Aquatic Insects Vol. 2 (1980), No. 3, pp. 177-189

# Life History and Ecology of *Stenonema modestum* (Banks) (Ephemeroptera: Heptageniidae) in Virginia, USA

by

Boris C. KONDRATIEFF and J. Reese VOSHELL, Jr.

ABSTRACT

The life history and ecology of *Stenonema modestum* was investigated in the North Anna River, a 5th order stream in the Piedmont Physiographic Province of Virginia. *S. modestum* subimagines emerged in late-afternoon to early-evening from April to October. The duration of the subimago stage was ca. 24 hrs. There was seasonal size variation among adults with larger individuals emerging in the spring. There was also seasonal fluctuation in fecundity positively correlated with the seasonal variation in adult size. Nuptial flights occurred just before dusk with males forming swarms of 30-50 individuals above large riffles. Copulation occurred in the air. *S. modestum* exhibited a multivoltine life cycle. Most of the overwintering brood emerged in April and deposited eggs; larvae from these eggs grew through the summer and emerged in mid-August. Sporadic emergence of stragglers from the overwintering brood occurred throughout June and July; larvae from these eggs emerged in September and October. It appears that differential egg hatching was responsible for the continuous emergence pattern. There were at least 14 to 15 instars for the overwintering brood. Larvae were found most frequently under loose cobble and boulders. Larvae of *S. modestum* were opportunistic generalists in their feeding habits, primarily ingesting detritus and diatoms and occasionally early instars of Chironomidae.

## INTRODUCTION

Mayflies are an important component of aquatic ecosystems, but the life history and ecology of most species are not known. The life histories of species must be elucidated in order to completely understand their functions in aquatic ecosystems. Many species appear and disappear throughout the year as different broods complete development in synchrony with seasonal climatic factors. The microhabitat preference and trophic specialization of many species change as the organisms develop. Therefore, it is not possible to completely understand the functional roles of organisms in aquatic ecosystems without considering their entire life histories. The objectives of this study were to elucidate the life cycle of *Stenonema modestum* (Banks), to analyze the physical and chemical characteristics of the larval habitat, and to determine the feeding habits of the larvae.

Members of the genus *Stenonema* are common inhabitants of streams and rivers in eastern North America. *S. modestum* was described by Banks (1910) from male imagines collected in the vicinity of the Potomac River at Washington, D.C. Bednarik and McCafferty (1979) recently revised the genus *Stenonema* and designated several common species of *Stenonema* as synonyms of *S. modestum*. Some cursory life history and ecology information has been reported for this widely distributed and highly variable species under other names, particularly *S. rubrum* (McDunnough) (Leonard and Leonard, 1962; Bell, 1969; Bell and Nebeker, 1969; Lewis, 1974; Shapas and Hilsenhoff, 1976; Flowers and Hilsenhoff, 1978).

## STUDY AREA

This study was conducted in the North Anna River, a tributary of the York River Basin, in Virginia. The York River Basin lies within the Piedmont Plateau and Coastal Plain Provinces of central and eastern Virginia. Most of the basin is forested (70%) or in cropland and pasture (22%), with very little land use classified as urban (2%) (Virginia Division of Water Resources, 1970). A sampling site was established on the North Anna River at the Fall Line approximately 32 km downstream of Lake Anna, a shallow mainstream impoundment. The Fall Line is the boundary between the Piedmont Plateau and Coastal Plain Provinces. Here the North Anna River is approximately 75 m wide and is typified by several cascading falls and small islands. The gradient of the study site is 21.8 m/km. *Justicia americana* (L.) (waterwillow) grows profusely in areas with slow current and on the islands. At this point the North Anna River is a 5th order stream that drains approximately $1.14 \times 10^5$ ha. The substrate consists primarily of coarse pebble (32-64 mm), cobble (64-256 mm), and boulder (> 256 mm). A complete description of the study site may be found in Kondratieff (1979).

## MATERIALS AND METHODS

Field studies were conducted from June 1977 to June 1978. Quantitative samples (3 replicates) were collected in riffle areas with an Ellis-Rutter Portable Invertebrate Box Sampler (0.1 $m^2$ area, 351 $\mu$m net). Samples were taken monthly in the winter (November to March) and every two weeks for the remainder of the year. All samples were preserved in 5% formalin. The following parameters were measured for each bottom sample: substrate (Cummins, 1962; Hynes, 1970), vegetation (dry weight), depth (meter stick), and current (General Oceanics, Inc., Model 2030, Mark II digital flowmeter). Additional benthic samples were collected with a D-frame kick net for gut analysis and rearing. To assist in determining emergence and flight periods, a blacklight trap and/or a white light (Coleman lantern) and sheet were used to collect adults. Other data such as timing, place of emergence, and flight patterns were recorded from direct observation in the field. The following physical-chemical parameters were measured according to the methods of the American Public Health Association et al. (1975): temperature, dissolved oxygen, total alkalinity, pH, conductivity, major cations, and major anions. All physical-chemical parameters were measured on each sampling date except cations and anions, which were measured monthly.

In this study the number of instars was determined by the method of Janetschek (1967). This method was devised for determining the number of instars for small insects that molt frequently. McClure and Stewart (1976) and Newell and Minshall (1978) have explained the use of the Janetschek method for other species of mayflies. *S. modestum* larvae were observed in an artificial stream regulated to temperatures of the natural habitat to help clarify instar separation. Size-frequency histograms were constructed to determine the number of generations per year and emergence times. Head capsule widths were measured immediately behind the compound eyes. Widths were estimated to the nearest unit of the ocular micrometer. Individuals could usually be sexed when their head capsule reached a width of 1.90 to 2.10 mm. Developing male genitalia were used for sexing larvae.

To determine habitat preferences of larvae each benthic sample was classified as follows: depth $< 20$ cm or $\geqslant 20$ cm, current $\leqslant 100$ cm/sec or $> 100$ cm/sec, substrate $> -7$ mean phi or $\leqslant -7$ mean phi, vegetation present or absent. The relative importance of individual habitat factors in determining distribution was analyzed by the indexing system of Williams and Hynes (1973).

Feeding habits were analyzed by the methods of Shapas and Hilsenhoff (1976). The percent by volume in each of four categories (detritus, diatoms, filamentous algae, animal) was estimated to the nearest 10%. Results were calculated by averaging five fields from each of three replicate slides.

A complete description of all field and laboratory methods can be found in Kondratieff (1979).

## RESULTS AND DISCUSSION

### *Subimago*

*S. modestum* subimagines emerged in late-afternoon to early-evening (ca. 6:30 PM to 8:00 PM). The full-grown larvae floated to the surface in areas with moderate to slow current and emerged instantaneously. They then flew upward to riparian vegetation, sometimes as high as 12 to 15 m. This crepuscular emergence was also noted for *S. smithae* Traver by Berner (1950) and *Epeorus fragilis* (Morgan) by Needham et al. (1935). The duration of the subimago stage was ca. 24 hrs. Therefore, the subimagines molted and became adults in the late afternoon of the following day.

*Adult*

There was seasonal size variation among adults of *S. modestum* (Fig. 1). Mean total body length was greatest in April (♂ 8.64 mm, ♀ 10.20 mm) and least in August (♂ 7.24 mm, ♀ 7.80 mm).

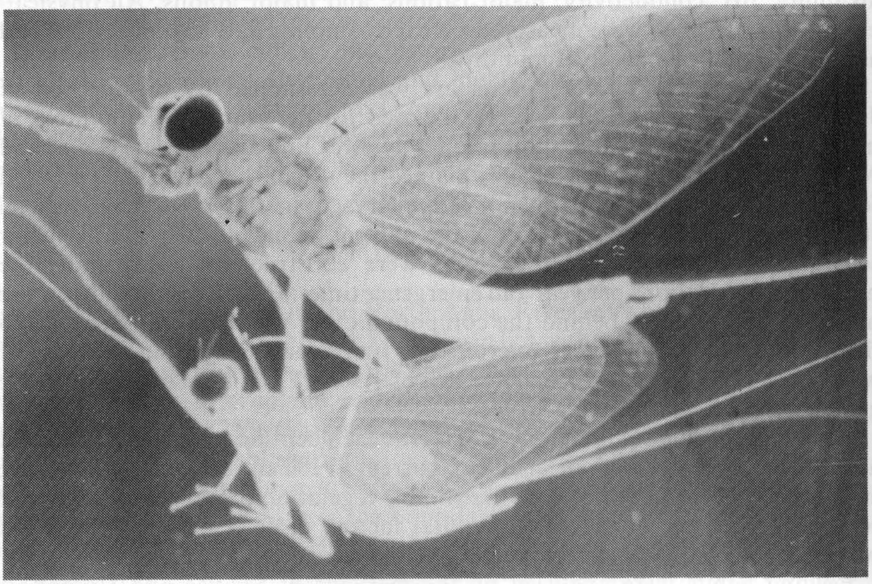

Fig. 1. *Stenonema modestum* imagines from the April (upper) and August (lower) broods.

Several large nuptial flights were observed. Just before dusk (ca. 8:30 PM) males began forming swarms consisting of 30-50 individuals above large riffles. The horizontal flight was rather constant with a rise and descent of only ca. 1 m. The swarming height varied from 2 to 6 m. The male remained in the same approximate locus until a female flew into the swarm. Immediate aerial copulation occurred, and the tandem pair immediately rose out of sight. Numerous tandem pairs were observed settling near the surface of the water; at this time the male separated and returned to the swarm. Swarming lasted until dark. The nuptial flight probably did not occur very long after dark (ca. 9:30 PM) because many females were observed ovipositing while it was still light. This type of nuptial flight was described by Cooke (1940) and Leonard and Leonard (1962) for *S. vicarium* (Walker) and for *S. smithae* by Berner (1950). One evening a thunderstorm developed, but the nuptial flights continued. Gusts of wind sent groups of males downstream. Lightning and moderate rain did not deter the flights. The same phenomenon was reported by Rawlinson (1939) for *Ecdyonurus venosus* (Fabricius).

*Egg*
Eggs which were removed from imagines fit the general description by Koss (1968). They measured 0.10 mm in diameter. Fertile eggs were obtained from ovipositing females in August. About 20% of the eggs hatched successfully in 25-28 days, but fungal contamination prevented further hatching. The first instars died soon after eclosion. The first instar resembled the figure by Ide (1935b) for *Stenacron interpunctatum canadense* (Walker). The head capsule width was 0.15 mm. Slight seasonal fluctuation in fecundity was noted. The average number of eggs (N = 4) was 515/♀ in April and 473/♀ in August.

*Larva*
The density of *S. modestum* averaged 391/$m^2$ (range 0 to 1090/$m^2$) (Fig. 2). Peak larval densities occurred in July, September, October, and December. July, September, and October densities corresponded with emergence peaks (Fig. 3). The high density in December reflected the overwintering of various developmental stages. The spring brood took ca. 202 days to develop and the fall and summer brood less than 120 days. The sex ratio of 125 larvae was 1♂:2♀. Richardson and Tarter (1976) also reported a ratio in favor of females for *S. vicarium* and *S. tripunctatum* (Banks). *Heptagenia marginalis* (Banks) was frequently found in association with *S. modestum*, along with a few individuals of *Stenonema integrum* (McDunnough).

The physical-chemical aspects of the environment are summarized in Table 1. The North Anna River is soft to medium in hardness with circumneutral pH, typical of Piedmont rivers. Dissolved oxygen concentrations remained near saturation in riffles. Water temperature ranged from a minimum of 2.5°C in February to a high of 29°C in July.

An analysis of the microdistribution of *S. modestum* by the methods of Williams and Hynes (1973) indicated a distinct preference for greater depths ($\geqslant$ 20 cm), slower current ($\leqslant$ 100 cm/sec), larger substrate (MØ $<$–7, coarse cobble to boulder), and no vegetation (water willow). The highest indices of preference for individual habitat factors were for larger substrate and slower current. The results of the analysis of the microdistribution of *S. modestum* are in general agreement with field observations. Larvae were found most frequently under loose cobble and boulders; they were rarely found under embedded rocks.

*Seasonal Cycle*
Correlation of seasonal head capsule widths with emergence peaks, adult collections, and presumed periods of growth without recruitment made it possible to interpret the seasonal cycle of *S. modestum* (Fig. 3). Adults that ermerged in April laid eggs; larvae from these eggs grew through summer and emerged in mid-August. The August adults were primarily responsible for the overwintering brood. "Straggler" adults that emerged in June and July produced larvae that grew through summer and emerged from September to October. Therefore, it appears that *S. modestum* followed a variation of Landa's (1968) B-1 life cycle: emergence of a fall (August) brood which initiated an

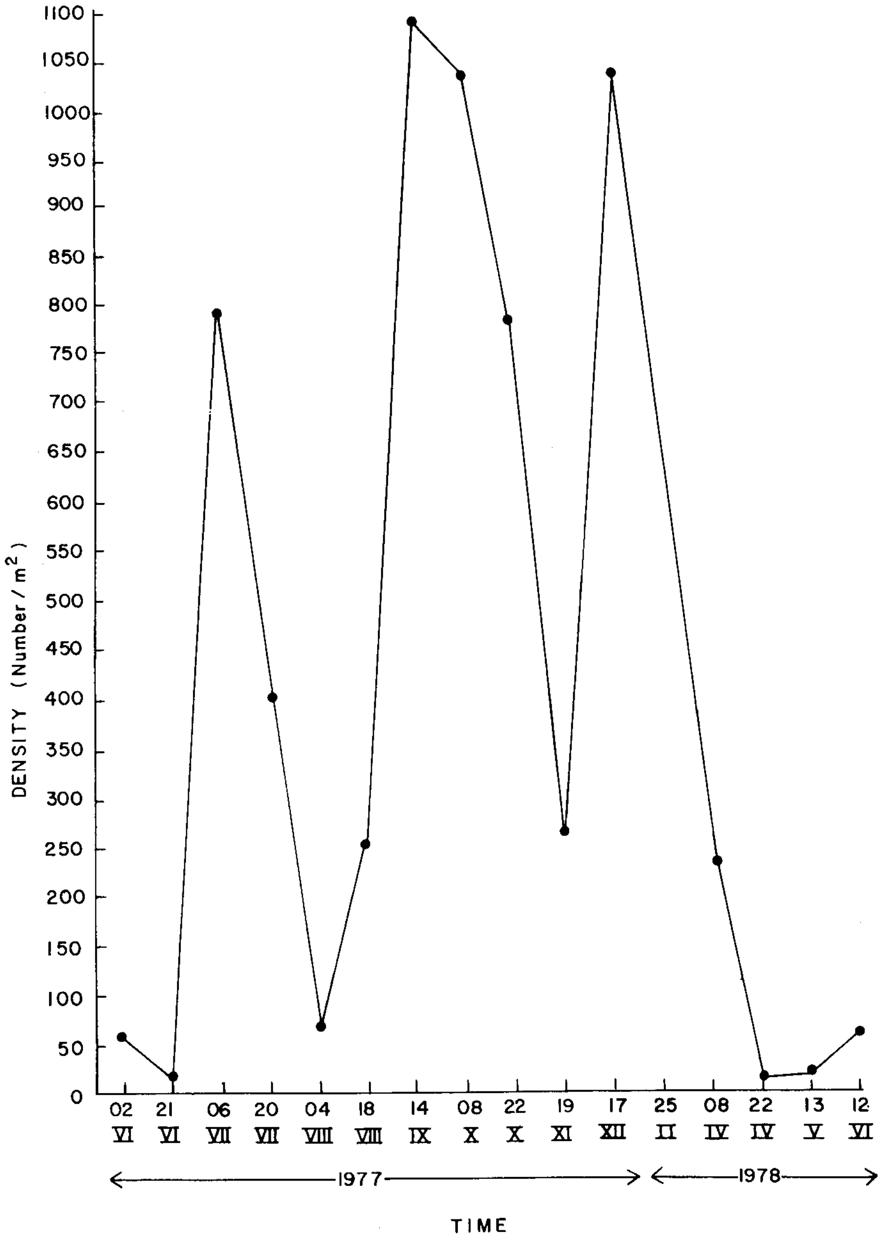


Fig. 2. Seasonal abundance of *Stenonema modestum* larvae in the North Anna River at the Fall Line.

Table 1. Basic physical and chemical properties of the North Anna River at the Fall Line from June 1977 to June 1978. The upper number is the mean and the lower numbers in parentheses are the range.

| Parameter | |
|---|---|
| Mean Daily Discharge ($m^3$/sec) | 12<br>(1-260) |
| Temperature (°C) | 18.7<br>(2.5-29.0) |
| Dissolved oxygen (ppm) | 9.8<br>(6.0-13.5) |
| Dissolved oxygen saturation (%) | 105<br>(79-127) |
| Total alkalinity (ppm $CaCO_3$) | 18<br>(12-29) |
| Hydrogen ion concentration (pH) | 7.00<br>(5.90-7.70) |
| Specific conductance ($\mu$mho/cm) | 61<br>(40-93) |
| Orthophosphate (ppm) | 0.03<br>(0.00-0.06) |
| Total phosphate (ppm) | 0.52<br>(0.00-3.56) |
| Nitrate nitrogen (ppm) | 0.615<br>(0.000-3.420) |
| Ammonia nitrogen (ppm) | 0.042<br>(0.000-0.096) |
| Sulfate (ppm) | 11<br>(8-15) |
| Calcium (ppm) | 2.66<br>(1.70-3.70) |
| Iron (ppm) | 0.30<br>(0.20-0.50) |
| Magnesium (ppm) | 7.66<br>(0.50-15.00) |
| Manganese (ppm) | 3.38<br>(1.50-5.00) |
| Potassium (ppm) | 2.68<br>(1.50-7.00) |
| Zinc (ppm) | 0.02<br>(0.00-0.10) |

overwintering brood with primary emergence in spring (April), but with some "stragglers" emerging throughout the summer.

The difference in the life cycle of *S. modestum* was that not all larvae passed the winter as "older larvae" but rather in various developmental stages. Ide (1935a) reported similar results for several species of *Stenonema*. Most of the overwintering brood emerged in April as large-sized adults, but the remaining overwintering larvae emerged June through July as smaller-sized adults. Differential egg hatching in the fall was probably responsible for the variety of developmental stages present during the winter. Ide (1935a) reported that *Stenacron interpunctatum canadense* eggs continued to hatch over a period of 6 weeks. The presence of very small larvae in April may indicate that some also overwintered as eggs that were most likely laid by late-emerging adults in September or even October. A portion of these late eggs may have hatched and been responsible for the small larvae in December. Failure to collect late instars in the riffles in June and July may be explained by the habit of many larvae of *Stenonema* species to seek quieter waters at the edge of the stream shortly before emergence. McCafferty and Huff (1978) also showed that *Stenacron interpunctatum* (Say) had three broods present in various stages of development at all times of the year in Indiana.

*Development*

Determination of larval instars by the Janetschek (1967) method indicated at least 14 or 15 instars for the overwintering brood (Fig. 4). Previous studies reported higher numbers of instars for related taxa. Ide (1935b) estimated 30-45 instars for *Stenacron interpunctatum canadense,* and Ide (1935a) estimated ca. 30 instars for *Epeorus vitreus* (Walker). However, Rawlinson (1939) reported 17 developmental stages for *Ecdyonurus venosus* (Fabricius). These developmental stages did not correspond to instars, but occurred independently at different instars. The palmen body indicated 14 instars. The number of instars derived by using the Janetschek method appears to be reasonable for *S. modestum* for the developmental period at the North Anna site.

The growth of *S. modestum* did not follow Dyar's rule (1890). A curved line resulted when the logs of the means of head capsule widths of the proposed instars were plotted versus instar number. There was a leveling off of growth during the winter, and then a speeding up during spring and summer. The progression factor was 1.11.

*Feeding Habits*

Gut contents of 22 larvae were analyzed to determine feeding habits (Fig. 5). Detritus and diatoms were present in all larvae; filamentous algae was present in most larvae. It appears that no filamentous algae was ingested in September or December. One larva contained Tanypodinae larvae (Diptera: Chironomidae). On the average *S. modestum* guts contained 55% detritus (range 15-94%), 38% diatoms (range 6-85%), 12% filamentous algae (range 0-32%), and 0.4% animal matter (range 0-2%). Shapas (1973) reported similar dietary components for Wisconsin *Stenonema* species; however, he reported that detritus made up a greater portion of the ingested food. Coffman et al. (1971) showed that young larvae of *S. fuscum* (Clemens) fed predominantly on detritus, but later, as they grew, they fed more on algae and eventually on some animal matter. The animal matter consisted of early instars of Chironomidae, resulting from the scraping and "vacuum cleaner" method of feeding exhibited by *Stenonema* species.

The dietary habits of *S. modestum* appeared to vary according to stage of development. In June the medium size class consumed mostly detritus and filamentous algae, while the large size class consumed a higher percentage of detritus. In December the medium size class consumed almost entirely detritus,

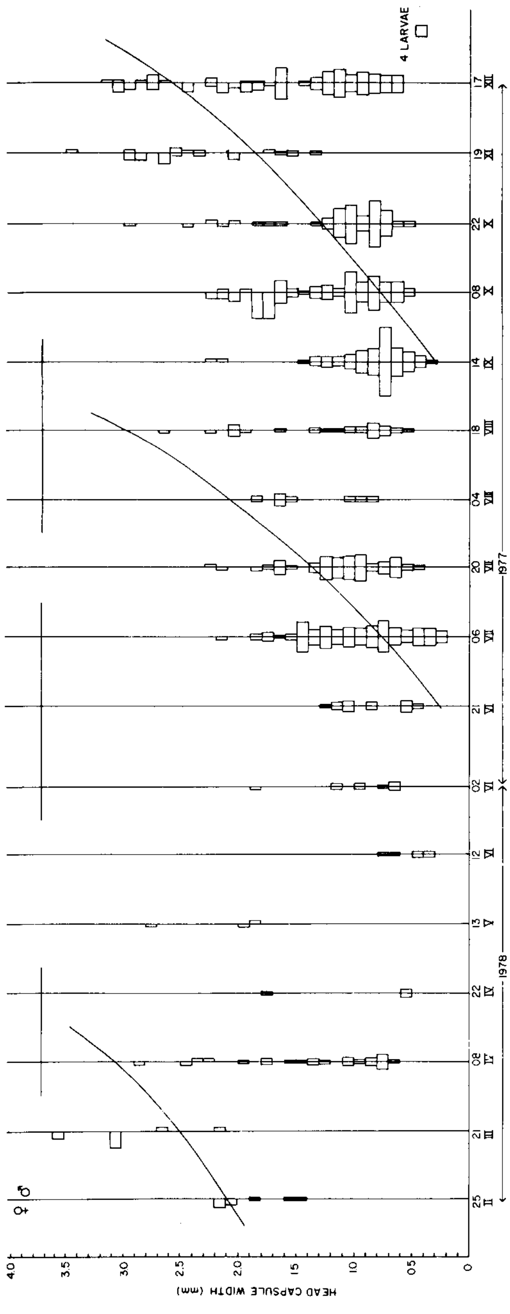


Fig. 3. Size frequency distribution of head capsule widths of *Stenonema modestum* in the North Anna River at the Fall Line. Curved lines indicate proposed generations. Horizontal lines indicate adult flight periods.

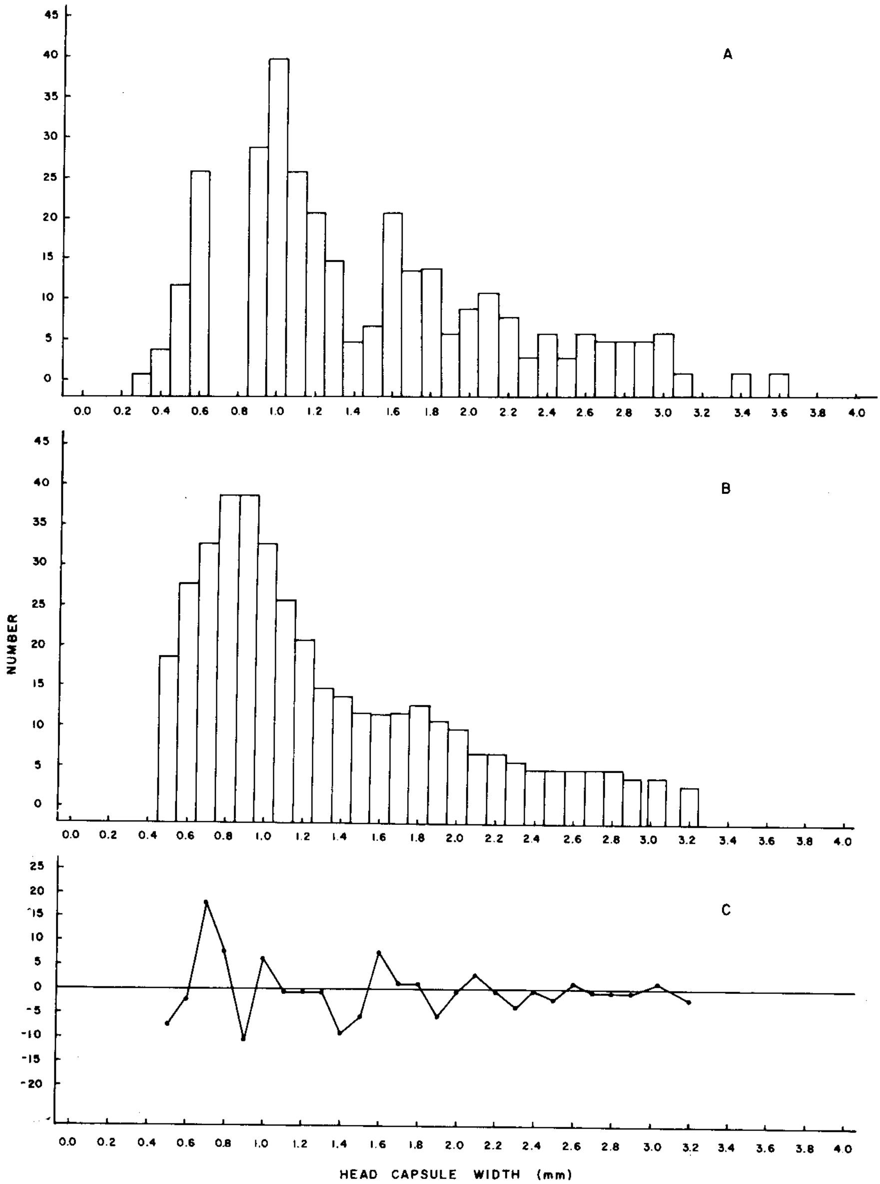


Fig. 4. Instar analysis of males and females in the overwintering generation of *Stenonema modestum* (N = 409) in the North Anna River at the Fall Line by the Janetschek model. A = size frequency histogram of head capsule widths; B = running mean of 5 of the frequencies; C = modal periodicity of instars (represents difference between A and B).

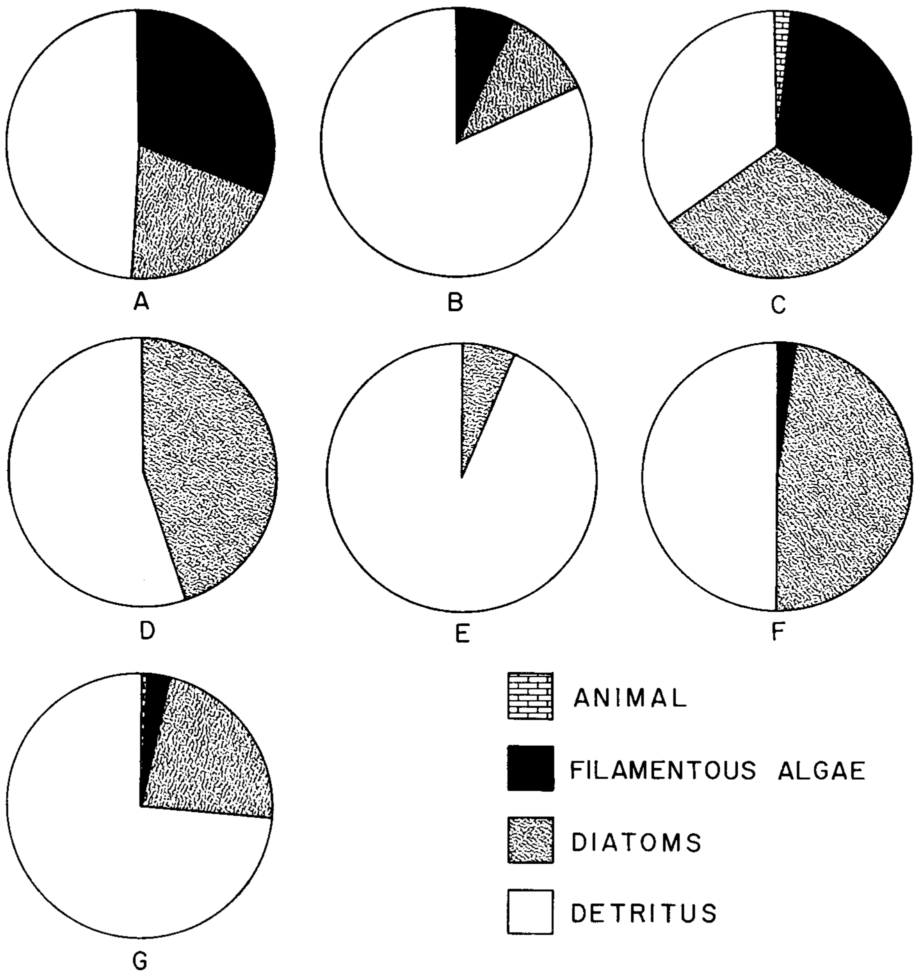


Fig. 5. Feeding habits of *Stenonema modestum* in the North Anna River at the Fall Line. Results are expressed as the percent of the total volume of gut contents. Larvae were grouped into two size categories by head capsule widths in mm and three temporal categories as follows: A, 1.3-2.2, 2 June 1977 (N = 4); B, 2.3-3.6, 2 June 1977 (N = 3); C, 1.3-2.2, 6 July 1977 (N = 6); D, 1.3-2.2, 14 September 1977 (N = 4); E, 1.3-2.2, 17 December 1977 (N = 4); F, 2.3-3.6, 17 December 1977 (N = 1); G, average of all larvae.

but the large size class consumed approximately equal percentages of detritus and diatoms. There were also some general seasonal trends in the food that was ingested. Detritus was the major component of the diet throughout the year. Filamentous algae comprised a greater percentage of the diet in early- to mid-summer, particularly in the smaller larvae. Diatoms were ingested more frequently from late-summer to winter, particularly by the larger larvae. These data indicate that *S. modestum* is an opportunistic generalist that changes its diet according to the seasonal changes in the food that is available in the environment.

## ACKNOWLEDGEMENT

We appreciate the generous technical assistance of Dr. George M. Simmons, Jr., Department of Biology, VPI & SU, and Charles R. Parker, Department of Entomology, VPI & SU. We thank Dr. Andrew Bednarik, University of Utah, for identifying our specimens of *S. modestum*.

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## LITERATURE CITED

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION, and WATER POLLUTION CONTROL FEDERATION (1975): Standard Methods for the Examination of Water and Waste Water. — Fourteenth Edition. New York: APHA. 1193 pp.

BANKS, N. (1910): Notes on our eastern species of the mayfly genus *Heptagenia*. — Can. Entomol., *42*: 197-202.

BEDNARIK, A. F. and W. P. McCAFFERTY (1979): A biosystematic revision of the genus *Stenonema* (Ephemeroptera: Heptageniidae). — Can. Bull. Fish. Aquat. Sci., *201*: 73 p.

BELL, H. L. (1969): Effect of substrate types on aquatic insect distribution. — J. Minn. Acad. Sci., *35*: 79-81.

BELL, H. L. and A. V. NEBEKER (1969): Preliminary studies on the tolerance of aquatic insects to low pH. — J. Kansas Entomol. Soc., *42*: 230-236.

BERNER, L. (1950): The mayflies of Florida. — Univ. Fla. Stud. Biol. Sci. Ser., *4*: 1-267.

COFFMAN, W. P., K. W. CUMMINS, and J. C. WUYCHECK (1971): Energy flow in a woodland stream ecosystem. I. Tissue support trophic structure of the autumnal community. — Arch. Hydrobiol., *68*: 232-276.

COOKE, H. G. (1940): Observations on mating flights of the mayfly *Stenonema vicarium* (Ephemerida). — Entomol. News, *51*: 12-14.

CUMMINS, K. W. (1962): An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. — Amer. Midl. Nat., *67*: 477-504.

DYAR, H. G. (1890): The number of moults of lepidopterous larvae. — Psyche, *5*: 420-422.

FLOWERS, R. W. and W. L. HILSENHOFF (1978): Life cycles and habitats of Wisconsin Heptageniidae (Ephemeroptera). — Hydrobiol., *60*: 159-171.

HYNES, H. B. N. (1970): The ecology of running water. — Univ. Toronto Press. 555 pp.

IDE, F. P. (1935a): The effect of temperature on the distribution of the mayfly fauna of a stream. — Univ. Toronto Stud., Biol. Ser., *39*: 3-76.

— (1935b): Post embryological development of Ephemeroptera (mayflies), external characters only. — Can. J. Res., *12*: 433-478.

JANETSCHEK, H. (1967): Growth and maturity of the springtail, *Gomphiocephalus hodgsoni*

Carpenter, from South Victoria Land and Ross Island. — Antarctic Res. Serv., *10,* Entomol. Antarctica. pp. 295-305.

KONDRATIEFF, B. C. (1979): The life history and ecology of two species of mayflies, with emphasis on the downstream effects of impoundment. — M. S. Thesis, Va. Polytech. Inst. and St. Univ., Blacksburg. 118 pp.

KOSS, R. W. (1968): Morphology and taxonomic use of Ephemeroptera eggs. — Ann. Entomol. Soc. Amer., *61*: 696-721.

LANDA, V. (1968): Development cycles of central European Ephemeroptera and their interrelationships. — Acta. Entomol. Bohemoslov., *65*: 276-284.

LEONARD, J. W. and F. A. LEONARD (1962): Mayflies of Michigan trout streams. — Cranbrook Inst. Sci., Bloomfield Hills, Mich. 139 pp.

LEWIS, P. A. (1974): Taxonomy and ecology of *Stenonema* mayflies (Heptageniidae: Ephemeroptera). — U.S.E.P.A. Environ. Monitoring Ser. Rept. EPA-670/4-74-006. 81 pp.

McCAFFERTY, W. P. and B. L. HUFF, Jr. (1978): The life cycle of the mayfly *Stenacron interpunctatum* (Ephemeroptera: Heptageniidae). — Great Lakes Entomol., *11*: 209-216.

McCLURE, R. G. and K. W. STEWART (1976): Life cycle and production of the mayfly *Choroterpes (Neochoroterpes) mexicanus* Allen (Ephemeroptera: Leptophlebiidae). — Ann. Entomol. Soc. Amer., *69*: 134-148.

NEEDHAM, J. G., J. R. TRAVER and Y. HSU (1935): The biology of mayflies. — Comstock Publ. Co., Ithaca. 759 pp.

NEWELL, R. L. and G. W. MINSHALL (1978): Life history of a multivoltine mayfly, *Tricorythodes minutus:* an example of the effect of temperature on life cycle. — Ann. Entomol. Soc. Amer., *71*: 876-881.

RAWLINSON, R. (1939): Studies on the life history and breeding of *Ecdyonurus venosus.* — Proc. Zool. Soc. B., *109*: 377-450.

RICHARDSON, M. Y. and D. C. TARTER (1976): Life histories of *Stenonema vicarium* (Walker) and *S. tripunctatum* (Banks) in a West Virginia stream (Ephemeroptera: Heptageniidae). — Amer. Midl. Nat., *95*: 1-9.

SHAPAS, J. T. (1973): General feeding habits of Wisconsin's predominant lotic-water insects. — M. S. Thesis. Univ. Wisconsin, Madison. 174 pp.

SHAPAS, T. J. and W. L. HILSENHOFF (1976): Feeding habits of Wisconsin's predominant lotic Plecoptera, Ephemeroptera, and Trichoptera. — Great Lakes Entomol., *9*: 175-188.

WILLIAMS, N. E. and H. B. N. HYNES (1973): Microdistribution and feeding of the net-spinning caddisflies (Trichoptera) of a Canadian stream. — Oikos, *24*: 73-84.

VIRGINIA DIVISION OF WATER RESOURCES (1970): York River Basin: Comprehensive Water Resources Plan. — Volume I - Introduction. Planning Bulletin 225. 112 pp.

Address of the Authors:
Boris C. KONDRATIEFF and Dr. J. Reese VOSHELL, Jr.
Department of Entomology
Virginia Polytechnic Institute and State University
Blacksburg, VA 24061 USA