth rates were on stream detritus, which also had the lowest respiration and ATP values. The highest values for ATP and respiration were on ground ash which had the highest larval growth rates.

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APPENDICIES

APPENDIX A

APPENDIX A

Table A-1. Current velocity and discharge data, B Avenue, Augusta Creek.

DATE	VELOCITY	DISCHARGE m^3/sec.	ft^3/sec.
22 June 1973	16.79	0.035	1.24
24 " "	16.11	0.034	1.20
28 " "	44.87	0.143	5.05
14 July "	26.46	0.067	2.37
6 August"	12.66	0.027	0.95
13 " "	12.20	0.025	0.88
20 " "	35.67	0.107	3.78
22 " "	14.50	0.033	1.17
27 " "	13.81	0.031	1.09
3 Sept. "	13.35	0.029	1.02
10 " "	12.20	0.025	0.88
25 " "	13.38	0.032	1.13
1 Oct. "	22.32	0.057	2.01
9 " "	16.80	0.040	1.41
15 " "	20.02	0.052	1.84
2 Nov. "	22.55	0.058	2.05
5 " "	17.40	0.044	1.55
11 " "	18.41	0.043	1.52
15 " "	67.42	0.263	9.28
16 " "	33.37	0.095	3.35
19 " "	20.71	0.045	1.59

Table A-1. (cont.)

DATE	VELOCITY	DISCHARGE m^3/sec.	ft^3/sec.
27 Nov. 1973	21.86	0.048	1.69
6 Dec. "	23.70	0.057	2.01
18 " "	17.26	0.040	1.41
28 " "	26.00	0.076	2.68
25 Jan. 1974	25.31	0.057	2.01
2 March "	34.52	0.090	3.18
20 " "	25.31	0.057	2.01
9 April "	25.31	0.069	2.44
30 " "	46.02	0.133	4.69
9 May "	29.91	0.074	2.61
16 " "	86.98	0.395	13.94
17 " "	62.13	0.236	8.33
29 " "	43.72	0.121	4.28
5 June "	22.55	0.050	1.77
12 " "	24.85	0.057	2.01
19 " "	28.30	0.065	2.29
27 " "	28.76	0.066	2.33
3 July "	33.37	0.074	2.61
10 " "	20.71	0.044	1.55
17 " "	19.56	0.041	1.45
25 " "	21.40	0.043	1.52
31 " "	18.41	0.037	1.31

Table A-1. (cont.)

DATE	VELOCITY	DISCHARGE m^3/sec.	ft^3/sec.
7 Aug. 1974	21.86	0.045	1.59
28 " "	21.40	0.047	1.66
4 Sept. "	25.31	0.052	1.84
11 " "	20.71	0.041	1.45
18 " "	17.95	0.037	1.30
25 " "	19.10	0.041	1.45
17 Oct. "	20.71	0.049	1.73
30 " "	52.92	0.171	6.04
2 Nov. "	23.01	0.053	1.87
24 " "	33.37	0.086	3.04
5 Dec. "	21.86	0.048	1.69
1 Jan. 1975	23.01	0.055	1.94

APPENDIX A

Table A-2. Current velocity and discharge data, Nagel site, Augusta Creek.

DATE			VELOCITY	DISCHARGE $m^3/sec.$	DISCHARGE $ft^3/sec.$
3	Oct.	1973	60.98	1.168	41.23
9	"	"	46.02	0.772	27.25
15	"	"	92.73	1.932	68.20
2	Nov.	"	55.91	1.043	36.82
5	"	"	57.06	0.996	35.16
11	"	"	55.91	0.909	32.10
15	"	"	68.57	1.266	44.69
16	"	"	78.23	1.577	55.67
19	"	"	66.27	1.212	42.78
27	"	"	64.43	1.157	40.84
6	Dec.	"	83.26	1.655	58.42
18	"	"	50.62	0.945	33.36
28	"	"	84.68	2.010	70.95
25	Jan.	1974	70.87	1.502	53.02
2	Mar.	"	72.02	1.403	49.53
20	"	"	75.93	1.557	54.96
9	April	"	85.83	2.111	74.52
30	"	"	88.13	1.911	67.46
9	May	"	46.71	0.928	32.76
17	"	"	100.09	2.287	80.73
29	"	"	71.33	1.312	46.31

Table A-2. (cont.)

DATE			VELOCITY	DISCHARGE m^3/sec.	ft^3/sec.
5	June	1974	61.67	1.012	35.72
12	"	"	62.13	1.154	40.74
19	"	"	75.47	1.328	46.88
27	"	"	69.03	1.168	41.23
1	July	"	52.92	0.846	29.86
3	"	"	55.22	0.873	30.82
10	"	"	49.01	0.789	27.85
17	"	"	36.82	0.550	19.42
25	"	"	35.67	0.533	18.82
31	"	"	30.60	0.458	16.17
7	Aug.	"	43.72	0.667	23.55
21	"	"	34.52	0.521	18.39
28	"	"	47.17	0.752	26.55
4	Sept.	"	49.01	0.789	27.85
11	"	"	37.51	0.572	20.19
18	"	"	39.12	0.631	22.27
25	"	"	41.42	0.646	22.80
17	Oct.	"	58.68	0.974	34.38
30	"	"	65.12	1.147	40.49
24	Nov.	"	66.73	1.232	43.49
5	Dec.	"	53.61	0.908	32.05
1	Jan.	1975	63.28	1.093	38.58

APPENDIX A

Table A-3. Current velocity and discharge data, Kellogg Forest, Augusta Creek.

DATE	VELOCITY * cm/sec. 1	2	DISCHARGE m3/sec.	ft^3/sec.
11 Nov. 1973	29.91	52.92	0.989	34.91
15 " "	37.97	60.98	1.472	51.96
16 " "	35.21	58.68	1.398	49.35
19 " "	31.18	42.57	1.083	38.23
27 " "	31.75	42.57	1.066	37.63
6 Dec. "	32.21	42.11	1.159	40.91
18 " "	29.91	52.92	1.140	40.24
28 " "	36.82	60.52	1.913	67.53
25 Jan. 1974	29.91	66.73	1.823	64.35
2 Mar. "	37.65	63.28	1.683	59.41
20 " "	42.57	66.73	1.824	64.39
9 April "	44.87	75.93	2.317	81.79
30 " "	40.96	54.07	2.050	72.37
9 May "	42.57	52.92	1.476	52.10
17 " "	65.12	89.74	2.810	99.19
29 " "	43.72	65.58	1.551	54.75
5 June "	37.97	59.83	1.224	43.21
12 " "	43.72	72.02	1.729	61.03
19 " "	44.87	67.42	1.619	57.15
27 " "	42.57	50.62	1.072	37.84
3 July "	36.82	49.01	0.957	33.78

Table A-3. (cont.)

DATE	VELOCITY cm/sec. 1	2	DISCHARGE m^3/sec.	ft^3/sec.
10 July 1974	39.12	53.61	1.033	36.46
17 " "	34.05	41.42	0.782	27.61
25 " "	32.21	43.72	0.760	26.83
31 " "	26.00	36.82	0.623	22.00
7 Aug. "	36.82	50.16	0.910	32.12
21 " "	29.91	50.16	0.706	24.93
28 " "	43.04	52.92	0.955	33.71
4 Sept. "	34.52	40.27	0.826	29.16
11 " "	26.00	23.70	0.499	17.61
18 " "	28.30	39.81	0.729	25.73
25 " "	25.77	48.78	0.781	27.57
14 Oct. "	36.36	49.01	1.087	38.37
15 " "	44.41	63.28	1.394	49.21
16 " "	33.63	53.68	1.092	38.55
30 " "	36.82	55.91	1.233	43.52
24 Nov. "	32.21	41.42	1.022	36.08
5 Dec. "	29.91	42.11	1.050	37.07
1 Jan. 1975	36.82	53.61	1.151	40.63

* current velocities taken at two locations at this site.

APPENDIX B

APPENDIX B

Table B-1. B Avenue temperature records from Oct. 1, 1971 to Sept. 30, 1972 (after Petersen, 1974).

PERIOD FROM	TO	MIN	MAX	MEAN DAILY	DEGREE DAYS
Sept 30	Oct 7	9.0	19.0	15.0	105.0
Oct 7	Oct 14	7.0	11.5	10.0	70.0
Oct 14	Oct 21	8.5	15.0	11.5	80.5
Oct 21	Oct 31	10.0	15.5	13.0	130.0
Oct 31	Nov 8	1.5	12.0	7.2	57.6
Nov 8	Nov 16	3.0	10.0	6.0	48.0
Nov 16	Nov 24	0.0	11.5	6.0	48.0
Nov 24	Dec 1	0.0	4.5	3.0	21.0
Dec 1	Dec 9	0.0	4.0	2.0	16.0
Dec 9	Dec 16	1.0	4.0	3.5	24.5
Dec 16	Dec 22	1.0	4.0	3.0	18.0
Dec 22	Dec 30	0.0	4.5	3.0	24.0
Dec 30	Jan 8	0.0	3.0	1.0	8.0
Jan 8	Jan 17	0.0	3.0	1.6	12.8
Jan 17	Jan 26	0.0	2.0	0.8	7.2
Jan 26	Feb 5	0.0	2.5	1.0	10.0
Feb 5	Feb 11	0.0	0.0	0.0	0.0
Feb 11	Feb 20	0.0	3.5	1.8	16.2
Feb 20	Mar 3	0.0	3.5	1.8	21.6
Mar 3	Mar 22	0.0	6.0	1.6	30.4
Mar 22	Apr 6	0.0	9.5	3.6	43.2

Table B-1. (cont.)

PERIOD FROM	TO	MIN	MAX	MEAN DAILY	DEGREE DAYS
Apr 6	Apr 11	0.0	11.0	4.2	21.0
Apr 11	Apr 20	3.0	13.0	8.6	77.4
Apr 20	May 4	4.0	17.0	11.3	158.2
May 4	May 11	5.0	17.5	12.0	84.0
May 11	May 17	8.5	18.5	12.5	75.0
May 17	May 24	9.0	18.5	13.0	91.0
May 24	Jun 5	10.0	19.0	14.0	154.0
Jun 5	Jun 14	11.5	19.5	14.3	128.7
Jun 14	Jun 21	12.0	19.0	15.0	105.0
Jun 21	June 28	13.0	20.0	16.5	115.5
Jun 28	Jul 5	12.0	19.5	15.5	108.5
Jul 5	Jul 11	12.0	19.5	15.0	105.0
Jul 11	Jul 19	10.0	19.5	14.3	114.4
Jul 19	Jul 28	10.0	19.5	15.0	135.0
Jul 28	Aug 4	10.0	19.5	15.0	105.0
Aug 4	Aug 13	10.0	19.0	14.0	140.0
Aug 13	Aug 24	11.0	18.5	14.5	160.0
Aug 24	Aug 31	12.0	19.0	14.5	101.5
Aug 31	Sept 6	12.0	19.5	17.0	204.0
Sept 6	Sept 17	10.5	18.0	16.5	173.3
Sept17	Sept 24	10.0	18.0	16.0	112.0
Sept24	Sept 30	9.0	17.5	15.6	90.0

APPENDIX B

Table B-2. B Avenue temperature records from Sept. 30, 1972 to Oct. 1, 1973.

PERIOD FROM	TO	MIN	MAX	MEAN DAILY	DEGREE DAYS
Sept 30	Oct 6	8.5	13.5	11.0	66.0
Oct 6	Oct 13	5.0	11.0	9.0	56.0
Oct 13	Oct 20	1.0	12.0	6.5	45.5
Oct 20	Oct 27	4.0	8.0	6.5	45.5
Oct 27	Nov 3	5.0	8.0	6.8	47.6
Nov 3	Nov 10	4.5	7.5	7.0	49.0
Nov 10	Nov 17	0.0	6.5	3.5	24.5
Nov 17	Nov 24	1.5	3.5	2.8	19.6
Nov 24	Dec 1	2.0	2.5	2.0	14.0
Dec 1	Dec 8	0.0	2.5	0.8	5.6
Dec 8	Dec 15	0.2	1.5	0.2	1.4
Dec 15	Dec 22	0.0	2.0	1.3	9.1
Dec 22	Dec 29	0.5	2.0	1.7	11.9
Dec 29	Jan 5	0.0	0.5	0.1	0.7
Jan 5	Jan 12	0.0	0.5	0.2	1.4
Jan 12	Jan 20	0.5	2.5	1.4	11.2
Jan 20	Jan 28	2.5	4.0	3.0	24.0
Jan 28	Jan 4	0.5	4.5	1.8	12.6
Feb 4	Feb 11	0.5	4.5	1.9	13.3
Feb 11	Feb 18	0.5	3.0	1.1	7.7
Feb 18	Feb 25	0.5	4.0	1.6	11.2
Feb 25	Mar 4	0.5	4.0	2.3	16.1

Table B-2. (cont.)

PERIOD FROM	TO	MIN	MAX	MEAN DAILY	DEGREE DAYS
Mar 4	Mar 11	2.5	9.0	5.0	35.0
Mar 11	Mar 18	1.0	10.5	6.2	43.4
Mar 18	Mar 25	0.5	10.5	4.5	31.5
Mar 25	Apr 2	2.5	12.0	7.7	53.9
Apr 2	Apr 9	5.0	14.0	7.8	54.6
Apr 9	Apr 16	2.5	14.5	6.6	46.2
Apr 16	Apr 23	5.0	18.0	12.5	87.5
Apr 23	May 2	6.0	18.0	11.3	79.1
May 2	May 9	7.0	17.5	11.5	80.5
May 9	May 17	8.0	16.5	11.0	88.0
May 17	May 24	6.0	16.5	11.8	82.6
May 24	May 31	9.5	17.0	13.8	96.6
May 31	Jun 7	12.5	18.5	15.8	110.6
Jun 7	Jun 15	12.5	19.5	16.5	132.0
Jun 15	Jun 22	14.5	18.5	15.9	111.3
Jun 22	Jun 29	14.0	17.0	15.4	107.8
Jun 29	Jul 7	14.0	18.0	15.0	120.0
Jul 7	Jul 14	13.5	19.5	17.0	119.0
Jul 14	Jul 21	14.0	17.5	15.3	107.1
Jul 21	Jul 29	16.0	18.5	16.5	115.5
Jul 29	Aug 6	16.0	18.5	16.5	115.5
Aug 6	Aug 13	16.0	18.0	16.5	115.5
Aug 13	Aug 20	15.0	17.0	15.5	108.5

Table B-2. (cont.)

PERIOD FROM	TO	MIN	MAX	MEAN DAILY	DEGREE DAYS
Aug 20	Aug 27	15.0	19.0	15.0	105.0
Aug 27	Sept 3	17.0	19.0	17.5	122.5
Sept 3	Sept 10	13.0	19.0	15.5	108.5
Sept 10	Sept 17	12.0	15.5	13.0	91.0
Sept 17	Sept 24	10.0	14.5	12.0	84.0
Sept 24	Oct 1	13.0	17.0	15.0	105.0

APPENDIX B

Table B-3. B Avenue temperature records from Oct. 15, 1973 to Nov. 1, 1974.

PERIOD		MIN	MAX	MEAN DAILY	DEGREE DAYS
Oct. 15	to Oct. 22	7.5	13.0	9.6	67.2
Oct. 22	Oct. 29	8.0	12.0	10.0	70.0
Oct. 29	Nov. 5	4.8	10.0	8.1	56.7
Nov. 5	Nov. 12	3.8	5.5	4.4	30.8
Nov. 12	Nov. 19	4.5	10.0	6.8	47.6
Nov. 19	Nov. 26	5.0	9.3	6.8	47.6
Nov. 26	Dec. 3	3.0	8.0	5.5	38.5
Dec. 3	Dec. 10	2.3	7.3	4.2	29.4
Dec. 10	Dec. 17	0.5	3.0	1.0	7.0
Dec. 17	Dec. 24	0.5	2.3	0.8	5.6
Dec. 24	Dec. 31	0.5	2.2	1.2	8.4
Dec. 31	Jan. 6	0.0	2.0	0.1	0.6
Jan. 6	Jan. 14	0.0	1.2	0.4	2.4
Jan. 14	Jan. 21	0.0	3.0	1.4	9.8
Jan. 21	Jan. 28	1.0	3.7	1.9	13.3
Jan. 28	Jan. 29	2.0	2.0	2.0	2.0
Jan. 29	Feb. 5	0.8	4.3	1.6	11.2
Feb. 5	Feb. 12	0.0	1.0	0.1	0.7
Feb. 12	Feb. 19	0.5	3.0	1.0	7.0
Feb. 19	Feb. 26	0.3	4.7	1.1	7.7
Feb. 26	Feb. 27	1.8	3.0	2.3	2.3
Feb. 27	Mar. 5	1.5	8.0	3.3	19.8

Table B-3. (cont.)

PERIOD		MIN	MAX	MEAN DAILY	DEGREE DAYS
Mar. 5	Mar. 12	2.5	10.0	4.6	32.2
Mar. 12	Mar. 19	0.5	7.0	3.5	24.5
Mar. 19	Mar. 26	0.2	6.5	2.8	19.6
Mar. 26	Apr. 2	1.2	7.5	3.4	23.8
Apr. 2	Apr. 9	1.9	12.1	6.3	44.1
Apr. 9	Apr. 16	2.6	16.0	8.9	62.3
Apr. 16	Apr. 23	4.5	15.5	10.3	72.1
Apr. 23	Apr. 30	4.5	17.0	11.0	77.0
Apr. 30	May 7	5.2	17.4	11.0	77.0
May 7	May 14	5.5	15.5	9.0	63.0
May 14	May 21	10.0	18.5	12.5	87.5
May 21	May 28	9.6	18.6	12.6	88.2
May 28	May 29	13.0	19.0	16.4	16.4
May 29	June 5	10.8	18.7	14.2	99.4
June 5	June 12	11.5	19.8	16.0	112.0
June 12	June 19	11.7	17.3	13.9	97.3
June 19	June 26	12.6	18.5	14.8	103.6
June 26	July 3	12.8	17.8	15.5	108.5
July 3	July 10	13.5	19.5	16.5	115.5
July 10	July 17	13.5	20.0	16.7	116.9
July 17	July 24	13.3	19.0	15.5	108.5
July 24	July 25	14.5	16.5	16.0	16.0
July 25	July 31	13.5	18.0	15.8	94.8
July 31	Aug. 7	13.2	17.0	15.0	105.0

Table B-3. (cont.)

PERIOD		MIN	MAX	MEAN DAILY	DEGREE DAYS
Aug. 7	to Aug. 14	14.8	18.0	16.3	114.1
Aug. 14	Aug. 21	14.7	17.3	15.5	108.5
Aug. 21	Aug. 28	13.0	17.8	15.8	110.6
Aug. 28	Sept 4	10.0	19.5	13.8	96.6
Sept 4	Sept 11	9.8	16.0	12.8	89.6
Sept 11	Sept 18	10.5	18.5	14.2	99.4
Sept.18	Sept 25	8.0	16.0	11.3	79.1
Sept 25	Oct 2	7.5	13.0	11.3	79.1
Oct 2	Oct 9	6.4	13.0	10.1	70.7
Oct 9	Oct 16	7.0	11.2	10.2	71.4
Oct 16	Oct 17	7.0	10.5	9.0	9.0
Oct 17	Oct 24	3.8	11.0	7.7	53.9
Oct 24	Oct 31	6.8	13.2	9.7	67.9
Oct 31	Nov 1	12.8	13.5	13.0	13.0

APPENDIX B

Table B-4. B. Avenue temperature records from Oct. 24, 1974 to May 15, 1975 (Mahan, D., KBS Pers. Comm.).

PERIOD		MEAN DAILY	DEGREE DAYS
Oct 24	to Nov 5	10.2	121.8
Nov 5	Nov 13	6.4	51.0
Nov 13	Nov 20	4.8	33.8
Nov 20	Nov 27	3.9	27.3
Nov 27	Dec 6	1.9	17.3
Dec 6	Dec 11	3.0	15.1
Dec 11	Dec 18	3.2	22.4
Dec 18	Dec 30	2.7	31.8
Dec 30	Jan 8	2.4	21.9
Jan 8	Jan 15	1.9	13.1
Jan 15	Jan 23	1.6	12.6
Jan 23	Jan 27	1.9	7.6
Jan 27	Jan 30	1.9	5.7
Jan 30	Feb 6	2.3	15.8
Feb 6	Feb 13	1.1	8.0
Feb 13	Feb 21	2.3	18.6
Feb 21	Feb 27	2.4	14.6
Feb 27	Mar 6	1.7	17.2
Mar 6	Mar 13	2.8	19.9
Mar 13	Mar 17	3.9	15.4
Mar 17	Mar 20	3.9	11.6

Table B-4. (cont.)

PERIOD		MEAN DAILY	DEGREE DAYS
Mar 20	Mar 27	4.0	28.0
Mar 27	Apr 4	3.7	29.5
Apr 4	Apr 10	4.1	24.8
Apr 10	Apr 17	3.9	27.3
Apr 17	Apr 24	13.2	92.6
Apr 24	May 1	11.0	77.0
May 1	May 8	12.7	88.6
May 8	May 15	14.8	103.6

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Table B-5. Nagel temperature records from Oct. 19, 1973 to Nov. 1, 1974.

PERIOD		MIN	MAX	MEAN DAILY	DEGREE DAYS
Oct 19 to	Oct 22	7.0	11.0	9.3	27.9
Oct 22	Oct 29	8.0	14.0	10.6	74.2
Oct 29	Nov 5	6.0	10.0	8.4	58.8
Nov 5	Nov 12	2.6	5.3	4.1	28.7
Nov 12	Nov 19	4.5	10.0	7.1	49.7
Nov 19	Nov 26	5.8	9.3	7.5	52.5
Nov 26	Dec 3	-	-	5.9	41.3
Dec 3	Dec 10	2.0	7.5	4.2	29.4
Dec 10	Dec 17	0.0	1.5	0.7	4.9
Dec 17	Dec 24	0.0	1.0	0.3	2.1
Dec 24	Dec 31	0.0	1.0	0.5	3.5
Dec 31	Jan 6	0.0	1.2	0.3	1.8
Jan 6	Jan 14	0.0	1.5	0.1	0.8
Jan 14	Jan 21	0.0	2.3	1.3	9.1
Jan 21	Jan 28	0.0	3.0	1.2	8.4
Jan 28	Jan 29	1.0	1.5	1.3	1.3
Jan 29	Feb 5	0.0	3.5	0.7	4.9
Feb 5	Feb 12	0.0	1.5	0.0	0.0
Feb 12	Feb 19	0.0	2.5	0.6	4.2
Feb 19	Feb 26	0.0	3.0	0.7	4.9
Feb 26	Feb 27	0.5	1.5	1.0	1.0
Feb 27	Mar 5	1.5	10.0	3.8	22.8

Table B-5. (cont.)

PERIOD		MIN	MAX	MEAN DAILY	DEGREE DAYS
Mar 5	to Mar 12	3.5	10.0	5.5	38.5
Mar 12	Mar 19	1.5	6.2	4.0	28.0
Mar 19	Mar 26	0.0	6.2	2.9	20.3
Mar 26	Apr 2	1.6	7.0	3.5	24.5
Apr 2	Apr 9	3.0	11.2	7.3	51.1
Apr 9	Apr 16	4.5	16.0	10.2	71.4
Apr 16	Apr 23	7.0	16.6	11.6	81.2
Apr 23	Apr 30	6.0	18.0	12.5	87.5
Apr 30	Apr 7	6.8	18.0	12.6	88.2
Apr 7	Apr 14	6.5	14.5	9.8	68.6
Apr 14	Apr 21	11.5	20.4	14.2	99.4
Apr 21	Apr 28	13.0	21.5	16.0	112.0
Apr 28	Apr 29	16.5	21.5	19.0	19.0
Apr 29	May 5	12.7	22.5	16.5	115.5
May 5	May 9	16.8	22.0	19.5	78.0
May 9	May 12	16.5	20.0	18.5	55.5
May 12	May 19	12.6	20.7	16.3	114.1
May 19	May 26	13.5	23.0	17.8	124.6
May 26	July 3	16.0	22.8	19.5	136.5
Jul 3	Jul 10	17.5	25.5	21.0	147.0
Jul 10	Jul 17	16.0	26.0	20.3	142.1
Jul 17	Jul 24	14.5	23.6	19.0	133.0
Jul 24	Jul 25	15.4	19.4	17.8	17.8

Table B-5. (cont.)

PERIOD	MIN	MAX	MEAN DAILY	DEGREE DAYS
Jul 25 to Jul 31	15.0	22.5	18.1	108.6
Jul 31 Aug 7	13.0	19.5	16.3	114.1
Aug 7 Aug 14	16.5	22.3	18.3	128.1
Aug 14 Aug 21	15.5	21.5	18.2	127.4
Aug 21 Aug 28	13.5	21.5	17.5	122.5
Aug 28 Sep 4	10.0	17.2	14.5	101.5
Sep 4 Sep 11	10.0	17.0	13.5	94.5
Sep 11 Sep 18	11.0	20.0	15.5	108.5
Sep 18 Sep 25	7.7	16.5	12.0	84.0
Sep 25 Oct 2	5.5	15.3	11.2	78.4
Oct 2 Oct 9	4.0	13.3	9.2	64.4
Oct 9 Oct 16	7.5	11.5	9.8	68.6
Oct 16 Oct 17	8.5	10.0	9.0	9.0
Oct 17 Oct 24	1.8	10.5	6.1	42.7
Oct 24 Oct 31	4.5	13.3	8.9	62.3
Oct 31 Nov 1	14.0	15.5	14.5	29.0

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Table B-6. Nagel temperature records from Oct. 24, 1974 to May 15, 1975 (Mahan, D., KBS Pers. Comm.).

PERIOD		MEAN DAILY	DEGREE DAYS
Oct 24 to	Nov 5	11.9	142.3
Nov 5	Nov 13	7.0	55.8
Nov 13	Nov 20	4.3	29.8
Nov 20	Nov 27	3.9	27.3
Nov 27	Dec 6	1.6	14.0
Dec 6	Dec 11	2.1	10.5
Dec 11	Dec 18	2.4	16.8
Dec 18	Dec 30	2.2	26.4
Dec 30	Jan 8	1.8	16.2
Jan 8	Jan 15	1.8	12.5
Jan 15	Jan 23	1.2	9.3
Jan 23	Jan 27	1.6	6.2
Jan 27	Jan 30	0.9	2.6
Jan 30	Feb 6	1.6	11.0
Feb 6	Feb 13	0.8	5.4
Feb 13	Feb 21	2.3	18.5
Feb 21	Feb 27	2.1	12.7
Feb 27	Mar 6	1.4	14.1
Mar 6	Mar 13	2.2	15.2
Mar 13	Mar 17	5.0	20.0
Mar 17	Mar 20	2.7	8.2

Table B-6. (cont.)

PERIOD		MEAN DAILY	DEGREE DAYS
Mar 20 to	Mar 27	5.2	36.3
Mar 27	Apr 4	3.8	30.1
Apr 4	Apr 10	4.9	29.3
Apr 10	Apr 17	7.6	53.5
Apr 17	Apr 24	10.3	72.0
Apr 24	May 1	6.3	44.0
May 1	May 8	19.3	135.4
May 8	May 15	16.8	117.6

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Table B-7. Spring Brook #1 temperature records from Nov. 19, 1973 to April 17, 1975.

PERIOD		MIN	MAX	MEAN DAILY	DEGREE DAYS
Nov 19 to	Dec 6	5.5	11.5	8.5	144.5
Dec 6	Dec 18	6.0	10.5	8.3	99.6
Dec 18	Dec 31	2.0	10.0	6.0	78.0
Dec 31	Jan 19	1.5	10.5	6.0	114.0
Jan 19	Jan 25	1.5	9.5	5.5	33.0
Jan 25	Jan 31	3.0	9.0	6.0	36.0
Jan 31	Mar 2	1.5	10.0	5.8	174.0
Mar 2	Mar 20	3.5	11.5	7.5	135.0
Mar 20	Mar 26	6.0	10.5	8.3	49.8
Mar 26	Apr 10	2.5	11.5	7.0	105.0
Apr 10	Apr 16	7.0	12.0	9.5	57.0
Apr 16	Apr 23	7.0	12.5	9.8	68.6
Apr 23	Apr 30	7.0	12.5	9.8	68.6
Apr 30	May 9	6.5	14.0	10.3	92.7
May 9	May 29	7.5	13.0	10.3	206.0
May 29	Jun 5	8.5	14.0	11.3	79.1
Jun 5	Jun 12	9.0	13.5	11.3	79.1
Jun 12	Jun 22	8.5	13.5	11.0	110.0
Jun 22	Jun 27	9.0	13.0	11.0	55.0
Jun 27	Jul 3	9.5	12.0	10.8	64.8
Jul 3	Jul 10	9.0	12.0	10.5	73.5
Jul 10	Jul 17	10.0	11.0	10.5	73.5

Table B-7. (cont.)

PERIOD		MIN	MAX	MEAN DAILY	DEGREE DAYS
Jul 17 to	Jul 25	9.5	10.5	10.0	80.0
Jul 25	Jul 31	9.5	12.0	10.8	64.8
Jul 31	Aug 8	9.5	11.0	10.0	80.0
Aug 8	Aug 21	10.0	11.0	10.5	136.5
Aug 21	Aug 28	10.0	13.0	11.5	80.5
Aug 28	Sep 4	10.0	11.0	10.5	73.5
Sep 4	Sep 11	9.5	10.0	9.8	68.6
Sep 11	Sep 18	9.5	12.0	10.8	75.6
Sep 18	Sep 25	9.0	10.0	9.5	66.5
Sep 25	Oct 1	9.0	11.0	10.0	60.0
Oct 1	Oct 18	9.0	10.0	9.5	161.5
Oct 18	Oct 30	10.0	11.0	10.5	126.0
Oct 30	Nov 24	7.5	10.0	8.8	220.0
Nov 24	Dec 5	8.0	9.5	8.8	96.8
Dec 5	Jan 1	6.0	8.0	7.0	189.0
Jan 1	Jan 28	4.5	8.0	6.3	170.1
Jan 28	Mar 1	3.5	8.5	6.0	198.0
Mar 1	Apr 17	4.0	9.0	6.5	305.5

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Table B-8. Spring Brook #2 temperature records from Nov. 19, 1973 to April 17, 1975.

PERIOD		MIN	MAX	MEAN DAILY	DEGREE DAYS
Nov 19 to	Dec 6	5.0	14.5	9.8	166.6
Dec 6	Dec 18	4.0	10.0	7.0	84.0
Dec 18	Dec 31	2.5	10.0	6.3	81.9
Dec 31	Jan 19	3.0	10.0	6.5	123.5
Jan 19	Jan 25	2.5	10.0	6.3	37.8
Jan 25	Jan 31	4.5	6.5	5.5	33.0
Jan 31	Mar 2	3.0	9.5	6.3	189.0
Mar 2	Mar 20	5.0	12.0	8.5	153.0
Mar 20	Mar 26	5.0	12.0	8.5	51.0
Mar 26	Apr 10	3.0	12.5	7.8	117.0
Apr 10	Apr 16	5.0	16.0	10.5	63.0
Apr 16	Apr 23	6.0	18.0	12.0	84.0
Apr 23	Apr 30	5.5	16.5	11.0	77.0
Apr 30	May 9	4.0	18.0	11.0	99.0
May 9	May 29	5.5	20.0	12.8	256.0
May 29	Jun 5	8.0	19.0	13.5	94.5
Jun 5	Jun 12	8.5	14.0	11.3	79.1
Jun 12	Jun 22	9.5	17.0	13.3	133.0
Jun 22	Jun 27	9.5	17.0	13.3	66.5
Jun 27	Jul 3	10.0	18.0	14.0	84.0
Jul 3	Jul 10	10.0	18.0	14.0	98.0
Jul 10	Jul 17	10.0	17.0	13.5	94.5

Table B-8. (cont.)

PERIOD		MIN	MAX	MEAN DAILY	DEGREE DAYS
Jul 17	to Jul 25	10.0	17.0	13.5	108.0
Jul 25	Jul 31	12.5	17.5	15.0	90.0
Jul 31	Aug 8	16.0	17.0	16.5	132.0
Aug 8	Aug 21	12.0	16.5	14.3	185.9
Aug 21	Aug 28	12.0	17.0	14.5	101.5
Aug 28	Sep 4	10.5	16.5	13.5	94.5
Sep 4	Sep 11	10.5	16.5	13.5	94.5
Sep 11	Sep 18	10.0	16.5	13.3	133.0
Sep 18	Sep 25	10.0	16.5	13.3	93.1
Sep 25	Oct 1	10.5	15.0	12.8	76.8
Oct 1	Oct 18	8.5	17.0	12.8	217.6
Oct 18	Oct 30	8.0	16.5	12.3	147.6
Oct 30	Nov 24	5.5	13.0	9.3	232.5
Nov 24	Dec 5	5.5	11.5	8.5	93.5
Dec 5	Jan 1	6.5	10.5	8.5	229.5
Jan 1	Jan 28	3.0	10.0	6.5	175.5
Jan 28	Mar 1	3.0	10.0	6.5	214.5
Mar 1	Apr 17	3.0	12.0	7.5	352.5

APPENDIX B

Table B-9. Kellogg Forest temperature records from Oct. 1, 1973 to Oct. 15, 1974 (Suberkropp, K., KBS Pers. Comm.)

PERIOD		MIN	MAX	MEAN DAILY	DEGREE DAYS
Oct 1 to	Oct 8	10.2	16.5	13.5	94.5
Oct 8	Oct 17	12.0	17.3	14.8	133.2
Oct 17	Oct 25	7.2	11.5	9.4	75.2
Oct 25	Oct 29	-	-	10.6	42.4*
Oct 29	Nov 5	-	-	8.4	67.2*
Nov 5	Nov 13	-	-	4.1	32.8*
Nov 13	Nov 20	3.9	9.6	6.7	46.9
Nov 20	Nov 27	5.6	9.1	7.1	49.7
Nov 27	Dec 4	2.2	9.3	5.6	39.2
Dec 4	Dec 11	0.5	8.1	3.6	25.2
Dec 11	Dec 14	0.0	1.5	0.5	1.5
Dec 14	Dec 20	0.0	0.5	0.0	0.0
Dec 20	Dec 31	0.0	1.5	0.4	4.4
Dec 31	Jan 1	0.0	0.0	0.0	0.0
Jan 1	Jan 12	0.0	0.5	0.0	0.0
Jan 12	Jan 23	0.0	1.5	0.6	6.6
Jan 23	Jan 31	0.0	3.0	1.1	8.8
Jan 31	Feb 5	0.0	2.8	0.1	0.5
Feb 5	Feb 12	0.0	0.0	0.0	0.0
Feb 12	Feb 20	-	-	0.6	4.8
Feb 20	Feb 28	0.0	2.8	0.0	0.0

Table B-9. (cont.)

PERIOD		MIN	MAX	MEAN DAILY	DEGREE DAYS
Feb 28	to Mar 9	1.2	9.5	4.5	40.5
Mar 9	Mar 16	5.5	12.2	9.0	63.0
Mar 16	Mar 23	0.8	9.0	4.0	28.0
Mar 23	Apr 2	6.0	10.8	8.4	84.0
Apr 2	Apr 9	5.7	13.2	9.5	66.5
Apr 9	Apr 16	3.2	13.5	7.9	55.3
Apr 16	Apr 23	8.2	19.0	15.0	105.0
Apr 23	Apr 30	8.8	19.0	13.2	92.4
Apr 30	May 7	7.8	16.8	13.2	92.4
May 7	May 15	8.8	18.5	14.0	112.0
May 15	May 22	8.3	17.8	13.0	92.0
May 22	May 29	13.5	18.5	15.2	106.4
May 29	Jun 5	11.5	23.0	18.0	108.0
Jun 5	Jun 12	17.5	26.0	21.5	150.5
Jun 12	Jun 15	-	-	16.3	48.9*
Jun 15	Jun 28	-	-	17.8	231.4*
Jun 28	Jul 4	17.0	23.0	19.2	115.2
Jul 4	Jul 11	17.5	25.0	22.0	154.0
Jul 11	Jul 18	16.0	24.2	19.2	134.4
Jul 18	Jul 25	17.0	22.5	19.5	136.5
Jul 25	Jul 30	-	-	18.1	90.5*
Jul 30	Aug 6	16.0	21.5	19.3	135.1
Aug 6	Aug 13	14.6	20.8	17.6	123.2

Table B-9. (cont.)

PERIOD			MIN	MAX	MEAN DAILY	DEGREE DAYS
Aug 13	to	Aug 20	15.7	22.2	18.7	130.9
Aug 20		Aug 27	13.6	22.0	18.8	131.6
Aug 27		Sep 3	10.6	18.5	14.7	102.9
Sep 3		Sep 10	10.2	17.5	13.2	92.4
Sep 10		Sep 17	11.3	19.1	15.2	106.4
Sep 17		Sep 24	7.8	16.4	12.4	86.8
Sep 24		Oct 1	8.6	14.8	11.6	92.8
Oct 1		Oct 8	4.8	13.5	9.0	63.0
Oct 8		Oct 15	6.8	11.5	10.0	70.0

* Data taken from Nagel temperature records.

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Table B-10. Kellogg Forest temperature records from Oct. 24, 1974 to May 15, 1975 (Mahan, D., KBS Pers. Comm.).

PERIOD		MEAN DAILY	DEGREE DAYS
Oct 24 to	Nov 5	11.2	134.0
Nov 5	Nov 13	6.9	55.0
Nov 13	Nov 20	4.7	32.8
Nov 20	Nov 27	4.0	28.0
Nov 27	Dec 6	1.4	13.0
Dec 6	Dec 11	2.6	13.1
Dec 11	Dec 18	2.8	19.2
Dec 18	Dec 30	2.4	28.6
Dec 30	Jan 8	2.2	19.4
Jan 8	Jan 15	1.9	13.0
Jan 15	Jan 23	1.1	8.7
Jan 23	Jan 27	2.0	8.1
Jan 27	Jan 30	1.1	3.2
Jan 30	Feb 6	1.8	12.3
Feb 6	Feb 13	0.1	6.0
Feb 13	Feb 21	1.9	15.3
Feb 21	Feb 27	2.1	12.5
Feb 27	Mar 6	1.6	15.8
Mar 6	Mar 13	2.4	16.5
Mar 13	Mar 17	5.8	23.1
Mar 17	Mar 20	3.1	9.3

Table B-10. (cont.)

PERIOD	MEAN DAILY	DEGREE DAYS
Mar 20 to Mar 27	6.0	42.2
Mar 27 Apr 4	4.0	32.3
Apr 4 Apr 10	5.0	29.7
Apr 10 Apr 17	7.2	50.1
Apr 17 Apr 24	10.5	73.2
Apr 24 May 1	6.6	46.4
May 1 May 8	19.6	137.3
May 8 May 15	15.7	109.8

APPENDIX C

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Table C-1. Larval dispersion characteristics at Nagel and Kellogg Forest sites.

SITE	DATE	n	$\bar{x}$	s^2	K_1	K_2	χ^2	DISPERSION ($P > 0.05$)
NAGEL								
Spring Brook #1	9 August 1973	10	79	7588	0.8	0.7	861.2	Contagious
"	26 January 1974	6	31	470	2.2	2.1	75.0	"
"	26 March 1974	8	22	480	1.1	0.9	153.4	"
"	14 June 1974	5	18	27	21.9	21.4	6.9	Random
"	9 July 1974	3	20	82	6.6	6.8	8.1	Contagious
Spring Brook #2	28 January 1974	15	14	133	1.6	1.5	134.6	"

Table C-1. (cont.)

SITE	DATE	n	$\bar{x}$	s^2	K_1	K_2	χ^2	DISPERSION ($P > 0.05$)
Spring Brook #2	20 March 1974	18	24	1126	0.5	0.5	799.8	Contagious
"	14 June 1974	6	70	2603	1.9	1.8	349	"
"	9 July 1974	6	42	1763	1.0	0.8	212	"
"	31 July 1974	6	322	90390	1.2	1.0	1404	"
KELLOGG FOREST								
Pool #1	26 July 1973	10	12	211	0.8	0.7	153	"
Pool #2	27 July 1973	9	11	109	0.8	0.7	120	"
Pool #3	27 July 1973	8	8	98	0.7	0.6	86	"

Table C-1. (cont.)

SITE	DATE	n	$\bar{x}$	s^2	K_1	K_2	χ^2	DISPERSION ($p > 0.05$)
KELLOGG FOREST								
Pool #4	31 July 1973	14	1.9	6	0.9	0.8	39	Contagious
Pool #5	31 July 1973	13	10.5	86	1.4	1.4	99	"
Pool #6	2 August 1973	12	7.7	56	1.2	1.1	80	"
Pool #6	11 August 1973	17	8.3	61	1.3	1.2	117	"
Pool #1	31 March 1974	6	8.5	15	11.7	11.3	9	Random
Pool #1	10 April 1974	11	6.4	17	3.9	3.8	26	Contagious

Table C-1. (cont.)

SITE	DATE	n	$\bar{x}$	s^2	K_1	K_2	χ^2	DISPERSION ($p > 0.05$)
KELLOGG FOREST								
Pool #2	10 April 1974	9	5.9	18	3.0	2.8	24	Contagious
Pool #1	3 July 1974	7	34.1	1417	0.8	0.7	250	"
Pool #2	3 July 1974	8	2.5	3	9.9	9.3	9	Random
Pool #1	1 August 1974	8	2.8	3	12.5	11.8	9	"
Pool #2	1 August 1974	8	2.5	5	2.4	2.1	14	"

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Table C-2. Larval densities at Nagel and Kellogg Forest sites.

SITE	DATE	n	NUMBER / m^2	S.D.	S.E.	C.V. as %
NAGEL						
Spring Brook #1	9 August 1973	10	4869	5349	1691	110
"	26 January 1974	6	1924	1330	543	69
"	26 March 1974	8	1336	1346	476	101
"	14 June 1974	5	970	320	143	33
"	9 July 1974	3	1249	557	322	45

Table C-2. (cont.)

SITE	DATE	n	$\frac{\text{NUMBER}}{m^2}$	S.D.	S.E.	C.V. as %
NAGEL						
Spring Brook #2	26 January 1974	15	847	708	183	84
	20 March 1974	18	1470	2061	486	140
	14 June 1974	6	4288	3133	1279	73
	9 July 1974	6	2548	2578	1052	101
	31 July 1974	6	19771	18460	7536	93
KELLOGG FOREST						
Pool #1	26 July 1973	10	761	892	282	117

Table C-2. (cont.)

SITE	DATE	n	NUMBER / m^2	S.D.	S.E.	C.V. as %
KELLOGG FOREST						
Pool #2	27 July 1973	9	696	798	266	115
Pool #3	27 July 1973	8	491	607	215	124
Pool #4	31 July 1973	14	118	147	39	125
Pool #5	31 July 1973	13	642	571	159	89
Pool #6	2 August 1973	12	471	461	133	98
Pool #6	11 August 1973	17	509	479	116	94

Table C-2. (cont.)

SITE	DATE	n	$\frac{\text{NUMBER}}{m^2}$	S.D.	S.E.	C.V. AS %
KELLOGG FOREST						
Pool #1	31 March 1974	6	522	235	96	45
Pool #1	10 April 1974	11	318	241	73	65
Pool #2	10 April 1974	9	362	258	86	71
Pool #1	3 July 1974	7	2096	2311	873	110
Pool #2	3 July 1974	8	154	108	39	71
Pool #1	1 August 1974	8	169	113	40	67

Table C-2. (cont.)

SITE	DATE	n	NUMBER / m^2	S.D.	S.E.	C.V. AS %
KELLOGG FOREST						
Pool #2	1 August 1974	8	154	139	49	91

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Table C-3. Larval dry weights and ash-free dry weights at Nagel and Kellogg Forest sites.

SITE	DATE	n	LARVAL AFDW (mg)	LARVAL DRY WEIGHT (mg)	S.D.	S.E.	C.V. as %
NAGEL							
Spring Brook #1	9 August 1973	88	0.668	0.841	0.435	0.046	51
"	26 January 1974	34	1.250	1.575	0.524	0.090	33
"	26 March 1974	47	1.664	2.097	0.537	0.078	26
"	9 July 1974	27	0.103	0.130	0.050	0.010	38
Spring Brook #2	18 December 1973	26	0.787	0.992	0.260	0.051	26
"	26 January 1974	57	0.529	0.667	0.284	0.038	43

Table C-3. (cont.)

SITE	DATE	n	LARVAL AFDW (mg)	LARVAL DRY WEIGHT (mg)	S.D.	S.E.	C.V. as %
Spring Brook #2	25 March 1974	57	1.135	1.430	0.418	0.055	29
"	8 July 1974	82	0.392	0.494	0.231	0.026	47
"	31 July 1974	59	0.603	0.846	0.278	0.036	33
"	28 August 1974	51	0.702	0.885	0.393	0.055	44
"	22 February 1975	38	0.726	0.914	0.347	0.056	38
"	24 April 1975	29	1.130	1.425	0.346	0.064	24

Table C-3. (cont.)

SITE	DATE	n	LARVAL AFDW (mg)	LARVAL DRY WEIGHT (mg)	S.D.	S.E.	C.V. as %
KELLOGG FOREST	1 July 1973	27	0.699	0.882			
"	2 August 1973	46	0.826	1.041	0.362	0.053	35
"	31 March 1974	48	1.346	1.697	0.541	0.078	32
"	3 July 1974	60	0.574	0.724	0.226	0.029	31
"	1 August 1974	50	0.913	1.150	0.431	0.061	38
"	22 February 1975	22	1.256	1.583	0.780	0.166	49

APPENDIX D

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7 days	tO_1	Initial animal weights Respiration
	tF_1 Feed Changed	Respiration ATP Carbon and Nitrogen
6-14 days	tO_2	Respiration ATP Carbon and Nitrogen
	tF_2	Final animal weights Respiration ATP Carbon and Nitrogen

Respiration: 3 to 5 replicates (one/chamber) at each sampling.

ATP: 3 replications (one/chamber) of 2 subsamples each at each sampling.

Carbon and Nitrogen: 3 replicates (1/chamber) of 2 subsamples each at each sampling.

Figure 8. Outline of sampling schedule for Respiration, ATP, Carbon and Nitrogen in 5 C and 15 C feeding experiment.

APPENDIX D

Table D-1. Growth experiment data for fourth instar S. annulicrus larvae on various foods at several temperatures.

Food Type	Temperature °C	Food Incubation Period(days)	Feeding Period (days)	Initial Animal Density	Percent Mortality	RGR mg/mg/day	Percent Gain/ day
Stream detritus	5	0	11	20	15.0	-0.012	-1.1
"	5	0	11	21	4.8	-0.006	-0.6
"	5	0	11	22	0.0	-0.008	-0.8
"	5	0	11	21	0.0	-0.002	-0.2
"	5	0	11	22	4.5	-0.002	-0.2
					$\bar{X}$ = 4.9	-0.006	-0.6
					S.E.= 2.7	0.001	0.2
					C.V.%= 126.1	53.4	74.6
Stream detritus	5	14	19	16	6.3	-0.003	-0.3
"	5	14	19	18	0.0	-0.001	-0.1
"	5	14	19	22	9.1	-0.001	-0.1
"	5	14	18	18	0.0	-0.012	-1.1
"	5	14	18	18	11.1	-0.002	-0.2
					$\bar{X}$ = 5.3	-0.004	-0.3
					S.E.= 2.3	0.001	0.2
					C.V.% = 96.8	85.4	119.9

Table D-1. (cont.)

Food Type	Temperature °C	Food Incubation Period(days)	Feeding Period(days)	Initial Animal Density	Percent Mortality	RGR mg/mg/day	Percent Gain/day
Tipula sp. feces	5	14	21	16	18.8	0.008	0.9
"	5	14	21	18	16.7	0.006	0.7
"	5	14	21	16	12.4	0.009	0.9
"	5	14	20	18	5.6	0.007	0.7
"	5	14	20	19	5.3	0.018	2.2
				$\bar{x}$ =	11.8	0.010	1.1
				S.E. =	2.8	0.002	0.3
				C.V.% =	52.8	47.2	58.5
Ground Ash Leaves	5	14	18	20	5.0	0.011	1.3
"	5	14	18	22	0.0	0.011	1.3
"	5	14	18	20	5.0	0.012	1.4
"	5	14	17	19	0.0	0.012	1.3
"	5	14	17	17	5.9	0.012	1.3
				$\bar{x}$ =	3.2	0.012	1.3
				S.E. =	2.9	0.0002	0.020
				C.V.% =	92.0	3.1	3.3

Table D-1. (cont.)

Food Type	Temperature °C	Food Incubation Period(days)	Feeding Period(days)	Initial Animal Density	Percent Mortality	RGR mg/mg/day	Percent Gain/ day
"Recalcitrant" Stream detritus	15	14	13	19	10.5	-0.007	- 0.6
"	15	14	13	19	47.4	-0.013	- 1.2
"	15	14	13	20	35.0	-0.006	- 0.6
				$\bar{x}$ =	31.0	-0.009	- 0.8
				S.E.=	10.8	0.002	0.2
				C.V.% =	60.6	39.9	44.4
Stream detritus	15	14	16	20	5.0	0.017	2.0
"	15	14	16	20	30.0	0.029	3.8
"	15	14	16	20	15.0	0.022	2.7
"	15	14	15	22	9.1	0.032	4.2
"	15	14	15	22	0.0	0.025	3.0
				$\bar{x}$ =	11.8	0.025	3.1
				S.E.=	5.2	0.002	0.4
				C.V.% =	97.8	22.0	28.4

Table D-1. (cont.)

Food Type	Temperature °C	Food Incubation Period(days)	Feeding Period(days)	Initial Animal Density	Percent Mortality	RGR mg/mg/day	Percent Gain/ day
Tipula sp. feces	15	14	17	18	22.2	0.044	7.1
"	15	14	17	18	0.0	0.039	5.9
"	15	14	17	19	0.0	0.037	5.4
"	15	14	16	20	0.0	0.052	8.8
"	15	14	16	22	4.5	0.062	12.4
				$\bar{x}$ =	5.3	0.047	7.9
				S.E. =	4.3	0.004	1.3
				C.V.% =	180.0	20.3	35.6
Ground Ash Leaves	15	14	18	23		0.078	26.1
"	15	14	18	23		0.080	28.7
"	15	14	18	21		0.052	9.9
"	15	14	17	17		0.055	10.2
"	15	14	17	21		0.059	6.1
				$\bar{x}$ =		0.065	16.2
				S.E. =		0.006	4.6
				C.V.% =		20.1	64.1