

## Life history and production of *Goerita semata* Ross (Trichoptera: Limnephilidae) in the southern Appalachian Mountains

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In western North Carolina, populations of *Goerita semata* are restricted to moss- or liverwort-covered rock faces located in small, heavily shaded high-elevation streams. The larval developmental period was completed in about 655 days with two distinct cohorts being present at any time. Growth was slow, averaging only 0.71% ash-free dry mass per day, with the highest growth rate of 1.52% per day measured for fifth instar larvae between March and April. Weight losses occurred in overwintering larvae. In spite of low growth rates, relatively high production (including silk expenditure) was maintained by high larval densities (mean =  $288 \cdot \text{m}^{-2}$ ). Production in the rock-face habitat was  $237.66 \text{ mg ash-free dry mass} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  or  $47.53 \text{ mg ash-free dry mass} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  when weighted by areal proportion of rock-face substrate for the entire stream. Most growth occurred during the spring when fifth instar larvae accrued >50% of the definitive larval weight. This period of enhanced growth was correlated with increases in water temperature and in diatom consumption by the larvae. During the spring, diatoms composed about 64% of the foregut contents. In contrast, amorphous detritus constituted about 91, 65, and 86% of the gut contents during the fall, winter, and summer, respectively. Diatom consumption was estimated to be responsible for 58% of the annual production.

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Dans l'ouest de la Caroline du Nord, les populations de *G. semata* sont restreintes aux surfaces couvertes de mousses ou d'hépatiques des pierres, dans les petits ruisseaux très ombragés de haute altitude. La période de développement larvaire a été évaluée à environ 655 jours et il y a toujours deux cohortes présentes. La croissance s'est avérée lente: 0,71% de masse sèche sans les cendres  $\cdot \text{jour}^{-1}$ ; le taux de croissance le plus élevé (1,52%  $\cdot \text{jour}^{-1}$ ) a été enregistré chez des larves de cinquième stade entre mars et avril. Les larves ont subi des pertes de masse au cours de l'hiver. En dépit des taux de croissance faibles, la production est relativement importante (y compris la production de soie) car les densités larvaires sont élevées ( $288 \cdot \text{m}^{-2}$  en moyenne). La production à la surface des pierres a été évaluée à  $237,66 \text{ mg masse sèche sans les cendres} \cdot \text{m}^{-2} \cdot \text{an}^{-1}$ , ou  $47,53 \text{ mg de masse sèche sans les cendres} \cdot \text{m}^{-2} \cdot \text{an}^{-1}$  lorsque la masse était évaluée en fonction de la proportion de surfaces de pierre dans tout le ruisseau. La croissance se produit surtout au printemps et la masse des larves de cinquième stade augmente de plus de 50% de la masse de la larve à maturité. Cette période de croissance accrue est reliée à l'augmentation de la température de l'eau et à l'augmentation de la consommation de diatomées. Au printemps, les diatomées constituent environ 64% des contenus stomacaux. Par ailleurs, les détritits amorphes constituent 91% des contenus stomacaux à l'automne, 65% à l'hiver et 86% en été. La consommation de diatomées est responsable de 58% de la production annuelle.

[Traduit par le journal]

### Introduction

The North American genera of the Goerinae (*sensu* Wiggins 1977) occupy a diverse assemblage of habitats, ranging from the water-saturated ooze associated with spring seeps to medium-size rivers (Wiggins 1977; Unzicker et al. 1982). On the basis of characters selected from all life-history stages, Wiggins (1973a, 1976) demonstrated that the five goerine genera occurring in North America should be placed within two tribes, the Lepaniini (*Lepania* Ross, *Goereilla* Denning) and the Goerini (*Goera* Stephens, *Goeracea* Denning, *Goerita* Ross). Trophically, members of the Lepaniini are shredders, feeding largely upon vascular plant detritus, whereas the taxa included in the Goerini are scrapers, removing and ingesting periphyton and fine particulate organic matter from mineral surfaces (Wiggins 1977). Of the three genera included in the Goerini, *Goera* is by far the most speciose and widespread, being well represented from spring brooks to medium-size rivers throughout much of North America (Wiggins 1977; Denning 1982; Unzicker et al. 1982). The remaining genera, *Goeracea* and *Goerita*, occur as local colonies associated with small mountain streams in the Pacific Northwest and the southern and central Appalachian Mountains, respectively (Wiggins 1973a).

Information concerning aspects of the biology of the North American goerine caddisflies is generally in the form of brief

field observations (Flint 1960; Wiggins 1973a, 1976, 1977) or presentations of specific ecological data such as trophic relations (Coffman et al. 1971), temporal growth patterns (Vannote and Sweeney 1980), and secondary production (Georgian and Wallace 1984). The latter three studies all concerned species of *Goera*. Little comprehensive life-history and ecological information is presently available for any goerine genera other than *Goera*.

Our investigation dealt with *Goerita semata* Ross in western North Carolina. Our objectives were (i) to determine the life history and estimate production of a population of *G. semata* in a small, high-elevation catchment located in the Nantahala Mountains; (ii) to examine its seasonal growth patterns and food utilization; and (iii) to estimate the trophic basis of production (Benke and Wallace 1980) in order to quantify the role of autochthonously derived food resources in the production biology of *G. semata*.

### Study area

The study was conducted in a first and second order headwater tributary of Ball Creek which drains watershed 27 (WS 27) of the Coweeta Hydrologic Laboratory (Macon County, North Carolina). WS 27 is a 38.8-ha control catchment with vegetation characterized as an undisturbed mixed hardwood – hemlock association. Riparian vegetation consists mainly of a dense understory of *Rhododendron* spp. The topography of WS 27 is rugged and of high relief (average

stream gradient ca. 28%) with the elevation of the stream ranging from 1035 to 1188 m above sea level. The relatively high elevation, the north-northeastern aspect, dense forest cover, and steep ridges forming the boundaries of the catchment combine to restrict insolation of the stream during much of the year. Therefore, a cool year-round climate results and the stream biota are able to accumulate only 2800 to 3300 degree-days per year. Stream substrate is heterogeneous, consisting of ca. 11% sandy pool, 15% pebble riffle, 35% cobble riffle, 6% boulder riffle, 20% rock face (bedrock outcrop), and 13% debris dam backwater (percent total stream bottom). Woody debris within the stream channel is abundant (21–24 kg ash-free dry mass  $\cdot$  m<sup>-2</sup>; J. B. Wallace and A. D. Huryn, unpublished data). Streamflow is perennial, with lowest and highest discharges during the early fall and late winter months, respectively. However, during dry periods, surface water at upper reaches may be largely restricted to a series of isolated pools. The lower stream channel is heavily braided, occasionally flowing in as many as four distinct channels. The average width (including the widths of all parallel channels) and depth of the stream varies with location and discharge with an average width of  $223.5 \pm 35.79$  cm (mean  $\pm$  95% CI) and depth of  $2.1 \pm 0.6$  cm measured during low flow on 5 July 1983, and corresponding values of  $307.7 \pm 51.4$  cm and  $2.8 \pm 0.5$  cm observed during high flow on 7 January 1984. Other pertinent data concerning stream chemistry and climatic data for WS 27 and the Coweeta basin in general is contained in Swank and Douglass (1977) and Swank et al. (1981).

## Materials and methods

### Benthic sampling

As part of a larger study designed to assess the population structure and secondary production of the macroinvertebrate community of a high elevation southern Appalachian stream, 20 benthic samples were taken monthly (September 1983 – August 1984) from randomly assigned locations along a 500-m section of Ball Creek extending upstream from the WS 27 weir. Three methods of sampling were utilized depending upon local flow and substrate characteristics. In pooled areas (e.g., debris dam backwaters) a 400-cm<sup>2</sup> coring device was driven into the substrate, and all material within the core was removed to a depth of ca. 15 cm where possible and placed in a bucket. Organic material in the bucket was removed by several elutriations through a 140- $\mu$ m sieve and preserved in a 6–8% formalin solution containing a small amount of phloxine B dye. In areas of coarse substrate, a 930-cm<sup>2</sup> Surbur Sampler (mesh, 230  $\mu$ m) was employed. Benthic materials located within the sampler frame and retained in the net were removed and treated as above. For areas of moss-covered, rock-face substrates, a 232-cm<sup>2</sup> area of moss was removed with a stiff brush, and the loosened material was washed into the Surber Sampler. At each sample site, estimates of percent composition of substrate by particle size and current velocity were measured as described by Gurtz and Wallace (1984). Temperature was recorded continuously at two stream sites (ca. 1035 and 1180 m above sea level) with recording thermographs.

### Life history

Adult males and females of *G. semata* were reared from field-collected pupae and late instar V larvae, confirming the previously tentative association of its adult and immature stages (Flint 1960; Wiggins 1973a, 1977). Flight period was determined from collections (Malaise trap) of adults made along the stream margin. Egg masses were located by searching possible oviposition sites during the adult flight period. The identification of the egg mass was made by hatching field-collected specimens in the laboratory and comparing them with field collected instar I larvae, as well as by comparing field-collected egg masses with those obtained from laboratory-reared females.

We were unable to separate larval instars by constructing head-width frequency histograms; however, measurements of the length of the prothoracic midcoxal line provided an index to the larval instar. The pattern of larval instar succession was determined by examination of relative instar frequency histograms constructed for each series of monthly benthic samples.

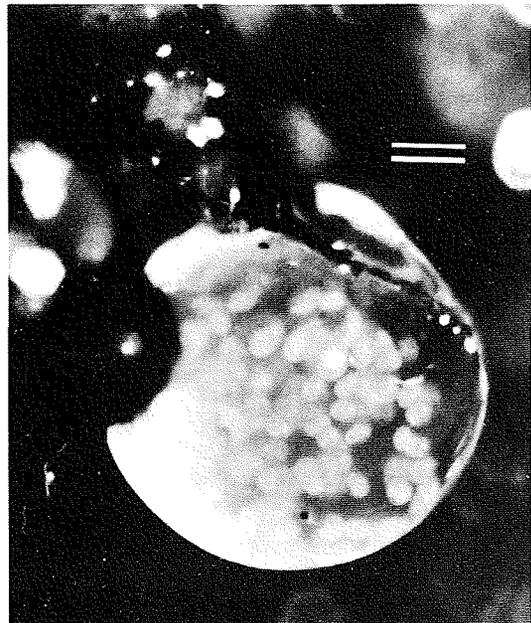


FIG. 1. Egg mass of *G. semata* photographed *in situ* on a moss-covered rock face in the headwaters of Ball Creek at the Coweeta Hydrologic Laboratory, Macon Co., NC (July 1984). Scale line represents 1.0 mm.

### Production

Monthly estimates of ash-free dry mass (AFDM) were usually based upon weights of a minimum of five individuals of each instar present; however, insufficient material occasionally resulted in the use of fewer specimens. AFDM of the mineral and silk larval cases were also measured to estimate silk expenditure. For the instar I larvae, 15 larvae were weighed simultaneously, and the mean individual weight was calculated. Larvae and cases used in weighings were selected from formalin-preserved samples and placed in a drying oven (55°C) for 24 h and then transferred to a desiccator for an additional 24 h. Oven-dried specimens were weighed on a Cahn 23 electrobalance to the nearest microgram to obtain dry mass and then ashed in a muffle furnace (500°C) for 1 h and reweighed to obtain AFDM.

Instantaneous growth rates (IGR) were calculated by the following formula:

$$\text{IGR} = (\ln W_f - \ln W_i) / t$$

where  $W_i$  and  $W_f$  are the initial and final larval AFDM observed during a period of growth ( $t$ ) measured in days (Mackay 1972).

Larval tissue and larval silk (obtained as AFDM of cases) production were calculated by the size-frequency method (Waters and Crawford 1973) and corrected for the cohort production interval (CPI) as proposed by Benke (1979).

### Gut analyses

Foregut contents of instar IV and V larvae were analyzed seasonally (autumn,  $n = 5$ ; winter,  $n = 5$ ; spring,  $n = 4$ ; summer,  $n = 4$ ). Slides for gut analyses were prepared using a modification of the Cummins (1973) membrane filter technique. Five food types were recognized: fine amorphous detritus, vascular plant detritus, fungal hyphae, filamentous algae, and diatoms. Ten randomly chosen fields were examined from each slide and outlines of individual particles were sketched using a compound microscope (400 $\times$  magnification) equipped with a camera lucida. Areas of outlines were measured with a HP 9864A digitizer interfaced to an HP 9825A desk-top computer to estimate the relative proportion of food types in each foregut. In all, 2604 particles were examined and measured. The values of annual production and the relative proportions of food types consumed by *G. semata* were combined with literature-derived bioenergetic data and used to estimate the amount of production attributable to each food type and the annual consumption of each (see Benke and Wallace 1980).

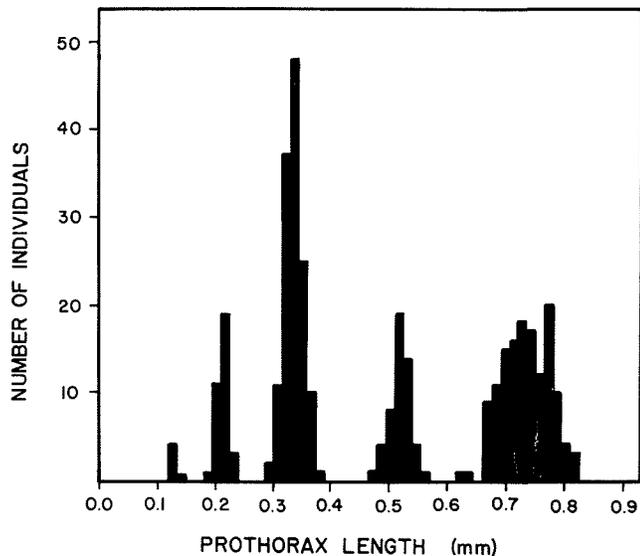


FIG. 2. Prothoracic length—frequency histogram used to determine five instars of *G. semata* in the headwaters of Ball Creek at the Coweeta Hydrologic Laboratory, Macon Co., NC (September 1983 – August 1984).

## Results

### Habitat and life history

Larvae and pupae of *G. semata* were found in aquatic mosses and liverworts located on rock faces. Less than 2% of all individuals collected during the investigation were from other substrate types. Water velocities over these habitats ranged from ca.  $114 \text{ cm} \cdot \text{s}^{-1}$  to 0, as active larvae were taken from moss located on a dry vertical rock face during the summer of 1983. This habitat differs from that described by Flint (1960) and Wiggins (1973a) who reported that larvae of *G. semata* occur on the undersides of rocks. The rock-face habitat of *G. semata* is similar to that described for *Goerita betteni* Ross (Wiggins 1973a).

Egg masses of *G. semata*, first observed on 21 June 1984, became increasingly numerous through the 1st week of July. Egg masses (Fig. 1) are typical for limnephilids, consisting of a spherical mass (ca. 0.5 cm diameter) of slightly amber spumaline. Eggs were regularly dispersed throughout the spumaline and each mass contained about  $83.0 \pm 4.3$  eggs. Egg masses clung to the substrate by their adhesive surface. Females oviposited away from water (in the strict sense of Wiggins 1973b), directly upon bare rock, mosses, or liverworts on vertical rock faces or under horizontal overhangs. Egg masses were most numerous under horizontal rock overhangs where local densities approached an estimated  $100 \cdot \text{m}^{-2}$ . Instar I larvae, first observed within egg masses in early July, remained within the spumaline for about 1 month. In early August, the egg masses abruptly began to disappear and those remaining were in various states of liquefaction.

The oviposition behavior of *G. semata* is similar to that reported for other Limnephilidae, most notably the Limnephilinae (Wiggins 1973b). We suggest that during dry summers, when extensive areas of rock face are dry, first instar larvae of *G. semata* escape desiccation by remaining within egg masses until adequate water flow returns. Wiggins (1973b) summarized similar desiccation avoidance mechanisms employed by other limnephilid taxa which inhabit temporary habitats.

Five larval instars could be identified from prothor-

acic length—frequency histogram (Fig. 2). The developmental period, from the time first instar larvae leave the egg mass to pupation, takes about 655 days (Fig. 3). Two distinct cohorts could be identified at any time. The cohort originating in 1982 and terminating in 1984 will be referred to as cohort "A." The cohorts originating in 1983 and 1984 will be designated as cohorts "B" and "C," respectively.

Free-living first instar larvae were initially observed in areas near oviposition sites during mid-August, coinciding with the dissolution of the egg masses. The duration of the first two stadia was short, and by October the majority of the larvae had attained instars III or IV. Larvae generally remained in these stadia until the following May. During this period some asynchrony in individual development of members of cohort B was apparent, with the members being apportioned among instars II–IV (Fig. 3). However, by June all members of the cohort were in instar IV, the stadium in which they passed the summer. These instar IV larvae, like the egg masses, are exposed to potential desiccation during low stream discharge in the summer months. Active instar IV larvae were collected from a dry, moss-covered, vertical rock face during July of 1983. The desiccation avoidance mechanisms of these larvae are not known; however, microclimatic factors within the moss may be involved.

During September, the majority of larvae of cohort A were in instar IV and entered the terminal instar (V) by mid-October (Fig. 3). Members of this cohort overwintered as instar V larvae and pupated in late May on vertical rock faces that were sparsely covered with moss and a thin film of water. Pupae were attached to the substrate by a stiff silken rod associated with the anterior closure (Flint 1960). Adults emerged by the 3rd week of June, and the main flight period extended through the 1st week of July (Fig. 3).

### Larval densities

Mean monthly densities of *G. semata* were variable, ranging from  $43 \pm 79 \cdot \text{m}^{-2}$  in June 1984 to  $905 \pm 1528$  in February 1984 in the rock-face habitat. The average density was  $288 \pm 103 \cdot \text{m}^{-2}$ . Variations in density were unpatterned with respect to the life-history events occurring within each cohort and are attributed to error associated with sampling a population of aggregated individuals. The numbers of individuals per sample was fitted to a Poisson distribution. The fit was not significant ( $p < 0.01$ ,  $\chi^2 = 477.80$ ,  $\text{df} = 65$ ), indicating a nonrandom distribution (Elliot 1977). The high coefficient of dispersion ( $33.61 > 1.0$ ) confirms that the population was composed of groups of aggregated individuals (contagious distribution) (Elliot 1977).

### Growth

Mean individual larval AFDM used in estimation of IGR was calculated as the sum of the product of each instars mean AFDM (including AFDM of case silk) and the instars relative frequency in its respective cohort (Table 1). Samples of individuals representing cohort B were inadequate to provide mean individual AFDM for December 1983 and January, April, and May 1984. Larval growth (AFDM ( $y$ ) vs. time ( $x$ )) was best described by exponential models for both cohort A ( $y = 0.395e^{0.004x}$ ,  $r^2 = 0.85$ ) and cohort B ( $y = 0.041e^{0.006x}$ ,  $r^2 = 0.86$ ). Growth of cohort A proceeded steadily (at an exponential rate) throughout the fall and early winter months (Fig. 4). However, between January and February an obvious decrease in AFDM occurred in both cohorts. This decrease coincided with the formation of an extensive ice sheet over most of the

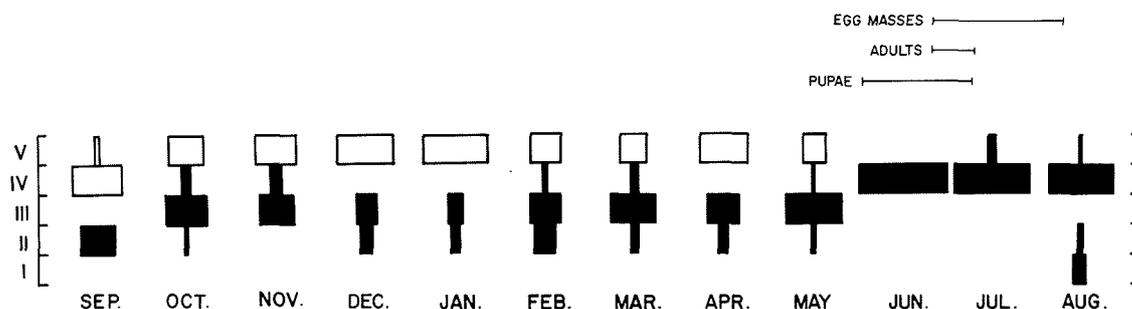


FIG. 3. Monthly instar frequency distributions for *G. semata* in the headwaters of Ball Creek at the Coweeta Hydrologic Laboratory, Macon Co., NC (September 1983 – August 1984). Instars are designated as I through V. Width of each bar represents the percentage of total individuals found in a given instar. Open, black, and stippled bars represent cohorts A, B, and C, respectively.

TABLE 1. Mean monthly larval ash-free dry mass (milligrams per individual) for three cohorts of *G. semata* in the headwaters of Ball Creek at the Coweeta Hydrologic Laboratory, Macon Co., NC (September 1983 – August 1984)

Date	Cohort A	Cohort B	Cohort C
29 Sep.	0.393	0.034	—*
23 Oct.	0.418	0.063	—*
21 Nov.	0.519	0.082	—*
19 Dec.	0.601	†	—*
20 Jan.	0.744	†	—*
21 Feb.	0.558	0.054	—*
22 Mar.	0.692	0.098	—*
20 Apr.	1.090	†	—*
29 May.	1.141	†	—*
22 Jun.	—*	0.259	—*
17 Jul.	—*	0.277	—*
15 Aug.	—*	0.367	0.011‡

NOTE: Mean individual AFDM (including case silk) was calculated as the sum of the products of each instar's mean AFDM and instar's relative frequency in its respective cohort.

\*Not occurring in stream on sample date.

†Insufficient material for estimation of weight.

‡Weight of case silk not available for first instar.

rock-face habitat during midwinter. A similar weight decrease was observed by Mutch and Pritchard (1984a) for *Philocasca alba* Nimmo in an ice-covered Rocky Mountain stream and was attributed to cessation of feeding. Most growth for each cohort occurred between February and June (Fig. 4). Between September and February, the IGR of cohort A was 0.24% per day; less than one-third the rate of 0.75% per day calculated for the period extending from February to May. The highest growth rate of 1.52% occurred between March and April. A similar pattern was observed for cohort B with growth rates of 0.31 vs. 0.82% per day observed for the same periods, respectively. From February to June, 78 and 62% of annual weight increase of cohorts A and B occurred, respectively. During this period, growth of cohort A alone was responsible for accruing over 50% of the definitive larval weight. The enhanced growth occurring between February and June is undoubtedly related to factors such as an increase in water temperature, insolation, and primary production as periphyton (see Seasonal food utilization and trophic basis of production, below).

#### Secondary production

Production of larval tissue and silk were calculated independently and the resulting values were summed to obtain total annual production. The summary data used in calculating production are given in Table 2. The final instar (V) was divided

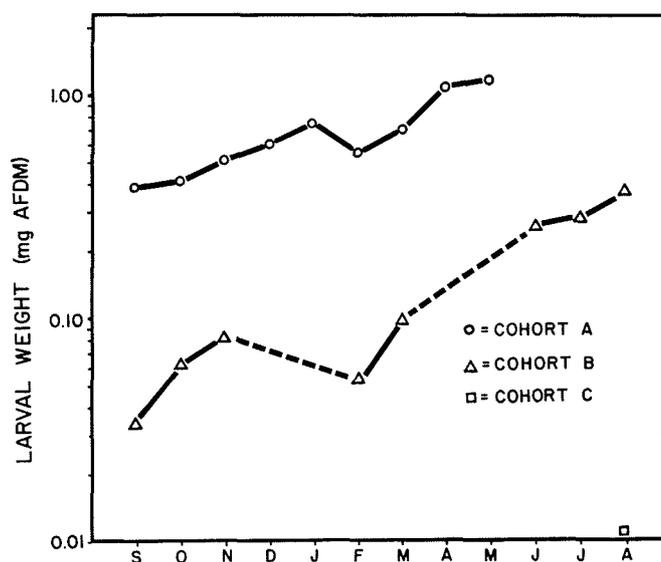


FIG. 4. Monthly changes in weight of three cohorts of *G. semata* in the headwaters of Ball Creek at the Coweeta Hydrologic Laboratory, Macon Co., NC (September 1983 – August 1984). The mean monthly individual ash free dry mass (AFDM) was calculated as the sum of the product of each instar's mean AFDM (including AFDM of case silk) and the instar's relative frequency in its respective cohort. Cohort "C" is represented by a single point (□) located in the lower right-hand corner of the graph.

into two size classes,  $V_1$  (October–March) and  $V_2$  (April–May), because of the abrupt increase in AFDM observed between the March and April collections. Negative values associated with the first two size classes were excluded, following the reasoning of Benke and Wallace (1980). These excluded values represented <4% of the total annual production (larval tissue + silk).

Total annual tissue and silk production (CPI corrected) for *G. semata* in the rock-face habitat was 237.66 mg AFDM  $\cdot$  m<sup>-2</sup>  $\cdot$  year<sup>-1</sup>. Larval tissue production accounted for 184.09 mg AFDM  $\cdot$  m<sup>-2</sup>  $\cdot$  year<sup>-1</sup> and silk production accounted for 53.57 mg AFDM  $\cdot$  m<sup>-2</sup>  $\cdot$  year<sup>-1</sup>. Silk production constituted 22.5% of the total annual production occurring in the rock-face habitat. This is similar to the 20–22% reported by Iverson (1980) for two populations of *Sericostoma personatum* Spence. Losses in the form of exuviae were not measured in the present study; however, this loss was probably minimal. Otto (1975) reported that losses of exuviae represented only 4% of the annual production of *Potamophylax cingulatus* (Stephens). The annual production to mean annual biomass ratio ( $P/B$ ) of *G. semata* was 2.67, well within the range expected for an insect with a

TABLE 2. Data used to calculate production of *G. semata* in the rock-face habitat in the headwaters of Ball Creek at the Coweeta Hydrologic Laboratory, Macon Co., NC (September 1983 – August 1984)

	Instar						No. · m <sup>-2</sup>	$\bar{B}$ (mg · m <sup>-2</sup> )	P (mg · m <sup>-2</sup> · year <sup>-1</sup> )	CPI (days)
	I	II	III	IV	V <sub>1</sub>	V <sub>2</sub>				
Density (No. · m <sup>-2</sup> )	5 (7)	37 (25)	80 (50)	76 (39)	79 (36)	11 (13)	288 (103)			
Tissue (mg)	0.002 (—)	0.018 (0.002)	0.055 (0.007)	0.186 (0.023)	0.429 (0.044)	0.909 (0.132)		62.87		
Case silk (mg)	NA	0.009 (0.004)	0.024 (0.003)	0.085 (0.010)	0.189 (0.014)	0.217 (0.033)		26.06		
Total								88.92	237.66	655

NOTE: Weights refer to ash free dry mass. Values in parentheses are 95% CI.

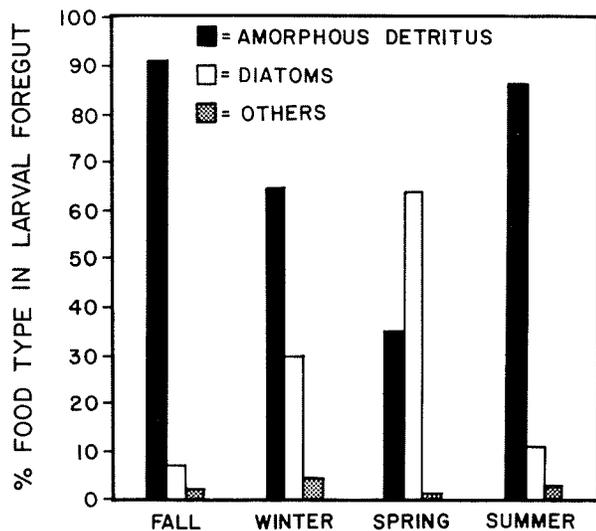


FIG. 5. Seasonal percentages of food types in the foreguts of *G. semata* in the headwaters of Ball Creek at the Coweeta Hydrologic Laboratory, Macon Co., NC (September 1983 – August 1984). The "others" category includes filamentous algae, fungal hyphae, and vascular plant detritus.

2-year life cycle (Waters 1977). When weighted by areal proportion of the rock-face habitat for the entire stream (see Study area), *G. semata*'s production is reduced to 47.53 mg AFDM · m<sup>-2</sup> · year<sup>-1</sup> (20% rock face · m<sup>-2</sup> × 237.66 mg AFDM · m<sup>-2</sup> · year<sup>-1</sup>).

Compared with the production of other scraping caddisflies occurring in open sunlit reaches of Shope Fork, a large (fourth order) Coweeta stream (Georgian and Wallace 1984), weighted annual production calculated for *G. semata* is considerably higher than *Agapetus* spp. (21 mg) and *Goera fuscata* Banks (9–16 mg) but lower than *Neophylax consimilis* Betten (150–176 mg) and *Glossosoma nigrior* Banks (612 mg). These values should be considered conservative since silk production was not measured by Georgian and Wallace (1984).

No data are available for production of scraping caddisflies occurring in low order (first or second), heavily shaded streams at Coweeta. However, Wallace and Gurtz (1985) reported production of a scraping mayfly (*Baetis* spp., Baetidae) that occurred in such a stream (WS 14, Hugh White Creek) as ca. 36 mg AFDM · m<sup>-2</sup> · year<sup>-1</sup>. This is comparable to the weighted production reported here for *G. semata* in WS 27. However, the rock-face production of *Baetis* was only 53 mg

AFDM · m<sup>-2</sup> · year<sup>-1</sup>, which was substantially lower than that of *G. semata* in WS 27.

Hence, the production of *G. semata* falls into the middle range of production values reported for other scraping caddisflies occurring in open, sunlit streams, yet it is considerably higher than that reported for a functionally similar mayfly inhabiting the rock-face habitat in a similar stream type. Despite the extended life cycle and the generally low IGR (ca. 0.71% per day), the level of production reported here was maintained by the high density of larvae occupying the rock-face habitat.

#### Seasonal food utilization and trophic basis of production

Seasonal gut analysis indicated that the primary food types consumed by *G. semata* were fine amorphous detritus (annual mean, 65%) and diatoms (annual mean, 32%) (Fig. 5). Filamentous algae, fungal hyphae, and vascular plant detritus collectively accounted for only 3% of the total annual food consumed. The proportion of each food category included in the diet varied substantially from season to season (Fig. 5). In fall, winter and summer, amorphous detritus predominated, composing 91, 65, and 86% of the gut contents, respectively. In contrast, diatom consumption predominated in the spring, composing 64% of the gut contents. This period of enhanced diatom ingestion coincided with increased insolation of the stream benthos as the sun became higher in its orbit. This moderated the shading effect of the high ridges surrounding the stream before leaves of the hardwood canopy developed. With the increase in insolation, stream temperature and diel fluctuation increased. On 1 March, the mean stream temperature was 1.8°C and the diel fluctuation was 0.3°C. On 1 April, 1 May, and 1 June, the mean temperatures rose to 4.8, 7.6, and 8.1°C and the diel fluctuations were 0.7, 0.9, and 0.5°C, respectively. By June, increases in both temperature and its diel fluctuation were moderated due to shading of the stream by the developing forest canopy. Periphyton production is known to increase with moderate increases in both light and temperature (Hornick et al. 1981; Bott 1983). Correspondingly, the most rapid period of growth observed in both cohorts of *G. semata* (Fig. 4; see Growth) correlated with increased diatom consumption and increases in both stream temperature and diel fluctuation.

The amount of production attributable to each food type consumed was estimated using the procedure of Benke and Wallace (1980). The methods and rationale of this procedure were detailed by Benke and Wallace (1980), as are justifications for the assimilation efficiencies (AE) and net production efficiencies (NPE) used in the present investigation. Based on

the rationale of this procedure, the food category contributing most to total annual production of *G. semata* was diatoms (58%) followed by fine amorphous detritus (39%), with the remaining food categories collectively contributing only 3% (Table 3). It should be stressed that diatoms may contribute substantially more than 58% to the total annual production of *G. semata*. This value was based on annual production and the proportional food type consumption averaged over the year. However, the elevated growth rates during the spring (Fig. 4, see Growth) indicated that the major proportion of production occurred during this season. Diatoms composed 64% of the spring diet and, therefore (based on assumptions of the above analysis), as much as 84% of the production during this period may be based on periphyton. Although the production data presented here do not allow for the assessment of seasonal dynamics, Wallace and Gurtz (1985) presented data indicating that production of *Baetis* responded positively to enhanced primary production.

Total annual consumption (milligrams AFDM per square metre per year) of each food category was estimated by dividing the amount of production attributed to each food type by its gross production efficiency (AE × NPE). From this relationship, *G. semata* was estimated to consume ca. 1680 and 644 mg AFDM·m<sup>-2</sup>·year<sup>-1</sup> of fine amorphous detritus and diatoms, respectively, in the rock-face habitat. When weighted by areal proportion of the rock-face habitat for the entire stream, these consumption rates are 336 and 129 mg AFDM·m<sup>-2</sup>·year<sup>-1</sup> of fine amorphous detritus and diatoms, respectively. Amounts of other food categories consumed are given in Table 3.

Stream net primary production in WS 14, a heavily shaded Coweeta catchment similar to WS 27, was estimated to be 2600 mg DM·m<sup>-2</sup>·year<sup>-1</sup> (Webster et al. 1983), which is equivalent to 2300 mg AFDM·m<sup>-2</sup>·year<sup>-1</sup> (Wallace and Gurtz 1985). Assuming that primary production in WS 27 is similar, the proportion of net primary production cropped by *G. semata*, diatoms and filamentous algae (ca. 184 mg AFDM·m<sup>-2</sup>·year<sup>-1</sup>), constituted ca. 7.1%. This proportion is remarkably similar to the 9.0% calculated for *Baetis* spp. in WS 14 (Wallace and Gurtz 1985).

### Discussion

The 2-year life cycle of *G. semata* is unusual for members of the Limnephilidae and for the Trichoptera in general (Wiggins 1977). Among the Limnephilidae, data suggesting 2-year life cycles have previously been reported only for *Alomyia* spp. (Wiggins 1977) and *Lepania cascada* Ross (Wiggins 1973a, 1977), and Mutch and Pritchard (1984a) found a 2- to 3-year life cycle for *Philocasca alba*. The extended life cycle of *G. semata* reported here is surprising since larvae attain a relatively small size prior to pupation (1.14 mg AFDM, including case silk). The prolonged developmental period is undoubtedly related to the harsh habitat of *G. semata*. The average annual temperature is lower, with only 2802–3300 degree-days per year. During midwinter, most of *G. semata*'s habitat is beneath massive ice sheets and larval weights decline. During dry summers, a large proportion of the habitat is dry, potentially contributing to an additional decline in growth.

The production of *G. semata* appears to be profoundly influenced, both actively and passively, by autochthonous primary production. The presence of aquatic mosses on rock outcrops is a passive influence enabling *G. semata* to occupy and

TABLE 3. Calculation of production attributed to each food type, the amount consumed, and the amount of feces produced by *G. semata* in the rock-face habitat in the headwaters of Ball Creek at the Coweeta Hydrologic Laboratory, Macon Co., NC (September 1983 – August 1984)

	% food type in foregut	Assimilation efficiency (AE)	Net production efficiency (NPE)	Relative amount to attributed production	% production attributed to each food type	Production from each food type (mg·m <sup>-2</sup> ·year <sup>-1</sup> )	Gross production efficiency (AE × NPE)	Amount of food consumed (mg·m <sup>-2</sup> ·year <sup>-1</sup> )	Feces produced* (mg·m <sup>-2</sup> ·year <sup>-1</sup> )
Detritus	65.4	0.1	0.5	3.27	39.27	93.33	0.05	1866.6	1679.9
Diatoms	32.2	0.3	0.5	4.84	58.04	137.94	0.15	919.6	643.7
Filamentous algae	0.5	0.3	0.5	0.08	0.96	2.28	0.15	15.2	10.6
Fungal hyphae	0.6	0.3	0.5	0.08	0.97	2.31	0.15	15.4	10.8
Vascular plant detritus	1.3	0.1	0.5	0.06	0.76	1.81	0.05	36.2	32.6

NOTE: To calculate values per square metre of the entire stream area, the values in this table should be weighted by the areal proportion of rock face (20%·m<sup>-2</sup>). Weights refer to ash free dry mass.

\*Feces produced = amount of food consumed – (amount of food consumed × AE).

maintain relatively high average annual densities on this substrate (ca.  $288 \cdot \text{m}^{-2}$ ). The importance of moss in the enhancement of invertebrate densities has been known for some time (Percival and Whitehead 1929; Hynes 1961) and documented for Coweeta streams (Gurtz and Wallace 1984). The production of *G. semata* ( $237.66 \text{ mg AFDM} \cdot \text{m}^{-2} \cdot \text{rock face} \cdot \text{year}^{-1}$ ) is maintained primarily by high areal density rather than high growth rates.

The major period of growth of *G. semata* (February to June) is correlated with increases in both quality of its diet, i.e., diatoms, and in stream water temperature, which influences both growth and foraging activity (Anderson and Cummins 1979). Periphyton is important to the biology of *G. semata*, being responsible for at least 58% of the annual production. In the rock-face habitat, *G. semata* egests  $>2300 \text{ mg} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  of fecal material of which 28% is periphyton based (Table 3). Therefore, a portion of this autochthonously derived energy source may be diverted into the detrital food web through coprophagy (Shepard and Minshall 1981, 1984). Hence, the autochthonously derived portion of *G. semata*'s feces, when combined with that of other grazers such as *Neophylax mitchelli* Carpenter, which occurs in high densities in stream habitats throughout WS 27 (unpublished data), may contribute substantially to secondary production of other functional groups.

Although allochthonous food resources probably overwhelm autochthonously derived resources in this heavily shaded headwater stream, the latter may influence total secondary production more than is generally realized. As suggested by McIntire (1973), Minshall (1979), Hornick et al. (1981), and Mutch and Pritchard (1984b), autochthonously based energy sources should not be overlooked when investigating stream ecosystem processes since they may contribute substantially, both directly and indirectly, to total secondary production and community structure.

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