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DIATOM UTILIZATION BY THE STREAM GRAZER, GLOSSOSOMA NIGRIOR (BANKS) (TRICHOPTERA:GLOSSOSOMATIDAE) IN TWO SOUTHERN MICHIGAN STREAMS

Michigan State University PH.D. 1983

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DIATOM UTILIZATION BY THE STREAM GRAZER, GLOSSOSOMA NIGRIOR (BANKS) (TRICHOPTERA:GLOSSOSOMATIDAE) IN TWO SOUTHERN MICHIGAN STREAMS

by

Mark Paul Oemke

A DISSERTATION

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ABSTRACT

DIATOM UTILIZATION BY THE STREAM GRAZER
GLOSSOSOMA NIGRIOR (BANKS) (TRICHOPTERA:GLOSSOSOMATIDAE)
IN TWO SOUTHERN MICHIGAN STREAMS

By

Mark Paul Oemke

The life history and utilization of diatoms as a food source were investigated in the larvae of Glossosoma nigrior (Banks) (Trichoptera:Glossosomatidae) in a first-order and third-order stream in southern Michigan. Five instars were determined from head capsule width measurements.

Growth of larvae fed periphyton from the two streams indicated that temperature, not diet was most significant in accounting for variability in weight gain over time. The impact of larval grazing was estimated from density estimates of larvae and diatoms. Field experiments indicated a mean gut filling time of 180 $\pm$ 40 minutes. Larvae generally ingested < 1-3% of the numerical diatom standing crop per day, although winter conditions indicated a potential maximum ingestion of 16-19% per day. The impact of grazing was most severe in the winter for both streams.

Diatom species lists were made for both streams. Diatoms surviving passage through the larval gut were identified. An assimilation efficienty of 73% was estimated for larvae feeding on natural periphyton.

Diet selection by larvae in the field, was determined to be affected by the diatom species composition. The presence of

Cocconeis placentula var. euglypta (Ehr.) Cl. increased diet selection.

Individual larval gut volumes and numbers and species of diatoms ingested by the respective instars were compared. Diatom samples were taken from natural substrates and glass slides to determine the availability of diatom species compared with the species observed in the larval gut contents. Certain diatom species were found in greater abundance within the larval guts than observed in the natural periphyton. Small, unicell diatoms were ingested more than diatoms which formed filaments or erect colonies. Comparisons of diatom species ingested against availability, indicated Cymbella sinuata Greg. was consistently ingested in preference to all other diatom species.

Glossosoma nigrior was found to be a grazer specialist, exhibiting distinct preferences for select diatom species. Preference rankings of diatom species ingested by larvae were nearly identical in a first and third-order stream. Possible consequences of selection and grazing pressure are discussed. All stream grazers should no longer be considered generalist feeders.

To Harold E. Oemke, my dad who helped me look for polliwogs each spring, and to Virginia L. Oemke, my mom who encouraged us both.

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1.0 INTRODUCTION

The Trichoptera are important stream invertebrates involved with processing both autochthonous and allochthonous materials. Previous trophic studies have analyzed the importance of trichopteran shredders (Hanna 1957, Smirnov 1962, Elliot 1971, Thorup and Iverson 1974, Iverson 1973, Anderson and Grafius 1975, Anderson 1976) trichopteran filter feeders (Rhame and Stewart 1976, McCullough et al. 1979, Wallace and Malas 1976 a,b, Mecom and Cummins 1964) predators (Thut 1969, Tachet 1965a, and 1965b) trichopteran detritivores (Cummins et al. 1973, Anderson and Sedell 1979, Minshall 1967) and trichopteran herbivores (Lehmkuhl 1970, Castro 1975, Resh 1976, Gersun 1974). Only a few studies have investigated the complex interactions between the stream flora and any stream insect grazer (Douglas 1958, Brown 1960, and 1961a,b, Castro 1975, Moore 1977a). Such few studies analyzing grazers and their periphyton food sources are surprising in that stream grazers have, perhaps, the main role in processing autochthonous production material (Anderson and Cummins 1979, Cummins and Klug 1979, Hawkins and Sedell 1981, McMahon et al. 1974, Minshall 1978, Perkins and Kaplan 1978). A detailed investigation was therefore undertaken to determine the interactions between a common stream grazer and its major food source.

If an organism scrapes indiscriminately on rock substrates, then

its food or gut contents may reflect the statement "Local conditions beget local results" (Muttkowski 1929). However, within this concept exist several unanswered questions. Are various food size categories excluded at different instars due to mouthparts to food size ratios? When fluctuations in food quantity or quality occur, what is the impact on the larval feeding strategy?

To answer these questions in a quantifiable manner it was necessary to analyze discrete food units which would remain separable and distinct from one another, and that could be manipulated experimentally and remain identifiable. Diatoms are one of the major food sources, other than detritus in many woodland streams (Cummins and Klug 1979, Minshall 1967) and usually are the major algal component (Patrick 1970), as well as being the most nutritious (McMahon et al. 1979). The silaceous valves of the diatoms often remain intact after passage through the gut and species identifications can be made on even partial remnants due to their consistent symmetry (Patrick and Reimer 1966). Diatoms therefore provided the ideal food unit for analysis of grazer periphyton interactions.

The placement of any organism in a trophic level impinges on the attempt to describe and explain why specific food is utilized by an organism rather than other available food. Factors known to influence trophic positioning include: 1) physical restrictions in food size; 2) morphology of the feeding apparatus (which will change for immatures which molt); 3) micro-habitat selection, where the organism is restricted to the range of food sources available (Cummins 1973); 4) chemical restrictions, including the presence of

toxic compounds, phagodeterrents, phagostimulants, or growth inhibitors (Gordon 1968); and 5) seasonal and temporal shifts in total food resource type and abundance. These confounding factors have led researchers to consider the same organism studied under different conditions and at different times to be a detritivore, carnivore, herbivore, or some combination of all three (Gatjen 1926, Gibbs 1963, Satija 1959a).

Aquatic stream systems may operate on a principle that would favor more generalized feeding to adapt to the fluctuating conditions found in most streams (Cummins 1973). If the caloric content and protein of available food is similar in aquatic systems, the selective preference within any type of feeding class would be rare, if the distributional properties of the food are equal. The excess time spent in selection must be compensated for by the increase in energy obtained by the selection process (House 1965). The trophic positioning of aquatic insects may depend on the general type of feeding apparatus, with specific criteria of food texture or particle size as constraints (Cummins 1973). It is possible that what may appear as an abundant food supply may in fact be essentially undesirable from a nutritional aspect, or physically restrictive in size or form for certain growth states of the herbivore.

The small trichopteran, Glossosoma nigrior (Banks) (Trichoptera: Glossosomatidae), was selected for study because of its food habits. G. nigrior larvae, recognizable by their turtle-like stone case (Wiggins 1977), occur on the surfaces of rocks and cobbles and obtain food through the scraping action of the mouthparts against the rock surfaces (Cummins 1973, 1975).

Cummins (1973) noted that G. nigrior in Linesville Creek, Pennsylvania consumed 92% diatoms and in Augusta Creek, Michigan, fed on 75% detritus. An intensive study examining all instars, conducted over seasonal changes may reveal the mechanism behind such reported discrepancies. The occurrence of G. nigrior in two streams, Spring Brook and Augusta Creek, located near to each other (Kalamazoo Co., Michigan), encouraged a comparison of the larvae's food habits between the two different streams. Spring Brook, located near Richland, Michigan, is a small, first order stream with a dense riparian vegetation which heavily shades the stream in summer. Augusta Creek, located near Gull Lake, Michigan, is a larger, third order stream which is open to sunlight in the mid-channel regions even during the summer. Analysis of diatom utilization in a first order and a third order stream should provide enough information to describe in detail specific larval-periphyton interactions for each individual stream, as well as any general grazing strategies of G. nigrior larvae common to both streams.

1.1 Objectives

The goal of this study was to determine the utilization of diatoms by larvae of G. nigrior through the larval life of the insect, in a first and third order stream. The specific ofjectives were:

1) Determination of larval growth on diets composed of different diatom species.
2) Ascertain if any larval diatom feeding preferences exist, and elucidate possible mechanisms of selection.
3) Determination of G. nigrior larval disgestive efficiency of diets composed of different diatom

species.

4) Determination of the diatom flora and the impact of larval grazing on the diatom community, including seasonal fluctuations in diatom species abundances.

2. DESCRIPTION OF THE STUDY SITES

2.1 Stream Descriptions

The interactions of G. nigrior with the available periphyton were studied in Augusta Creek, Kalamazoo Co. Michigan (TRS T.1S,R.9W). A small riffle section about 50 meters in length was chosen for intensive study. The study site was located 100 m downstream from C Ave. and was approximately 8 m wide. The riparian vegetation consisted of whorled loosestrife, Decodon verticillatus (L.) Ell., dogwood, Cornus spp., wild rose, Rosa palustris L., and several willows, Salix, spp. The shoreline vegetation did not form a closed canopy over the stream at C Ave. and permitted sunlight to penetrate throughout the year in the mid-channel. Deciduous trees along the watershed included black ash, Fraxinus nigra Marsh., American elm, Ulmus americana L., red maple, Acer rubrum L. as the dominant tree species but with associations of basswood, Tilia americana L., yellow birch, Betula lutea Michx., and several oak species, Quercus spp. (Howard 1975).

Substrate in the riffle zone consists of sand, gravel and some large cobble. Augusta Creek is a third order brook and brown trout stream (Ward and Cummins 1978). The drainage basin is 72.3 km^2 in area with a total stream length, including tributaries, of 69.3 km (Mahan and Cummins 1978). Groundwater recharge to the stream comes after percolation through soils of glacial outwash and morainic origin; Kalamazoo loam is a moderately permeable soil and contributes medium surface runoff, Oshtemo loam is moderately rapid in permeability and slow to moderate for runoff, Houghton muck is also present in low areas along the drainage basin (U.S.D.A. 1979).

Water alkalinity averages 230 mg/l $CaCO_3$ and average total hardness is 280 mg/l (Mahan and Cummins 1978). The average discharge is 1.19 m^3/s (42 cfs) and the gradient is about 1-2%. Phosphorus as PO_4 is between .001-.04 mg/l and the nitrate concentration of the groundwater is between 2-5 mg/l (Mahan and Cummins 1978).

The second stream from which organisms and algae were collected was Spring Brook, a first order stream west of Augusta Creek, also in Kalamazoo Co., Michigan (TRS T.1S, R.10W). The study site was a riffle zone located 100 m south from C Ave., on private land. The stream is about 1.5 m wide and the banks are densely covered with overhanging vegetation of (dogwood, Cornus sp., several willows, Salix spp., and large clumps of grasses and sedges). The riparian vegetation completely covers the stream in the summer permitting little light to penetrate to the streambed.

Substrate consists of large cobble and rocks embedded in deposits of clay. Large amounts of sand are present as are occasional pieces of peat dislodged from adjacent marshland. The plants of the stream include water cress, Nasturtium officinale R.Br., and a moss which grows attached to rocks (Family Hypnaceae). The drainage basin is 27.2 km^2 in area. The surrounding soils consist of Spinks loamy sand, which is rapidly permeable to water and contributes little surface runoff, Oshtemo sandy loam, which is moderately rapid in permeability and may contribute slow to rapid runoff depending of the slope of the land bordering the stream. Houghton muck, is also present in low marshy areas along the stream basin (U.S.D.A. 1979).

Water alkalinity averages 190 mg/l $CaCO_3$ and total hardness is 220 mg/l. The discharge ranged from .13-.15m^3/s (4.7-5.3 cfs) and

the velocity between .89 - 1.02 m/s. The discharge is very uniform throughout the year because of the groundwater supplied to the stream from nearby springs, and the limit of surface runoff due to the nature of the surrounding soils.

Temperature readings were taken each week for Augusta Creek during the sampling period. The average temperature was below 25°C (77°F) in the summer and ranged from 0°C to 30°C (32°F-86°F). Spring Brook temperature was monitored daily with a tricorder equipped with a temperature sensor for the ambient air temperature, a sensor for the water temperature of the stream, and a sensor for the temperature of the stream substrate. Air temperature ranged from -5° to 94°F (Appendix Figure A-1), water temperatures averaged approximately 51°F and ranged from 28°F-62°F (Appendix Figure A-2), substrate averaged 48°F and ranged 30°f-62°F (Appendix Figure A-3).

3.0 BIOLOGY OF G. NIGRIOR (BANKS)

3.1 METHODS

3.1.1 Qualitative sampling of larvae

The most efficient sampling method to obtain large numbers of G. nigrior larvae was to remove randomly selected rocks and cobbles and remove all visible larvae. The larvae, which often cling with considerable force to the rock faces, did not often become dislodged with this technique. Samples were taken across each stream's riffle zone to insure an adequate collection of larvae in different regions of

the riffle. Larvae were placed immediately in 75% ethanol and 5% formalin mixture for quick fixing of the tissues and the algae of the gut contents. The advantages of this procedure are that it is very fast, does not disrupt the habitat if the stones are replaced, and can therefore be done often. Samples were taken weekly from June through October and at least monthly from November through May using this method.

3.1.2 Quantitative sampling

Many researchers have discussed the importance of sampling both in regards to use of devices, as well as to timing of sample collections (Hynes 1970,Elliot 1971, Resh 1974, Merritt and Cummins 1981). Sampling intervals were thus shorter during periods of larval changes either in growth or in density (Resh 1979) to correlate with changes in periphyton density and species composition changes.

The depth of the water in the riffle zones plus the current speeds indicated a stovepipe corer (Merritt and Cummins 1978) would be best suited for the study areas. Two plexiglas stovepipe samplers were used. A 24.5 cm diameter pipe was used to collect from Augusta Creek, and 14.25 cm pipe was used to sample from the smaller Spring Brook. Samples were taken across randomly chosen transects of each stream's riffle area to combine organism density estimates from the edges with density estimates from mid-channel. The sampler was twisted into the stream bed substrate and all rocks, gravel, and sediments removed to a depth of 10 cm. Sample water was removed from the sampler pipe and poured through a plankton net (mesh size=40 microns) to assure

retention of early instars. All material was preserved in the field with 70% ethyl alcohol and 5% formalin and returned to the lab for sorting under a dissection microscope.

Laboratory sorting was done under 10 x magnification for coarse substrates and at 40 x magnification, when sorting sand and sediments for early instars.

Emergence traps covering .25 m^2 of stream bottom were used to estimate timing and densities of adult emergence (May to November 1978). The tent-shaped traps were .25 m^2 at the base and approximately 1.5 m in height. The sides of the trap were covered with nylon window screen (mesh = 1.5 mm) with a door on one side for removal of specimens. The top of each trap was covered with 12 cm wide piece of wood to provide shelter for the adults during rain. The nylon mesh sides extended below the water surface but allowed water to flow under the trap (Anderson and Wold 1972). Traps were placed in riffle areas at each stream where the substrate was gravel, rocks and small rubble. Insects were collected weekly.

3.1.3 Morphometric data

A general investigation into the biology of G. nigrior was necessary to understand the temporal distribution of the larval stages, relative instar weights, mouthpart structure and function, and gut measurements. These areas of study were essential to aid in understanding the interactions of G. nigrior organism, at any one life stage, with its food sources.

G. nigrior larvae collected from the field in both qualitative and quantitative samples were measured with a Zeiss dissection microscope fitted with an ocular micrometer. Magnification was at 40X for larger instars, and 100X for small instars. Measurements were taken of larval head capsule widths collected from both streams to the nearest .5 ocular unit (.006 or .01 mm.). This represented a precision of 2-5%.

Selected specimens were retained from qualitative collections for mouthpart examinations. Several heads were removed from specimens for S.E.M. examination. These heads were transferred from the field fixitive and placed in absolute ethyl alcohol. Heads were mounted intact on S.E.M. stubs and air dried. Individual mouthparts were removed from other specimens and then similarly treated.

Larvae and pupae were collected from both Spring Brook and Augusta Creek for dry weight measurements. The larvae were killed with carbonated soda water to prevent regurgitation of gut contents, and oven dried at 60°C for 24h then placed in a dessicator until weighed. All specimens were weighed on a Cahn Model 21 electrobalance.

Each individual larval gut was measured at the time of dissection with a Zeiss microscope fitted with an ocular micrometer. The total length of the excised gut was measured, from behind the proventriculus to a point just behind the insertion of the malpighian tubules. The width of the gut was measured at the widest part, immediately posterior to the proventriculus. The gut volume for each individual was then calculated based on the approximation of the gut to a cylinder, using the measurements of gut length and gut width (Trama 1957).

Additional individual measurements of volume of gut contents were also made after removing the gut wall from the actual gut

contents. A more accurate measurement of volume of gut contents was then calculated using anterior, mid, and posterior widths of the gut contents. The volume of the contents was then calculated using the formula for the volume of two conic sections, which were then summed to give the total gut contents volume.

3.2 Diel Feeding Analysis

G. nigrior larvae were collected every four hours from Spring Brook for a 24 hour period to determine feeding activity patterns. Each group of larvae was immediately killed in carbonated water to prevent regurgitation and placed in 75% ethyl alcohol to preserve gut contents. Gut examination was made immediately after return to the lab. The length of the gut filled with food was compared to the total length of the gut (Resh 1976, Mecom 1970) to determine the percent of the gut filled.

3.1.5 Field Ingestion Rates

Determination of gut filling times was measured in Spring Brook. Two dyes were used, Methylene Blue and Basic Fuschin. The dyes were mixed in concentrated form and poured slowly over naturally occurring periphyton on the rocks temporarily removed from the stream bed. The rocks were selected on the basis of adequate periphyton growth and also, the presence of populations of G. nigrior. After allowing several minutes for the dye to penetrate the periphyton, the rocks were lowered back into the stream. Larvae were then collected from the treated rock

surfaces every 15 minutes over a 3 hour period. Comparing the total length of time an individual had been exposed to the periphyton with the length of the gut filled with unstained periphyton, an approximate gut filling time was estimated (Cummins 1973).

3.2.3 Gut Emptying Times

Groups of field collected larvae were transferred to aerated bowls without food. Larvae were removed every 3-4h and the percent of the gut filled was estimated by comparing the length of the gut filled with food to the total length of the gut.

3.1.7 Dry Weights and Ash Free Dry Weights of Feces

V instars and IV instars (28 and 86 respectively) were collected from Spring Brook and 46 IV-V instars were collected from Augusta Creek in April, 1981. Larvae were removed from their cases and transferred to jars containing filtered stream water. After 1.5 hrs. the larvae were removed and the water and feces filtered through a .4 micron millipore membrane filter to remove the fecal material. The filters were placed in a drying oven at 60°C for 24 hrs. The fecal material was then carefully scraped from the filters unto preweighed foil squares and weighed on a Cahn ®, Model 21 electrobalance. The material was then ashed at 500°C for 90 minutes and returned to a dessicator before ash free dry weight determinations were made (Conover 1966).

3.2 RESULTS

3.2.1 Instar Analysis

Table 1 shows the distribution of larvae by head widths. Five instar groupings appear distingushable. Most caddis flies have five larval instars (Lepneva 1964) and work by Cummins (unpub.) has indicated that the number of instars for G. nigrior is five. When the growth differences, as determined from head width measures, are compared between instars, an average growth ration of 1.4336 between instars is apparent. Head width calculations based on Dyar's Law (Dyar 1890) using the average growth ratio closely predicted the measured head width values for later instars (Table 2). Dyar's law states that the linear dimension of the head capsule in lepidoptera larvae is a nearly constant factor, and that no further widening of the head capsule occurs between molts. Although this rule is a generalization and many exceptions to this "law" occur, there is some validity in using the calculations to compare against actual measures if careful interpretation is followed (Ghent 1956). Comparisons of actual measurements against those calculated by using Dryar's growth ratio indicated close agreement between actual instar head widths and those predicted by Dyar's law.

3.2.2 Temporal Distribution

Combining the data from all larval quantitative samples across time with the data from the qualitative samples, a complete instar

Table 1. Measured head capsule widths for G. nigrior larvae collected from Spring Brook and Augusta Creek.

	Head width (mm)	Number of Spring Brook larvae	Number of Augusta Creek larvae	Total number measured
Instar	.135	1		
	.138	1		
I	. 14	16		52
	.145	17	3	
	.150	12	1	
	.155	1		
	.180	1	1	
	.193	3	3	
II	.205	7	9	46
	.218	5	1	
	.230	11	3	
	.250	2		
	.285	20		
	.298	22		
III	.310	57	17	153
	.323	5	18	
	.335	3	10	
	.410	7	2	
	.440	26	11	
IV	.453	12	4	117
	.465	23	19	
	.478	2	2	
	.490	1	8	
	.540		4	
	.565	18	7	
V	.590	46	12	182
	.615	36	13	
	. 64	14	14	
	.665		12	
	.690		6	

Table 2. Head capsule widths for all larvae by instar [combined S.B. & A.C. Data].

Instar	n	mean head width	ratio next instar head width to current instar head width	calculated head width using Dyar's Law (A.G.R.=1.4336)	% error (actual vs Dyar)
I	52	.1444	1.4785		
II	46	.2135	1.4468	.2070	3.04
III	153	.3089	1.4681	.2968	3.92
IV	117	.4535	1.3409	.4254	6.20
V	182	.6081		.6099	0.30
	550				

Average Growth Ratio = (A.G.R.) 1.4336

distribution over time can be drawn. The number of larvae measured for instar group separation was 1,376 for Augusta Creek and 3,618 for Spring Brook. First instars were most abundant in the fall of the year for both streams, while fifth instars appeared in maximal number in December and May (Figures 1 and 2). The instar distributions indicate a bivoltine population with pupation in early spring and in late fall. The presence of the first instars in December of 1978 for Spring Brook suggests a potential egg diapause of unknown length. This is not unexpected, since Anderson and Bourne (1974) found that eggs collected from Agepetus bifidus Denning, (Glossosomatidae) in August did not hatch until the following March.

Adult emergence occurred between May 12, 1978 and June 2, 1978 for Augusta Creek. This approximately four week flight period contrasts to an emergence period between May 18, 1978 and August 18, 1978 for Spring Brook. Minshall (1968) found a short adult flight period for Glossosoma intermedium Klap. and a lengthy larval period, while Ulfstrand (1968) found a long adult flight period, a short larval period (all had pupated by November), and a long pupal stage. Anderson and Bourne (1974) and Anderson and Wold (1972) determined an overlaping bivoltine population for Glossosoma penitum Banks.

Cummins (1975) recorded a bivoltine G. nigrior population with a winter generation and a summer generation. The winter generation in Augusta Creek and Spring Brook had more early instars, which show peak percentages of the total larval population in September for both streams (Figures 1 and 2).

3.2.3 Density Measurements

Figure 1. Percent abundances by instar and by month for Augusta Creek.

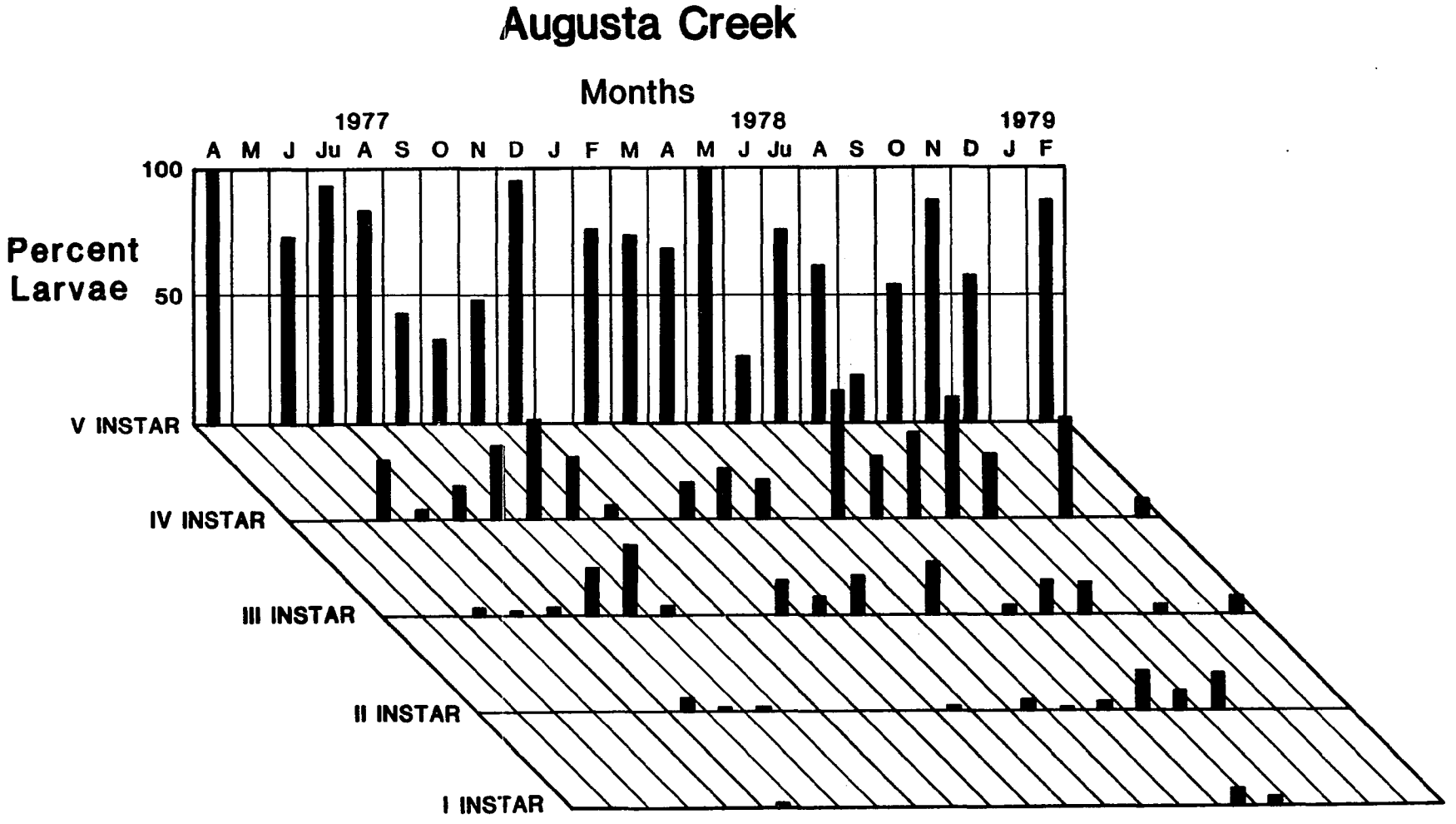
Augusta Creek
Months
1977
1978
1979
A M J Ju A S O N D J F M A M J Ju A S O N D J F
100
Percent Larvae
50
V INSTAR
IV INSTAR
III INSTAR
II INSTAR
I INSTAR

Figure 1.

Figure 2. Percent abundances by instar and by month for Spring Brook.

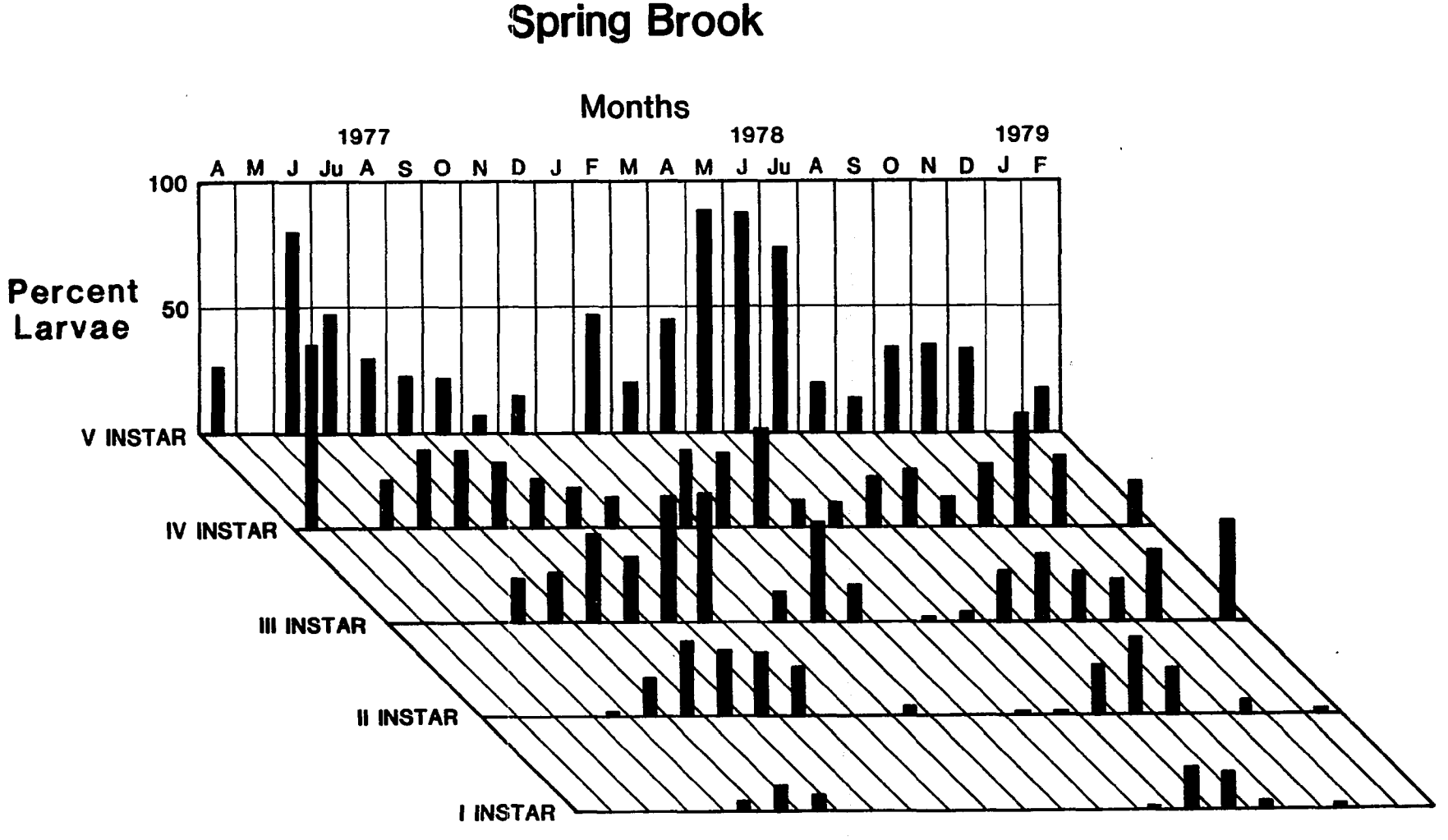
Spring Brook
Months
1977
1978
1979
A M J Ju A S O N D J F M A M J Ju A S O N D J F
100
50
Percent Larvae
V INSTAR
IV INSTAR
III INSTAR
II INSTAR
I INSTAR

Figure 2.

The estimation of population densities in each stream was based on 42 quantitative benthic samples. Average population densities were higher in Spring Brook (724.76 $\pm$ 121.65/m^2) than in Augusta Creek (97.26 $\pm$ 23.43/m^2) (Table 3). The density of summer-growing larvae and pupae is 566.04/m^2 for Spring Brook which is roughly 50% of the winter population density (1,090.14/m^2). Augusta Creek densities with estimates are 42.55 and 219.86 /m^2 respectively for the summer and winter samples (collected on July 8, 1978 and February 22, 1979) (Table 3). Instar specific and pupal densities (Table 4) averaged over all sampling periods indicated a sampling bias in estimating I-II instar densities from Spring Brook and in estimating I-II-III instars from Augusta Creek. Elliott (1971) used D, as an estimate of precision in sampling, where D represents the standard error expressed as a proportion of the mean, D = S.E/x. The usual 'tolerated' precision for running water bottom samples should be between 10 and 40% or D = 0.10 to 0.40 (Cummins 1975). The precision estimates (Table 4) fall below the 40% level except for those age specific distributions which are not common during all sampling periods, namely the I-II instars and pupae. This sampling bias is based on a sampling interval that over estimates larval growth stages that are of longer duration and are present during a greater proportion of the life cycle. The total densitites of combined life states (Table 3) show a greater precision (D less than 25% for Augusta Creek and 17% for Spring Brook). The population of G. nigrior larvae is approximately eight times greater in the smaller Spring Brook stream than in Augusta Creek (Table 3).

3.2.4 Description of the Mouthparts

Table 3. Total G. nigrior density estimates by sample date (based on combined instar and pupal counts n = number of samples).

	SPRING BROOK				AUGUSTA CREEK		
Date	n	X (#/m^2)	S.E.	D(S.E./X)	n	X(#/m^2)	S.E.	D(S.E./X)
March	3	649.8	317.24	.4881	3	99.3	18.76	.1890
April	3	566.0	297.22	.5251	3	156.0	83.61	.5359
May	3	251.5	130.92	.5204	3	42.6	12.27	.2887
July	3	566.0	288.21	.5092	3	42.6	12.27	.2887
October	3	1,069.1	36.31	.0340	3	56.7	18.76	.3307
Nov	3	880.5	412.42	.4684	3	63.8	21.28	.3333
Feb	3	1,090.1	545.07	.5000	3	219.9	127.86	.5815
Total mean average	21	724.8	121.65	.1678	21	97.3	23.43	.2408

Table 4. Age specific instar densities for Spring brook and Augusta Creek. Based on combined quantitative samples (n=21)

	SPRING BROOK					
	INSTAR					
	I	II	III	IV	V	Pupae
$X(\#/m^2)$	8.9659	53.7956	230.6100	218.6289	152.7421	57.5346
$S.E.(\#/m^2)$	8.9659	18.7968	64.5708	45.6497	31.7704	28.7443
$D(^{s.e}/x)$	1.0000	.3490	.2800	.2088	.2080	.4996
	AUGUSTA CREEK					
$X(\#/m^2)$	1.0128	3.0404	8.1064	17.2234	30.3957	36.4745
$S.E(\#/m^2)$	1.0128	2.2198	4.2745	6.3348	9.1187	13.8640
$D(^{s.e}/x)$	1.0000	.7301	.5273	.3678	.3000	.3801

Very few investigators have examined in detail the feeding mechanism of the organism they were studying for trophic analysis. Notable exceptions include the work by Brown (1960, 1961) on mayflies and Satija (1959a, 1959b) and Wallace and Malas (1976) on trichoptera.

The labrum of G. nigrior is covered ventrally with dense rows of stout brush-like setae. These brushes are clustered at the distal tip of the labrum, some of which appear as star shaped clusters, particularly near the lateral edges of the labrum (Figure 3-4). The labrum, equipped with these brushes, apparently functions as a scraping tool to remove the tightly attached diatoms and algae upon which the larvae feed. More proximal brushes, located ventrally on the labrum, all point or bend posteriorly into the preoral cavity. These may serve to prevent material which has been removed by the tip of the labrum from being dislodged or moving out of the mouth cavity.

The mandibles operate together, with one fitting inside of the other to remove the algae from the opposite mandible, at the same time moving the food posteriorly into the esophageal opening (Figure 3-3). The esophagus opens directly at the base of the mandibles. The anterior edge of the mandibles is scoop shaped, perhaps to aid in holding more dislodged material (Figure 3-6). The ventral side of each mandible has a shearing edge which probably serves as a cutting blade to remove algae or stalked diatoms. The mandibles are also equipped with specialized setae (Figure 3-6). One group of evenly spaced long setae extend mesally from the base. These may serve as a net when overlapped with those from the opposite mandible (Figure 3-3) to keep clumps of detached algae from falling out of the mouth cavity while allowing mineral particles or sand grains through. The other set of

Figure 3 - 1) Lateral view of head and mouthparts of G. nigrior larva (X 100).

2) Dorsal view of head of G. nigrior larva with mandibles extended (X 100).

3) Dorsal view of inner mouthparts with labrum excised showing the long setae at the bases of the left and right mandible, and the numerous setae located at the tip of the labial complex (X 225)

4) Antero-ventral view of labrum, showing extensive setal clusters or brushes (X 300).

5) Close view of long setae which extend from the base of the scooped out portion of the mandible (X 1500).

6) Ventral view of left mandible, showing the two groups of long setae arising from the base of the mandibular scoop and along the mesal edge (X 450).

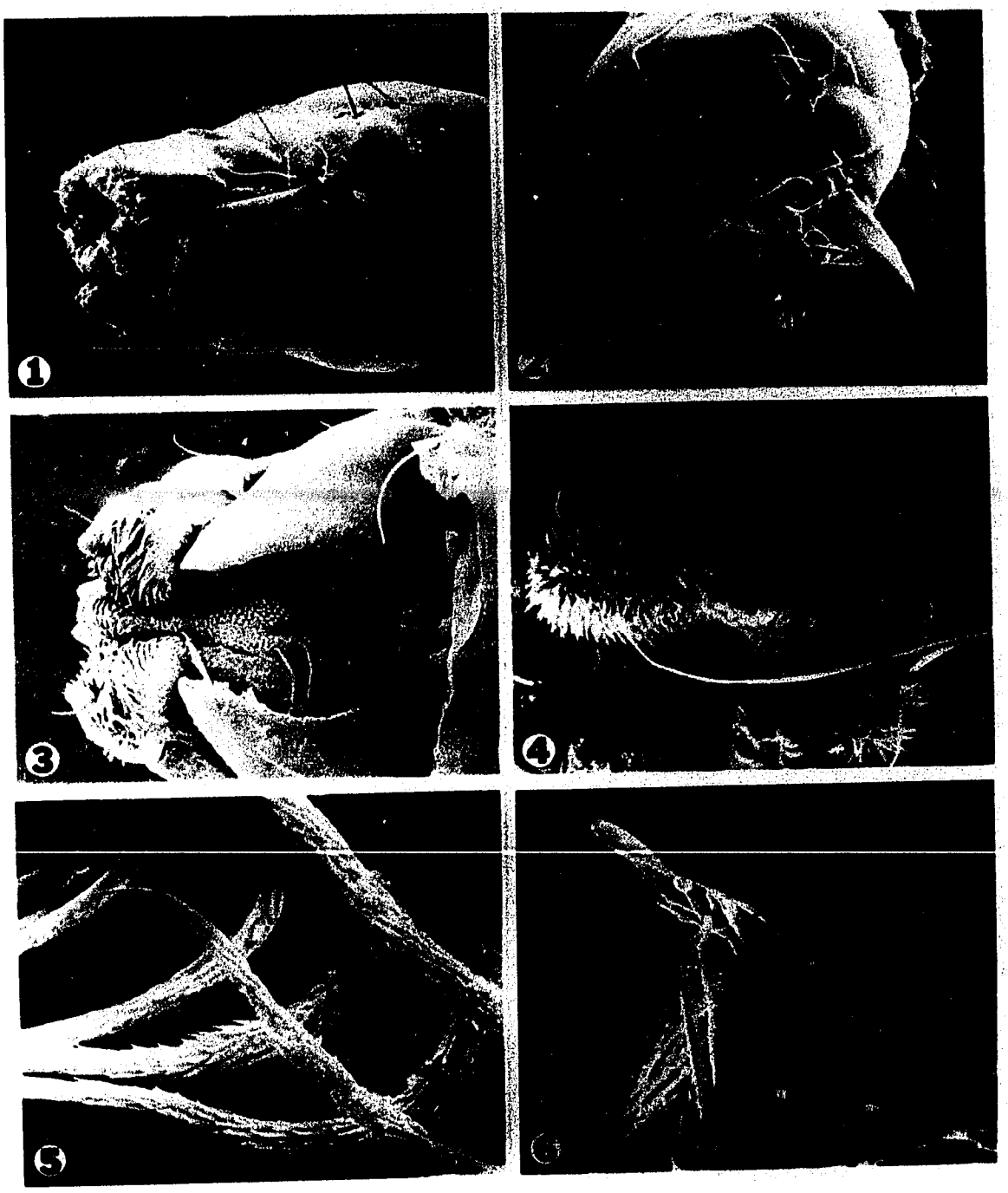

Figure 3.

mandibular setae emerges from the base of the scoop portion of each mandible (Figure 3-6). These setae may aid in cleaning the mandible of food and assist in removing food adhering to the ventral setae of the labrum.

The maxillae, labium, and hypopharynx are united as a large complex similar to that found in caterpillar larvae (Snodgrass 1935). This complex serves as a base against which the labrum and mandibles can sweep, scrape, and remove small food particles effectively. The somewhat angular profile to the entire ventral mouthpart complex allows the larvae to feed with the head held in a near vertical position, while remaining sheltered by the overhanging stone case. This feeding style and predator protection permits G. nigrior (MacKay and Wiggins 1979) to feed actively throughout the day. This feeding operation is very efficient, as evidenced by the ingestion of diatom species considered unharvestable by other grazing organisms because of strong adherence to the substrate or small cell size (see section 5).

The silk forming labial glands open through a duct located on the median lobe between the terminal lobes of the maxillae. The hypopharynx is fused with a small prementum (Snodgrass 1935). Labial palpi are represented by a pair of small papillae located at the sides of the spinneret. The function of the fused labium, maxillae, and hypopharynx is probably involved with silk spinning for case construction, and for support against which the mandibles and labrum can press for food removal and to aid in food transport into the esophagus. The dorsal surface of this combined structure is also covered with posteriorly directed setae (Figure 3-3).

3.2.2 Gut Filling and Gut Emptying

The length of time for larvae to completely eliminate their gut contents ranged from 7 to 10 days (Table 5). Because of the long time interval necessary to void the gut, larvae were held at least 8 days without food before attempting to establish a rate of gut filling. Moore (1975) determined a 1 day gut emptying time at 15°C and 3 days at 5°C for Asellus aquaticus L. and 18h and 40h for Gammarus pulex L. at the same temperatures. Zimmerman and Wissing (1978) determined gut-loading times of 12.48 to 4.11 h at 5°-20°C and gut-emptying times of 12.9 to 5.01 h for Hexagenia limbata Serville. Cummins (1975) estimates that most aquatic herbivores have a gut loading time between 2-12 hours. Cummins (1973) indicates gut loading times of 8 to 24 hours for Neophylax oligius Ross and 4 to 8 hours for Hydropsyche betteni Ross. The gut filling time for G. nigrior appears to be between 3 and 7 hours from laboratory studies (Table 6), although appreciable gut filling occurs even at 10°C after 2 hours. The gut loading time in Table 6 reflects the rate for starved larvae. The possible dispersion of gut contents within such larvae raises questions as to the measurements of the percent of gut filled, as these relate to factors of gut contents compression, which depend upon the amounts of water and food present. A more precise measurement technique, using a colored food source, was introduced to larvae grazing in the streams under natural conditions. The length of gut filled with the colored food was compared to total gut length over time (Cummins 1973, Zimmerman and Wissing 1978). Regression calculations using the mean values indicate a time of 180.30 $\pm$ 46.91 (X, 95% CL $P < .001$) minutes

Table 5. Relative proportion of gut remaining filled after G. nigrior larvae held without food.

Temp.	n	Proportion filled (± S.E.)	Time (hrs)
20°C	7	0.41 ± .12	19
20°C	7	0.29 ± .08	67
10°C	8	0.67 ± .06	24
10°C	7	0.22 ± .06	72
10°C	5	0.13 ± .04	120
10°C	7	0.01 ± .007	240

Table 6. Proportion of gut filled after starved larvae of G. nigrior exposed to food.

Temp(°C)	n	Proportion filled (X ± S.E.)	Time(hrs)
10°	9	.32 ± .058	1
	7	.63 ± .052	2
	9	.92 ± .043	4
	6	.98 ± .017	6
20°	5	.75 ± .107	3

for 100% of the food material in the gut, to be the red color of basic fuschin (R^2 = .97) and a time of 150.51 $\pm$ 41.80 (X, 95% CL P < .001) minutes for methylene blue (R^2 = .91), (Figure 4).

Larval field feeding habits were examined over a 24h period to determine if G. nigrior fed as most herbivores, with constant feeding, or if certain periods of the day were used. Field collections made every four hours and subsequent gut analysis indicated that feeding was continous. 95% confidence intervals show .83 to .95 of the gut is filled with food at any one time over a 24 hour period (Table 7).

3.2.6 Feces Weights

Weight measurements of the feces collected from IV and V instar larvae from Spring Brook and Augusta Creek, based on total weight of feces collected and calculated per individual over time, indicate the likely ranges for egestion rates between these instars (Table 8). The IV instars collected from Spring Brook contribute aboute 20% the amount contributed by V instars fecal production.

To understand the efficiency of digestion in a relative fashion a comparison of the dry weights to ash-free dry weights of feces was made. This method used by Conover (1966), while underestimating the losses of certain dissolved organics in the feces, nevertheless gives comparable results with other more complex assimilation measurement techniques (Hargrave 1970). The method uses the differences in dry weight to A.F.D.W. ratios between food and feces to determine assimilation efficiencies. The organic content of the feces was

Figure 4. a) Percent of gut filled over time by larvae feeding on Fuschin stained periphyton in the stream ($\bar{x} \pm$ S.D).

b) Percent of gut filled over time by larvae feeding on Methyl blue stained periphyton in the stream ($\bar{x} \pm$ S.D).

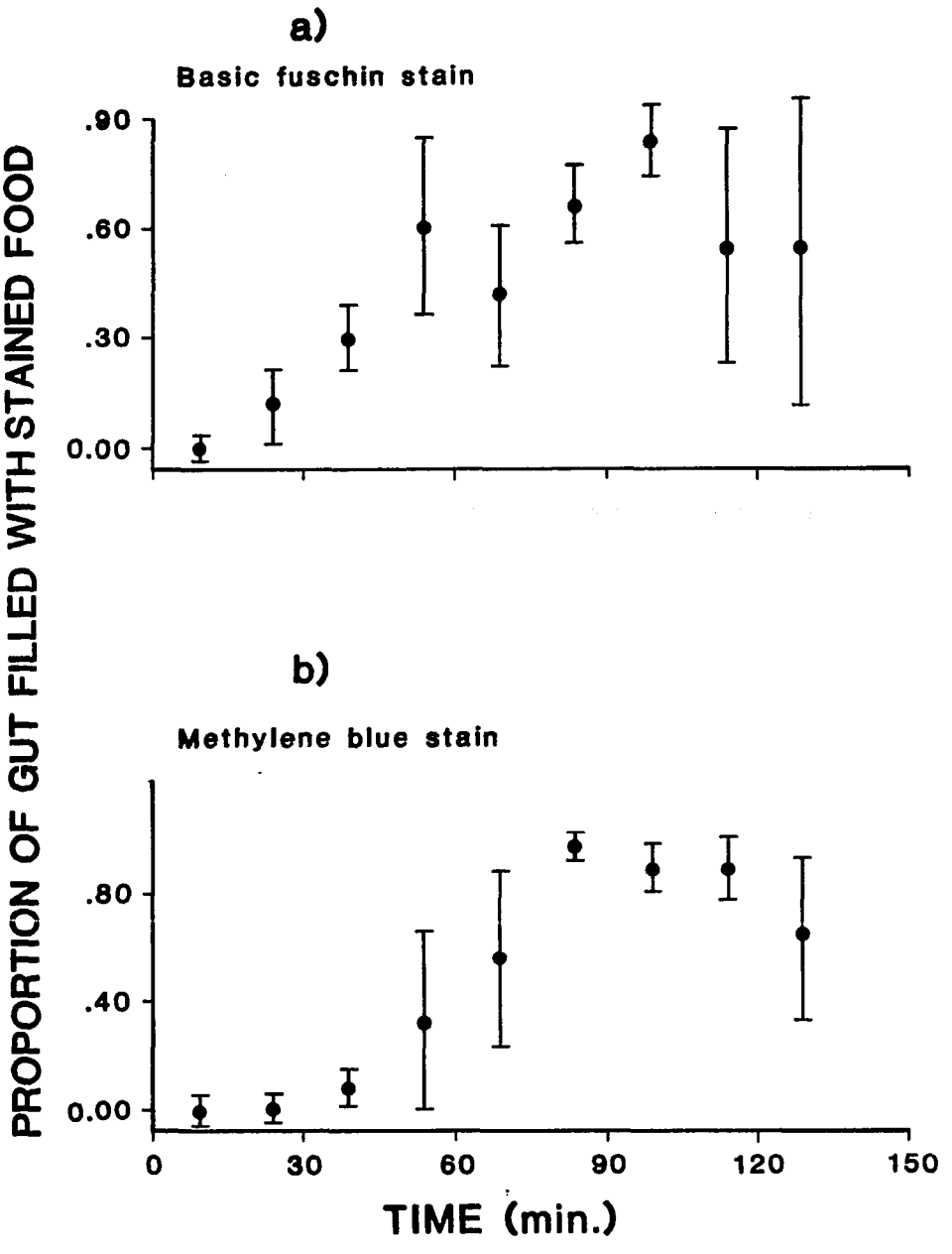
a)
Basic fuschin stain
.90
.60
.30
0.00
b)
Methylene blue stain
.80
.40
0.00
PROPORTION OF GUT FILLED WITH STAINED FOOD
0
30
60
90
120
150
TIME (min.)

Figure 4.

Table 7. Proportion of gut filled, for larvae collected in the field over 24 hour period (X ± S.E.) (Time 0 = noon)

Time(h)	n	Percent gut filled
0	20	0.90 ± .06
4	18	0.90 ± .05
8	15	0.80 ± .06
12	19	0.88 ± .04
16	15	0.86 ± .05
24	17	0.98 ± .01

Table 8. Egestion rates for G. nigrior IV and V instar larvae from Spring Brook and Augusta Creek (Based on feces total dry weights obtained after 1.5 calculated per individual)

Stream	Instar	n	Egestion Rate mg feces/1.5h	Egestion Rate mg feces X lar^{-1} X d^{-1}
Spring Brook	V	28	.185	2.960
Augusta Creek	IV-V	46	.171	2.728

similar between streams, and between IV and V instars larvae averaging between 49-50% (Table 9).

3.2.7 Gut Volumes

Spring Brook V instar larvae show the lowest gut volumes in December of 1977, May 1978, and November of 1978 (Figure 5, Appendix Table A-1). This reduction in gut volume may reflect the period of gut emptying prior to forming the pupal case. At this time the gut was flattened by extensive fat bodies formed along its length. The times of maximum gut volumes preceed these periods and represent the large amount of food consumed by the final instar before pupation. Gut volumes for V instars at Spring Brook were greatest in July and October 1977 and July and September 1978 (Figure 5). A November decrease in gut volume is shown for IV and III instars also (Figure 5). Generally gut volumes appear greatest in the summer and early fall periods, and lowest in early to late winter. Data from Augusta Creek larvae indicate March-April-May as well as September-October as times of peak gut volumes (Appendix Table A-2 and Figure 5). Lowest gut volumes were reached in February-March for IV and III instars, and December and June-July for V instars. Augusta Creek IV and V instar gut volumes were significantly larger than those from Spring Brook (Table 10).

3.2.8 *G. nigrior* Larval and Pupal Weights

Larvae from Spring Brook and Augusta Creek were collected in September and November 1978 and dry weights determined (Appendix,

Table 9. Dry weights and A.F.D.W. of IV and V instar G. nigrior feces.

Stream	Instar	Feces total dry weight (mg)	Feces total A.F.D.W. (mg)	Feces total A.F.D.W.% D.W.
S.B.	V[1]	5.192	2.666	.5135
S.B.	V[2]	3.511	1.656	.4716
A.C.	IV-V[3]	7.842	3.848	.4907

[1]Based on 28 larvae

[2]Based on 86 larvae

[3]Based on 46 larvae

Figure 5. Gut volumes for III-V instars by sample date for Spring Brook (left side) and Augusta Creek (right side).

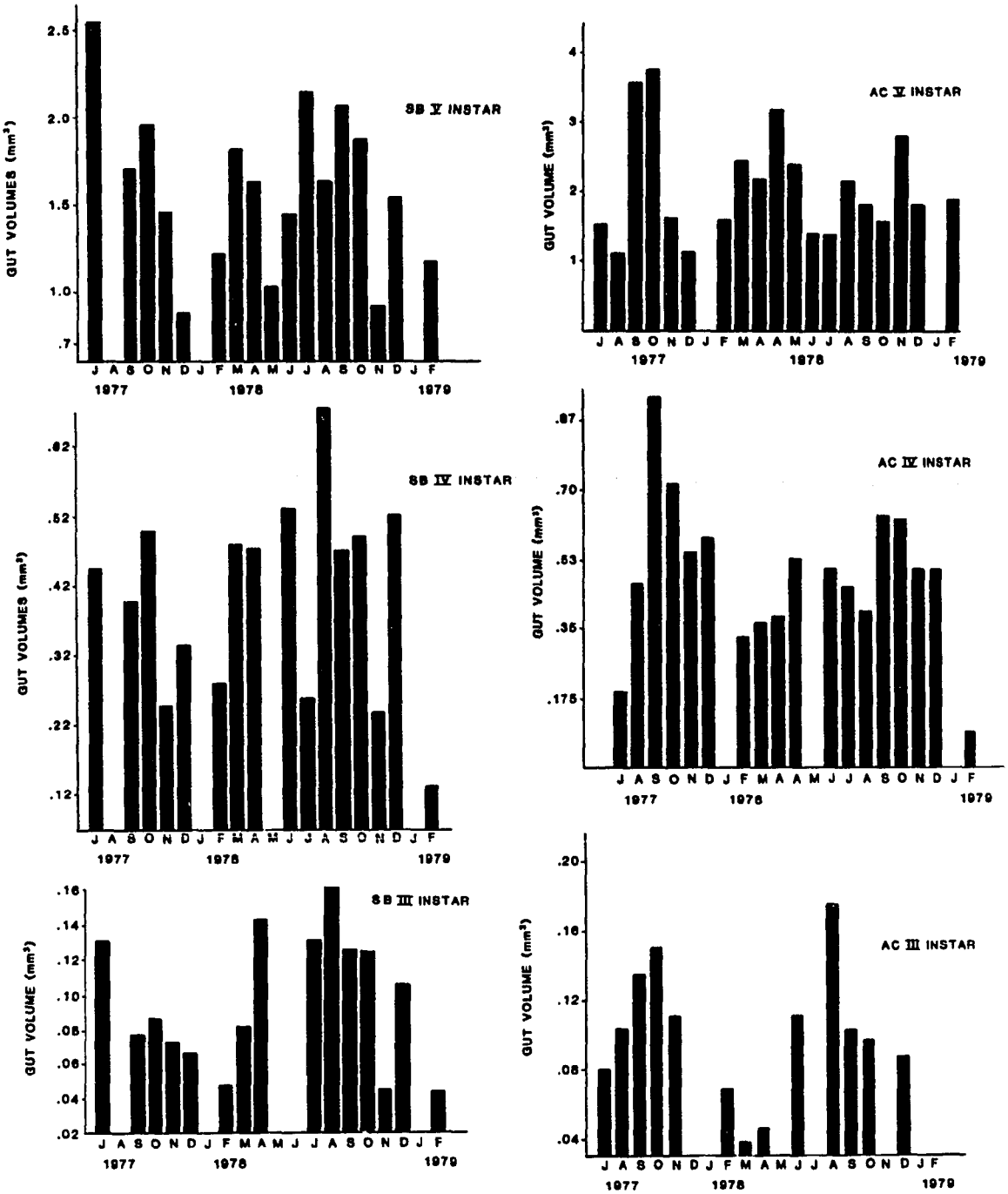
SB V INSTAR
AC V INSTAR
SB IV INSTAR
AC IV INSTAR
SB III INSTAR
AC III INSTAR
GUT VOLUMES (mm³)
GUT VOLUME (mm³)
J A S O N D J F M A M J J A S O N D J F
1977
1978
1979

Figure 5.

Table 10. Gut volume comparison for I-V instars from Spring Brook and Augusta Creek (X ± S.E.)[1]

	Instar	n	Gut volume (mm^3)
Spring Brook	V[2]	128	1.55 ± .07
	IV[3]	111	0.433 ± .032
	III	77	0.094 ± .006
	II	44	0.027 ± .002
	I	33	0.0095 ± .0009
Augusta Creek	V	95	1.98 ± .12
	IV	65	0.542 ± .031
	III	46	0.111 ± .007
	II	11	0.022 ± .002
	I	2	0.0089 ± .0015

[1] Based on larvae collected from July 1977 to Feb. 1979 total 393 from S.B. and 219 from A.C.

[2] Significant difference from A.C., (t-test, $p < 0.01$)

[3] Significant difference from A.C., (t-test, $p < 0.05$)

Table A-3). Pupae were collected from both sites in November 1978. Augusta Creek V instars and pupae were significantly heavier than those from Spring Brook ($P < .001$) (Figure 6).

4.0 DIATOM STUDIES

4.1 METHODS

4.1.1 Qualitative Samples

The most accurate method for assessing the diatom species present was to remove periphyton from natural substrates. Several investigators have commented on the localization by diatom species in specified micro-habitats on the rock face, in regards to current flows, and light penentration (Butcher 1946, Blum 1956, Jones 1951, Roff 1969). Care was taken therefore to collect areas from the front and back faces of stones, as well as the sides and tops. This method assures the maximum number of species enumerated from the total species universe present, as well as providing the best estimates of relative dominance (Sladeckova 1962). Scrapings were made from the tops of rocks where larvae were also collected for later gut analysis. This was repeated several times to insure adequate representation of major diatom species. The top surface of the stone was scraped with a knife blade, the stone turned upside down and the surface rinsed with distilled water from a squeeze bottle. The runoff containing the algal specimens was collected by holding a container under the rock. Final qualitative analysis to determine the availability of particular diatom

Figure 6. Growth curve based on the mean instar specific dry weights for Spring Brook and Augusta Creek ($\pm$ S.E.) curves were fitted by eye.

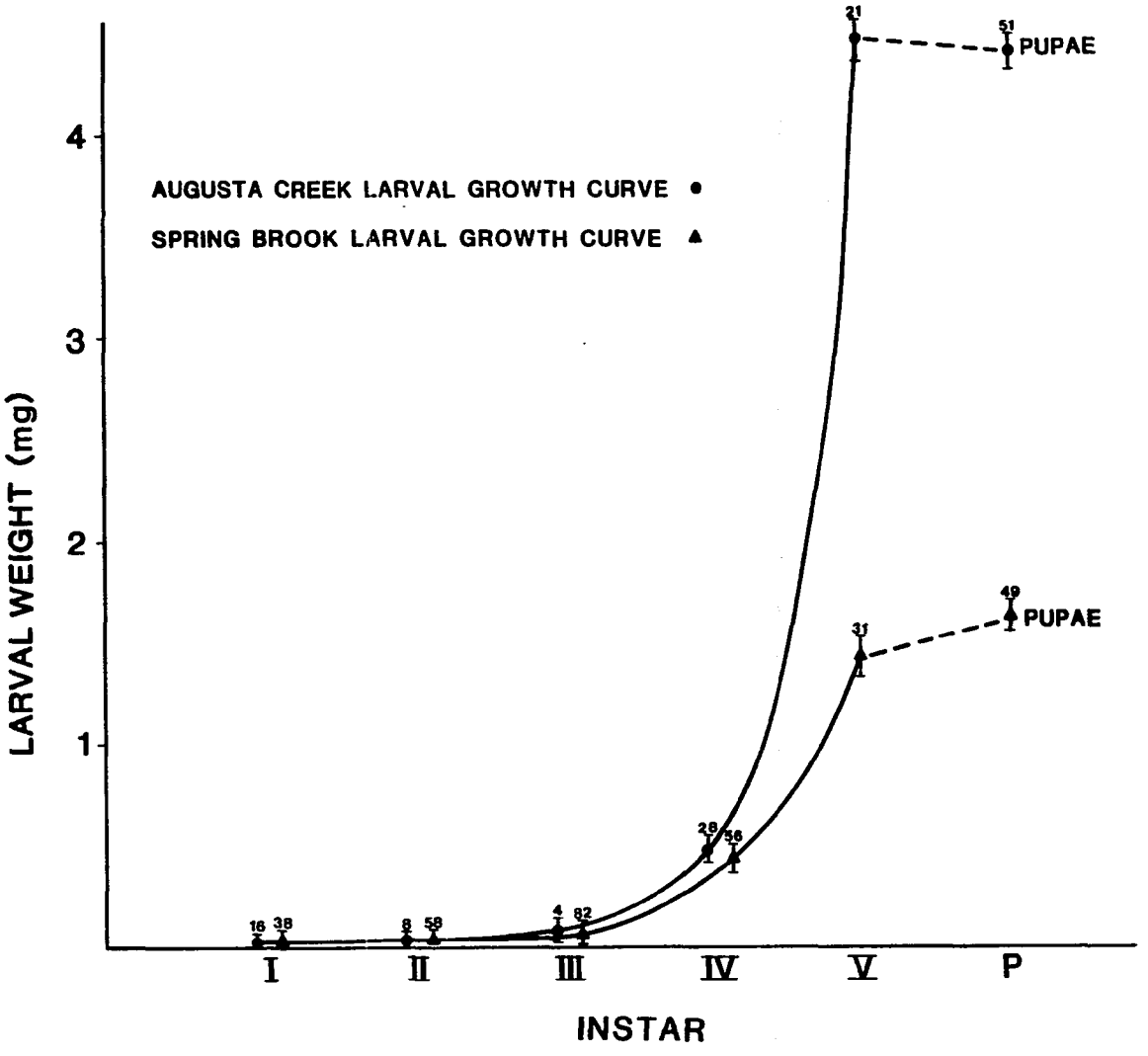
AUGUSTA CREEK LARVAL GROWTH CURVE ●
SPRING BROOK LARVAL GROWTH CURVE ▲
LARVAL WEIGHT (mg)
4
3
2
1
21
51
PUPAE
49
PUPAE
31
28
36
4
82
8
58
16
38
I
II
III
IV
V
P
INSTAR

Figure 6.

species was performed by combining at least five individual samples together and subsampling the resulting composite sample.

4.1.2 Quantitative sampling

Glass slides are commonly used by researchers for quantitative studies and density estimates of available diatom species (McMahon, et al. 1974, Patrick et al. 1954, Sladecek and Sladeckova 1964, Hohn and Hellerman 1963, Withford and Schumacher 1963, Dillard 1971).

Glass slides were placed on the tops of bricks, held with ruber bands and placed on the stream bed. This horizontal placement allows a periphytic biomass similar to natural substrates (Castenholz 1961). Samples were removed from the slides with a razor blade. This method is known to be quantitatively accurate (Wetzel and Westlake 1969) and diatom density per unit area of glass slide cleaned can then be extrapolated to calculate measurements of cell volumes or cell weights per unit area.

Other quantitative algal collections were taken with a device modified from Loeb (1981), consisting of two 60 cc. syringes. The scraping syringe with the tip section removed and a scraping brush attached to the plunger would be placed against a rock surface and the plunger twisted down and rotated to remove the attached algae. The plunger would then be withdrawn, aspirating the removed algae and water into the chamber of the syringe. The collection syringe, attached to the side of the scraping syringe, could then remove a sample from the scraping syringe with little loss of water or sample material. This technique allowed precise measurement of a given area of natural

4.1.3 Slide Preparation

Diatom taxonomy is based on the sculpturing on the siliceous cell wall. Proper identifications require that the inner organic material be removed so that critical cell wall features can be observed.

The Aufwuchs and epilithic periphyton from qualitative and quantitative samples were treated with 27% hydrogen peroxide and the addition of a small quantity of potassium dichromate. The resulting exothermic reaction sufficiently oxidizes the organic material. After dilutions with distilled water and repeated settlings, a small quantity of the cleaned frustrules was mounted in Hyrax (refractive index 1.71). Occasional quantitative samples were prepared by a burning method, utilizing a hot plate set at 500-600°C to oxidize the organic material within the diatoms. This method is less vigorous than peroxide cleaning and allows more fragile forms and colonial groups to remain intact. From each quantitative sample 1 ml portions were transferred to 22 mm^2 glass coverslips, and then placed on the hot plate until the organics were volatilized. Additional portions were added until sufficient valves were present for an accurate count. After the specimens were cleaned a Hyrax mount was prepared.

4.1.4 Quantitative Density Determinations

Density measurements were made from diatom collections made from known substrate areas. Counts and species determinations were made at 1600 X magnification on a Leitz Ortholux microscope using brightfield and phase-contrast illumination. An oil immersion fluorite objective

(N.A. 1.32) and a phase contrast objective (N.A. 1.32) were used. Approximately 250-350 valves were identified and tabulated from each quantitative sample to insure that correct proportions of the major diatom species populations were determined. The counts were made along a randomly selected transect on the coverslip until sufficient numbers had been counted. Additional slides were scanned for rare taxa to complete the diatom species' lists. The field area for each objective was calculated using a stage micrometer and multiplied by the length of the transect measured to determine the precise area examined. The density of cells/mm^2 of substrate area (for total diatom density or for individual species density) was calculated according to the formula:

$$\text{Density} = \text{Number of cells counted} \times \frac{\text{Total Area of Coverslip}}{\text{Area Counted}} \times \frac{\text{Total Volume Periphyton Sample}}{\text{Volume of Subsample on Coverslip}} \times \frac{1}{\text{Substrate Area Sampled}}$$

4.1.5 Diatom Species Abundances

Qualitative and quantitative diatom collections were examined and the relative percent of each species was determined as a proportion of the total number of cells counted. Chi-squared test of preliminary data were conducted to determine the correct number of cells that should be counted for correct percent diatom species' abundances. Nine preliminary comparisons were made covering five sampling periods and 12,290 diatoms were counted and identified. The test compared the relative percentages obtained from counting 50, 100, 200, 300, 500,

1000, and 2000 diatoms. Eight of nine comparisons indicated no significant differences at the 95% level between the major diatom species abundances as determined from counts of 200-300 cells against counts of 2,000 cells. This agrees with the results of Moore and Beamish (1973) in the number of cells necessary to count and identify before accurate species abundances could be determined (250-300 cells). All slide counts of diatom species abundances therefore ennumerated between 200 and 350 individual diatom cells.

4.1.6 Diatom Volume Measurements

The relative contribution of an individual diatom species to the diet of G. nigrior can be estimated by converting cell numbers to cell volumes. This prevents a very small, but numerous diatom species like Achananthes linearis from appearing numerically dominant in the gut of G. nigrior or in the periphyton, while occupying a small volumetric percent of the total gut contents or substrate area, compared to other larger diatom species.

Volume determinations were calculated from length, width, and depth measurements of major diatoms at 1600 X magnification. In most cases, depth was determined from measurements made of diatom cells resting in girdle view. Appropriate geometric solids formulae were then used, based on the shape of the diatom (Findenegg 1969). Volumes of diatom species of irregular shape like Meridion circulare (Grev.) Agardh var. circulare were calculated using the closest geometric shape, in this case a truncated cone with two parts. Other species volumes were calculated using the formulae for spheres, cones,

cylinders, pyramids, or frustums. Although some volumetric calculations on diatom species currently exist (Nalewajko 1966, Nauwerck 1963, Moore 1974), the volume differences of the same diatom species from different waters and at different times of the year (Findenegg 1969) made individual cell volume measurements necessary. Several individuals of each major species were measured and volumes calculated to provide a range of representative volumes.

4.1.7 Periphyton Dry Weight and Ash Free Dry Weight

The periphyton from artificial substrates removed from both streams was oven dried (60°C for 24h) for dry weight determinations. Dry weight samples were placed in preweighed foil packets and ashed at (550°C for 1h) and reweighed for ash free dry weight measurements.

4.2 RESULTS

4.2.1 Augusta Creek and Spring Brook Flora

A total of 159 total taxa were identified from the Augusta Creek diatom flora, representing 27 genera (Table 11).

A total of 134 total taxa were identified from the Spring Brook diatom flora from June 1977 to February 1979 (Table 12). A total of 55 distinct diatom species were only found in Augusta Creek and 30 taxa were only found in Spring Brook (Table 13). Six more species of Navicula and four more species of Cymbella were identified from the Augusta Creek samples. The genera Eunotia, Hantzschia, and Rhopalodia

Table 11. List of the Diatom Flora from Augusta Creek.

Achnanthes affinis Grun. var. affinis
clevei Grun. var. clevei
clevei var. rostrata Hust.
conspicua A. Mayer var. conspicua
deflexa Reim. var. deflexa
exigua Grun. var. exigua
exigua var. heterovalva Krasske
hungarica (Grun.) Grun. var. hungarica
lanceolata (Bréb.) Grun. var. lanceolata
lanceolata var. apiculata Patr.
lanceolata var. dubia Grun.
lanceolata var. omissa Reim.
latissima A. Cleve var. latissima
lemmermanni Hust var. lemmermanni
linearis (W.Sm.) Grun. var. linearis
linearis f. curta H.L.Sm.
minutissima Kütz. var. minutissima
rupestris Krasske var. rupestris
stewartii Patr. var. stewartii
wellsiae Reim. var. wellsiae
sp. 6
sp. 7

Amphora ovalis (Kütz.) Kütz. var. ovalis
ovalis var. libyca (Ehr.)Cl.
ovalis var. pediculus (Kütz.)V.H. ex DeT.
perpusilla (Grun.) Grun. var. perpusilla
sp. 3

Asterionella formosa Hass. var. formosa

Caloneis bacillaris var. thermalis (Grun.) A.Cl.
ventricosa var. minuta (Grun.) Patr.
sp. 2

Cocconeis diminuta Pant. var. diminuta
disculus (Schum.) Cl. var. disculus
pediculus Ehr. var. pediculus
placentula Ehr. var. placentula
placentula var. euglypta (Ehr.) Cl.
placentula var. lineata (Ehr.) V.H.
sp. 2
sp. 3
sp. 4

Cyclotella comta (Ehr.)Kütz. var. comta
meneghiniana Kütz. var. meneghiniana

Cymatopleura solea (Bréb.)W.Sm. var. solea

Cymbella affinis Kütz. var. affinis
aspera (Ehr.)H. Perag. var. aspera

Table 11. (continued)

	hybrida Grun.ex Cl.var. hybrida
	mexicana (Ehr.) Cl. var. mexicana
	mexicana var. janischii (A.S.)Reim.
	microcephala Grun. var. microcephala
	minuta var. silesiaca (Bleisch ex Rabh.) Reim.
Cymbella	prostrata (Berk.)Cl. var. prostrata
	sinuata Greg. var. sinuata
	sinuata f. antiqua (Grun.) Reim
	tumida (Bréb.)V.H. var. tumida
	tumidula Grun. ex A.S. var. tumidula
Diatoma	anceps (Ehr.) Kirchn. var. anceps
	tenue var. elongatum Lyngb.
	vulgare Bory var. vulgare
	vulgare var. linearis V.H.
Diploneis	interrupta (Kütz.)Cl. var. interrupta
	oblongella (Naig. ex Kütz) var. oblongella
Eunotia	curvata (Kütz.) Lagerst. var. curvata
Fragilaria	brevistriata Grun. var. brevistriata
	brevistriata var. capitata Hérib.
	brevistriata var. inflata (Pant.) Hust.
	construens (Ehr.) Grun. var. construens
	leptostauron (Ehr.)Hust. var. leptostauron
	leptostauron var. dubia (Grun.)Hust.
	vaucheriae (Kütz.)Peters var. vaucheriae
	virescens Ralfs var. virescens
Frustulia	rhomboides (Ehr.) DeT. var. rhomboides
	vulgaris (Thwaites)DeT.var. vulgaris
Gomphonema	acuminatum Ehr. var. acuminatum
	affine Kütz. var. affine
	affine var. insigne (Greg.) Andrews
	angustatum (Kütz.)Rabh. var. angustatum
	angustatum var. citera (Hohn & Hellerm.) Patr.
	dichotomum Kütz. var. dichotomum
	gracile Ehr. emend V.H. var. gracile
	grunowii Patr. var. grunowii
	insigne var. subclavatiformis Mayer
	olivaceum (Lyngb.) Kütz. var. olivaceum
	olivaceum var. calcarea (Cl.)Cl.
	parvulum (Kütz.)var. parvulum
	sphaerophorum Ehr. var. sphaerophorum
	tenellum Kütz. var. tenellum
	ventricosum Greg. var. ventricosum
	sp. 2
	sp. 5

Table 11. (continued)

Gyrosigma attenuatum (Kütz.)Rabh. var. attenuatum

Hantzschia amphioxys var. maior Grun.

Melosira varians Ag. var. varians

Meridion circulare (Grev.)Ag. var. circulare
circulare var. constrictum (Ralfs)V.H.

Navicula bacillum Ehr. var. bacillum
cryptocephala Kütz. var. cryptocephala
cryptocephala var. veneta (Kütz.)Rabh.
cuspidata (Kütz.)Kütz. var. cuspidata
decussis Ostr. var. decussis

Navicula graciloides Mayer var. graciloides
lagerstedtii Cl. var. lagerstedtii
lanceolata (Agardh)Kütz. var. lanceolata
menisculus bar. upsaliensis (Grun.)Grun.
minnewaukonensis Elm. var. minnewaukonensis
oblonga Kütz. var. oblonga
pelliculosa (Bréb. ex Kütz.) Hilse var. pelliculosa
pseudoreinhardtii Patr. var. pseudoreinhardtii
pseudoscutiformis Hust. var. pseudoscutiformis
pupula Kütz. var. pupula
pupula var. elliptica Hust.
pupula var. rectangularis (Greg.)Grun.
radiosa Kütz. var. radiosa
radiosa var. parva Wallace
radiosa var. tenella (Bréb. ex Kütz.)
reinhardtii (Grun.)Grun. var. reinhardtii
rhynchocephala Kütz. var. rhynchocephala
salinarum var. intermedia (Grun.)Cl.
scutelloides W.Sm. ex Greg. var. scutelloides
seminulum Grun. var. seminulum
subhamulata var. undulata Hust.
subrhynchocephala Hust. var. subrhynchocephala
tantula Hust. var. tantula
tripunctata (O.F.Mull)Bory var. tripunctata
tripunctata var. schizonemoides (V.H.) Patr.
viridula (Kütz.)Kütz. emend. V.H. var. viridula
viridula var. avenacea (Bréb.)V.H.
viridula var. linearis Hust.
viridula var. rostellata (Kütz.) Cl.
sp. 5
sp. 6

Neidium dubium (Ehr.)Cl. var. dubium
iridis var. ampliatum (Ehr.)Cl.

Nitzschia acicularis W.Sm. var. acicularis

Table 11. (continued)

amphibia Grun. var. amphibia
apiculata (Greg.) Grun. var. apiculata
capitellata Hust. var. capitellata
dissipata (Kütz.)Grun. var. dissipata
fonticola Grun. var. fonticola
frustulum Kütz. var. frustulum
heufleriana Grun. var. heufleriana
kutzingiana Hilse. var. kutzingiana
linearis (W.Sm.) var. linearis
palea (Kütz.)W.Sm. var. palea
sigmoidea (Ehr.)W.Sm. var. sigmoidea
thermalis var. minor Hilse

Opephora martyi Hérib. var. martyi

Rhoicosphenia curvata (Kütz.)Grun. var. curvata

Rhopalodia gibba var. ventricosa (Ehr.)Grun.

Stauroneis smithii Grun. var. smithii

Surirella angusta Kütz. var. angusta
linearis W.Sm. var. linearis
linearis var. helvetica (Brun.)Meister
ovata Kütz. var. ovata

Synedra goulardi Bréb var. goulardi
parasitica W.Sm. var. parasitica
parasitica var. subconstricta Grun.
rumpens var. familiaris (Kütz.)Hust.
ulna (Nitz.)Ehr. var. ulna
ulna var. contracta Ostr.

Table 12. List of the Diatom Flora from Spring Brook.

Achnanthes affinis Grun. var. affinis
clevei Grun. var. clevei
clevei var. rostrata Hust.
conspicua A.Mayer var. conspicua
deflexa Reim. var. deflexa
exigua Grun. var. exigua
hauckiana Grun. var. hauckiana
hauckiana var. rostrata Schulz.
hungarica (Grun.)Grun. var. hungarica
lanceolata (Bréb.)Grun. var. lanceolata
lanceolata var. apiculata Patr.
lanceolata var. dubia Grun.
lanceolata var. lanceolatoides (Sov.)Reim.
lanceolata var. omissa Reim.
linearis (W.Sm.)Grun. var. linearis
linearis f. curta H.L.Sm.
marginulata Grun. var. marginulata
minutissima Kütz. var. minutissima
peragalli var. fossilis Temp. & Perag.
rupestris Krasske var. rupestris
wellsiae Reim. var. wellsiae
sp. 1
sp. 2
sp. 3

Amphora hemicyla Stoerm. & Yang var. hemicyla
perpusilla (Grun.)Grun. var. perpusilla
sp. 1
sp. 2

Asterionella formosa Hass. var. formosa

Caloneis bacillaris var. thermalis (Grun.)A.Cl.

Cocconeis diminuta Pant. var. diminuta
pediculus Ehr. var. pediculus
placentula Ehr. var. placentula
placentula var. euglypta (Ehr.)Cl.
placentula var. lineata

Cyclotella kutzingiana Thwaites var. kutzingiana
meneghiniana Kütz. var. meneghiniana

Cymatopleura solea (Bréb.) W.Sm. var. solea

Cymbella angustata (W.Sm.)Cl. var. angustata
microcephala Grun. var. microcephala
minuta var. silesiaca (Bleisch ex Rabh.)Patr.
sinuata Greg. var. sinuata
sinuata f. antiqua (Grun.) Reim.
subaequalis Grun. var. subaequalis
tumidula Grun. var. tumidula
sp. 3

Table 12. (continued)

Diatoma hiemale var. mesodon (Ehr.)Grun.
tenue var. elongatum Lyngb.
vulgare Bory var. vulgare

Diploneis oblongella (Naig. ex Kütz.) var. oblongella

Fragilaria brevistriata var. inflata (Pant.)Hust.
construens var. venter (Ehr.)Grun.
leptostauron var. dubia (Grun.)Hust.
pinnata Ehr. var. pinnata
vaucheriae (Kütz.)Peters var. vaucheriae

Frustulia vulgaris (Thwaites)DeT. var. vulgaris

Gomphonema acuminatum Ehr. var. acuminatum
affine Kütz. var. affine
angustatum (Kütz.)Rabh. var. angustatum
angustatum var. citera (Hohn & Hellerm.) Patr.
dichotomum Kütz. var. dichotomum
gracile Ehr. emend V.H. var. gracile
instabilis Hohn & Hellerm. var. instabilis
olivaceum (Lyngb.)Kutz. var. olivaceum
olivaceum var. calcarea (Cl.)Cl.
parvulum (Kütz.) var. parvulum
subclavatum (Grun.)Grun. var. subclavatum
subclavatum var. commutatum (Grun.) A.Mayer
tenellum Kütz. var. tenellum
truncatum Ehr. var. truncatum

Gyrosigma sciotense (Sulliv. & Wormley)Cl. var. sciotense

Melosira varians Ag. var. varians

Meridion circulare (Grev.)Ag. var. circulare
circulare var. constrictum (Ralfs)V.H.

Navicula amphibola Cl. var. amphibola
bergenensis Hohn var. bergenensis
bryophila Østr. var. bryophila
capitata Ehr. var. capitata
cryptocephala Kütz. var. cryptocephala
cryptocephala var. veneta (Kütz.)Rabh.
decussis Østr. var. decussis
elginensis (Greg.)Ralfs var. elginensis
graciloides Mayer var. graciloides
integra (W.Sm.)Ralfs var. integra
lagerstedtii Cl. var. lagerstedtii
lanceolata (Agardh)Kütz. var. lanceolata
minnewaukonensis Elm. var. minnewaukonensis
nigrii DeNotaris var. nigrii
oblonga Kütz. var. oblonga

Navicula pseudoscutiformis Hust. var. pseudoscutiformis

Table 12. (continued)

pupula var. rectangularis (Greg.)Grun.
radiosa Kütz. var. radiosa
radiosa var. parva Wallace
radiosa var. tenella (Bréb. ex Kütz.)
reinhardtii (Grun.)Grun. var. reinhardtii
rhynchocephala Kütz. var. rhynchocephala
salinarum var. intermedia (Grun.)Cl.
scutelloides W.Sm. ex Greg. var. scutelloides
tripunctata (O.F. Mull)Bory var. tripunctata
viridula (Kütz.)Kütz. emend. V.H. var. viridula
viridula var. avenacea (Bréb.)V.H.
sp. 5
sp. 6
sp. 7

Neidium binode (Ehr.)Hust. var. binode

Nitzschia acicularis W.Sm. var. acicularis
amphibia Grun. var. amphibia
angustata (W.Sm.)Grun. var. angustata
apiculata (Greg.)Grun. var. apiculata
dissipata (Kütz.)Grun. var. dissipata
fonticola Grun. var. fonticola
frustulum Kütz. var. frustulum
heufleriana Grun. var. heufleriana
kutzingiana Hilse. var. kutzingiana
linearis (W.Sm.) var. linearis
obtusa W.Sm. var. obtusa
palea (Kütz.)W.Sm. var. palea
tropica Hust. var. tropica

Opephora martyi Hérib. var. martyi

Pinnularia viridis var. minor Cl.

Rhoicosphenia curvata (Kütz.) Grun. var. curvata

Stauroneis smithii Grun. var. smithii

Stephanodiscus astraea var. minutula

Surirella ovata Kütz. var. ovata
linearis W.Sm. var. linearis

Synedra goulardi Bréb. var. goulardi
parasitica var. subconstricta Grun.
rumpens var. familiaris (Kütz.)Hust.
socia Wallace var. socia
ulna (Nitz.)Ehr. var. ulna
ulna var. contracta Østr.
sp. 1
sp. 2

Table 13. List of Diatom taxa found only in August Creek or only in Spring Brook.

Augusta Creek	Spring Brook
Achnanthes exigua v. heterovalva	Achnanthes hauckiana
A. latissima	A. hauckiana v. rostrata
A. lemmermanni	A. lanceolata v. lanceolatoides
A. stewartii	A. marginulata
	A. peragalli v. fossilis
Amphora ovalis	Amphora hemicycla
A. ovalis v. libyca	
A. ovalis v. pediculus	
Caloneis ventricosa v. minuta	
Cocconeis disculus	
Cyclotella comta	Cyclotella kutzingiana
Cymbella affinis	Cymbella angustata
C. aspera	C. subaequalis
C. hybrida	
C. mexicana	
C. mexicana v. janischii	
C. prostrata	
C. tumida	
Diatoma anceps	Diatoma hiemale v. mesodon
D. vulgare v. linearis	
Diploneis interrupta	
* Eunotia curvata	
Fragilaria brevistriata v. capitata	Fragilaria pinnata
F. leptostauron	
F. virescens	
Frustulia rhomboides	
Gomphonema affine v. insigne	Gomphonema instabilis
G. grunowii	G. subclavatum
G. insigne v. subclavatiforme	G. subclavatum v. commutatum
G. sphaerophorum	G. truncatum
G. ventricosum	
Gyrosigma attenuatum	Gyrosigma sciotense
* Hantzschia amphioxys v. maior	

Table 13. (continued)

Augusta Creek	Spring Brook
Navicula bacillum	Navicula amphibola
N. cuspidata	N. bergenensis
N. menisculus v. upsaliensis	N. bryophila
N. pelliculosa	N. capitata
N. pseudoreinhardtii	N. elginensis
N. pupula v. pupula	N. integra
N. pupula v. elliptica	N. nigrii
Navicula seminulum	
N. subhamulata v. undulata	
N. subrhynchocephala	
N. tantula	
N. tripunctata v. schizonemoides	
N. viridula v. linearis	
N. viridula v. rostellata	
Neidium dubium	Neidium binode
N. iridis v. ampliatum	
Nitzschia capitellata	Nitzschia angustata
N. sigmoidea	N. obtusa
N. thermalis v. minor	N. tropica
* Rhopalodia gibba v. ventricosa	Pinnularia viridis v. minor
	* Stephanodiscus astraea v. minutula
Surirella linearis v. helvetica	
S. angusta	
Synedra parasitica	Synedra socia
Total 55	Total 30

* genera which were not recorded from both streams

were not found in Spring Brook samples, while the genus Stephanodiscus was absent from Augusta Creek samples examined.

4.2.2 Diatom Species Availabilities

The relative percents of Achanthes spp. show the importance of this group as a constituent of the total diatom community both in Spring Brook and in Augusta Creek (Figure 7). Achnanthes affinis accounted for 58% of the diatom community in late April 1978 in Augusta Creek, and 38% in December. Achnanthes linearis accounted for 42% on December, 1977 and 35% on September, 1978 for Augusta Creek. The Achnanthes spp. in Spring Brook, while major contributors, never accounted for more than 38% per individual species (Achnanthes affinis 38% on November 1978 and Achnanthes lanceolata 37% on September 1977). Cocconeis placentula var. euglypta showed an October 1978 maximum of 73% for Spring Brook. The same diatom in Augusta Creek reached peak abundance levels in mid summer through early fall; 40% in July 1977, 63% and 48% in July and August 1978. Cymbella sinuata were less than 2% of the total diatoms throughout the study at Spring Brook and less than 6% in Augusta Creek. The winter diatom community appeared dominated by various Gomphonema spp. for both Spring Brook and Augusta Creek, as reflected by the high percentage of G. olivaceum in February and April,(28-35% in Spring Brook and 43-70% for February and March in Augusta Creek). The colonial diatom, Meridion circulare showed a rapid rise in dominance in February, March, and April for Spring Brook, reaching a maximum level of 65%. M. circulare showed a similar pattern in Augusta Creek although accounting for only 7-12% of the total diatom

Figure 7. Relative percent abundances for selected major diatom species by sample date for Spring Brook and Augusta Creek.

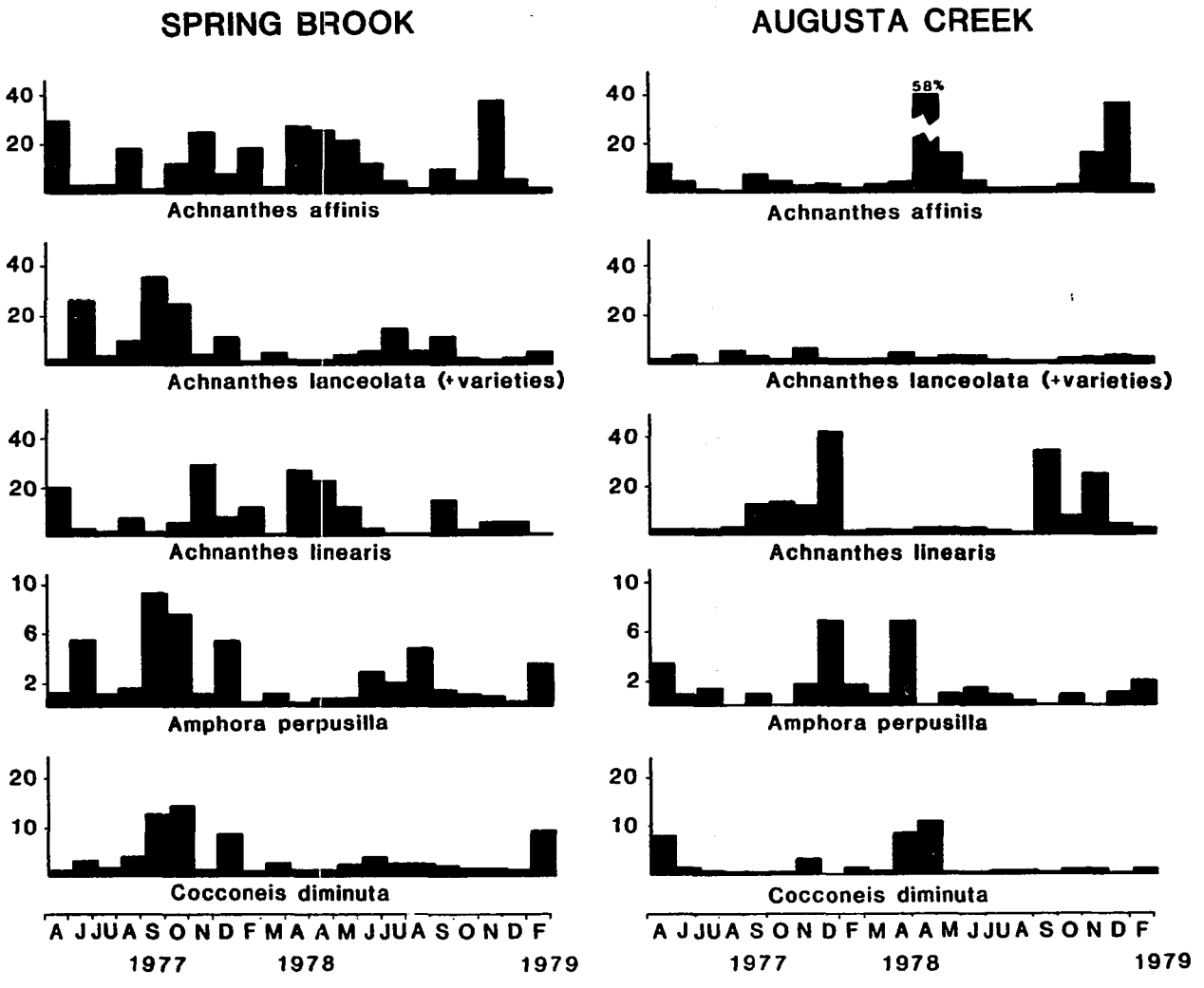
SPRING BROOK
AUGUSTA CREEK
40
20
58%
Achnanthes affinis
Achnanthes lanceolata (+varieties)
Achnanthes linearis
10
6
2
Amphora perpusilla
Cocconeis diminuta
A J J U A S O N D F M A A M J J U A S O N D F
1977
1978
1979

Figure 7.

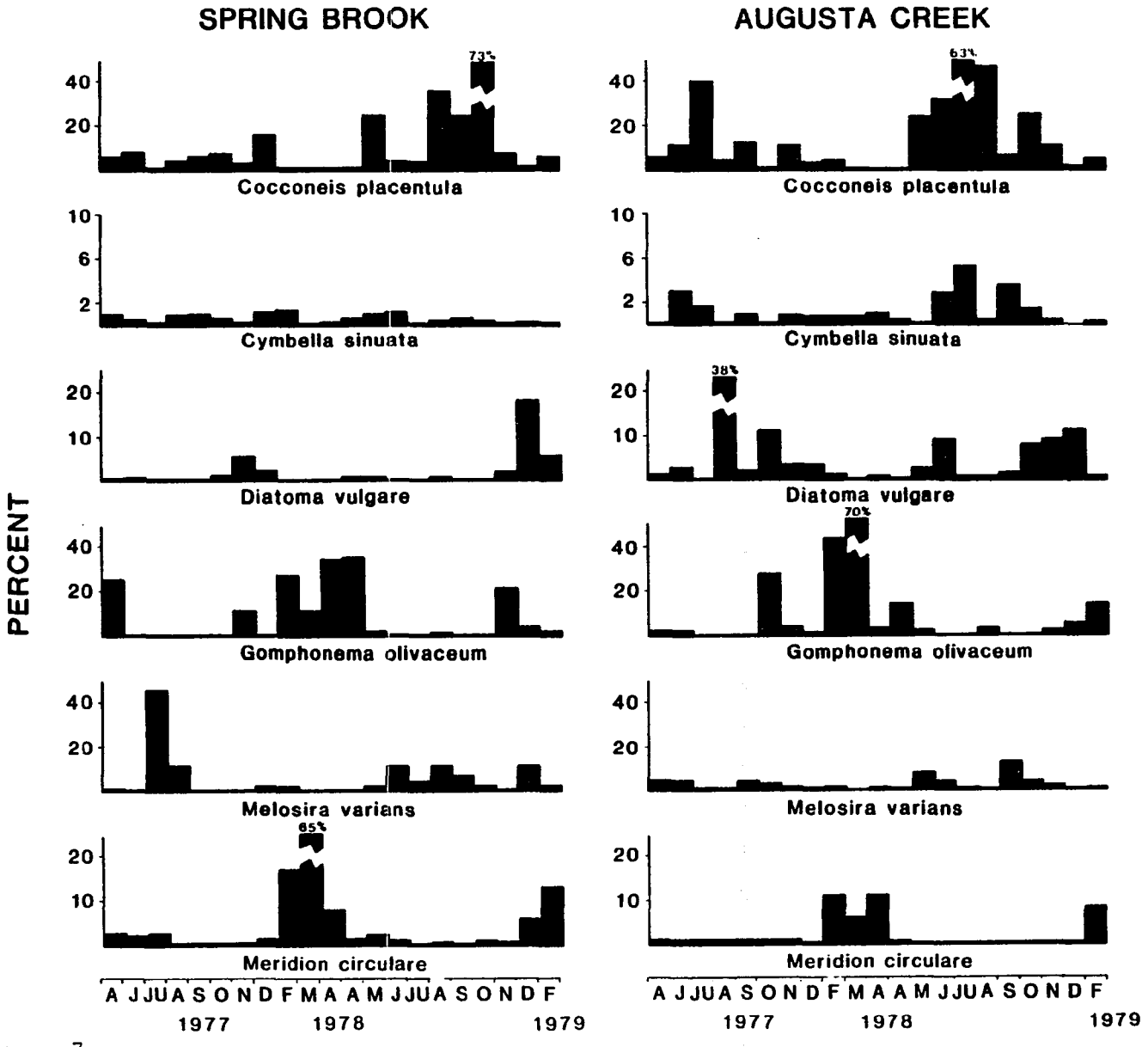
SPRING BROOK
AUGUSTA CREEK
PERCENT
Cocconeis placentula
Cymbella sinuata
Diatoma vulgare
Gomphonema olivaceum
Melosira varians
Meridion circulare
73%
63%
38%
70%
65%
A J J U A S O N D F M A A M J J U A S O N D F
1977
1978
1979

Figure 7.

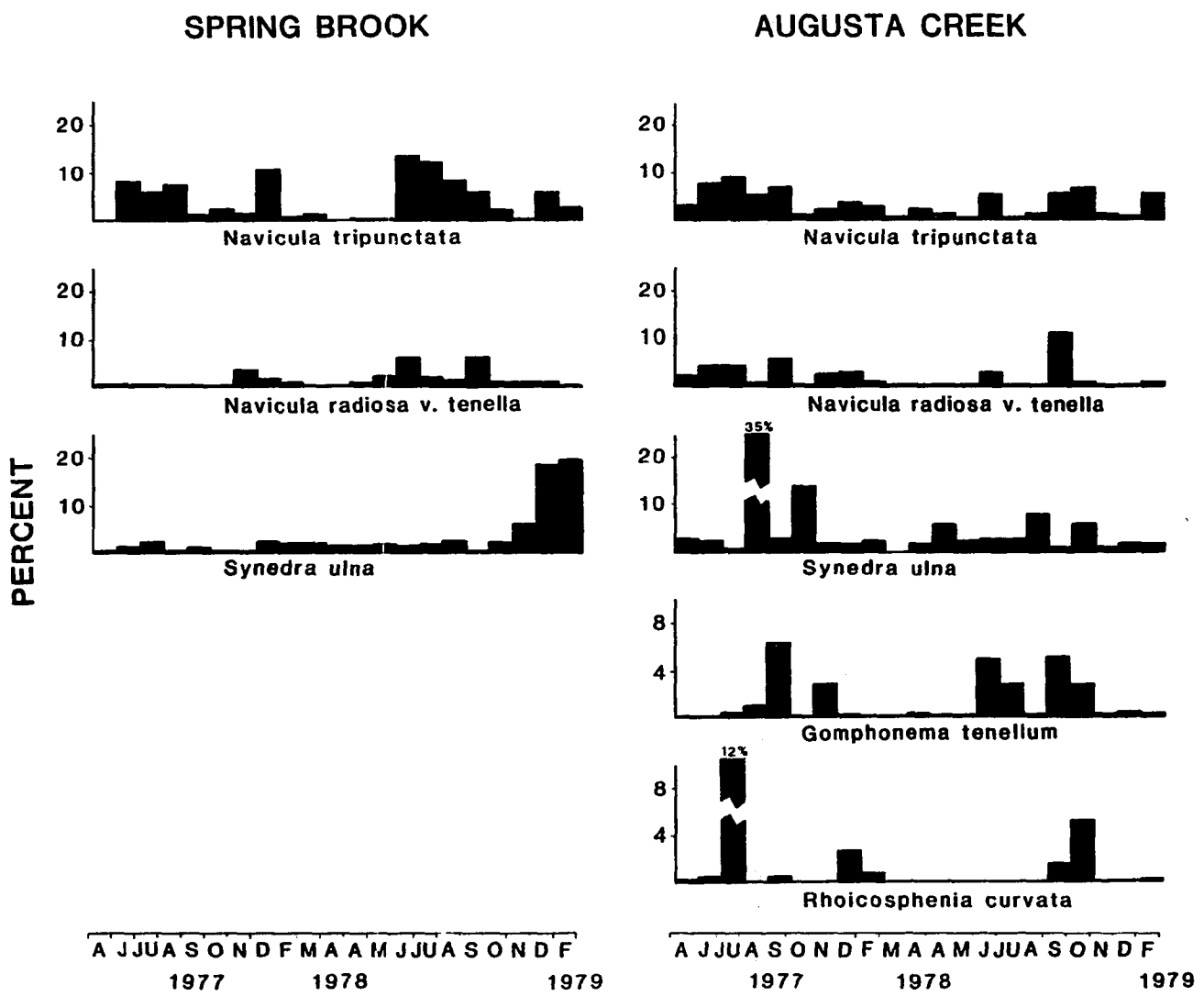
SPRING BROOK
AUGUSTA CREEK
PERCENT
20
10
Navicula tripunctata
Navicula radiosa v. tenella
Synedra ulna
35%
8
4
Gomphonema tenellum
12%
Rhoicosphenia curvata
A J J U A S O N D F M A A M J J U A S O N D F
1977
1978
1979

Figure 7.

community at this time. Moore (1972) observed Cocconeis spp. maxima in the fall, as did Butcher (1946). These researchers' data agree with the fall peak observed in Augusta Creek. The dominant winter species of M. circulare, G. olivaceum, and D. vulgare agree with results by Blum (1954) for the Saline River in Southern Michigan.

4.2.3 Diatom Densities

Augusta Creek diatom density levels ranged from a low of 2.21 X 10^2 cells/mm^2 in February 1978 to a peak of 3.58 X 10^4 cells/mm^2 in March 1978 (Figure 8). Spring Brook populations ranged from 9.38 X 10^2 cells/mm^2 on February 1978 to a high of 1.55 X 10^4 cells/mm^2 in March 10 1978. Diatom fluctuations of similar magnitude have been recorded by Moore (1972), Butcher (1932), and Gruendling (1971). A fall maximum was observed in Augusta Creek in November, although Spring Brook showed only a moderate increase (Figure 8). The diatom populations levels appear to fluctuate more widely in Augusta Creek than in Spring Brook. While the peak levels of diatoms are 2-3 times larger in Augusta Creek than in Spring Brook over the periods of the March and November maxima, during the remaining sample periods the Spring Brook diatom levels were greater. This is particularly noticeable in comparisons of February 1979 densities between the two streams (Figure 8). Analysis of variance between the two mean density measurements showed no significant difference between the populations over the time periods studied. Mean ($\pm$ S.E.) diatom densities of 8.15 X $10^3 \pm 4.71$ cells/mm^2 for Augusta Creek and 5.65 ± 1.62 X 10^3 cells/mm^2 for Spring Brook were calculated.

Figure 8. Diatom numerical density comparison between Augusta Creek and Spring Brook (log conversions; $\bar{X} \pm$ S.E., average n=3) from Feb. 1978 to Feb. 1979.

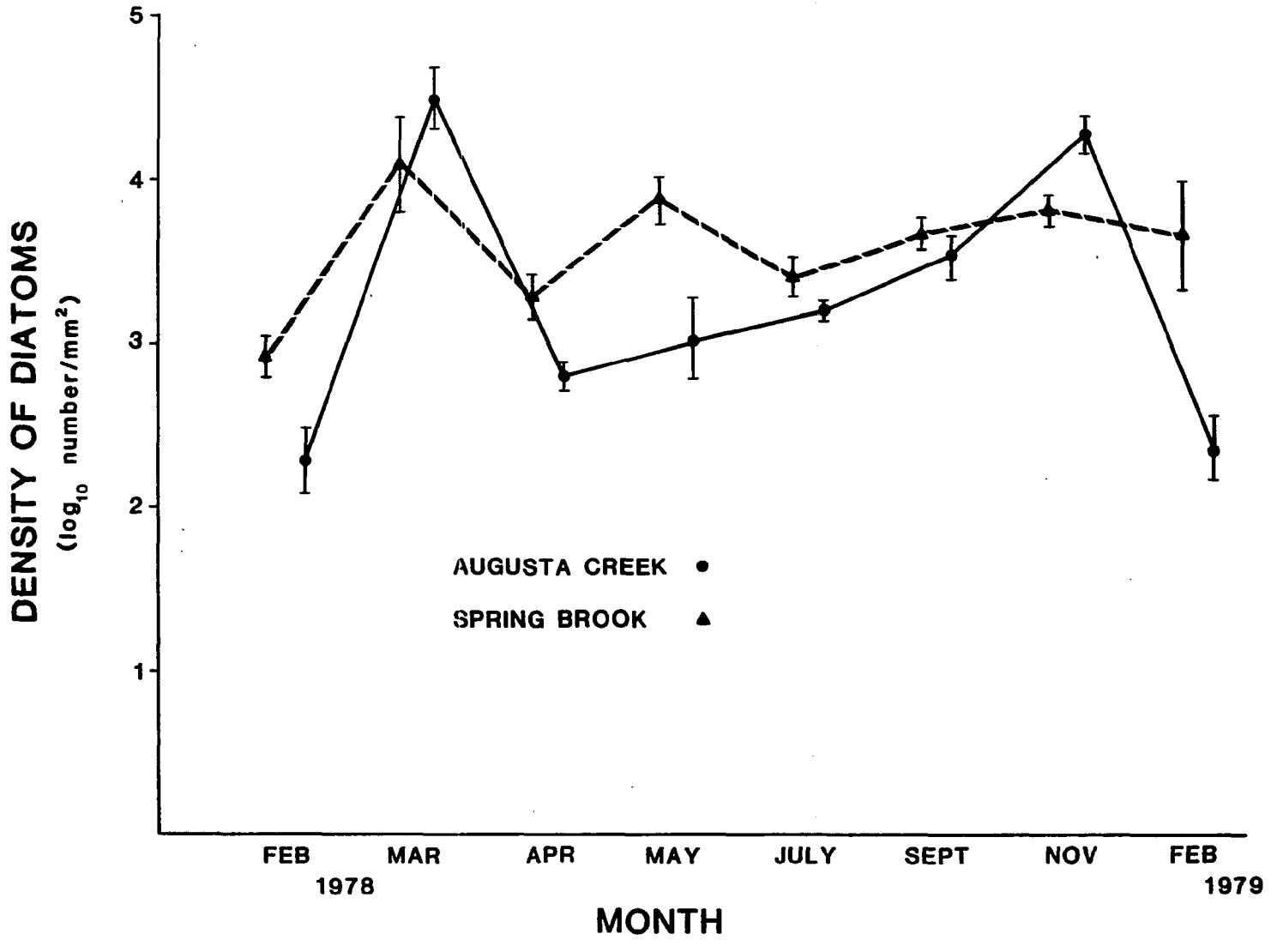
DENSITY OF DIATOMS
(log_{10} number/mm^2)
5
4
3
2
1
AUGUSTA CREEK
SPRING BROOK
FEB
1978
MAR
APR
MAY
JULY
SEPT
NOV
FEB
1979
MONTH

Figure 8.

4.2.4 Diatom Cell Volumes

The largest of the most abundant diatoms were Diatoma vulgare, Synedra ulna (and varieties), Melosira varians and Navicula viridula. All had volumes in excess of 3,000 cubic microns (Table 14). The smallest diatom volumes were measured from Amphora perpusilla, Cocconeis diminuta, Achnanthes sp. Gomphonema tenellum, and Navicula radiosa var. tenella. All had volumes below 150 cubic microns. Volume differences of 30 or 40X between these small species and the larger ones were common.

When numerical densities of individual diatom species were transferred to volumes, the analysis of variance of the average individual cell volumes between streams for the periods studied showed no significant difference between the mean diatom cell volume present on the substrate in Augusta Creek and the mean volume present in Spring Brook (data from Table 15). Comparing the total diatom species cell volumes/mm^2 in Augusta Creek to Spring Brook showed unequal variances, but also no significant differences. However, the total cell volumes were not proportional to diatom numbers, illustrating the value of the volume calculations (Figure 9).

4.2.5 Periphyton Dry Weights and Ash Free Dry Weights

Samples were collected primarily in winter and early spring to assess the dry weight and ash-free dry weight of the periphyton. The mean ($\pm$ S.E.) periphyton dry weight was 0.027 $\pm$ .008 mg/mm^2 (n=5) for Spring Brook, and the mean ash-free dry weight/dry weight ratio was

Table 14. Cell volumes for some major diatom species ($\bar{x} \pm$ S.E. in μ^3) in Augusta Creek and Spring Brook.

Species	$\bar{x} \pm$ S.E. (μ^3)	n
Diatoma vulgare	4,975.1 ±213.7	13
Synedra ulna v. contracta	4,703.6 ±265.0	10
Melosira varians	3,664.0 ±449.9	27
Navicula viridula	3,391.5 ±245.6	4
Cocconeis pediculus	1,977.4 ± 47.8	19
Navicula tripunctata	1,523.1 ± 49.7	16
Nitzschia dissipata	1,457.3 ±414.6	6
Navicula tripunctata var. schizenemoides	1,270.9 ± 61.3	4
Rhoicosphenia curvata	1,084.9 ± 85.8	10
Fragilaria vaucheriae	803.5 ± 28.6	12
Meridion circulare	802.9 ± 41.8	38
Gomphonema olivaceum	649.0 ± 57.6	19
Gomphonema angustatum	644.0 ± 14.6	6
Cymbella minuta v. silesiaca	486.0 ± 14.3	6
Fragilaria leptostauron var. dubia	436.5 ± 45.2	15
Cymbella sinuata	367.8 ± 22.9	35
Cocconeis placentula var. euglypta	323.7 ± 23.3	58
Navicula radiosa var. tenella	134.3 ± 5.4	11
Gomphonema tenellum	127.2 ± 8.8	8
Achnanthes clevei	126.7 ± 13.4	8
Achnanthes linearis	103.6 ± 2.7	23
Achnanthes affinis	97.8 ± 3.6	18
Cocconeis diminuta	66.7 ± 3.2	18
Amphora perpusilla	17.2 ± 1.7	14

Table 15. Diatom numerical densities and diatom total volume estimates for Augusta Creek and Spring Brook

Date	Stream	Diatom Density ($\#/mm^2$)	Total cell volumes of Diatom species present (mm^3/mm^2)	Average individual cell volume (mm^3)	(μ^3)
Feb '78	A.C.	$2.2089\ 10^{10}$	$1.71\ 10^{-4}$	$7.74\ 10^{-7}$	774
Mar '78	A.C.	$3.5795\ 10^{4}$	$2.61\ 10^{-2}$	$7.29\ 10^{-7}$	729
Apr '78	A.C.	$6.6685\ 10^{2}$	$4.75\ 10^{-4}$	$7.12\ 10^{-7}$	712
May '78	A.C.	$1.0469\ 10^{3}$	$9.16\ 10^{-4}$	$8.75\ 10^{-7}$	875
Aug '78	A.C.	$1.707\ 10^{3}$	$1.36\ 10^{-3}$	$7.97\ 10^{-7}$	797
Oct '78	A.C.	$3.7849\ 10^{3}$	$4.77\ 10^{-3}$	$1.26\ 10^{-6}$	1260
Nov '78	A.C.	$2.1718\ 10^{4}$	$1.07\ 10^{-2}$	$4.93\ 10^{-7}$	493
Feb '79	A.C.	$2.4911\ 10^{2}$	$2.68\ 10^{-4}$	$1.08\ 10^{-6}$	1080

Table 15 continued

Date	Stream	Diatom Density ($\#/mm^2$)	Total cell volumes of Diatom species present[1] (mm^3/mm^2)	Average individual cell volume (mm^3)	(μ^3)
Feb '78	S.B.	$9.375\ 10^2$	$5.45\ 10^{-4}$	$5.81\ 10^{-7}$	581
Mar '78	S.B.	$1.5469\ 10^4$	$1.18\ 10^{-2}$	$7.63\ 10^{-7}$	763
Apr '78	S.B.	$2.2018\ 10^3$	$8.46\ 10^{-4}$	$3.84\ 1-\bar{0}^7$	384
May '78	S.B.	$7.3318\ 10^3$	$2.61\ 10^{-3}$	$3.56\ 10^{-7}$	356
Aug '78	S.B.	$2.5345\ 10^3$	$2.35\ 10^{-3}$	$9.27\ 10^{-7}$	927
Oct '78	S.B.	$5.1216\ 10^3$	$1.73\ 10^{-3}$	$3.38\ 10^{-7}$	338
Nov '78	S.B.	$6.974\ 10^3$	$6.28\ 10^{-3}$	$9.0\ 10^{-7}$	900
Feb '79	S.B.	$4.6596\ 10^3$	$5.29\ 10^{-3}$	$1.14\ 10^{-6}$	1140

Figure 9. Comparisons of total diatom cell volumes to numerical diatom density (μ^3/mm^2 vs. log numbers/mm^2).

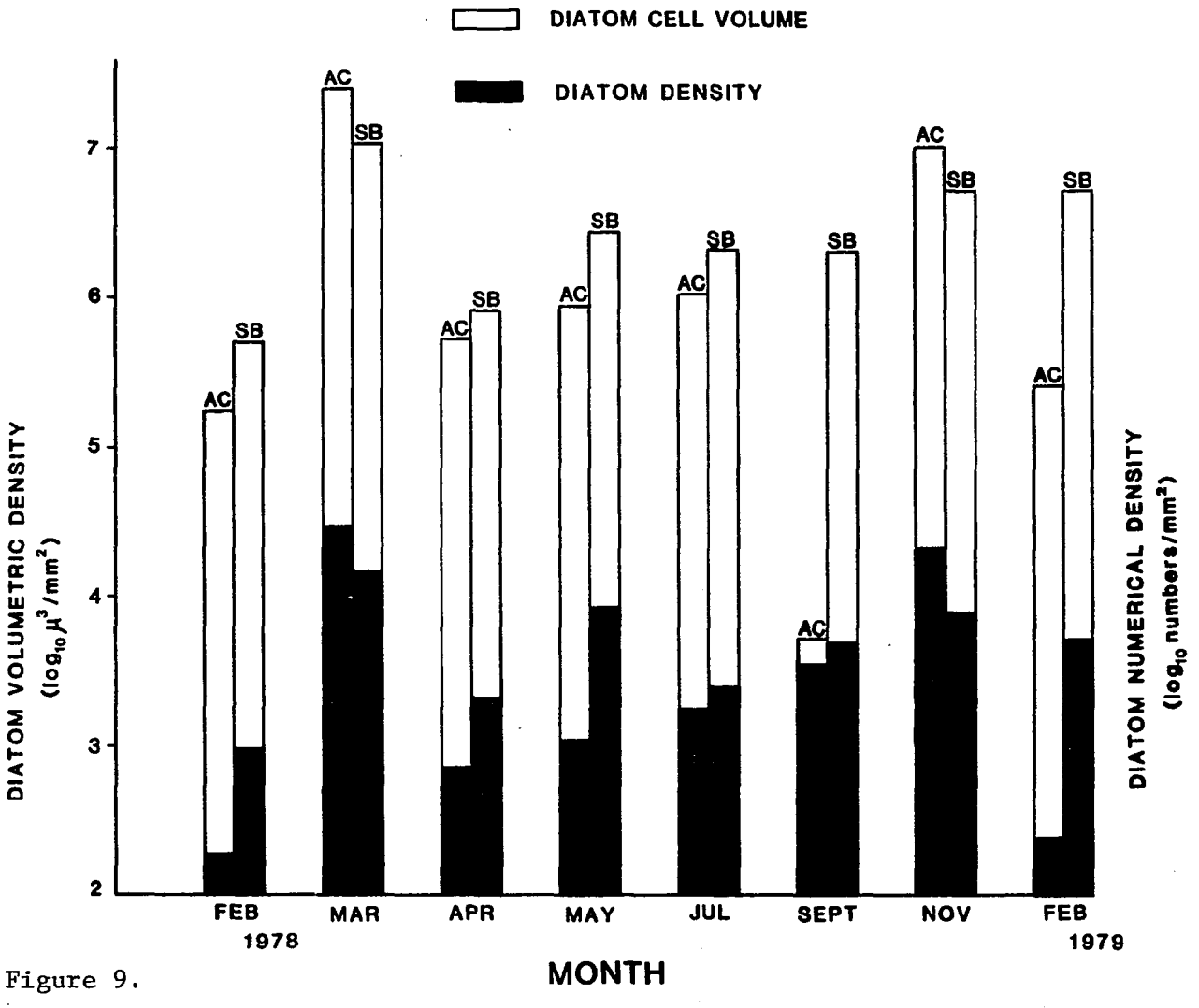
DIATOM CELL VOLUME
DIATOM DENSITY
DIATOM VOLUMETRIC DENSITY
(log10 μ3/mm2)
DIATOM NUMERICAL DENSITY
(log10 numbers/mm2)
2
3
4
5
6
7
AC
SB
FEB
1978
MAR
APR
MAY
JUL
SEPT
NOV
FEB
1979
MONTH

Figure 9.

0.7587 $\pm$ .078 (n=5) (Table 16). Augusta Creek had respective values of 0.041 $\pm$ .014 (n=8) and 0.7887 $\pm$ .030 (n=8).

The diatom numerical density data was converted to dry weight and caloric equivalents using factors from Trama (1957), Roff (1969) and Cummins et.al. (1966) (Table 17). Calculated yearly means for Spring Brook using these factors and information from Table 17, indicated a mean dry weight periphyton biomass of 47.15 mg/m^2 (S.E. = 13.51, n = 8) and a caloric value of 151.7 $Kcal/m^2$. Augusta Creek calculations indicated 67.96 mg/m^2 (S.E. = 39.28, n = 8) dry weight biomass and 218.7 $Kcal/m^2$.

Table 16. Periphyton dry weights (mg/mm^2) and ash-free dry weight: dry weight ratios ($X \pm S.E.$).

Stream	Date	n	D.W. mg/mm^2 X	D.W. mg/mm^2 S.E.	Exposure Period (Days)	A.F.D.W. / D.W. X	A.F.D.W. / D.W. S.E
S.B.	Jan 81	1	.0179	------	28	.9578	-----
S.B.	Mar 81	2	.0093	±.0022	35	.5223	±.1416
S.B.	Apr 81	5	.0558	±.0191	28	.8678	±.0421
S.B.	Apr 81	3	.0213	±.0134	16	.6490	±.0266
S.B.	May 81	3	.0306	±.0083	23	.7961	±.0201
A.C.	Oct 80	2	.0276	±.0117	28	.7893	±.0085
A.C.	Dec 80	3	.1205	±.0315	28	.8244	±.0185
A.C.	Jan 81	1	.0165	------	28	.7904	------
A.C.	Jan 81	2	.0732	±.0162	83	.9032	±. 001
A.C.	Mar 81	3	.0101	±.0067	28	.6044	±. 077
A.C.	Apr 81	5	.0621	±.0095	28	.7656	±.0382
A.C.	Apr 81	3	.0078	±.0051	16	.8192	±.0356
A.C.	May 81	3	.0082	±.0021	35	.8131	±. 035

Table 17. Empirical standing crop for periphyton in Augusta Creek and Spring Brook based on quantitative samples.

Date	Stream	Diatom density ($\bar{X} \pm$ S.E.) (no./mm^2)	Diatom dry weight (mg/mm^2) ($\times 10^{-3}$)	Caloric equivalent[3] (Kcals/mm^2) ($\times 10^{-6}$)	
Feb 1978	Augusta Creek	$2.2089 \pm 0.092\ 10^2$	1.840 ± 0.077	5.92 ± 0.25	
Mar		$3.5195 \pm 0.530\ 10^4$	298.500 ± 0.440	960.57 ± 141.60	1
Apr		$6.6685 \pm 0.270\ 10^2$	5.562 ± 0.230	17.90 ± 0.74	
May		$1.0469 \pm 0.990\ 10^3$	8.731 ± 8.257	28.10 ± 26.60	
Aug		$1.7070 \pm 0.105\ 10^3$	14.240 ± 0.880	45.82 ± 2.83	
Oct		$3.7849 \pm 1.600\ 10^4$	31.570 ± 13.340	101.59 ± 42.93	
Nov		$2.1718 \pm 0.430\ 10^2$	181.600 ± 36.360	584.39 ± 116.87	2
Feb 1979		$2.4911 \pm 0.920\ 10^2$	2.078 ± 0.770	6.69 ± 2.48	
Feb 1978	Spring Brook	$9.3750 \pm 1.860\ 10^2$	7.819 ± 1.550	25.16 ± 4.99	
Mar		$1.5469 \pm 0.900\ 10^4$	129.010 ± 75.060	415.15 ± 241.50	1
Apr		$2.2018 \pm 0.440\ 10^3$	18.360 ± 3.670	59.08 ± 11.82	
May		$7.3318 \pm 3.250\ 10^3$	61.150 ± 27.110	196.78 ± 87.24	
Aug		$2.5345 \pm 1.090\ 10^3$	21.140 ± 9.090	68.03 ± 29.25	
Oct		$5.1216 \pm 0.430\ 10^3$	42.710 ± 3.590	137.44 ± 11.55	
Nov		$6.9740 \pm 1.400\ 10^3$	58.160 ± 11.630	187.16 ± 37.43	2
Feb 1979		$4.6596 \pm 1.810\ 10^3$	38.860 ± 15.100	125.05 ± 48.59	

1--March 31, 1978 greatest standing crop.
2--Fall maxima.
3--Based on 3,218 gm-cal/gm dry weight conversion factor from Trama (1957).

5.0 Interactions between G. nigrior larvae and the diatom flora

5.1 METHODS

5.1.1 Growth experiments

Field collected larvae taken from Spring Brook on September 9, 1979 were used to measure growth on different periphyton food sources at 10°, 15° or 20°C. Thirty eight larvale were dried and weighed to determine a mean original weight. Groups of 30 larvae were then placed in quart jars filled with stream water filtered through a .4 micron millipore filter. Small rocks with naturally occurring periphyton from Augusta Creek or Spring Brook provided food sources for the larvae. Fresh stream water was added every week and rocks with fresh periphyton. replaced the old rocks. All jars were aerated with bubbling airstones and the water levels maintained by addition of filtered stream water when necessary. Four replicates (jars) were used for each food source Each week several specimens were removed from each of the four jars dried as above and weighed.

A three way ANOVA was run without replication (J.H.Stapleton, M.S.U. Statistics Dept., pers. comm.) because the cell variances were close and the number of specimens per treatment combination was similar. All main effects of temperature, time, and diet were fixed treatments, fitting a Model I ANOVA (Sokal and Rohlf 1969). The analytical procedure for unbalanced factorial data or the Federer-Zelen method (Gill 1978), was also used.

5.1.2 Determination of Diatom Survivorship after Ingestion

Larvae of various instars were collected on the same day from both streams and returned in aerated water which was kept cold using ice and styrofoam chests. Larvae were placed in separate containers in the laboratory, at 10°C and at 21°C. Fresh feces were examined each hour to determine the extent of digestion, as determined by disintegration of the diatoms' chloroplasts observed under the microscope. Several hours were spent examining and identifying intact diatoms remaining in the feces to determine if differences existed in diatom species survivorship between streams or between temperatures. Examinations of diatoms were made using a Leitz Ortholux microscope at 1600X magnification with phase contrast illumination. Diatom species were considered intact if either the chloroplasts showed no dissolution of contents or no color changes, or if the diatom exhibited normal motility. On several occasions feces were removed to sterilized diatom culture medium (Lehman 1976, with minor modifications) to indicate if viable diatom species were capable of reproduction after passage through the insect's gut.

5.1.3 Larval Gut Analysis Techniques

All larvae collected for gut analysis were separated by head capsule width into instar group and placed in 70% alcohol with 5% formalin to preserve gut contents. Larvae of each instar were dissected using fine forceps and minuten pins to remove the intact midgut, using a Zeiss dissection microscope at either 40X or 100X

magnification. An average of 5 (range 1-7) individuals of each instar group were dissected and gut slides made by combining the excised midguts. The guts were transferred to a microscope slide coverslip, a small amount of distilled water added and the guts teased apart with the minuten pins. The gut contents were dispersed across the entire coverslip. Pieces of alimentary canal were removed from the coverslip and the water allowed to evaporate. The coverslip was then placed on a hotplate and left at high temperature until the organic material had been removed. This technique removed all but the silaceous cell of the diatoms and rendered species determinations possible (Patrick and Reimer 1966).

Midgut length and width measurements were taken at the time of dissection using an ocular micrometer at either 40X or 100X magnification, to permit precise quantification of the gut volumes.

Diatoms were counted and identified from each gut slide until between 250-350 had been enumerated. A diatom species list was then made for each gut slide examined, by date and by instar group. Gut analysis was made at least monthly during spring, summer and fall in both streams and all instar groups present were examined to determine diatom species present in the gut contents. Each individual diatom species abundance was compared to the total number of diatoms of all species present in the gut contents and the percent relative abundance determined. This was done for all instar groups.

5.1.4 Periphyton Preference Experiments

Food discrimination by G. nigrior larvae was measured by a series of field experiments designed to determine if selection of food items by the larvae was possible. The first experiment used 1" and 1 1/2" square ceramic tiles that had been placed in Augusta Creek and Spring Brook for differing exposure periods, to provide different periphyton "diets". The tiles were exposed for 28 days in both streams and then arranged in both a random grid and a patterned grid. The grids were placed in Spring Brook and about 60 larvae placed in the center of each grid. Every 15 minutes the position of the larvae were determined for a two hour period.

The second experiment increased the number of available diets to three, also using a patterned and random placement of the diet tiles on a grid. The second test was conducted in both Spring Brook and in Augusta creek to determine if G. nigrior larvae were discriminating on the basis of their own stream's periphyton. Tiles were used that had been exposed for different periods in both riffle and pools from each stream to provide the different diets.

5.1.5 Diatom species preferred by G. nigrior larvae

Larval diatom species preferences were determined by the comparison of usage and availability of each diatom species. Extensive gut analyses of the larvae were done to determine usage, and quantitative and qualitative sampling of the stream flora was done to determine availability. The statistical analysis techniques were those of Johnson (1980). The analysis determined preference ranks of diatom food species based on both usage and availability; the null hypothesis

was that all diatom species were equally preferred. The difference between usage rank and availability rank provides a measure of relative preference. This relative preference value permits rankings in order of preference, similar to Ivlev's index of electivity (Ivlev 1961) and similar to the model in optimal foraging theory which orders food types in rank orders from most preferred to least preferred (Pyke et al. 1977). In this analysis a usage rank of 1 (most commonly ingested diatom species) minus an availability rank of 6 (6th most common diatom species in periphyton) equals a difference of -5 which would indicate a high degree of preference over diatoms in which usage ranked lower than availability. This analysis also provides a test of significance on the diatoms species based on their respective rank order.

5.2 RESULTS

5.2.1 Larval Growth

Weeks three and four showed the largest increases in weights particularly at the higher temperatures (Figure 10). Mortality appeared the highest for the Spring Brook diet at the high temperatures with only a single larva surviving the four week test at the 20°C temperature. Statistical analysis indicated that interaction between main effects was not significant and that only the time factor significantly increased the weights ($P < .01$). With the interaction effects not significantly contributing to the source of variation, the analysis was performed again using the error mean square to test for significance of the three main effects; diet, temperature, and time in

Figure 10. Comparisons of larval weights ($\bar{X}$ -95%CL) held at three temperatures (10^{o}, 15^{o}, and 20^{o} C), supplied with two different diets, and measured weekly for four weeks.

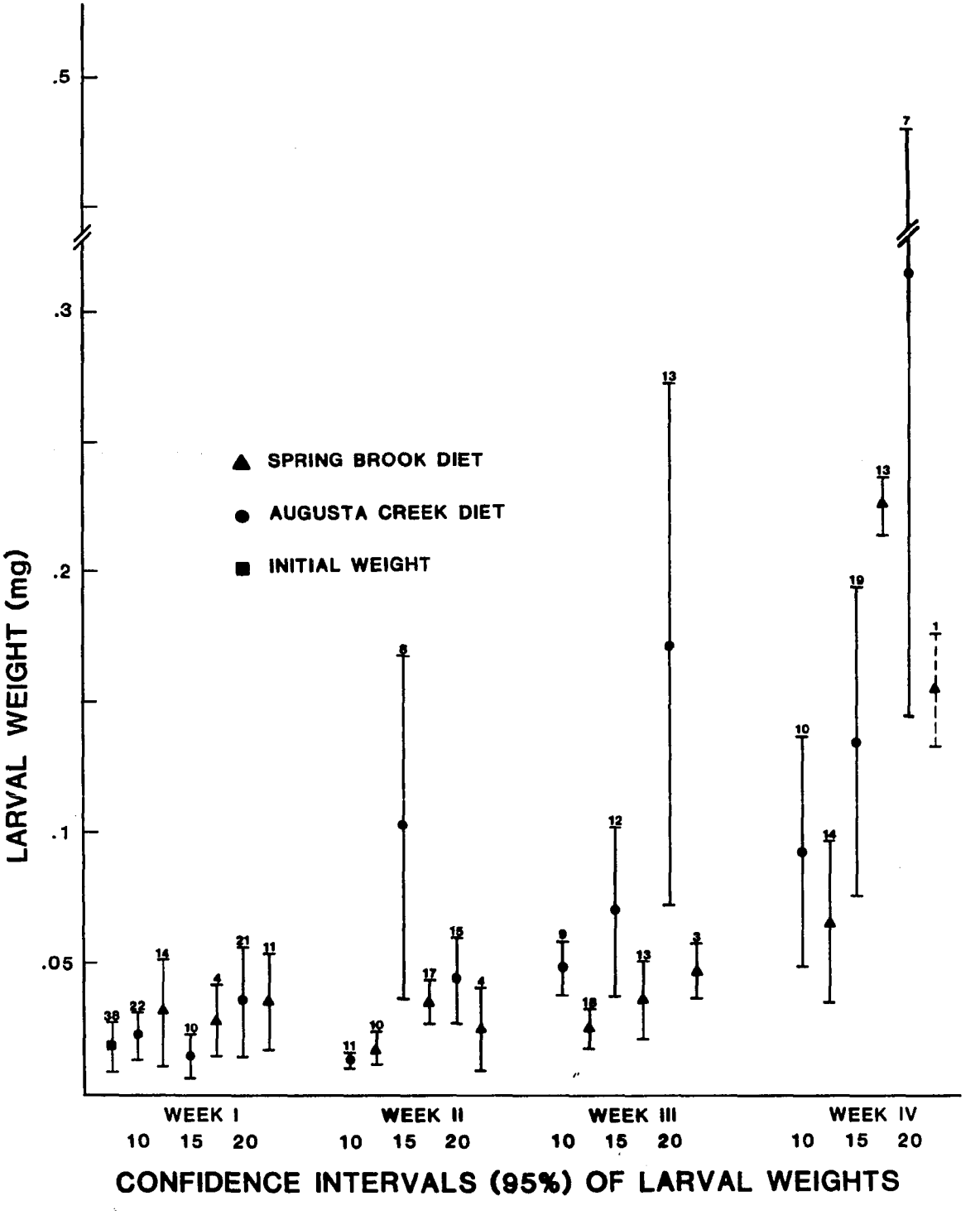
LARVAL WEIGHT (mg)
.5
.3
.2
.1
.05
SPRING BROOK DIET
AUGUSTA CREEK DIET
INITIAL WEIGHT
WEEK I
WEEK II
WEEK III
WEEK IV
10 15 20
CONFIDENCE INTERVALS (95%) OF LARVAL WEIGHTS

Figure 10.

weeks. The difference in diets between available periphyton from Spring Brook and Augusta Creek was not significant in contributing to differences observed in weight gains, while temperature was the most significant main effect ($P < .001$) contributing to weight gains, followed by time in weeks ($P < .01$) (Table 18).

The greatest percentage of growth per day occured at 15°C on the Spring Brook diet (Table 19). The Augusta Creek diet showed a constant increase in percentage of growth per day for the larvae as the temperature increased. But the total growth was maximum at 15°C on the Spring Brook diet. The drop in growth rates for larvae reared at 20°C on the Spring Brook diets corresponded with the highest mortality levels at this treatment combination (90%). It is possible that the 15°-20°C temperature represents some critical level for diatom growth (Dillard 1971). Temperature changes are known to effect diatom and other algal populations (Patrick et al. 1969, Patrick 1971). The 20°C temperature may have reduced the Spring brook diatom population to low levels reducing potential growth rates and increasing larval mortality. The Augusta Creek diet if it contained different diatom species or algal types, may have been less affected by the temperature increase.

5.2.2 Periphyton Assimilation

Comparisons of the ash-free dry weight to dry weight ratios between the periphyton food source and the feces can roughly determine the percent of the food assimilated (Conover 1966). Larvae collected on April 9, 1981 from Augusta Creek and Spring Brook were used for fecal ash-free dry weights, and periphyton sampled at the same time was

Table 18. Analysis of variance of the weight gains of G. nigrior larvae supplied with Augusta Creek periphyton (Diet I) and with Spring Brook Periphyton (Diet II). Three temperatures 10°, 15°, 20°C were used over 4 weeks.

SOURCE OF VARIATION	D.F	S.S	M.S.	F-RATIO
DIET A	1	.0008	.0004	.04
TEMP B	2	.2266	.1133	11.33***
WEEKS C	3	.1242	.0414	4.14**
ERROR	252	2.5188	.010	

*** F.001 [2,252] = 10.8

** F.01 [3,252] = 3.87

Table 19. Comparison of G. nigrior growth rates (mg dry wt.) on two different diets at three temperatures

TEMP	REL GROWTH RATES[1] (mg/mg . d^{-1}) X ± S.E.	% TOTAL GROWTH INCREASE	GROWTH % /DAY	TOTAL GROWTH mg/larva X ± S.E.
		SPRING BROOK DIET		
10°	.0518 ± .008	240.31	8.58	.0471 ± .014
15°	.1062 ± .040	1,057.65	37.77	.2073 ± .047
20°	.0402 ± .006	142.35	6.78	.0279 ± .002
		AUGUSTA CREEK DIET		
10°	.0662 ± .012	376.53	13.45	.0738 ± .021
15°	.0595 ± .023	583.67	20.85	.1144 ± .028
20°	.0894 ± .056	1,494.90	53.39	.1364 ± .068

[1] the means are from sets of 4 chambers with initial larval density the same.

used to determine the food source ash-free dry weight. The mean percent assimilated was 73.83 ± .014 (X ± S.E.) for Spring Brook IV and V instars and 73.81 ± .001 for Augusta Creek IV-V (Table 20). These results are similar to the 73% assimilation efficiency found by Hargrave (1970) for Hyallela azteca L. when grazing on epiphytic algae which consisted primarily of diatoms.

5.2.3 Diatom Survivorship in the Feces

Cymbella minuta var. silesiaca survived intact about 75% of the time and Melosira varians almost 99% of the time (Table 21). Members of the genus Cymbella have been reported to be more resistant to digestion in other insects guts also (Moore 1975), while members of the genus Amphora were found to be resistant in the gut of larval lampreys (Moore and Beamish 1973). Calow (1975) found a 60% absorption efficiency when Achnanthes spp. were supplied as food to gastropods, compared to the 20% survivorship reported here. The importance of precise diatom species identification can be seen in the comparison of the survivorship of two species of the genus Gomphonema. Gomphonema olivaceum shows a survivorship of approximately 10% while Gomphonema angustatum shows a survivorship of over 40%. While evidence from diet preference tests preference test and gut analysis implicates larger diatoms, including filamentous or colonial forms as being physically too large to eat it is of interest to note that Melosira varians, Synedra ulna and Diatoma vulgare, three out of the top four diatom species showing high survivorship after passage through the gut, are

Table 20. Estimates of assimilation efficiencies for larvae from Spring Brook and Augusta Creek based on techniques of Conover (1966).

STREAM	INSTAR [1]	FECES A.F.D.W./D.W.	PERIPHYTON A.F.D.W./D.W.	% ASSIMILATED
SPRING BROOK	V	.5143	.7858 ± .0481	71.13
	V	.5178	.7858 ± .0481	70.73
	V	.5065	.7858 ± .0481	72.02
	IV	.4291	.7858 ± .0481	79.51
	IV	.4859	.7858 ± .0481	74.24
	IV	.4748	.7858 ± .0481	75.36
AUGUSTA CREEK	IV-V	.4786	.7852 ± .0273	74.89
	IV-V	.5093	.7852 ± .0273	71.61
	IV-V	.4781	.7852 ± .0273	74.94

[1] n= 28 V instars from Spring Brook; n = 86 IV instars from Spring Brook; n = 46 IV-V instars from Augusta Creek.

Table 21. Rankings of survivorship for major diatom species surviving intact after passage through the larval gut ($\bar{X}$ + S.E.)(Based on combined data from both streams from October, December, and March).

	Diatom species	Percent surviving ($\bar{X} \pm$ S.E.)
1.	Melosira varians	98.75 ± 1.30
2.	Cymbella minuta v. silesiaca	75.88 ± 9.90
3.	Synedra ulna	56.85 ± 13.10
4.	Diatoma vulgare	57.00 ± 43.00
5.	Gomphonema angustatum	40.50 ± 7.50
6.	Amphora perpusilla	38.84 ± 1.30
7.	Navicula radiosa v. tenella	25.15 ± 4.00
8.	Achnanthes affinis & linearis	20.61 ± 4.50
9.	Nitzschia dissipata	16.50 ± 14.30
10.	Navicula tripunctata	10.25 ± 10.25
11.	Gomphonema olivaceum	9.58 ± 6.40
12.	Cocconeis placentula v. euglypta	2.92 ± 2.90

also either large in size or form some filamentous colony. Perhaps the ability of these species to survive intact in the herbivore's gut, rather than cell largeness, or colony type, determine the extent to which they are ingested. It is also noteworthy that, Cocconeis placentula var. euglypta, the diatom species found most difficult to remove from rock surfaces by other herbivores, is the species showing the least survivorship (3%) in the feces of G. nigrior larvae.

5.2.4 Diatom Species Abundances in Larval Guts

Cymbella sinuata and Cocconeis placentula var. euglypta showed gut abundances generally above abundances recorded from the periphyton (Figure 11). For example, II-III-IV instar gut analysis for Spring Brook in August of 1977 indicated over 78% of gut diatoms are C. placentula var. euglypta while the periphyton diatom community showed this same species as comprising only approximately 5% of the total. This is particularly clear for comparisons between Cymbella sinuata availability in the periphyton and its uptake by larvae of G. nigrior for almost all sampling periods.

5.2.5 Analysis of Diatom Abundance

The importance of diatoms to the diet of G. nigrior instars was also measured by transferring numerical densities of diatom species to volumetric equivalents, using the previously measured diatom volumes (Table 14). Examing the mean diatom cell volume calculated for each

Figure 11. Diatom species abundance in the instar guts (vertical bars) and abundance in the stream periphyton (dashed line) by month.

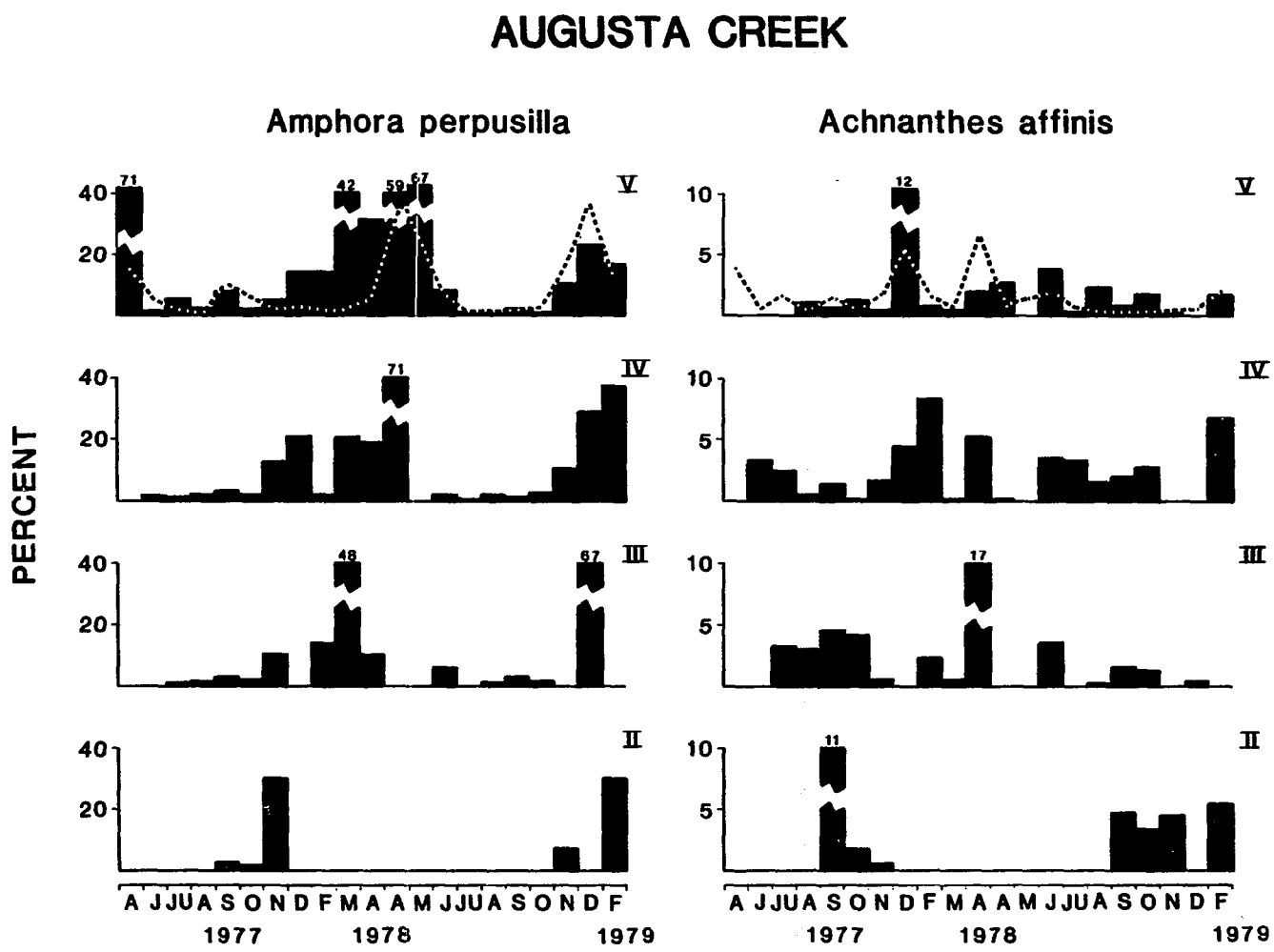
AUGUSTA CREEK
Amphora perpusilla
Achnanthes affinis
PERCENT
V
IV
III
II
A J J U A S O N D F M A A M J J U A S O N D F
1977
1978
1979

Figure 11.

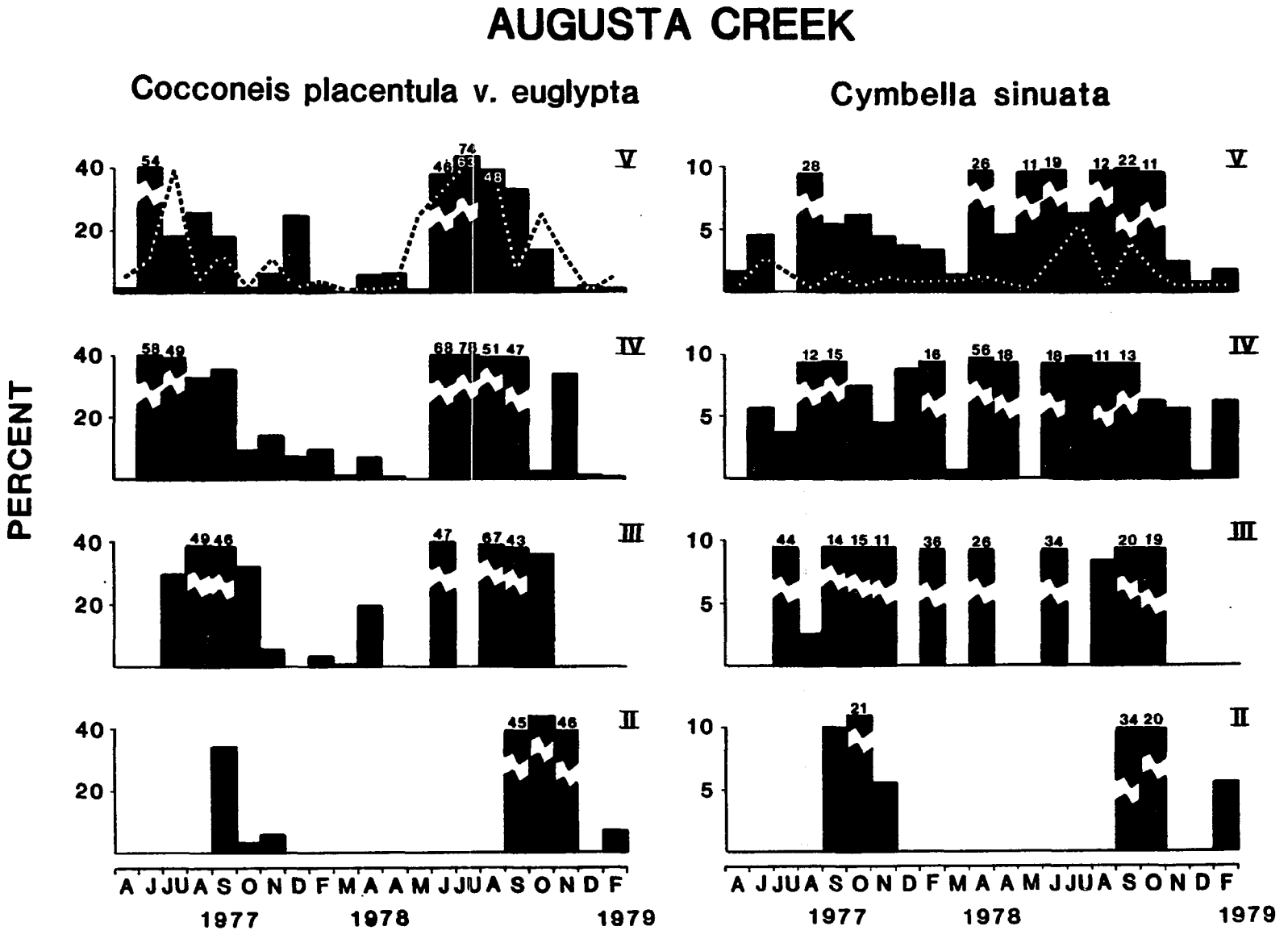
AUGUSTA CREEK
Cocconeis placentula v. euglypta
Cymbella sinuata
PERCENT
V
IV
III
II
A J J U A S O N D F M A A M J J U A S O N D F
1977
1978
1979

Figure 11.

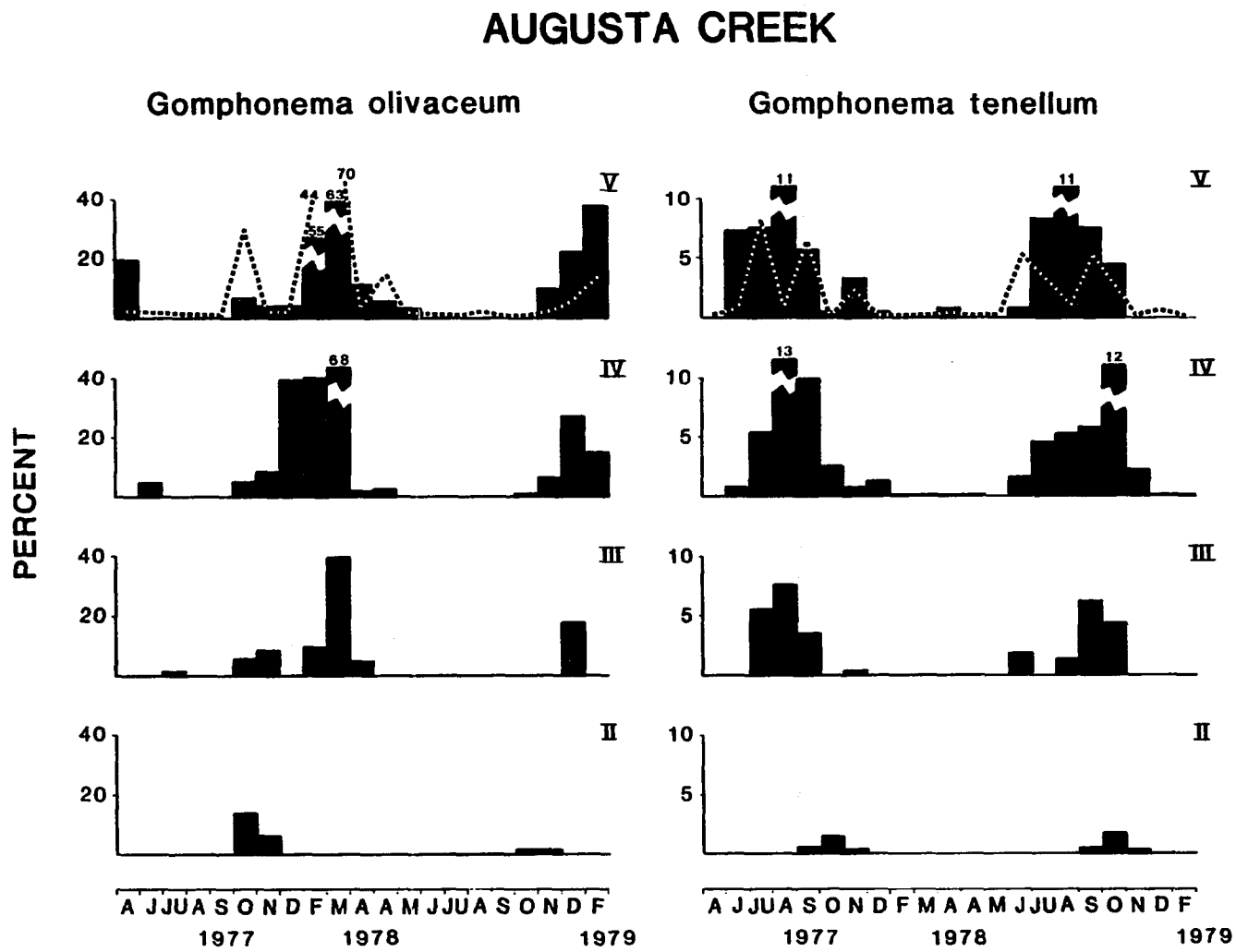
AUGUSTA CREEK
Gomphonema olivaceum
Gomphonema tenellum
PERCENT
V
IV
III
II
70
44
63
55
68
11
13
12
40
20
10
5
A J J U A S O N D F M A A M J J U A S O N D F
1977
1978
1979

Figure 11.

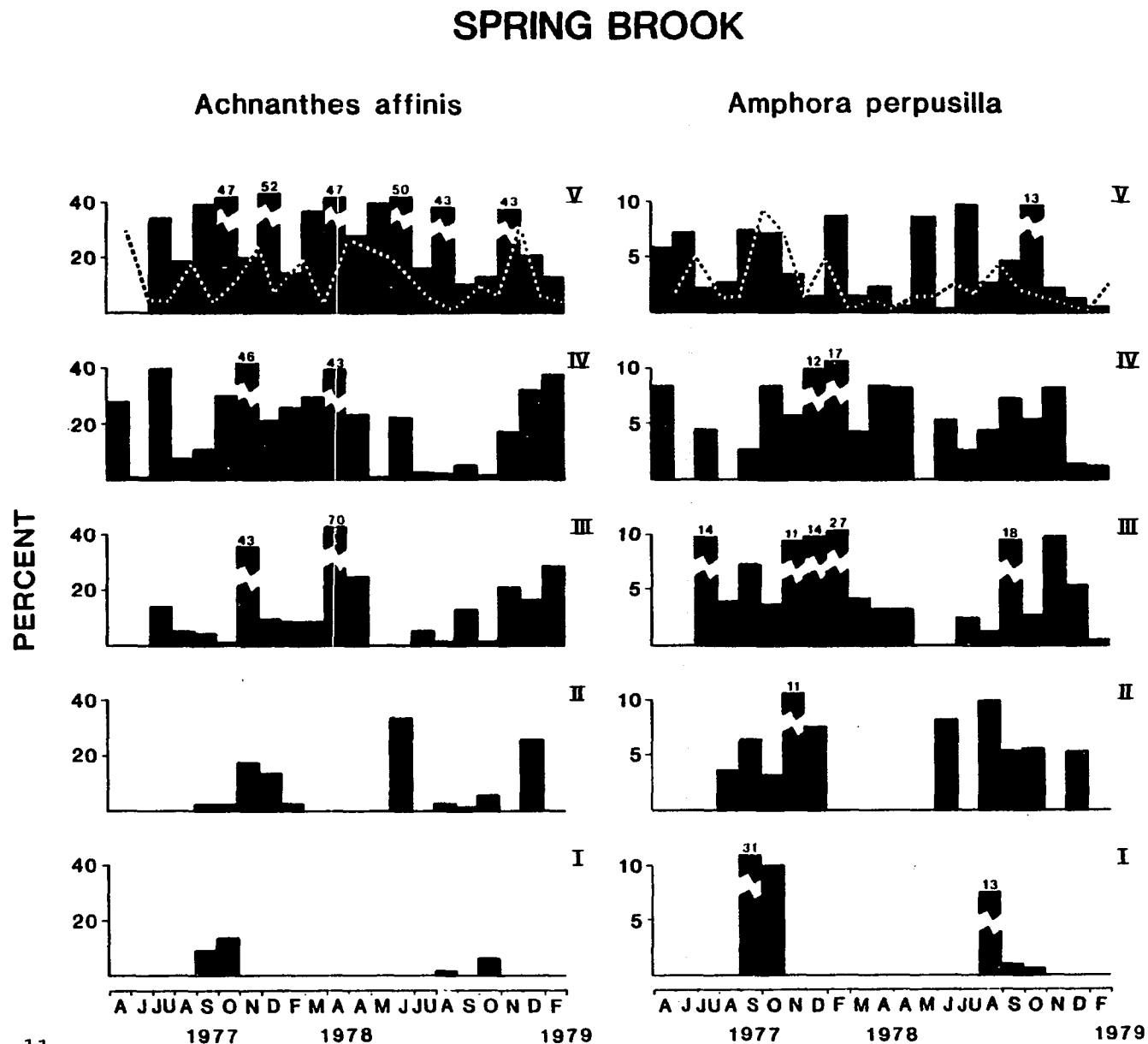
SPRING BROOK
Achnanthes affinis
Amphora perpusilla
PERCENT
40
20
10
5
47 52 47 50 43 43
13
46 43
12 17
43 70
14 11 14 27 18
11
31 13
V
IV
III
II
I
A J J U A S O N D J F M A A M J J U A S O N D J F
1977
1978
1979

Figure 11.

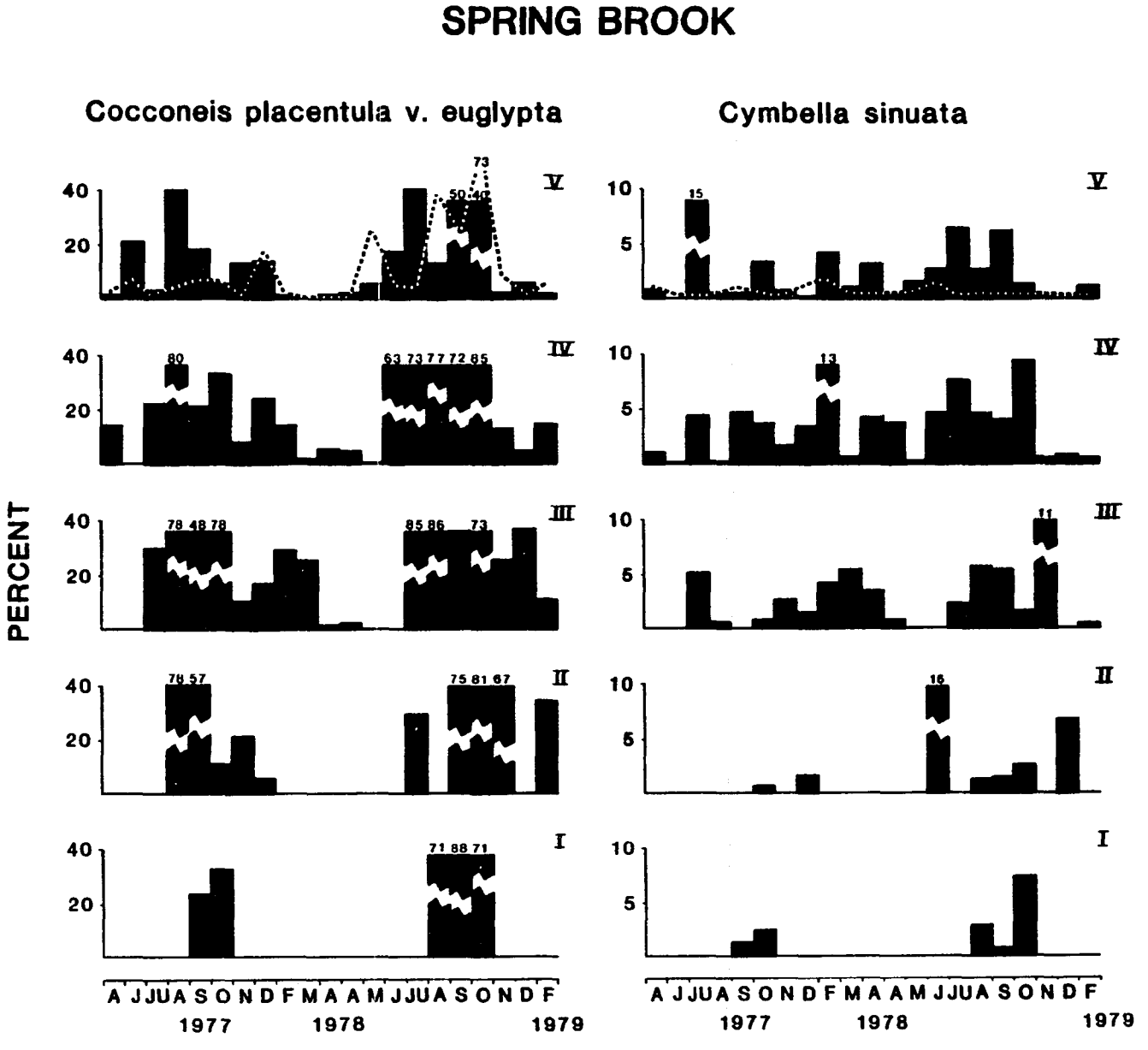
SPRING BROOK
Cocconeis placentula v. euglypta
Cymbella sinuata
PERCENT
40
20
10
5
V
IV
III
II
I
73
50 40
15
80
63 73 77 72 85
13
78 48 78
85 86 73
11
78 57
75 81 67
16
71 88 71
A J J U A S O N D F M A A M J J U A S O N D F
1977
1978
1979

Figure 11.

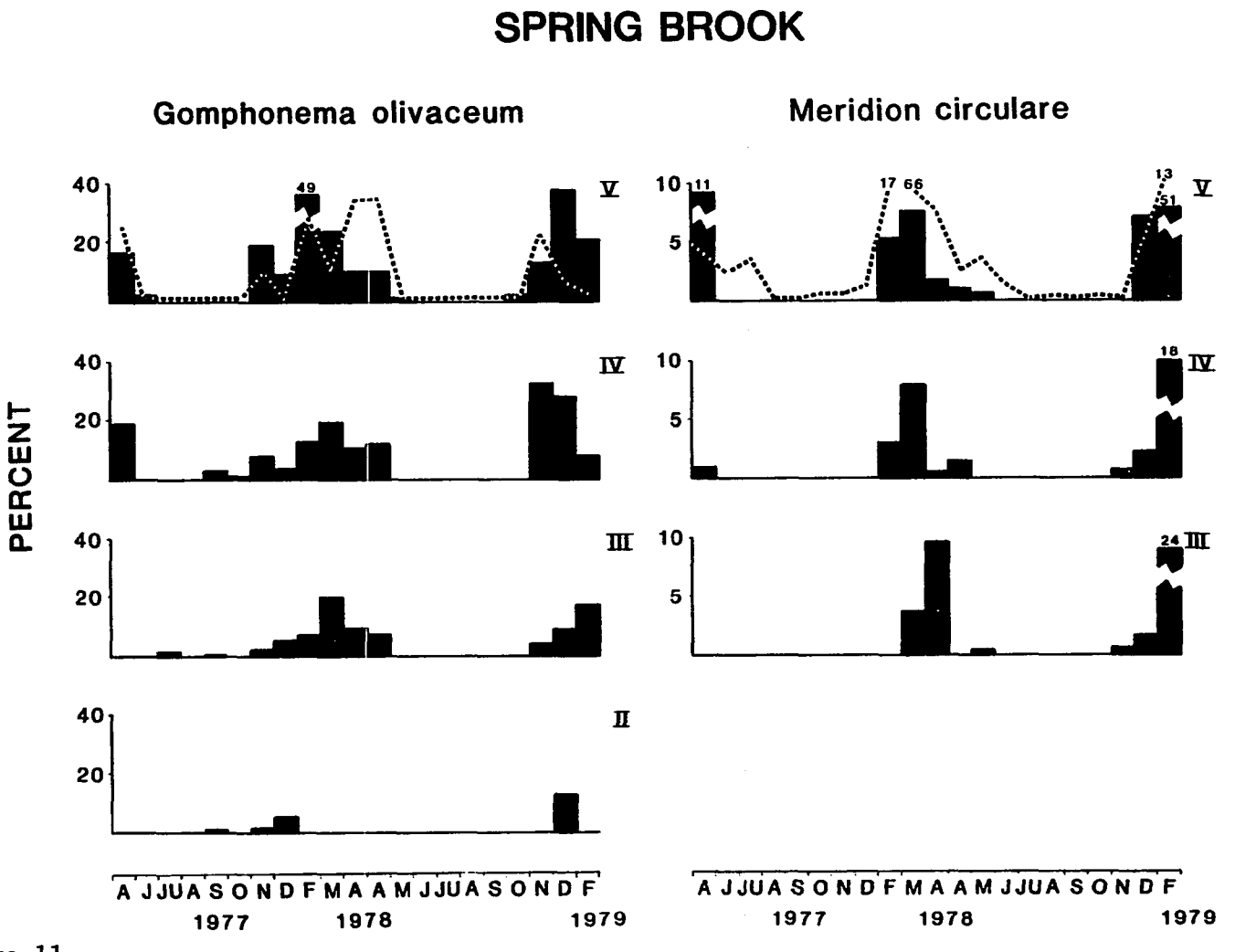
SPRING BROOK
Gomphonema olivaceum
Meridion circulare
PERCENT
40
20
10
5
49
11
17
66
13
51
18
24
V
IV
III
II
A J J U A S O N D F M A A M J J U A S O N D F
1977
1978
1979

Figure 11.

Figure 12. The average diatom cell volume found in the gut contents of instars I-V ($\bar{X} \pm$ S.E.) from Augusta Creek and Spring Brook.

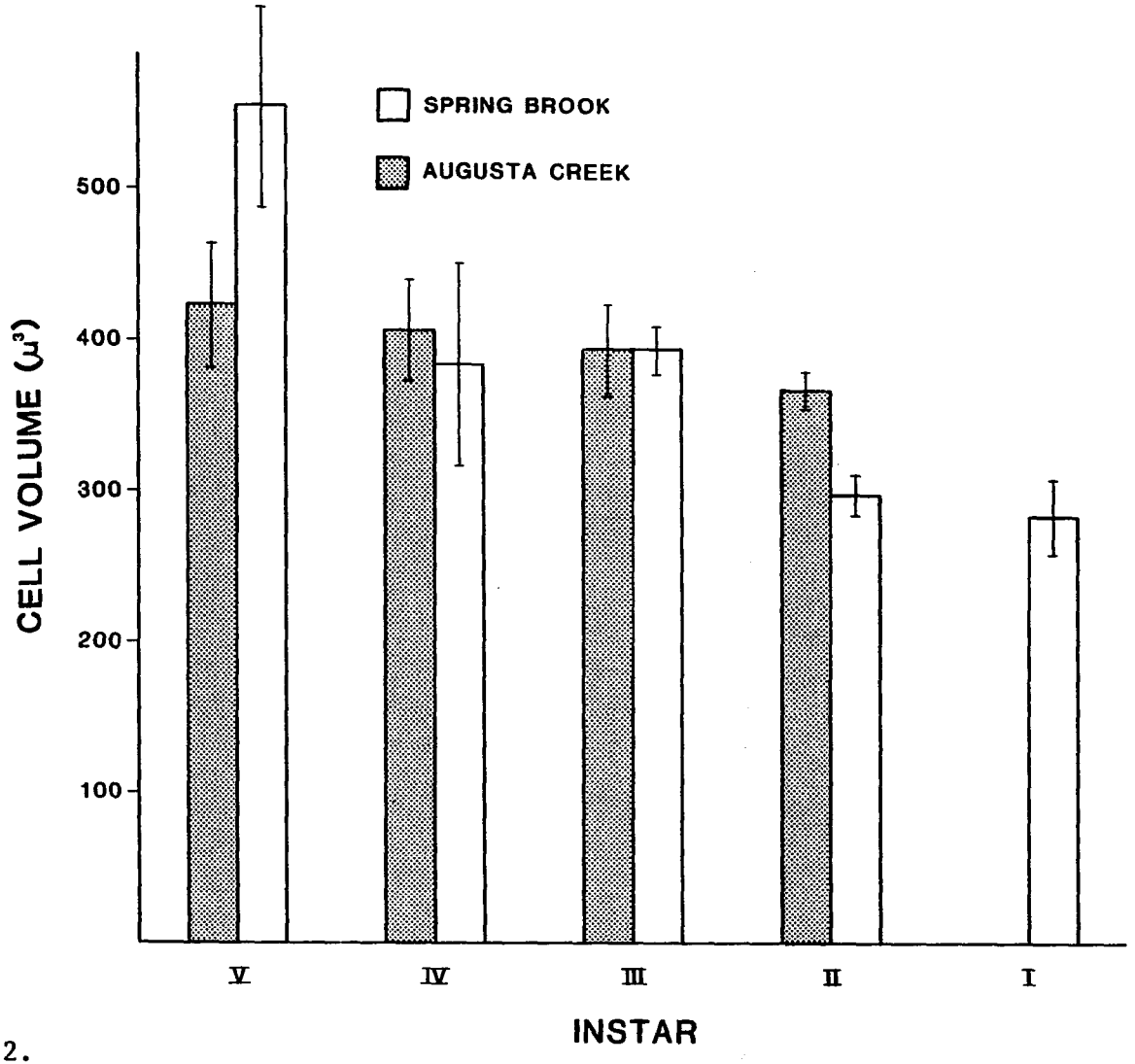
SPRING BROOK
AUGUSTA CREEK
CELL VOLUME (μ³)
500
400
300
200
100
V
IV
III
II
I
INSTAR

Figure 12.

instar, indicated a general trend towards smaller diatoms ingested with decreasing larval size (Figure 14).

Correlation coefficients between the mean volume of available diatoms on the stream substrates and the mean diatom volume found in the gut contents of each mean diatom voluyme in the instar showed generally low values (Table 22). This supports the fact that the mean diatom volume in the larval gut contents does not accurately reflect the mean available diatom volume from the periphyton community. The overall correlation from combining all instar data (16 dates), based on the mean diatom cell volume for all instars found on that date, showed an overall r value of 0.47. The higher r value of 0.71 for combined III instars reflects the high individual correlation obtained separately for Spring Brook III instars between size available and size ingested (r = 0.89).

Comparing the number of diatoms per mm^3 of gut contents with the number of diatoms per mm^2 substrate available, indicated that only the I and II instars gut volumes appeared influenced by the surrounding substrate diatom concentrations (R^2 = .62). This may indicate a more restricted feeding space for early instars covering less area because of their smaller size, and thus a greater dependence on readily available food.

A regression of the total volume of diatoms present in the gut against the total number of diatoms present on the stream substrates (Table 23), indicated that the I through IV instars showed the greatest similarity between gut diatom volume, and gut diatom numbers (Table 24). If the early instars ingest a more limited size range of diatoms one might expect a greater similarity between numbers of diatoms

Table 22. Correlation coefficients between mean diatom cell volume available in the periphyton and mean diatom cell volume measured from the gut samples.

Instar	n[1]	r	Significance
V	16	0.17	ns
IV	14	0.18	ns
III	12	0.71	**
I-II	7	0.49	ns

1--Number of sample dates from which an average of 5 larval guts per date were examined.

Table 23. Results of larval feeding studies comparing diatom gut analysis with stream diatom availability.

Date	Instar	Number of diatoms in gut	Gut content's volume (mm^3)	Actual diatom volume (mm^3)	Proportion of gut contents filled w/ diatoms	Diatom concentration in stream ($no.s/mm^2$)
			Spring Brook			
Feb 1978	V	8.773×10^4	.4182	.0039	.0093	9.375×10^2
	IV	2.870×10^4	.0873	.0073	.0836	
	III	2.483×10^3	.0215	.0007	.0326	
Mar 1978	V	1.275×10^5	.2789	.0425	.1524	1.5496×10^4
	IV	4.100×10^4	.1705	.0081	.0475	
	III	1.280×10^3	.0279	.0005	.0179	
Apr 1978	V	3.250×10^5	.5812	.0595	.1024	2.2018×10^3
	IV	9.103×10^4	.1665	.0188	.1129	
	III	8.290×10^3	.0402	.0014	.0348	
May 1978	V	6.170×10^4	.5304	.0101	.0190	7.3318×10^3
Aug 1978	V	2.320×10^4	.5871	.0070	.0119	2.5345×10^3
	IV	4.58×10^4	.2422	.0149	.0615	
	III	1.775×10^4	.0439	.0055	.1253	
	II	2.120×10^3	.0059	.0006	.1017	
	I	5.660×10^2	.0012	.0001	.0833	
Oct 1978	V	8.488×10^4	.7015	.0640	.0912	5.1216×10^3
	IV	2.701×10^4	.1732	.0088	.0508	
	III	2.623×10^3	.0349	.0008	.0229	
	II	2.470×10^3	.0070	.0008	.1143	
	I	3.120×10^2	.0013	.0001	.0077	
Nov 1978	V	1.270×10^5	.2409	.0801	.3325	6.9740×10^3
	IV	1.170×10^4	.0771	.0103	.1336	
	III	8.520×10^2	.0207	.0006	.0290	
Feb 1979	V	8.140×10^4	.3581	.0721	.2011	4.6596×10^3
	IV	1.250×10^4	.0364	.0060	.1639	
	III	1.250×10^3	.0204	.0008	.0382	

Table 23 (continued)

Date	Instar	Number of diatoms in gut	Gut content's volume (mm^3)	Actual diatom volume (mm^3)	Proportion of gut contents filled w/ diatoms	Diatom concentration in stream ($no.s/mm^2$)
			Augusta Creek			
Feb 1978	V	$5.880x10^4$	.5324	.0316	.0594	$2.2089x10^2$
	IV	$3.530x10^3$	.1175	.0016	.0136	
	III	$2.020x10^3$	.0257	.0008	.0311	
Mar 1978	V	$7.280x10^4$	.9748	.0268	.0275	$3.5795x10^4$
	IV*	$6.610x10^3$	.1281	.0035	.0273	
	III*	$3.590x10^3$	.0197	.0013	.0660	
Apr 1978	V	$1.097x10^5$	.8536	.0315	.0369	$6.6685x10^2$
	IV	$8.730x10^3$	.1364	.0025	.0183	
	III	$4.778x10^2$	.0212	.00014	.0066	
May 1978	V	$1.690x10^5$	.9236	.0332	.0359	$1.0469x10^3$
Aug 1978	V	$3.368x10^4$	.8626	.0155	.0180	$1.7070x10^3$
	IV	$3.032x10^4$	.1423	.0143	.1005	
	III*	$1.006x10^4$	.0472	.0047	.0996	
Oct 1978	V	$7.056x10^4$	.6019	.0493	.0819	$3.7849x10^3$
	IV	$5.743x10^4$	.2236	.0139	.0622	
	III	$3.275x10^3$	.0312	.0014	.0449	
	II	$8.357x10^2$	.0046	.0003	.0652	
Nov 1978	V*	$8.101x10^4$	1.1483	.2210	.1925	$2.1718x10^4$
	IV	$2.724x10^4$	.1762	.0138	.0783	
	II*	$3.829x10^3$	.0046	.0011	.2391	
Feb 1979	V	$8.140x10^4$	.7280	.0386	.0530	$2.4911x10^2$
	IV*	$1.311x10^4$	.0230	.0050	.2174	
	II*	$1.380x10^3$	.0032	.0007	.2188	

*based on one larval gut examined for that date.

Table 24. Parameters of regression equations relating volume of diatoms in the gut to numbers of diatoms in the gut.

INSTAR	n^1	a	b	r^2	SIGNIFICANCE
			Augusta Creek		
V	8	.0600	4.79×10^{-9}	.01	ns
IV	7	.0022	2.65×10^{-7}	.73	*
III	5	-.0002	4.81×10^{-7}	.99	***
			Spring Brook		
V	8	.0259	1.44×10^{-7}	.18	ns
IV	7	.0053	1.44×10^{-7}	.72	*
III	7	.0001	2.80×10^{-7}	.93	***
			Augusta Creek and Spring Brook		
I-II	7	2.2960×10^{-5}	2.99×10^{-7}	.89	***

1--Number of months from which an average of 5 larval guts per month were examined.

ingested and the diatom volumes (high R^2). Instars I-IV showed significant similarity between numbers and volumes ($R^2 > .72$). If the larger V instars ingest a larger size range of diatom cells, the resulting volumetric calculations of diatoms in the gut may show greater variability when regressed against diatom numbers. The low coefficients of determination for V instars from Spring Brook (.18) and Augusta Creek (.01) indicate that estimating gut diatom volume from gut diatom density is not reliable for this stage.

Diatoms fill between 1-32% of gut contents of Spring Brook larvae while the percentage of diatoms in the gut of Augusta Creek ranges between 1-23% (Figure 13), based on summing individual diatom volumes. Diatoms are thus a very significant component of the gut contents and probably contribute significantly to the overall nutrition of the larvae. Calculating the total diatom gut contents volume using a mean individual diatom cell volume measured from each instar group and from each stream (data from Figure 12), multiplied by the number of diatoms found in the gut gives the total diatom volume. When the total diatom volume is calculated as a proportion of the gut contents volume, the percentage of gut contents occupied by diatoms can be determined over all sampling periods (Figure 14). Comparing gut diatom volumes from III-V instars indicates that Spring Brook larvae generally ingest a larger proportion of diatoms than do Augusta Creek larvae (Figure 14). Diatoms may therefore be a more important food source for the early and late instars from Spring Brook, than for the late instars from Augusta Creek.

The mean proportion of gut contents filled by diatom cells ranged from 6-10% for Spring Brook and 5-14% for Augusta Creek (Table 25).

Figure 13. Percentage of larval gut contents filled with diatoms of measured cell volumes, from Augusta Creek and Spring Brook quantitative samples.

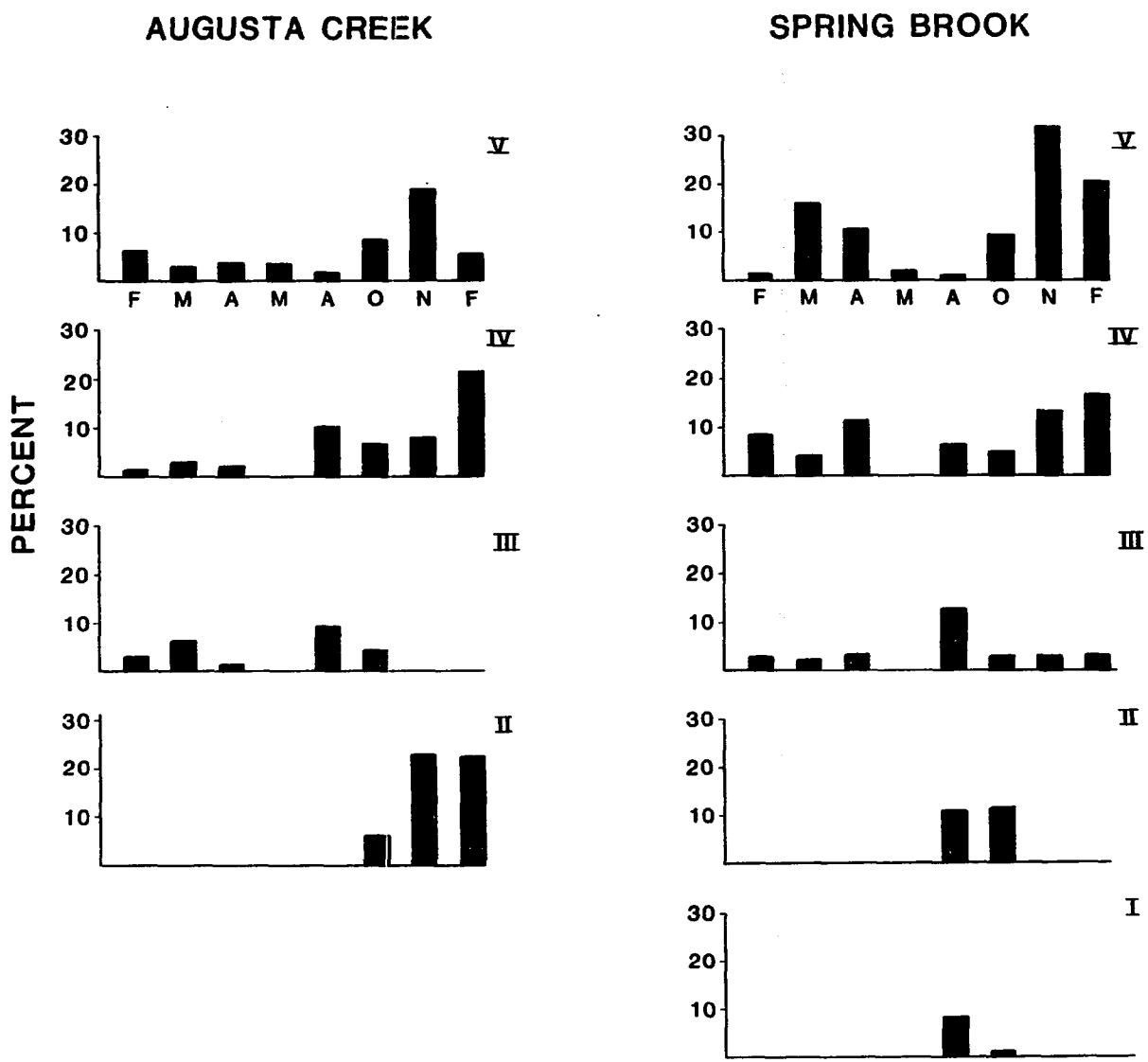
AUGUSTA CREEK
SPRING BROOK
PERCENT
30
20
10
F M A M A O N F
V
IV
III
II
I

Figure 13.

Figure 14. Percentage of larval gut contents volume filled with diatoms by month for Augusta Creek and Spring Brook (based on the average mean diatom cell volume for each instar).

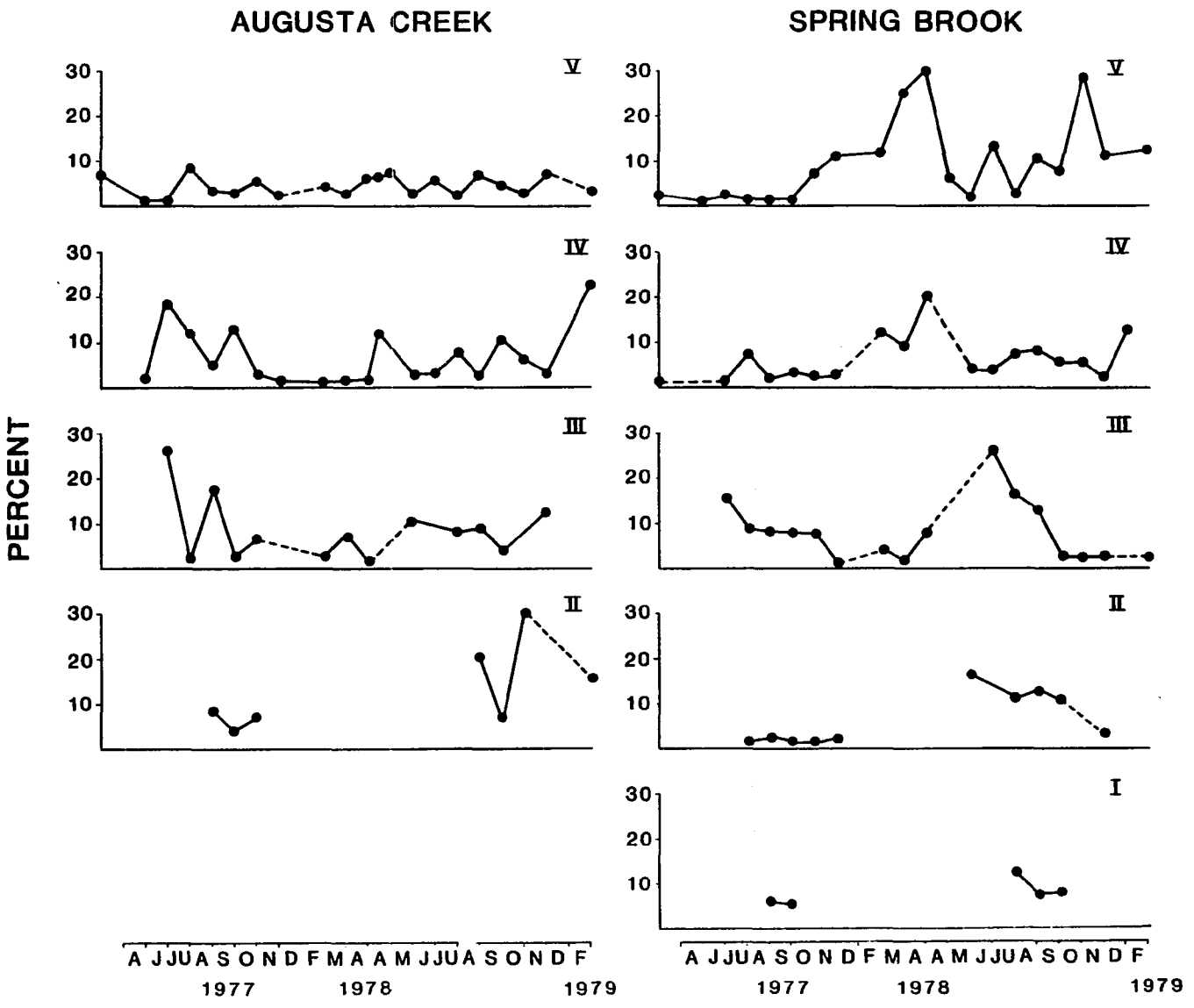
AUGUSTA CREEK
SPRING BROOK
PERCENT
30
20
10
V
IV
III
II
I
A J J U A S O N D F M A A M J J U A S O N D F
1977
1978
1979

Figure 14.

Table 25. Mean proportion of gut contents filled by Diatoms (X ± S.E.)

INSTAR	S.B.[1]	n	A.C.[1]	n	Significant
V	.0976 ± .021	20	.0480 ± .005	21	*
IV	.0648 ± .118	18	.0750 ± .015	19	ns
III	.0804 ± .017	16	.0878 ± .020	13	ns
II	.0616 ± .018	10	.1361 ± .036	7	*
I	.0770 ± .014	5	.0765 ±	1	

*P < .05

1 Based on a calculated mean diatom cell volume for each instar from February 1979).

Tests of significance between the means from Augusta Creek and Spring Brook larvae showed significant ($P < .05$) differences between the percent of the gut contents filled by diatom cells for V and II instar larvae. Spring Brook V instars contained almost twice the percentage of diatoms in their gut contents as V instars from Augusta Creek. Second instar Augusta Creek larvae contained 13.6% diatom gut volume versus only 6.2% for Spring Brook larvae. This illustrates again the importance of diatoms to the diet of early Augusta Creek instars and early and late instars from Spring Brook.

5.2.6 Diet Preference Experiments

The results of the first diet selection experiment indicated that the distribution of larvae on the tiles containing different periphyton food sources was not random (chi-squared test, ($P < .01$). G. nigrior larvae selected the Spring Brook tiles three times as often as the Augusta Creek tiles in both patterned and random arrangements of the diets. Tile arrangement was not a significant factor influencing diet selection during these experiments. Analysis of the periphyton food sources on the tiles from Augusta Creek and Spring Brook showed several differences in major diatom species composition and densitites between the two diets (Figure 15-B). Several diatom species were more abundant in the Augusta Creek periphyton; Synedra ulna, Gomphonema olivaceum, and Achnanthes spp. One particular species, Cocconeis placentula var. euglypta, was less abundant in Augusta Creek's periphyton yet, composed over 50% of the total density of the Spring Brook periphyton. While the total density of diatoms was higher in the Augusta Creek

periphyton, this did not appear to effect selection frequency. From this visual analysis, it began to appear that the diatom species composition of the two available diet choices was determing selection, and that Cocconeis placentula var. euglypta was the factor most likely to have influenced positive selection of the Spring Brook diet over the Augusta Creek diet.

The second experiment increased the number of diet choices available and was run in Spring Brook, using Spring Brook larvae, and in Augusta Creek, using Augusta Creek larvae, to determine if larvae were acclimated to the food sources available in their own stream. An analysis of the distribution of the larvae on the available diets from the Augusta Creek experiment using contigency tables indicated significant differences in diet selection frequency ($P < .005$). There was a uniform trend over time for Augusta Creek larvae to select the Augusta Creek pool diet, over the Augusta creek riffle diet, over the Spring Brook diet (Figure 16). The same experiment in Spring Brook also showed significant differences in diet selection when the results were tested using contingency tables ($P < .05$). In both experiment I and II, tests for heterogeneity between times and diets indicated no significant effects. A two way ANOVA (without replication) was also performed on the second experiment in Spring Brook and indicated that diet selection was significant ($P < .001$) in explaining the larval movement through time (Table 26). This difference in diet selection could be contrasted to the relative concentrations, and abundances of two main diatom species, Cocconeis placentula var. euglypta and Meridion circulare (Figure 15-A). As the concentration of C. placentula var. euglypta increased, selection frequency of that diet

Figure 15. Major diatom species concentrations available on each diet. Diets were; ACP-Augusta Creek pool, ACR-Augusta Creek riffle, SB-Spring Brook riffle. Number after refers to time in days each tile exposed in a riffle or pool. Left side (A) is experiment II which was run in Spring Brook and Augusta Creek, right side (B) is experiment I which was run only in Spring Brook.

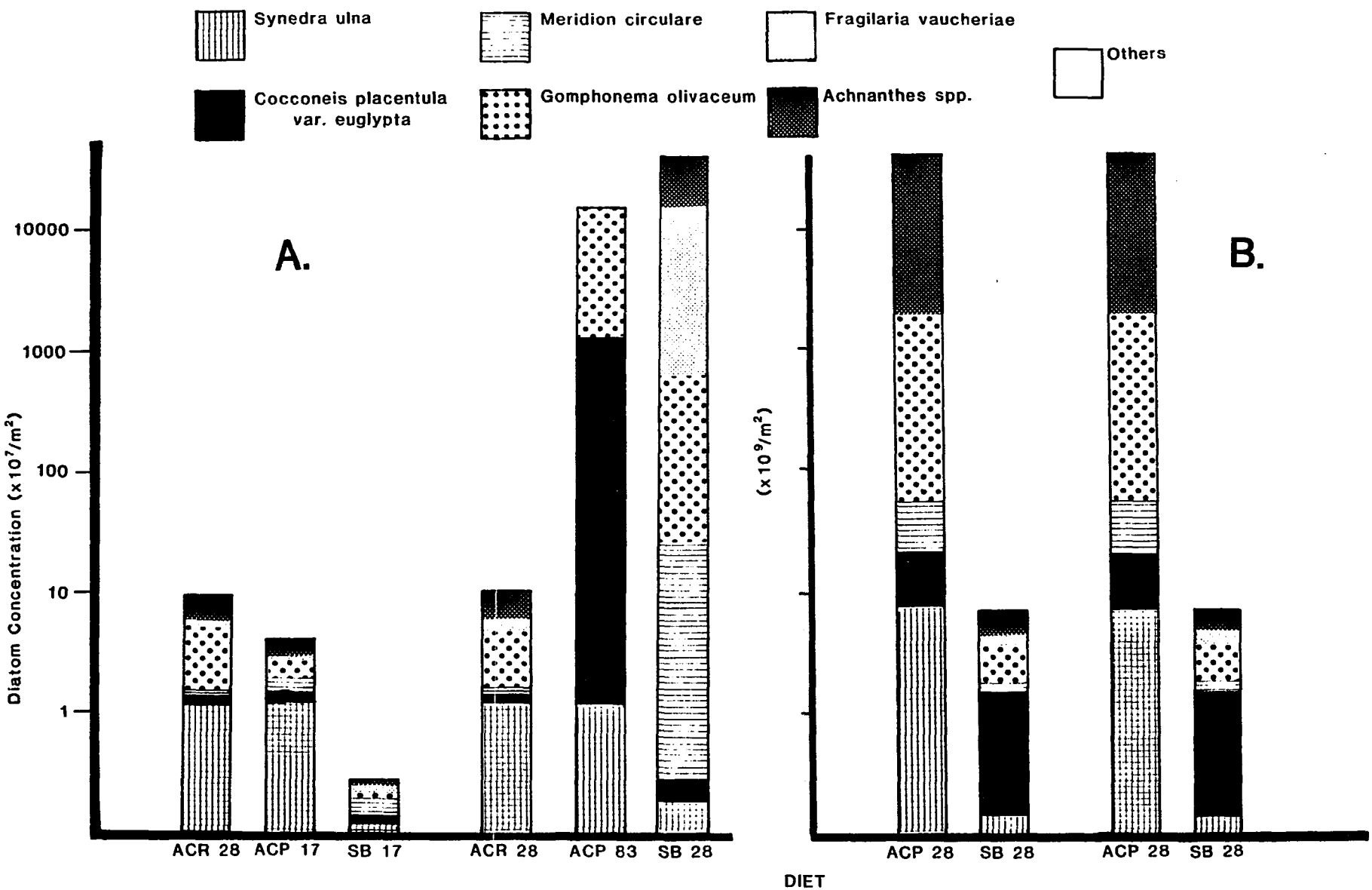
Synedra ulna
Meridion circulare
Fragilaria vaucheriae
Others
Cocconeis placentula var. euglypta
Gomphonema olivaceum
Achnanthes spp.
A.
B.
Diatom Concentration (x10⁷/m²)
(x10⁹/m²)
10000
1000
100
10
1
ACR 28
ACP 17
SB 17
ACR 28
ACP 83
SB 28
ACP 28
SB 28
ACP 28
SB 28
DIET

Figure 15.

Figure 16. Results of Test II, showing diatom concentrations in each diet and for two important species.

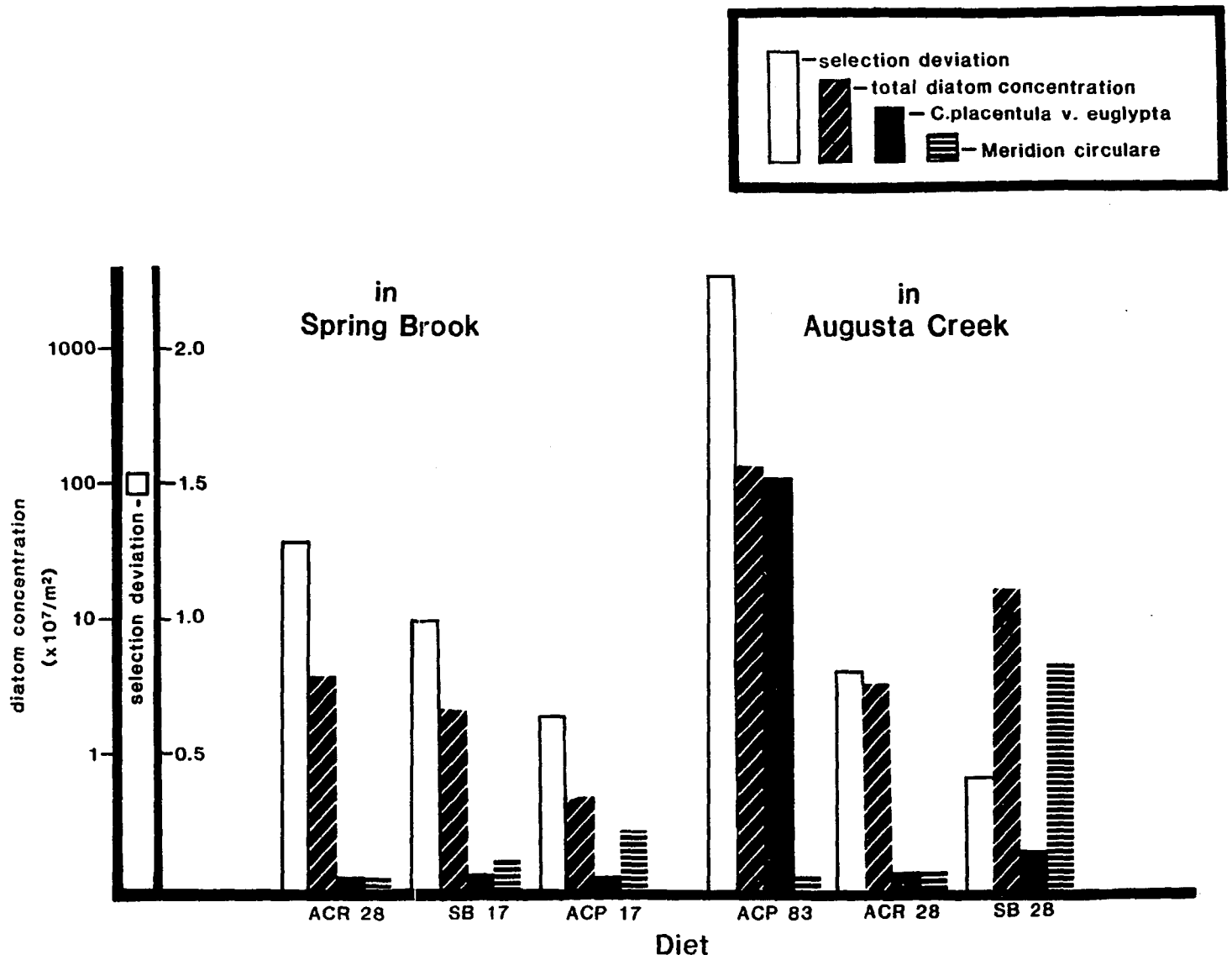
selection deviation
total diatom concentration
C.placentula v. euglypta
Meridion circulare
in
Spring Brook
in
Augusta Creek
diatom concentration
(x10⁷/m²)
selection deviation
1000
100
10
1
2.0
1.5
1.0
0.5
ACR 28
SB 17
ACP 17
ACP 83
ACR 28
SB 28
Diet

Figure 16.

Table 26. Analysis of variance from experiment II, testing the significance of time and diet in accounting for larval movements when offered a diet choice.

Two way ANOVA (without replication).

Source of var.	D.F.	S.S.	M.S.	F.
TIMES	7	102.9	14.7	1.39
DIETS	3	136.4	454.8	43.03**
ERROR	21	22.1	10.6	

** F(3,21).001 = 7.94

increased, and when the concentration of Meridion ciruculare increased in the diet, selection frequency was decreased (Figure 16).

Using a selection deviation index, based on numbers of larvae observed on a diet divided by the number expected, allowed comparisons which included information and results from all diets from both experiments (Figure 17). Selection deviation for each diet was then regressed on the log concentrations of Cocconeis placentula var. euglypta minus Meridion circulare (Figure 18). An R^2 value of .80 indicated that most of the variability in the selection deviation values could be accounted for by the concentrations of these two diatom species. It appeared that C. placentula var. euglypta indeed acted as a stimulator species, and M. circulare as an inhibitor species (negative effect on diet selection). A step wise multiple regression including the log of the total diatom concentration, gave an overall R^2 value of .92. This indicated that the total concentration of diatoms was less a determining factor in diet selection for these two experiments than were the respective concentrations of the two individual diatom species. A negative coefficient indicated that total diatom concentration had a negative effect on diet selection at the concentrations present during the tests.

5.2.7 Diatom Species Preferred by G. nigrior Larvae

The gut contents of instar groups were analyzed for G. nigrior larvae collected from Augusta Creek and Spring Brook from April 15, 1977 to February 23, 1979. Twenty four major diatom species were followed and relative gut percentage abundances recorded for each

Figure 17. Combined experimental results showing selection deviation, total diatom concentration, and concentration of two important diatom species for each diet.

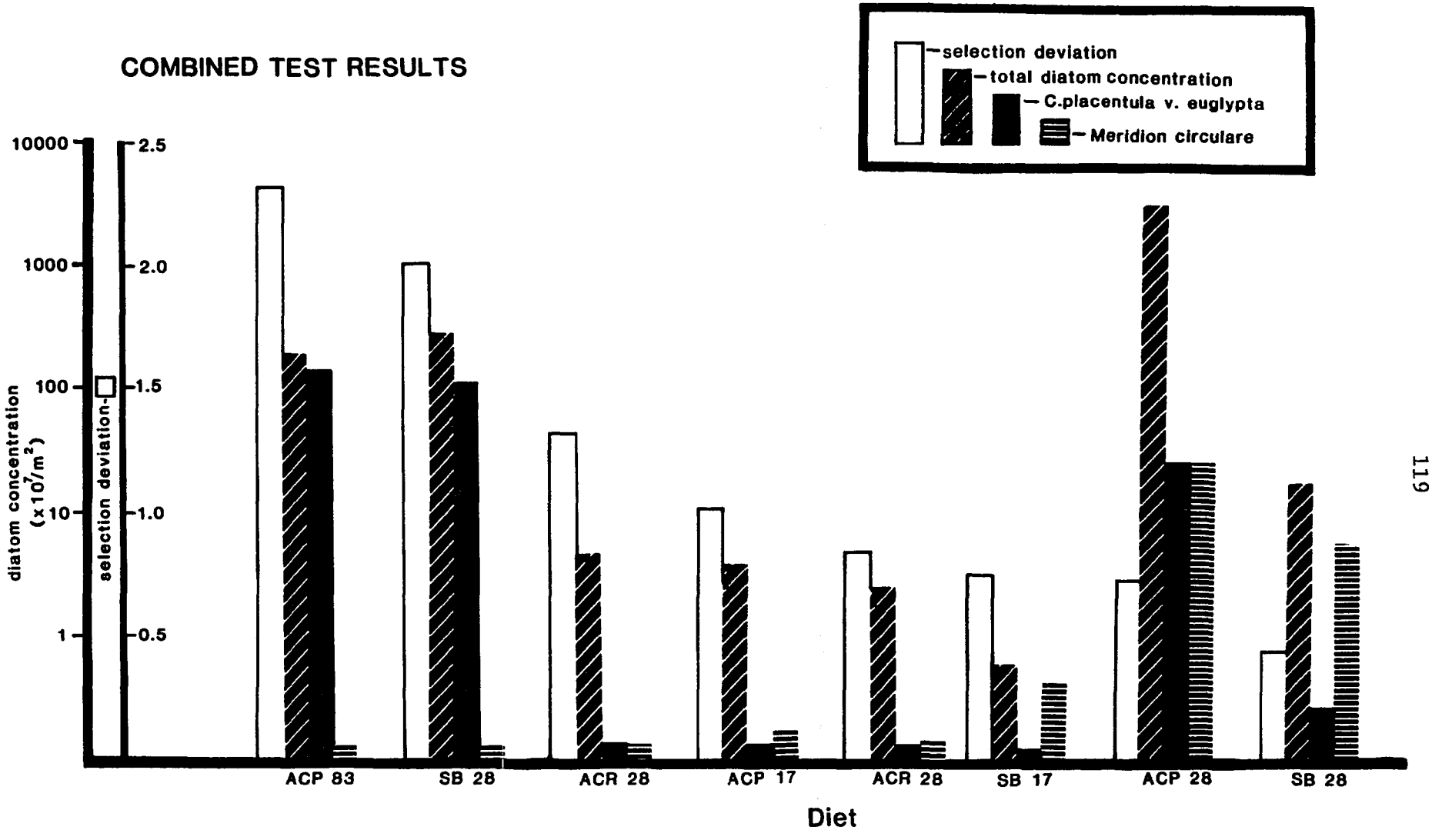
COMBINED TEST RESULTS
selection deviation
total diatom concentration
C.placentula v. euglypta
Meridion circulare
10000
1000
100
10
1
diatom concentration (x10⁷/m²)
selection deviation
2.5
2.0
1.5
1.0
0.5
ACP 83
SB 28
ACR 28
ACP 17
ACR 28
SB 17
ACP 28
SB 28
Diet

Figure 17.

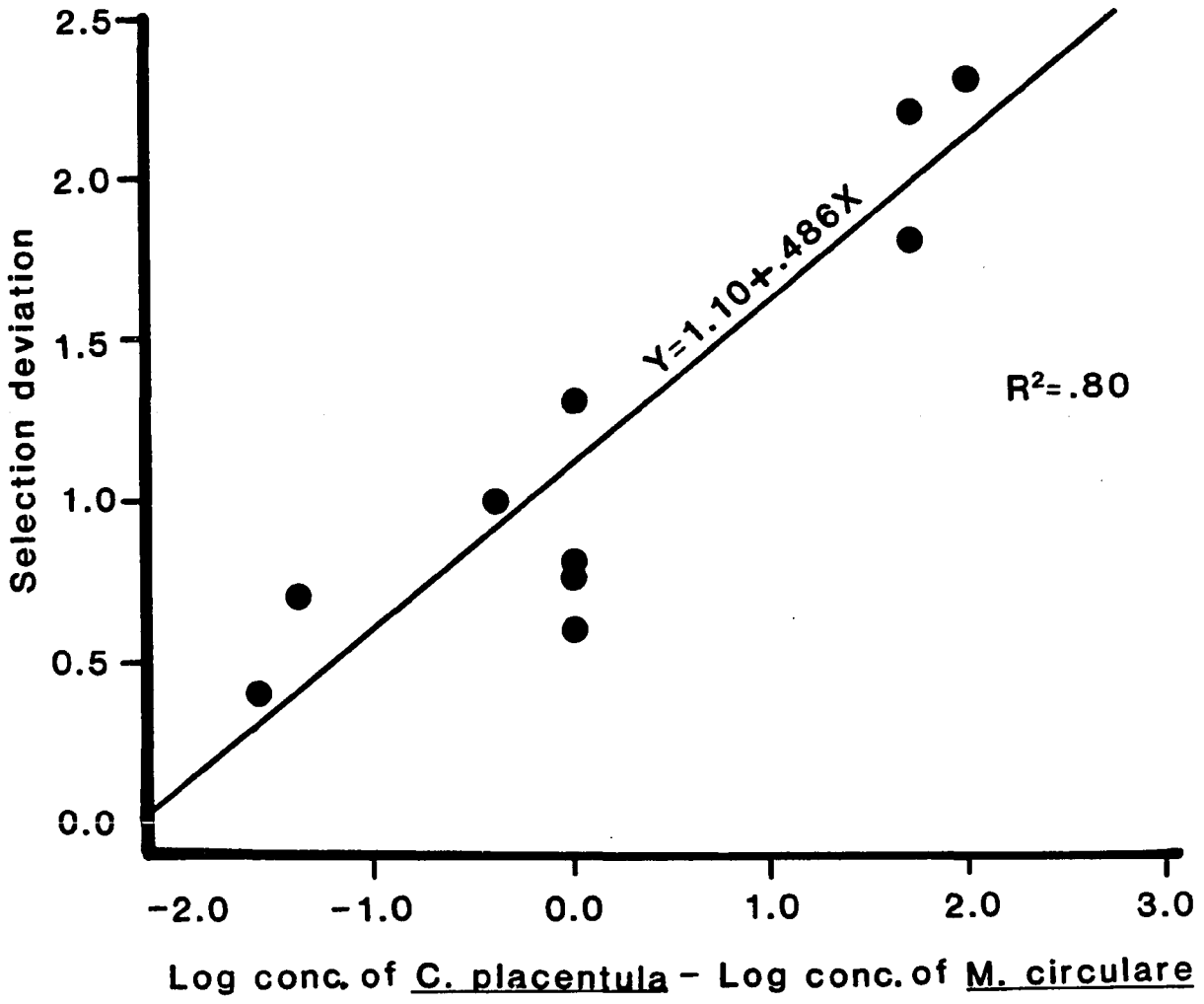

Figure 18. Regression line obtained from relating selection deviation to the concentrations of the two diatom species, Cocconeis placentula v. euglypta and Meridion circulare.

diatom species by instar group I-V, over twenty two sample dates for Augusta Creek. Twenty two major diatom species were followed for twenty sample dates from Spring Brook. The relative percent availabilities of these main diatom species were measured from periphyton samples collected at the same time as the larvae. A total of 216 larval guts were examined from Augusta Creek and approximately 15,250 diatom cells ennumerated. Spring Brook guts examined totaled 344 with approximately 17,250 diatoms identified and counted. The results of the diatom usage-availability analysis from Johnson (1980), showed considerable differences of usage rank and availability rank among major diatom species for Augusta Creek larvae, and for Spring Brook larvae (Table 27 and 28). Diatom preferences were observed to change between season and between instars within each stream (Table 27 and 28). Cocconeis placentula var. euglypta ranked 10th in preference value for all instars measured in the fall, 8th in the winter, and 3rd in the spring and summer for Augusta Creek (Table 27). C. placentula var. euglypta ranked 7th in preference value in the fall, 6th in winter, and 3rd in spring and summer for Spring Brook (Table 28). Considering that over 500 guts were examined with over 30,000 diatoms counted, this similarity between preference value rankings for the same diatom species from two different order streams is remarkable.

The overall diatom preference ranking using mean values for all instar group combined across sampling seasons are shown for Augusta Creek in Table 29 and for Spring Brook in Table 30. A comparison of the preference rankings of the diatom species between the two streams also shows a remarkable consistency in both those species most preferred (top of the list) and those least preferred (bottom of the

Table 27. Difference between usage rank and availability rank (=preference value, P.V.) and resulting preference rank for 24 major diatom species from Augusta Creek. Based on results from computer program "PREFER" (JOHNSON 1980) .

DIATOM SPECIES	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK
	-- FALL[1] --		-- WINTER --		-- SPRING --		-- SUMMER --		-- V-INSTAR[2] --		-- IV-INSTAR --		-- III-INSTAR --		-- II INSTAR --		-- IV-V INSTAR --		--I+II+III INSTAR --	
Achnanthes affinis	0.23	12	-3.57	2	-0.88	2	0.54	7	-4.33	3	-1.55	5	0.23	8			-3.24	4	-0.71	10
Achnanthes clevei	1.52	17	-0.04	5									1.92	13			0.76	17	-0.45	11
Achnanthes lanceolata	2.92	19			1.62	7	1.73	11	5.43	21	2.07	17	1.88	12			2.23	19		
Achnanthes linearis	0.23	13	-1.64	3			-0.77	4	-5.07	2	-0.42	9	-0.78	4	1.43	6	-2.60	7	-1.26	7
Amphora perpusilla	-7.67	2	0.39	9			-0.41	5	2.28	15	-2.66	3	-2.08	2	-1.14	2	-2.66	6	-6.64	2
Cocconeis diminuta	2.25	18															3.93	21		
Cocconeis pediculus	1.10	15							0.50	11	-0.32	10	-1.00	3	-1.00	3	0.01	12	-1.59	6
Cocconeis placentula v. euglypta	-0.63	10	0.32	8	-0.38	3	-1.00	3	-2.76	4	-1.55	6	-0.50	5	0.00	4	-1.11	11	-1.00	9
Cymbella minuta v. silesiaca	3.14	20	0.11	6	-0.38	4	1.64	10	3.33	17	0.42	12	1.50	10	1.93	7	0.24	15	0.05	12
Cymbella sinuata	-9.83	1	-3.68	1	-3.06	1	-2.63	1	-6.57	1	-6.76	1	-4.12	1	-1.79	1	-9.23	1	-8.23	1
Diatoma vulgare	9.10	24							3.74	18							5.44	22	4.81	17
Fragilaria vaucheriae	-0.71	9	2.39	12							1.16	14					0.61	16		
Gomphonema angustatum	-2.50	8	1.11	10	0.81	6	1.50	9	0.29	10	-0.08	11					-2.11	9	0.50	13
Gomphonema olivaceum	-3.39	6	0.11	7	0.125	5			-2.62	6	-0.82	7	-0.12	7			-1.95	10	-1.09	8
Gomphonema tenellum	-2.58	7					0.77	8	-2.45	7	-2.55	4	1.46	9	-0.29	5	-3.30	3	-2.02	4
Melosira varians	7.89	23															2.25	20		
Meridion circulare	-3.77	4	2.36	11					1.40	13							-2.19	8		
Navicula cryptocephala	-3.77	5	-0.36	4					-2.00	8	0.42	13					0.09	14	-1.69	5
Navicula radiosa v. tenella	-0.58	11					-0.18	6	-2.74	5	-0.47	8	1.58	11			3.05	5	0.52	14
Navicula salinarum v. intermedia	1.3C	16							1.52	14	1.50	16					1.18	18	2.45	16
Navicula tripunctata	6.48	22	2.50	13	2.13	8			2.54	16	6.87	18					5.50	23	6.59	19
Nitzschia dissipata	0.35	14							0.52	12	1.39	15					0.03	13	0.90	15
Rhoicosphenia curvata	-6.65	3					-1.18	2	-0.86	9	-3.92	2	-0.23	6	-0.71	3	-4.52	2	-4.14	3
Synedra ulna	5.42	21							4.10	20							8.04	25	5.67	18

1--Based on gut analysis for all instars found by season.

2--Based on gut analysis from all dates when instars present.

Table 28. Difference between usage rank and availability rank (=preference value, P.V.) and resulting preference rank for 22 major diatom species from Spring Brook. Based on results from computer program "PREFER" (JOHNSON 1980) .

DIATOM SPECIES	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK	P.V.	RANK
Achnanthes affinis	-0.81	9	-4.94	1	0.15	5	-4.00	5	-2.36	6	-2.71	4	-1.79	5	0.10	5	0.50	4	-2.72	6	-2.32	6
Achnanthes clevei	2.51	19	0.21	8			-1.70	7	0.00	12	0.97	12	2.82	14	0.80	7			0.35	12	1.91	16
Achnanthes lanceolata	0.61	14	1.32	9	1.05	8	0.27	10	1.40	15	1.50	13	2.03	12	0.55	6			1.34	15	0.16	11
Achnanthes lanceolata v. dubia	1.48	16	-4.18	5	0.05	4	-0.19	9	-0.52	10	-0.24	8	-0.29	9	0.90	8	1.30	5	-0.68	9	-1.09	9
Achnanthes linearis	-1.96	4	-2.15	7	1.30	9	-4.19	4	-1.81	7	-2.29	7	-1.76	6	2.05	10			-2.32	7	-1.73	7
Achnanthes rupestris	-1.50	6					-5.11	2	-2.50	4	-2.71	5	-2.76	4					-3.05	5	-3.89	3
Amphora perpusilla	-4.43	2	-4.88	3	-2.35	1	-3.94	6	-3.86	2	-4.45	2	-4.09	2	0.21	2	0.20	3	-4.56	2	-5.37	2
Coconeis diminuta	3.59	20	2.29	12			4.22	16	6.07	21	5.37	19	3.74	16	1.65	9			6.00	22	2.23	17
Cocconeis pediculus	4.52	21	1.85	11			2.10	13	1.64	16	2.89	16	3.32	15					2.31	17	3.32	20
Cocconeis placentula v. euglypta	-1.35	7	-3.41	6	-1.56	3	-4.92	3	-1.76	8	-3.71	3	-1.88	3	-2.30	1	-0.40	2	-3.05	4	-3.73	4
Cymbella sinuata	-8.07	1	-4.59	4	-1.90	2	-10.36	1	-6.43	1	-7.24	1	-6.03	1	-0.45	4	-1.60	1	-7.59	1	-8.62	1
Diatoma vulgare	2.16	17	4.26	15					0.95	13	2.50	14							1.79	16	2.83	19
Fragilaria vaucheriae	-1.78	5	2.82	13			3.05	14	2.23	17	2.58	15	2.79	13					2.42	18	1.56	14
Gomphonema olivaceum	-2.56	3	-4.94	2	0.60	7			-3.38	3	-2.68	6	-1.38	8	-1.20	3			-3.46	3	-3.06	5
Melosira varians	2.22	18	4.17	14			9.97	18	4.29	20	4.12	17							4.59	20	5.69	21
Meridion circulare	-0.61	11	1.82	10	2.45	10	-0.61	8	1.21	14	0.95	11	2.03	11					1.05	14	0.55	13
Navicula radiosa v. tenella	-0.15	12							-2.43	5	-0.21	9	-1.44	7					-1.62	8	-1.67	8
Navicula species #1	-0.72	10					2.27	12	-0.26	11	-0.03	10	0.59	10					-0.35	10	0.34	12
Navicula tripunctata	6.41	22	4.58	16			9.27	17	4.07	19	5.13	18	6.12	17					4.81	21	8.25	22
Nitzschia dissipata	-0.85	8			0.20	6	3.36	15	-0.55	9									0.51	13	1.93	15
Nitzschia linearis	0.24	13																	0.24	11	0.03	10
Synedra ulna	1.04	15	5.74	17			0.69	11	3.97	18									4.00	19	2.90	18
	-- FALL[1] --		-- WINTER --		-- SPRING --		-- SUMMER --		-- V INSTAR[2] --		-- IV- INSTAR --		-- III INSTAR --		-- II INSTAR --		-- I INSTAR --		-- V+IV INSTAR --		--I+II+III-- INSTAR	

1--Based on gut analysis for all instars found by season.

2--Based on gut analysis from all dates when instars present.

Table 29. Diatom species preference rankings for all instars over all seasons from Augusta Creek.

Rank	Diatom species
1.	Cymbella sinuata
* 2.	Rhoicosphenia curvata
3.	Achnanthes affinis
4.	Amphora perpusilla
* 5.	Gomphonema tenellum
6.	Achnanthes linearis
7.	Cocconeis placentula var. euglypta
8.	Gomphonema olivaceum
* 9.	Navicula cryptocephala
10.	Navicula radiosa var. tenella
11.	Cocconeis pediculus
12.	Meridion circulare
* 13.	Gomphonema angustatum
* 14.	Cymbella minuta var. silesiaca
15.	Achnanthes clevei
16.	Fragilaria vaucheriae
17.	Nitzschia dissipata
18.	Achnanthes lanceolata
* 19.	Navicula salinarum var. intermedia
20.	Navicula tripunctata
21.	Cocconeis diminuta
22.	Diatoma vulgare
23.	Melosira varians
24.	Synedra ulna

*--Diatom species analyzed for larval feeding preferences from Augusta Creek only.

Table 30. Diatom species preference rankings for all instars over all seasons from Spring Brook.

Rank	Diatom species
1.	Cymbella sinuata
2.	Amphora perpusilla
3.	Cocconeis placentula var. euglypta
* 4.	Achnanthes rupestris
5.	Gomphonema olivaceum
6.	Achnanthes affinis
7.	Achnanthes linearis (inc. f. curta)
8.	Navicula radiosa var. tenella
9.	Achnanthes lanceolata var. dubia
* 10.	Navicula sp. 1
11.	Nitzschia dissipata
12.	Achnanthes lanceolata
* 13.	Nitzschia linearis
14.	Meridion circulare
15.	Achnanthes clevei
16.	Fragilaria vaucheriae
17.	Diatoma vulgare
18.	Cocconeis pediculus
19.	Synedra ulna
20.	Cocconeis diminuta
21.	Melosira varians
22.	Navicula tripunctata

*--Diatom species analyzed for feeding preferences from this stream only.

list). In both streams the most preferred species was Cymbella sinuata, and the next to the last preferred was Melosira varians. Amphora perpusilla also appears high on the preference list from both streams, as do Gomphonema olivaceum, Achnanthes affinis, and Achnanthes linearis. While the precise rank of the preferred diatom species shifted from season to season (Tables 27 and 28), Cymbella sinuata remained in the most preferred position for all instar groups from Augusta Creek averaged over all sampling periods and seasons. This same diatom species was constantly ranked in the top four for all analyses run from Spring Brook.

The last analysis of diatom preferences included combining all the gut study data from Spring Brook and Augusta Creek. The large IV and V instars were considered together, and the smaller I-III instars together. Rankings for the major diatom species are shown in Table 31. C. sinuata was again significantly more preferred than all other diatom species available in both analysis.

The preferred selection by larvae in two different streams for C. sinuata provides support for the existence of a very precise selection mechanism being used by grazing larvae. This diatom occurred on natural substrates at relative abundance levels nearly always less than 6% of the total diatom community in Augusta Creek and less than 2% in Spring Brook. However, relative abundance of this diatom in the guts of the larvae on occasion exceeded 16% for Spring Brook and over 56% for Augusta Creek larvae (Figure 11). While such differences between availability and usage existed for some other diatom species like, Cocconeis placentula var. euglypta and Achnanthes spp., no other diatom

Table 31. Preference rank for the common diatom species ingested by instars I-V from Augusta Creek and Spring Brook.

Rank	Diatom species
1.	Cymbella sinuata
2.	Amphora perpusilla
3.	Gomphonema olivaceum
4.	Achnanthes affinis
5.	Cocconeis placentula var. euglypta
6.	Achnanthes linearis
7.	Navicula radiosa var. tenella
8.	Meridion circulare
9.	Achnanthes clevei
10.	Achnanthes lanceolata
11.	Nitzschia dissipata
12.	Cocconeis pediculus
13.	Fragilaria vaucheriae
14.	Diatoma vulgare
15.	Cocconeis diminuta
16.	Melosira varians
17.	Synedra ulna
18.	Navicula tripunctata

species showed the nearly constant, number one preference rank when analyzed statistically across instars for both streams.

The reasons for such a distinct choice remain at present obscure. It is possible that a biochemical analysis may indicate some essential nutrient only available in this diatom species. It is likewise possible that selection may be governed by the presence of allelochemicals (Slansky 1981). Terrestrial phytophagous insects are known to be strongly influenced by olfactory and gustatory stimuli resulting from compounds present in their food (Chapman 1974, Dethier 1980, Gordon 1968). Recent work indicates that mosquito larvae can respond to the presence of minute quantities of chemical substances released into the water from cells of water soaked seeds (Barber et al. 1982). Similar chemical compounds released from the cells of Cymbella sinuata could, theoretically stimulate or promote larval feeding. Future research will hopefully elucidate such possibilities. Precise selection for a single species of diatom by a large density of grazers might significantly decrease the diatom's abundance in the periphyton. The fact that Spring Brook periphyton contained a smaller average abundance for Cymbella sinuata (2% vs. 6% for Augusta Creek) and also had a much larger larval density than Augusta Creek might imply some cause and effect. Warren (1971) suggested that in systems of very similar capacity to produce food, largest consumer biomass is associated with lowest food standing crops, i.e., resource depression occurs. The observed lack of significance between measured diatom densities throughout this study between Augusta Creek and Spring Brook might indicate the similarity of these two streams in the production of diatoms, and support the idea that the larger grazer densities measured

in Spring Brook have in fact lowered the density of the most preferred diatom species. If, however, the production capacity of Augusta Creek was greater than Spring Brook one might expect to see a greater grazer biomass (Hawkins and Sedell 1981). Because the comparisons of diatom density showed no significant differences does not mean that total production between the two streams was the same. Augusta Creek revealed much more algae when green algae and blue-greens, along with diatoms were measured than Spring Brook. It thus may be that the quality of the food or the "right production" of algal species is necessary before increases in grazer biomass can be expected to occur.

5.2.8 Impact of larval grazing on diatom densities

The number of diatoms present in the gut contents of each instar show a substantial range in values over the duration of this study. Table 32 presents the mean values calculated for each instar group from their respective stream and shows the ranges of diatom gut densities encountered. Fluctuations in gut diatom concentration for the same instar group of nearly 40 fold were observed when measured at different months of the year. A great proportion of these fluctuations in gut contents were attributable to changes in diatom densities in the streams.

To better understand the consequences of these fluctuations, the respective instar densities were used to calculate the potential impact of each instar group on the diatom density by calculating the numbers of diatoms ingested for each instar group on a daily basis (Table 33). Periods of seasonal change were selected for analysis to cover corresponding periods of change in both larval and periphyton densities. Larval grazing shows the least effect on the diatom community in the spring of the year, ingesting only between 0.1-1.2% of the available periphyton. In Augusta Creek the larvae would graze less than 1% of the available food, daily throughout the spring, summer, and fall. In winter however, the larvae in Augusta Creek would ingest about 16% of the total available diatoms on a daily basis, assuming no reproduction by diatoms. The ingestion rate used for this calculation was measured at approximately $10^{o}C$ and may be substantially lower for larvae feeding in the winter water temperatures near $0^{o}C$ recorded from Augusta Creek. However, even if the ingestion rate is

Table 32. Total mean gut diatom concentrations for I-V instars from Spring Brook and Augusta Creek. (From all sample periods April 1977 - February 1979)

# MONTHLY SAMPLES	STREAM	INSTAR	MEAN NUMBER DIATOMS IN GUT	RANGE
20	Spring Brook	V	$8.375\ 10^{4}$	$1.6 \times 10^{4} - 3.2 \times 10^{5}$
21	Augusta Creek	V	$8.647\ 10^{4}$	$8.9 \times 10^{3} - 2.0 \times 10^{5}$
18	Spring Brook	IV	$2.347\ 10^{4}$	$2.5 \times 10^{3} - 9.1 \times 10^{4}$
19	Augusta Creek	IV	$2.659\ 10^{4}$	$6.6 \times 10^{3} - 6.4 \times 10^{4}$
16	Spring Brook	III	$7.147\ 10^{3}$	$7.1 \times 10^{2} - 2.6 \times 10^{4}$
13	Augusta Creek	III	$6.885\ 10^{3}$	$4.8 \times 10^{2} - 1.9 \times 10^{4}$
10	Spring Brook	II	$1.391\ 10^{3}$	$1.6 \times 10^{2} - 4.9 \times 10^{3}$
7	Augusta Creek	II	$3.214\ 10^{3}$	$4.6 \times 10^{2} - 1.1 \times 10^{4}$
5	Spring Brook	I	$3.656\ 10_{2}^{2}$	$3.1 \times 10^{2} - 5.7 \times 10^{2}$
1	Augusta Creek	I	$4.148\ 10$	

Table 33. Seasonal impact of larval grazing on stream diatom concentrations. Calculations based on quantitative samples of larvae and diatoms.

SPRING BROOK

Season	Instar	Instar-Density (No./m^2)	Diatoms ingested[1] (No./IND.·Day^{-1})	Percent of available[4] diatoms ingested by population[2]
Spring (1978)	II	39.0	1.1128×10^4	0.003
	III	312.0	1.0231×10^4	0.021
	IV	149.5	3.2826×10^5	0.317
	V	123.5	1.0198×10^6	0.814
		642.0		1.155
Summer (1978)	I	62.3	4.5266×10^3	0.011
	II	118.9	1.6958×10^4	0.080
	III	164.0	1.4204×10^5	0.919
	IV	181.0	3.6636×10^5	2.616
	V	39.6	1.8596×10^5	0.291
		565.8		3.907
Fall (1978)	II	119.1	1.9727×10^4	0.039
	III	281.5	1.3903×10^4	0.065
	IV	389.8	1.5463×10^5	1.000
	V	184.1	8.4744×10^5	2.579
		974.5		3.683
Winter (1978)	II	21.8	6.7583×10^3	0.003
	III	436.0	1.0011×10^4	0.094
	IV	207.0	9.9816×10^4	0.443
	V	185.3	6.5154×10^5	2.591
		850.1		3.131
Winter (1979)	II	21.8	1.1128×10^4	0.026
	III	436.0	1.9863×10^4	0.924
	IV	207.0	2.2952×10^5	5.068
	V	185.3	7.0187×10^5	13.870
		850.1		19.887

Table 33 (continued)

Augusta Creek

Season	Instar-Density (No./m^2)		Diatoms ingested[1] (No./IND.·Day^{-1})	Percent of available[4] diatoms ingested by population[3]
Spring (1978)	III	13.9	$3.5931 \times 10^{3}_{3}$	0.001
	IV	28.8	$6.6104 \times 10^{3}_{4}$	0.001
	V	56.6	7.2800×10^{4}	0.092
		99.3		0.094
Summer (1978)	V	7.0	5.4640×10^{4}	0.179
		7.0		0.179
Fall (1978)	I	3.5	$4.1480 \times 10^{2}_{3}$	0.001
	II	10.6	$1.8428 \times 10^{3}_{3}$	0.001
	III	7.0	$4.0762 \times 10^{3}_{4}$	0.001
	IV	31.8	9.2068×10^{4}	0.180
		52.9		0.183
Winter (1978)	--	--	--	--
Winter (1979)	III	6.6	$2.0200 \times 10^{3}_{3}$	0.001
	IV	6.6	$3.5300 \times 10^{3}_{4}$	0.001
	V	85.7	5.8800×10^{4}	16.200
		98.9		16.202

1--Based on a gut filling time of 3 hours, with gut diatom concentrations measured on date collected.

2--Spring Brook diatom densities: March-1978 $1.5469 \times 10^{10}/m^2$, August-1798 $2.5345 \times 10^{9}/m^2$, Oct. and Nov.-1978 $6.0478 \times 10^{9}/m^2$. Feb.-1979 $4.6596 \times 10^{9}/m^2$, Feb.-1978 $9.3750 \times 10^{8}/m^2$.

3--Augusta Creek diatom densities: March-1978 $3.5795 \times 10^{10}/m^2$, August-1978 $1.7070 \times 10^{9}/m^2$, Oct. and Nov.-1978 $1.2751 \times 10^{10}/m^2$, Feb.-1979 $2.4911 \times 10^{8}/m^2$.

4--Percent of available diatoms ingested per day, assuming no diatom reproduction.

halved, the larvae would still be ingesting approximately 8% of the available food on a daily basis. Spring Brook data show that larvae ingested consistently more of the available periphyton, about 3.6% from summer, fall and winter periods. It is possible that Spring Brook larvae have a significant effect of the algae throughout the year by constantly depleting algae from rock surfaces, which continually opens additional sites for algal colonization while keeping total algal densities low. McIntire (1973) observed that a low periphyton biomass could support a high biomass of herbivores if the system was adequately productive. The large effect the Spring Brook larvae have on the available diatom populations indicates that only the high turnover of algae in this stream maintains the high densities of G. nigrior larvae. The very large effect grazing may exert on the periphyton population is shown for Spring Brook during the winter season (February) of 1978 in Table 33, when the combined total larval grazing accounted for approximately 20% of the total diatom population per day. This is very close to the observed (16%) maximum daily effect calculated for Augusta Creek in the winter of 1979.

The relative abundance of each instar group in the total larval population can also shift the impact of grazing on the diatom populations. The relationships between the amounts of diatoms ingested by each instar group shows that V instars consume over 4 times the number of diatoms as IV instars and 250 times the number as I instars (Figure 19). A large population of IV and V instars actively feeding throughout the winter period could severely depress periphyton

Figure 19. Gut diatom concentrations for instars I-V and relative differences between instars, data from both streams over all sampling periods.

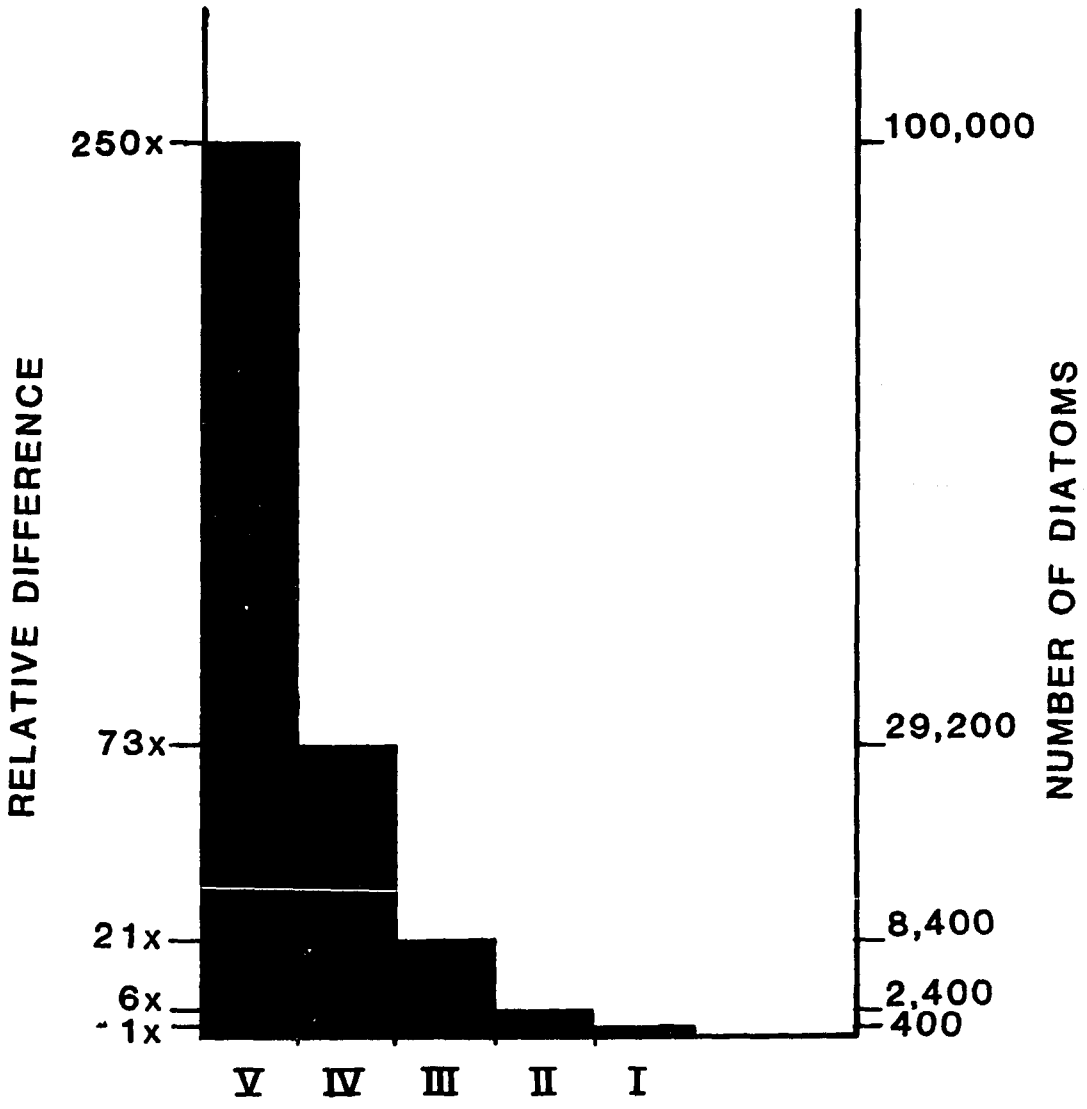
250x
73x
21x
6x
1x
RELATIVE DIFFERENCE
100,000
29,200
8,400
2,400
400
NUMBER OF DIATOMS
V
IV
III
II
I

Figure 19.

density levels. It is also noteworthy that the winter period of low periphyton production is associated with high proportions of diatoms in the larval guts (Figures 15-16) and high densities of V instars (Table 33). Potential overgrazing in winter periods may strip surfaces clean of algae, facilitating algal colonization and potential rapid increases in diversity during spring, when light and nutrient levels rise. In this manner high larval grazing pressures may serve to reset the algal community to low algal concentration levels immediately prior to peak spring growth of the periphyton. The scouring effects of floods on the periphyton community during spring and the potential overgrazing by larvae in winter may keep periphyton communities at reduced levels or in early stages of succession (Hunter 1980).

In Spring Brook maintaining early successional stages of algae would favor the continued periphyton dominance by small diatom unicells. High grazing pressure may thus be self-serving to the G. nigrior larval populations in Spring Brook by providing open rock surfaces throughout the year which act as colonization sites for rapidly growing diatom unicells, which are ingested in preference to larger diatoms. Cocconeis placentula var. euglypta is a rapid colonizer and thus, may be maintained at high substrate concentrations by continually high grazing pressure. Intensive grazing in diatom dominated headwaters may thus, decrease algal diversity by reducing all algal levels because of the high feeding rates, thus favoring diatom unicells which are quickly replaced through their rapid growth, while larger algae are not (Laws 1975). This keeps algal diversity

low or at early successional stages (Summer and McIntire 1982).

In Augusta Creek the high grazing pressure in the winter (Table 33) and the possible depression of the algal standing crop may serve to prevent filamentous or colonial algae from completely dominating the substrates and eventually eliminating diatom unicells. Grazers in third order streams may increase diversity by mechanically dislodging large filamentous algae during feeding movements, or possibly ingesting the larger algal forms in the case of late instars. Both activities serve to increase light penetration and nutrient exposure to underlying cells and even to open new sites for diatom unicell colonization. These activities maintain higher food quality (low C:N ratio) by stimulating diatom growth (increased nitrogen) and reducing the amounts of filamentous green algae which contain more cellulose (high C:N ratio) in their cell walls (Hunter 1980).

Grazers may thus modify the quantity of available algae, through feeding, as well as the quality of the available algae, through preferentially selecting preferred algal species. This later selection may ultimately further enhance food quality by maintaining a high turnover or vigorous growth of the preferred algal species.

6.0 SUMMARY AND CONCLUSIONS

Glossosoma nigrior larvae were separated by head capsule width into five instars. Temporal distributions compared the contribution of each instar to the total larval population. Temporal distributions and gut volume calculations indicated that the fifth instar is present throughout most of the season and that this last instar ingests the most diatoms. Examinations of feeding rates and gut contents volume over 24 hours permitted calculations of grazing impact to assess the importance of each larval instars feeding on the standing crop of the periphyton. The continuous feeding by the instars can remove up to 20% of the diatom standing crop on a daily basis, assuming no growth by the diatoms. High assimilation efficiencies of 73% agreed with results obtained by other researchers for other invertebrates feeding on diatoms (Hargrave 1970). The high assimilation efficiency indicated that diatoms are a good source of nutrition for the larvae.

Diatom mean volumes determined for each instar indicated that in general the smaller the larvae, the smaller the volume of the diatom likely to be ingested. The differences in mean diatom cell volumes between instars infers some mechanism for selection of diatom species based on microscopic volume differences. The actual volumes of even the larger individual diatom cells are much smaller than mouthpart sizes of even the smallest I instars. Yet, when individual diatoms grow together, their colony or total aggregated size may be large enough to deter selection, particularly by the samll instars. Since many of the larger diatoms measured grew either colonially or as

filaments (Diatoma and Melosira), basing diatom preferences on the individual diatom species cell volume may be incorrect. Large V instars were capable of ingesting colonial diatoms while early instars were not. The larger mean diatom cell volume in the guts of increasingly larger instars probably reflected the fact that colonial diatoms could be harvested more easily and not that selection of diatoms was based on the individual cell volume.

Diatom species lists indicated that the common diatom species present in both streams were similar, with only 1-6 out of the top 25 major species different for each stream. Diatoms most preferred by all larvae were small unicells, while larger, colonial or filamentous diatoms were least preferred. The similarity between the top diatom species preferred and the bottom species least preferred was very high, comparing Augusta Creek results to Spring Brook's. Analysis of survivorship of diatoms in the feces indicated that some of the diatoms least preferred had the highest percent survivorship in the feces, particularly some large colonial forms. Cocconeis placentula var. euglypta, one of the top preferred diatoms showed the least percent survivorship in the feces.

Larvae were tested and found able to discriminate between periphyton diets. Analysis indicated that discrimination was based on the species composition of the diets, with certain species of small unicells increasing selection rates and other species of colonial habit decreasing selection. Larval growth measured in the laboratory, using two periphyton diets from Augusta Creek or Spring Brook, indicated that temperature was the most significant factor contribut-

ing to variability in weight gains, rather than diet ($P<.001$, Table 18). Several researchers have found the interaction of temperature and food quality and quantity hard to separate (Anderson and Cummins 1979, Ward and Cummins 1978, Merritt et al. 1982). It may be virtually impossible to separate the contributing factors of temperature and food which may affect larval growth in stream grazers, particularly if a single species of diatom, preferentially selected from the many different species available, might greatly influence the grazer's overall nutrition. Changes in water temperature can profoundly influence the diatom community by completely changing the diatom species composition (Patrick et al. 1969, Patrick 1971, Whitford and Schumacher 1963, Dillard 1971). It would be hard to separate the effects of a temperature change which are so coupled with species changes in the available periphyton food sources.

Instars I-III showed a greater correlation between the mean volume of diatom present in the gut contents and the mean volume available in the periphyton ($r=.71, P<.05$), than did instars IV-V. The small size of the mouthparts of these early growth stages could make efficient harvesting of diatom unicells impossible when growing intermixed with strands of filamentous algae or very dense growths of diatoms. Such factors may account for the increased abundance of early instars reported by stream researchers in the shaded headwater regions of streams. The cooler temperatures and reduced lighting would encourage a diatom growth of unicells throughout the year in low densities appropriate for efficient operation

of specialized scraping mouthparts. Late instars, having larger feeding structures, would not be restricted from grazing in the downstream zones, where water temperature is increased, light penetration greater, and the resulting periphyton often a mixture of filamentous green and blue-green algae along with more colonial and fewer unicellular diatoms (Patrick 1971).

G. nigrior instars were shown to have similar preferences in selection of diatom species regardless of stream order. Slight differences in preference rank occurred for some diatom species with changes in season or instar. Generally, however, the same diatom species occupied the top and bottom of the preference rankings in both streams. It appears that G. nigrior larvae are discriminating feeders and do not ingest periphyton randomly or based only on availability. The degree of similarity between diatom species most preferred and those least preferred for Augusta Creek and Spring Brook larvae indicated a consistent selection and rejection mechanism operating independantly of stream order.

The dominance by unicellular diatoms in shaded streams throughout the year (Lyford and Gregory 1975) agrees with the observed gut analysis results from Spring Brook. Cocconeis placentula var. euglypta, a small unicell, is a diatom which grows tightly appressed to the rock surfaces and resists ingestion by several other grazing organisms, which are unable to remove it (Moore 1975, 1977a, 1977e, Patrick 1970). The mouthparts of G. nigrior are specialized for harvesting such small diatoms and may even be hindered by filamentous or colonial diatom or algal growths present. Evidence

by Scott (1958) on the interference of silt with effective feeding by Glossosoma indicates the necessity of relatively clean surfaces against which the larval mouthparts can function. The negative effect of increasing diatom density observed in the diet selection tests, gives further support to the existence of an optimal level of periphyton density above which level less selection occurs, because harvesting efficiency diminishes. It is very likely that high grazer densities would not develop in stream regions where silting, or filamentous or colonial algae populations made food harvesting difficult throughout the year. What 'appears' as a large, available food supply in Augusta Creek may be unsuitable regardless of the presence of the preferred food species because of the interference with the mouth parts and labral brushes or tactile organs of G. nigrior larvae by strands of filamentous green or blue-green algae, or even colonial diatoms. These observations may lend support to the idea of McIntire (1973), that a very low biomass of the 'correct' preferred food species can support a large biomass of grazers.

In small headwater regions intensive grazing during the winter period may serve as the stream periphyton reset mechanism. This may be of particular significance in regard to the infrequent occurrence of severe scouring resulting from spring flooding in these smaller headwater streams (Hynes 1970).

In larger third order streams like Augusta Creek, the larvae have less of a direct impact on periphyton because of the greater overall production of periphyton and lower grazer densities. Nevertheless, the results of grazing, coupled with the effects of spring

scouring, may help to maintain a more diverse periphyton community. Intensive grazing may act synergistically with scouring to keep a mixture of the preferred diatom unicells growing with the less preferred filamentous, or colonial diatoms or other algal types.

The greater algal production generally observed in third order streams over first order streams (Hawkins and Sedell 1981, Cummins 1974) may offer a range in periphyton communities from physically simple to complex, from one dominated by unicellular diatoms throughout the year (Lyford and Gregory 1975), to one where diatoms, green algae, and blue-green algae fluctuate in seasonal dominance. The preferences exhibited by G. nigrior larvae for selection of small unicells and their avoidance of diets containing colonial diatoms indicate that the physical make-up of the periphyton and its exact species composition are critical constraints which may affect both the final size of the grazer, as well as its distribution along a stream course.

APPENDIX

Table A-1. Gut volumes for Spring Brook larvae (X ± S.E.) by collection date (mm^3).

	FIFTH INSTAR		FOURTH INSTAR		THIRD INSTAR		SECOND INSTAR		FIRST INSTAR	
date	Mean ± S.E.	n	Mean ± S.E.	n	Mean ± S.E.	n	Mean ± S.E.	n	Mean ± S.E.	n
7/77	2.55 ± .304	6	.491 ± .103	5	.131 ± .023	6				
9/77	1.73 ± .354	4	.399 ± .048	5	.079 ± .011	5	.021 ± .002	5	.008 ± .001	6
10/77	1.96 ± .392	5	.499 ± .127	5	.087 ± .023	5	.033 ± .010	6	.017 ± .003	6
11/77	1.47 ± .151	5	.245 ± .079	5	.072 ± .016	5	.028 ± .005	5		
12/77	0.89 ± .203	4	.334 ± .094	5	.068 ± .022	5	.026 ± .006	5		
2/78	1.15 ± .261	13	.262 ± .068	5	.049 ± .014	4				
3/78	1.89 ± .467	4	.482 ± .117	5	.080 ± .020	6				
4/78	1.63 ± .398	5	.471 ± .083	5	.142 ± .030	2				
5/78	1.03 ± .115	4								
6/78	1.47 ± .252	4	.525 ± .159	4			.036	1		
7/78	2.43 ± .283	12	.254 ± .082	3	.134	1				
8/78	1.65 ± .402	4	.672 ± .301	5	.161 ± .038	5	.026 ± .004	7	.008 ± .002	8
9/78	2.08 ± .457	3	.477 ± .114	5	.126 ± .025	5	.022 ± .006	5	.008 ± .001	7
10/78	1.89 ± .203	5	.489 ± .117	5	.124 ± .026	5	.029 ± .004	7	.009 ± .002	5
11/78	0.92 ± .278	5	.235 ± .041	5	.045 ± .017	5				
12/78	1.56 ± .318	5	.521 ± .112	5	.109 ± .008	5	.035 ± .008	3		
2/79	1.18 ± .155	4	.127 ± .044	5	.043 ± .015	5				
10/80	1.30 ± .124	36	.491 ± .042	34	.097 ± .016	8			.001	1
	TOTAL	128		111		77		44		33

Table A-2. Gut volumes for Augusta Creek larvae (X ± S.E.) by collection date (mm^3).

	FIFTH INSTAR A.C.		FOURTH INSTAR A.C.		THIRD INSTAR A.C.		SECOND INSTAR A.C.		FIRST INSTAR A.C	
date	Mean ± S.E.	n	Mean ± S.E.	n	Mean ± S.E.	n	Mean ± S.E.	n	Mean ± S.E.	n
7/77	1.55 ± .087	5	.185	1	.080	1				
8/77	1.13 ± .412	4	.471 ± .035	2	.107 ± .008	2				
9/77	3.57 ± .722	5	.953 ± .137	5	.136 ± .013	6			.009 ± .0047	2
10/77	3.74 ± .819	5	.688 ± .087	5	.150 ± .019	9	.018	1		
11/77	1.66 ± .259	4	.549 ± .069	5	.113 ± .011	2	.027	1		
12/77	1.17 ± .322	5	.570 ± .138	2						
2/78	1.66 ± .393	10	.342 ± .033	2	.070 ± .005	2				
3/78	2.46 ± 1.042	4	.370	1	.039	1				
4/78	2.20 ± 1.734	2	.393 ± .010	5	.047 ± .010	3				
4/78	3.18 ± 0.500	5	.536	1						
5/78	2.35 ± 0.697	2								
6/78	1.42 ± 0.230	5	.514 ± .090	5	.111 ± .014	5				
7/78	1.41 ± 0.153	13	.477 ± .038	5						
8/78	2.22 ± 0.306	5	.407 ± .060	5	.177	1				
9/78	1.84 ± 0.420	5	.646 ± .112	5	.102 ± .013	7	.024 ± .004	5		
10/78	1.68 ± 0.383	5	.623 ± .162	5	.097 ± .011	5	.022 ± .005	2		
11/78	2.82	1	.497 ± .091	5			.022	1		
12/78	1.82 ± 0.534	5	.515 ± .079	5	.088 ± .013	2				
2/79	1.94 ± 0.445	5	.091	1			.018	1		
	TOTALS	95		65		46		11		2

Table A-3. Mean dry weights of Augusta Creek and Spring Brook I-V instars and pupae.

Stream	n	Instar	Dry weight (X ± S.E.)
Aug. Ck.	16	I	0.0194 ± .002
	8	II	0.0204 ± .01
	4	III	0.0462 ± .007
	28	IV	0.4598 ± .04
	21	V	4.5101 ± .091 ***
	51	Pupae	4.459 ± .089 ***
Spring Brook	38	I	0.0196 ± .002
	58	II	0.0213 ± .004
	82	III	0.0437 ± .009
	56	IV	0.4409 ± .031
	31	V	1.4451 ± .108 ***
	49	Pupae	1.6244 ± .053 ***

*** $p < .001$

Figure A-1. Daily maximum and minimum air temperatures recorded at Spring Brook (^{o}F).

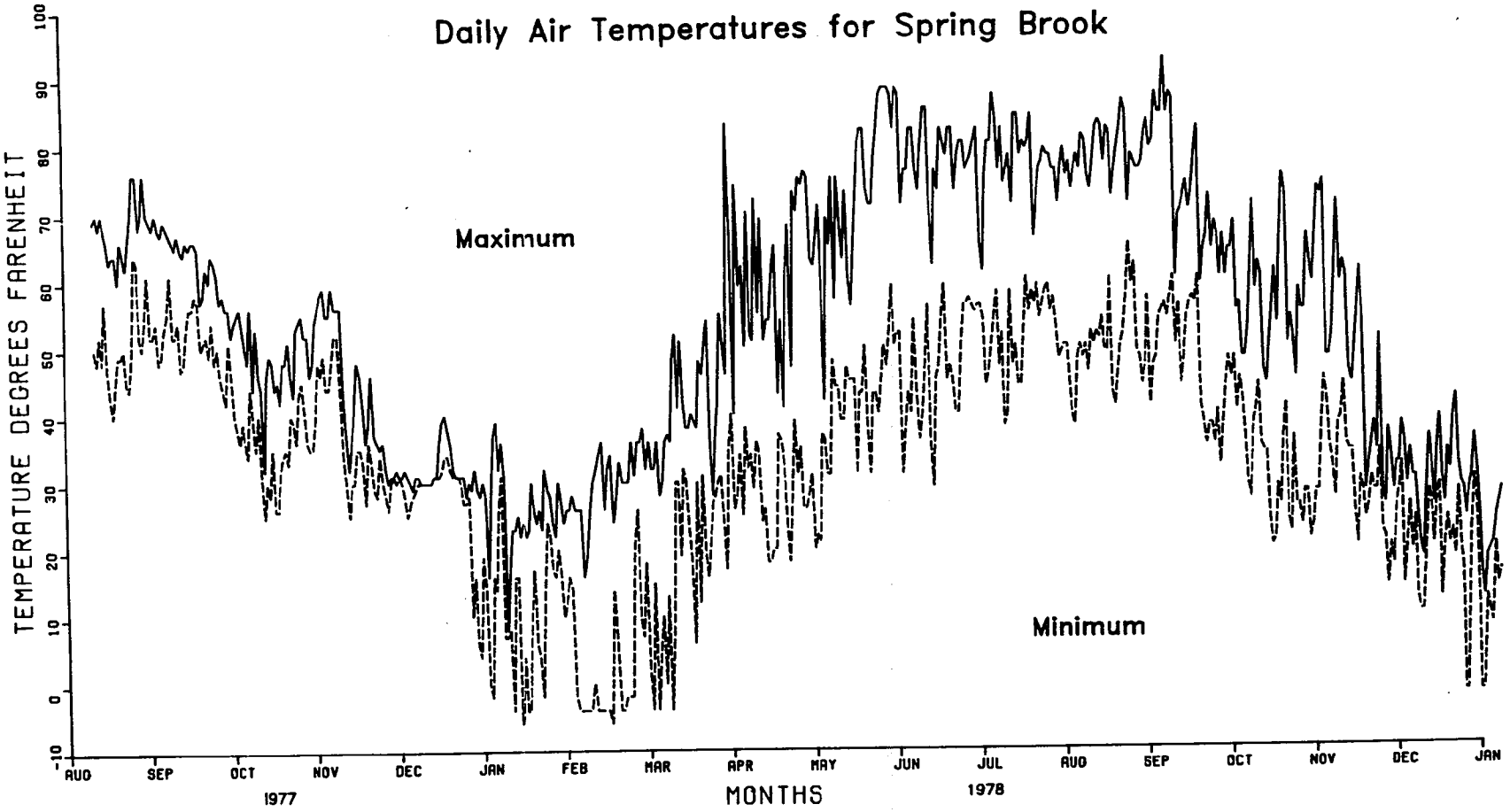
Daily Air Temperatures for Spring Brook
TEMPERATURE DEGREES FARENHEIT
100
90
80
70
60
50
40
30
20
10
0
-10
Maximum
Minimum
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
1977
MONTHS
1978

Figure A-1.

Figure A-2. Daily maximum and minimum water temperatures from Spring Brook (^{o}F).

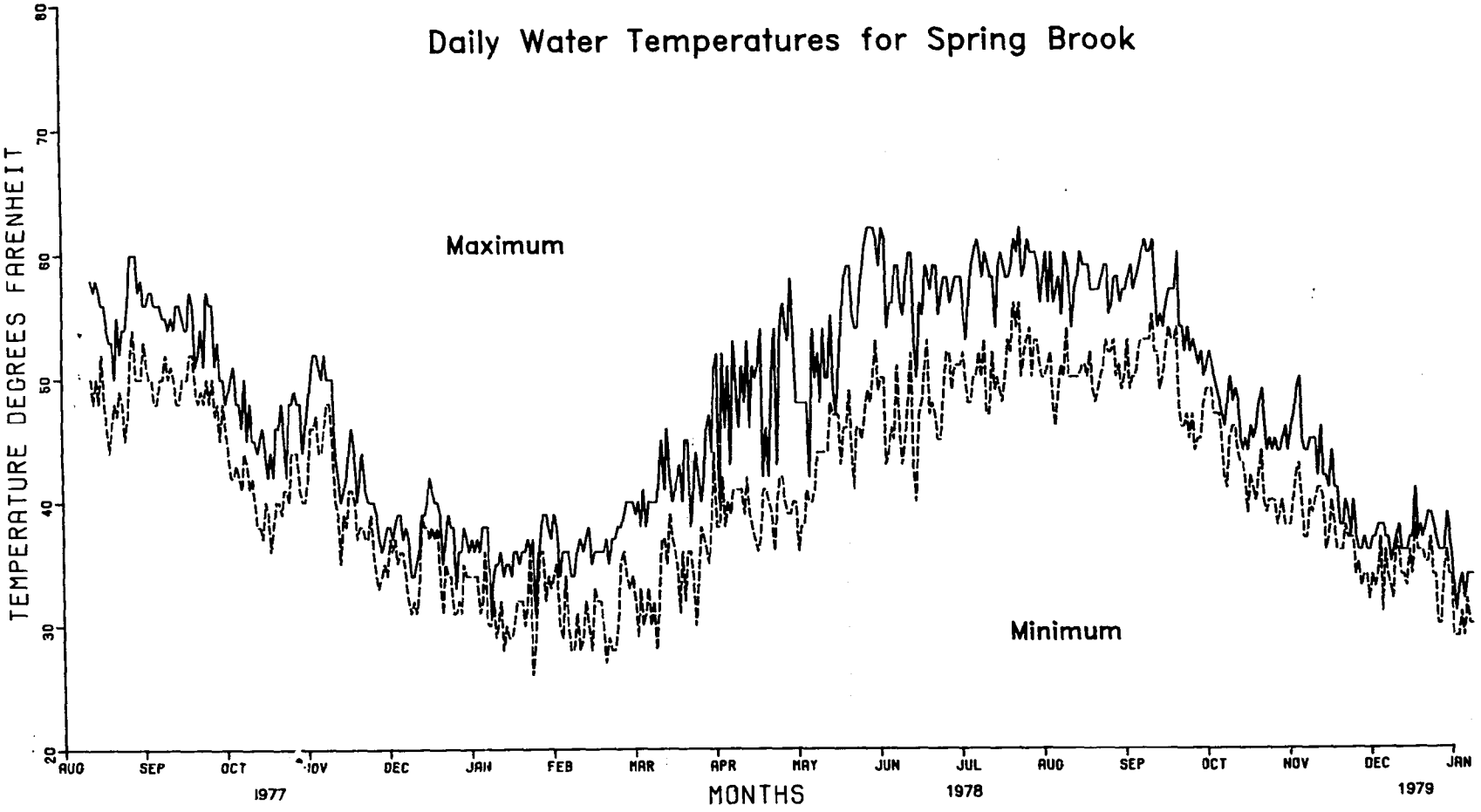
Daily Water Temperatures for Spring Brook
TEMPERATURE DEGREES FARENHEIT
80
70
60
50
40
30
20
Maximum
Minimum
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
1977
1978
1979
MONTHS

Figure A-2.

Figure A-3. Daily maximum and minimum streambed temperature records for Spring Brook (^{O}F).

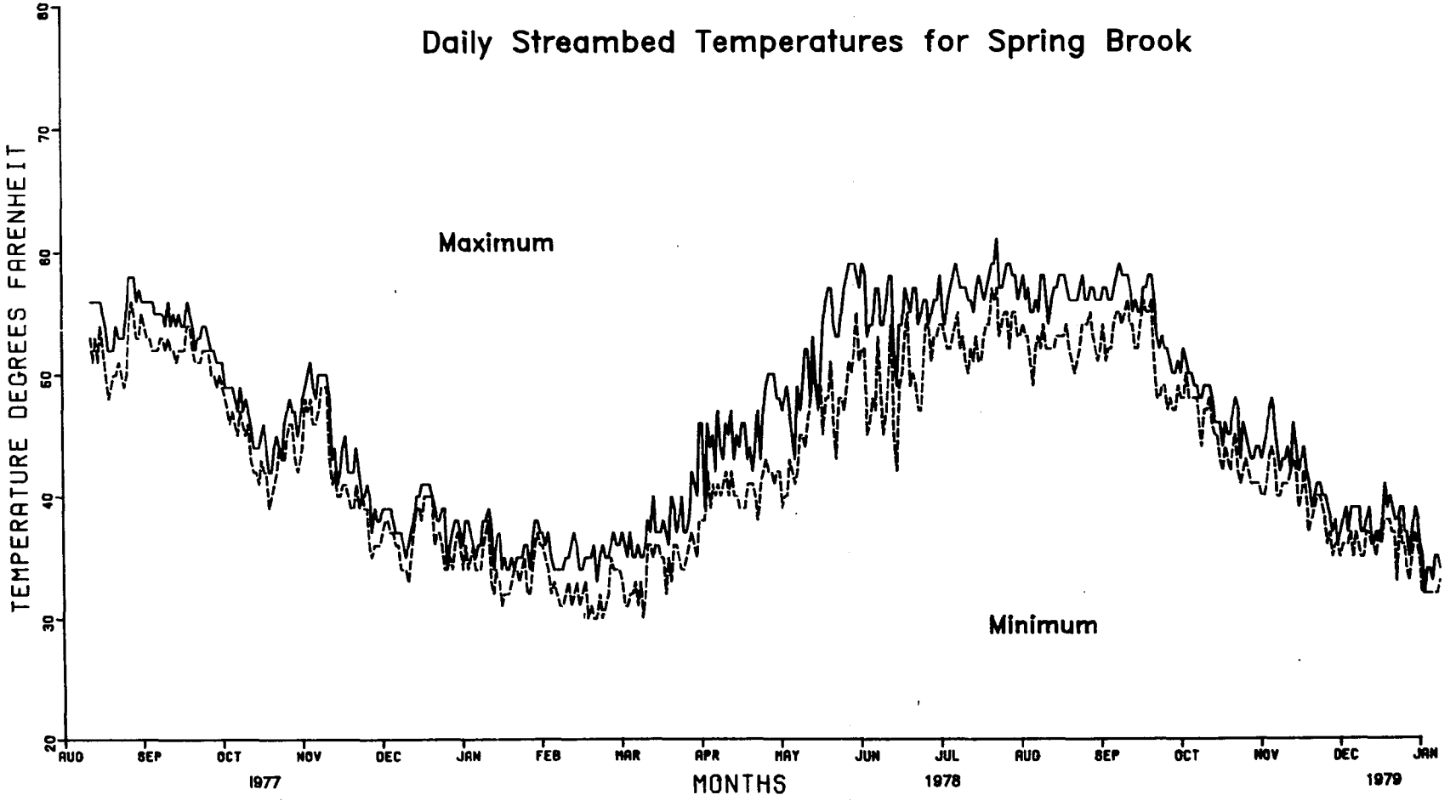
Daily Streambed Temperatures for Spring Brook
Maximum
Minimum
TEMPERATURE DEGREES FAHRENHEIT
80
70
60
50
40
30
20
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
1977
1978
1979
MONTHS

Figure A-3.

BIBLIOGRAPHY

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American Public Health Association. 1976. Standard methods for the examination of water and wastewater, 14 th edition. American Public Health Association, Washington, D.C. 1193p.

Anderson, N. H. 1976. Carnivory by an aquatic detritivore, Clistronia magnifica (Trichoptera: Limnephilidae). Ecology 57:1081-1085.

Anderson, N. H. and J. L. Wold. 1972. Emergence trap collections of Trichoptera from an Oregon stream. Can. Ent. 104:189-201.

Anderson, N. H. and J. R. Bourne. 1974. Bionomics of three species of Glossosomatid caddis flies in Oregon. Can. J. Zool. 52:405-411.

Anderson, N. H. and E. Grafius. 1975. Utilization and processing of allochthonous material by stream trichoptera. Verh.Int.Verein. Limnol. 19:3083-3088.

Anderson, N. H. and K. W. Cummins. 1979. Influences of diet on the life histories of aquatic insects. J.Fish.Res.Bd.Can. 36:335-42.

Anderson, N. H. and J. R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Ann.Rev.Entomol. 24: 351-377.

Bamforth, S. S. 1982. The variety of artificial substrates used for microfauna, p.115-130. in: Artificial substrates, J. Cairns Jr. (ed.). Ann Arbor Science Pub., Michigan.

Barber, J. T., E. G. Ellgaard, and K. Herskowitz. 1982. The attraction of Culex pipiens quinquefasciatus Say to ribonucleic acid and nucleotides. Journ. Ins. Physiol. 28:585-588.

Begres, F. M. 1971. The diatoms of Clear Lake and Ventura Marsh, Iowa. Unpublished Ph.D. thesis, Iowa State Univ., Iowa. 199p.

Blum, J. L. 1954. Two winter diatom communities of Michigan streams. Pap. Mich. Acad. Sci. 39:3-7.

Blum, J. L. 1956. The ecology of river algae. Bot. Rev. 22:291-341.

Brown, D. S. 1960. The ingestion and digestion of algae by Chloen dipterum. Hydrobiologia 16:81-96.

Brown, D. S. 1961a. The food of the larvae of Chloeon dipterum L. and Baetis rhodani (Pictet). J. Anim. Ecol. 30:55-75.

Brown, D. S. 1961b. The morphology and functioning of the mouthparts of Chloeon dipterum L. and Baetis rhodani (Pictet). Proc. Zool. Soc. Lond. 136:147-176.

Butcher, R. W. 1932. Studies in the ecology of rivers. II. Microflora of rivers with special reference to algae on the river bed. Ann. Bot. Lond. 46:813-862.

Butcher, R. W. 1946. Studies in the ecology of rivers. VI. The algal growth in certain highly calcareous streams. Jour.Ecol.Lond. 33:268-283.

Cairns, J., Jr. 1981. Predicting toxicological response from one level of biological organization to another. Abstract in Abstracts for second annual meeting of SETAC, 1981, Virginia.

Calow, P. 1975a. On the nature and possible utility of epilithic detritus. Hydrobiologia 46:181-89.

Calow, P. 1975b. Defaecation strategies of two fresh water gastropods, Ancyclus fluviatilis and Planorbis contortus with a comparison of field and laboratory estimates of food absorption rate. Oecologia 20:51-63.

Castenholz, R. W. 1961. The effect of grazing on marine littoral diatom populations. Ecology 42:783-814.

Castro, L. B. 1975. Okologie und produktionsbiologie von Agapetus fuscipes Curt. im Breitenbach 1971-72. Arch. Hydrob. Suppl. 45:305-375.

Chapman, R. F. 1974. The chemical inhibition of feeding by phytophagous insects: a review. Bull. Entomol. Res. 64:339-63.

Conover, R. J. 1966. Assimilation of organic mater by zooplankton. Limnol. and Oceanog. 11:338-345.

Cummins, K. W. 1973. Trophic relations of aquatic insects. Ann. Rev. Ento. 68:183-206.

Cummins, K. W. 1974. Structure and function of stream ecosystems. Bioscience 24:631-41.

Cummins, K. W. 1975. Macroinvertebrates, p. 170-198 in B. Whitten (ed.) River Ecology, Blackwell Sci., England 725 p.

Cummins, K. W., W. P. Coffman, and P. A. Roff. 1966. Trophic relations in a small woodland stream. Mitt. Int. Ver.Theor.Ang. Limnol. 16:627-638.

Cummins, K. W., R. C. Peterson, F. O. Howard, J. C. Wuycheck, and V. I. Holt. 1973. Utilization of leaf litter by stream detritivores. Ecology 54:336-345.

Cummins, K. W. and M. J. Klug. 1979. Feeding ecology of stream invertebrates. Ann. Rev. Ecol.Syst. 10:147-72.

Dethier, V. G. 1954. Evolution of feeding preference in phytophagous insects. Evolution 8:33-54.

Dethier, V. G. 1980. Evolution of receptor sensitivity to secondary plant substances with special reference to deterrents. Am.Nat. 115:45-66.

Dillard, G. E. 1971. An epilithic diatom community of a North Carolina sandhills stream. Rev. Algol. 10:118-127.

Douglas, B. 1958. The ecology of the attached diatoms and other algae in a small stony stream. Journ. Ecol. 46:295-322.

Dyar, H. G. 1890. The number of molts of lepidopterous larvae. Psyche 5:420-422.

Elliott, J. M. 1971a. The life history and biology of Apatania muliebris McLachlan (Trichoptera). Ent. Gaz. 22:245-251.

Elliott, J. M. 1971b. Some methods for the statistical analysis of samples of benthic invertebrates. Sci. Publ. Freshwat. Biol. Assoc. 25. 144p.

Findenegg, I. 1969. Expressions of populations, p. 16-17 in R. A. Vollenweider (ed.) A manual on methods for measuring primary production in aquatic environments, Blackwell Sci. England 213p.

Gatjen, D. G. 1926. Nahrungsuntersuchungen bei Phryganiden larven (Phrygania und Neuronia). Arch. Hydrobiol. 16:649-667.

Gersun, U. 1974. The associations of algae with arthropods. Rev. Algol. 11:18-41.

Ghent, A. W. 1956. Linear increment in width of the head capsule of two species of sawflies. Can. Ent. 88:17-23.

Gibbs, D. G. 1967. The proventriculus of some trichopterous larvae. J.Zool.Lond. 152:245-56.

Gill, J. L. 1978. Design and analysis of experiments. Iowa State Univ.Press, Iowa 409p.

Gordon, H. T. 1968. Quantitative aspects of insect nutrition. Am. Zool. 8:131-138.

Gruendling, G. K. 1971. Ecology of the epipelic algal communities in Marion Lake, British Columbia. J.Phycol. 7:239-49.

Hanna, H. M. 1957. A study of the growth and feeding habits of the larvae of four species of caddisflies. Proc.Roy.Ent.Soc.Lond. 32:139-146.

Hargrave, B. T. 1970. Utilization of benthic microflora by Hyalella azteca (Amphipoda). J.Anim.Ecol. 39:427-37.

Hawkins, C. P. and J. R. Sedell. 1981. Functional groups in streams. Ecology 62:387-397.

Hohn, M. H. and J. Hellerman. 1963. The taxonomy and structure of diatom populations from three eastern North American rivers using three sampling methods. Trans.Am.Mic.Soc. 82:250-329.

House, H. L. 1965. Insect nutrition, p.769-813, in M. Rockstein (ed.) The physiology of insecta, Acad. Press, N.Y.

Howard, F. O. 1975. Natural history and ecology of Pycnopsyche lepida, P. guttifer and P. scabripennis (Trichoptera: Limnephilidae) in a woodland stream. Unpub. Ph.D. thesis, Michigan State Univ., Michigan 115p.

Hunter, R. D. 1980. Effects of grazing on the quantity and quality of fresh water aufwuchs. Hydrobiologia 69:251-259.

Hynes, H. B. N. 1970a. The ecology of running waters. Univ.Toronto Press, Toronto, Canada 555p.

Hynes, H. B. N. 1970b. The ecology of stream insects. Ann.Rev.Ent. 15:25-42.

Iversen, T. M. 1973. Decomposition of autumshed beech leaves in a springbrook and its significance for the fauna. Arch. Hydrobiol. 72:305-312.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, Connecticut.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Jones, J. R. E. 1951. An ecological study of the River Towy. J. Anim.Ecol. 20:68-86.

Laws, E. A. 1975. The importance of respiration losses in controlling the size distribution of marine phytoplankton. Ecology 56:419-426.

Lehman, J. T. 1976. Photosynthetic capacity and luxury uptake of carbon during phosphate limitation in Pediastrum duplex. J.Phyc. 12:190-193.

Lehmkuhl, D. M. 1970. A North American trichopteran larvae which feeds on fresh water sponges. Am.Mid.Nat. 84:278-280.

Lepneva, S. G. 1964. Larvae and pupae of annulipalpia, Trichoptera. Fauna of the U.S.S.R. Zool. Inst. Akad. Nauk. S.S.S.R., N.S. 88:1-638,(Transl. Israel Program Sci. Transl. 1971).

Loeb, S. L. 1981. An in situ method for measuring the primary production and standing crop of the epilithic periphyton community in lentic systems. Limnol. and Oceanog. 26:394-399.

Lyford, J. H. and S. V. Gregory. 1975. The dynamics and structure of periphyton communities in three Cascade Mt. streams. Ver.Int.Ver. Theor.Ang.Limnol. 19:1610-1616.

Mackay, R. J. and G. B. Wiggins. 1979. Ecological diversity of Trichoptera. Ann.Rev.Ent. 24:185-208.

Mahan, D. C. and K. W. Cummins. 1978. A profile of Augusta Creek in Kalamazoo and Barry Counties, Michigan. Mich.State Univ., W.K. Kellogg Biol. Sta. Tech. Rep. No. 3.

McCullough, D. A., G. W. Minshall, and C. E. Cushing. 1979. Bioenergetics of lotic filter feeding insects Simulium spp. and Hydropsyche occidentalis and their function in controlling organic transport in streams. Ecology 60:585-96.

McIntire, C. D. 1973. Periphyton dynamics in laboratory streams: a simulation model and its implication. Ecol.Monogr. 43:399-420.

McMahon, R. F., R. D. Hunter, and W. D. Hunter. 1974. Variaton in Aufwuchs at six freshwater habitats in terms of carbon biomass and C:N ratios. Hydrobiologia 45:391-404.

Mecom, J. 1970. Evidence of diurnal feeding activity in Trichoptera larvae. J.Grad.Res.S.M.U. 38:44-57.

Mecom, J. O. and K. W. Cummins. 1964. Preliminary study of trophic relations of larvae Brachycentrus americanus (Banks) (Trichoptera: Brachycentridae). Trans.Amer.Mic.Soc. 83:233-243.

Merritt, R. W., D. H. Ross, and G. J. Larson. 1982. Influence of stream temperature and seston on the growth and production of overwintering larval black flies (Diptera:Simuliidae). Ecology 63:1322-1331.

Merritt, R. W. and K. W. Cummins. 1978. An introduction to the aquatic insects of North America. Kendall Hunt, Iowa. 441p.

Minshall, G. W. 1967. Role of allichthonous detritus on the trophic structure of a woodland springbrook community. Ecology 48:139-149.

Minshall, G. W. 1968. Community dynamics of the benthic fauna in a woodland springbrook. Hydrobiologia 32:305-339.

Minshall, G. W. 1978. Autotrophy in stream ecosystems. Bioscience 28:767-771.

Moore, J. W. 1972. Composition and structure of algal communities in a tributary stream of Lake Ontario. Can.J.Bot. 50:1663-74.

Moore, J. W. 1974. Benthic algae of S. Baffin Island, III. Epilithic and epiphytic communities. J.Phycol. 10:456-462.

Moore, J. W. 1975. The role of algae in the diet of Asellus aquaticus and Gammarus pulex. J.Anim.Ecol. 44:719-30.

Moore, J. W. 1977a. Some aspects of the feeding biology of benthic herbivores. Hydrobiologia 53:139-146.

Moore, J. W. 1977b. Some factors effecting algal consumption in subarctic Ephemeroptera, Plecoptera, and Simuliidae. Oecologia 27:261-273.

Moore, J. W. and F. W. H. Beamish. 1973. Food of the larval sea lamprey (Pteromyzon marinus) and the american brook lamprey (L. lamottei). J.Fish.Res.Bd.Can. 30:7-15.

Muttkowski, R. A. and G.M. Smith. 1929. The food of trout stream insects in Yellowstone National Park. Ann.Roosevelt Wildlife 2:241-63.

Nalewajko, C. 1966. Dry weight, ash, and volume data for some freshwater planktonic algae. J.Fish.Res.Bd.Can. 23:1285-88.

Nauwerck, A. 1963. Die Beziehungen swischen zooplankton und phytoplankton im See Erken. Symb. Bot. Upsal. 17:1-163.

Patrick, R. 1948. Factors effecting the distribution of diatoms. Bot.Rev. 14:473-524.

Patrick, R. 1970. Benthic stream communities. Amer.Sci. 58:546-549.

Patrick, R. 1971. The effects of increasing light and temperature on the structure of diatom communities. Limnol. and Oceanog. 16:405-421.

Patrick, R., M. Hohn, and J. Wallace. 1954. A new method for determining the patterns of the diatom flora. Not.Nat. 259:1-12.

Patrick, R., B. Crum, and J. Coles. 1969. Temperature and manganese as determining factors in presence of diatoms or blue-green floras in streams. Proc.Nat.Acad.Sci. 64:672-678.

Patrick, R. and C. W. Reimer. 1966. The diatoms of the United States. Phila.Acad.Nat.Sci., Philadelphia. 688p.

Perkins, M. A. and L. A. Kaplan. 1978. Epilithic periphyton and detritus studies in a subalpine stream. Hydrobiologia 57:103-109.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52: 137-154.

Resh, V. H. 1974. Use of transect sampling in estimating single species productions of aquatic insects. Ver.Int.Ver.Theor.Ang. Limnol. 19:3089-3094.

Resh, V. H. 1976. Life histories of coexisting species of Ceraclea caddisflies (Trichoptera:Leptoceridae): the operation of independent functional units in a stream ecosystem. Can.Ent. 108:1303-1318.

Resh, V. H. 1979. Sampling variability and life history features: Basic considerations in the design of aquatic insect studies. J.Fish.Res.Bd. Can. 36:290-311.

Rhame, R. E. and K. W. Stewart. 1976. Life cycles and food habits of three Hydropsychidae species in the Brazos River, Texas. Trans.Amer.Entomol.Soc. 97:91-121.

Roff, P. A. 1969. The seasonal periodicity and microdistribution of the diatom flora of a riffle in Linesville Creek (Crawford County, Pennsylvania). Unpub. Ph.D. thesis, University of Pittsburgh, PA. 281 p.

Satija, G. R. 1959a. The structure of the alimentary canal and mouthparts of Trichoptera larvae with special reference to food and feeding habits. Res. Bull. Punjab Univ. N.S. 10:131-146.

Satija, G. R. 1959b. The structure of the alimentary canal and mouthparts of Trichoptera larvae with special reference to food and feeding habits. Res Bull. Punjab Univ. N. S. 10:147-168.

Satija, G. R. 1964. The structure of the alimentary canal and mouthparts of Trichoptera larvae with special reference to food and feeding habits of Tinodes waeneri, Arthripsodes alboguttatus, Rhyacophila dorsalis, and Agapetus fuscipes. Res. Bull. Punjab Univ. N.S. 15:221-224.

Scott, D. 1958. Ecological studies on Trichoptera of the River Dean, Cheshire. Arch. Hydrobiol. 54:340-392.

Sládečková, A. 1962. Limnological investigation methods for the periphyton (Aufwuchs) community. Bot. Rev. 28:286-350.

Sládeček, V. and A. Sládečková. 1964. Determination of the periphyton production by means of the glass slide method. Hydrobiologia 23:125-158.

Slansky, F., Jr. 1982. Insect nutrition: an adaptionist's perspective. Florida Ent. 65:45-71.

Smirnov, N. N. 1962. On nutrition of caddis worms Phryganea grandis L. Hydrobiologia 19:252-261.

Snodgrass, R. E. 1935. Principles of insect morphology. Mcgraw Hill, N.Y. 667p.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco 776p.

Sumner, W. T. and C. D. McIntire. 1982. Grazer-periphyton interactions in laboratory streams. Arch. fur Hydrobiol. 93:135-157.

Tachet, H. 1965a. Recherches sur l'alimentation des larves de Polycentropus (Trichoptera) dans leur milieu naturel. Ann.Soc. Ent. France 1:627-633.

Tachet, H. 1965b. Influence du stade larvaire et de la saison sur l'alimentation des larves de Polycentropus (Trichoptera) dan des conditions naturelles. Ann.Soc. Ent. France 1:635-640.

Thorup, J. and T. M. Iverson. 1974. Ingestion by Sericostoma personatum Spence (Trichoptera:Sericostomatidae). Arch. Hydrobiol. 74:39-47.

Thut, R. N. 1969. Feeding habits of larvae of seven Rhyacophila species with notes on other life history features. Ann.Ent.Soc.Am. 62:894-898.

Trama, F. B. 1957. The transformation of energy by an aquatic herbivore, Stenonema pulchellum (Ephemeroptera). Unpub. Ph.D. Thesis, Univ. Michigan, Michigan 140p.

Ulfstrand, S. 1968. Life cycles of benthic insects in Lapland streams. Oikos 19:167-90.

U.S. Department of Agriculture. Soil survey of Kalamazoo County, Michigan. 1979.

Waldbauer, G. P. 1968. The consumption and utilization of food by insects. Adv.Insect.Physiol. 5:229-282.

Wallace, J. B. and D. Malas. 1976a. Significance of elongate rectangular mesh found in capture nets of fine particle filter feeding Trichoptera larvae. Arch. fur Hydrobiol. 77:205-212.

Wallace, J. B. and D. Malas. 1976b. The fine structure of capture nets of larval Philopotamidae (Trichoptera) with emphasis on Dolophilodes distinctus. Can.J.Zool. 54:1788-802.

Ward, G. M. and K. W. Cummins. 1978. Life history and growth pattern of Paratendipes albimanus in a Michigan headwater stream. Annls. Ent. Soc. Am. 71:272-284.

Warren, C. E. 1971. Biology and water pollution control. W.B. Saunders, Phila. 434p.

Wetzel, R. G. and D. F. Westlake. 1969. Periphyton, p.33-40 in R. A. Vollenweider (ed.) A manual on methods for measuring primary production in aquatic environments, Blackwell Sci., England 213p.

Wiggins, G. B. 1977. Larvae of the North American caddisfly genera (Trichoptera). Univ. Toronto Press, Ontario, Canada 401p.

Withford, C. A. and G. J. Schumacher. 1963. Communities of algae in North Carolina streams and their seasonal relations. Hydrobiologia 22:133-196.

Zimmerman, M. C. and T. E. Wissing. 1978. Effects of temperature on gut-loading and gut-clearing times of the burrowing mayfly, Hexagenia limbata. F. W. Biol. 8:269-277.