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Life histories, abundance and distribution of some macroinvertebrates from a South Carolina, USA coastal plain stream

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Abstract

The life histories, densities and distribution patterns of the most abundant macroinvertebrates, exclusive of chironomids and oligochaetes, are reported for a low-gradient, second-order, blackwater stream on the Coastal Plain of South Carolina, USA. Univoltine life histories were found for all species of Coleoptera (*Ancyronyx variegata, Macronychus glabratus, Dubiraphia quadrinotata* and *Hydroporus clypealis*) and most species of Ephemeroptera (*Eurylophella temporalis, Paraleptophlebia volitans* and *Hexagenia munda*), although the mayfly *Stenonema modestum* was at least bivoltine. Both univoltinism (*Macrostemum carolina* and *Pycnopsyche luculenta*), partial bivoltinism (*Nyctiophylax affinis*) and complete bivoltinism (*Hydropsyche decalda, Cheumatopsyche* sp., *Phylocentropus placidus* and probably *Chimarra florida*) were found among the Trichoptera. Odonate species were both univoltine (*Calopteryx dimidiata, Enallagma divagans* and *Epitheca cynosura*) and semivoltine (*Boyeria vinosa, Gomphus lividus* and *Macromia georgina*). The alderfly *Sialis aequalis* and the isopod *Asellus laticaudatus* were univoltine, while the blackfly *Simulium taxodium* produced at least 6 generations per year. Groups of functionally-related species within the orders Odonata, Trichoptera and Coleoptera each exhibited possible temporal and/or spatial segregation.

Introduction

Information on the life histories and distribution of macroinvertebrates is essential for the understanding of the functional role of these organisms in streams. In particular, this information is necessary for secondary production estimates, the development of energy budgets for streams, and for environmental impact assessment. Although some information on the life histories and distribution of macroinvertebrates exists for several of the larger rivers of the Coastal Plain of the southeastern United States (Cudney & Wallace, 1980; Benke *et al.*, 1984), very little information has been published on the life histories of the macroinvertebrates inhabiting the low gradient, headwater streams of this area.

As part of a larger study (Smock *et al.*, 1985; Smock & Roeding, 1986), the macroinvertebrate communities at three sites on a second-order blackwater stream on the Coastal Plain of South Carolina, USA were studied. Here we present the life histories, densities, and distribution patterns of the most abundant macroinvertebrates, exclusive of chironomids and oligochaetes, in that stream. The 24 species included account for 19–37% of the total macroinvertebrate (>0.15 mm pore-size sieve) production at the three sites and 85–89% of production of species exclusive of chironomids and oligochaetes (Smock *et al.*, 1985).

Site Description

Sampling was performed at three sites on Cedar Creek, a relatively undisturbed second-order blackwater stream flowing through the Congaree Swamp National Monument in the upper Coastal Plain of Richland County, South Carolina. The stream is fully canopied with water tupelo (*Nyssa aquatica* L.), bald cypress (*Taxodium distichum* (L.) Rich.), and other hardwoods typical of seasonally-inundated southeastern floodplain forests. One sampling site was a low-flow swamp area with sediments of silt and refractory organic matter. The other two sites were approximately 5 km up and downstream of the swamp site. Their substrate consisted of loose sand with mud banks. Trunks and branches of fallen trees (snags) were common in the channel at all three sites.

A survey of substrate availability indicated that the predominant habitat at all three sites, measured as the percentage of the total available surface area in the stream, was the main channel sediments, accounting for from 49–70% of the total surface area at the swamp and downstream sites, respectively. The other major habitats included muddy bank areas (7–27%), snags (8–19%), leaf packs (5–12%), and leaf blades of the macrophyte *Sparganium americanum* Nutt. (0–6%) (see Smock *et al.*, 1985 for detailed information on habitat availability).

Water temperature ranged from 4–28 °C from October 1980 to September 1981, the duration of the sampling period, with an annual average of 17.6 °C. Annual average pH and conductivity were 5.6 and 29 μS/cm, respectively. Channel width ranged from 8–12 m; water depth ranged from 0.3 to 2 m. Mean annual discharge was 1.22 m^3/s (United States Geological Survey, personal communication).

Methods

Macroinvertebrates were collected monthly from the major habitats at each site. Main channel and bank sediments were sampled with a 4.4-cm inner diameter polyethylene corer. In addition, a 1-mm pore-size dip net was swept along the muddy bank over a 0.19 m^2 area to estimate densities of the larger, rarer macroinvertebrates. All snag samples (2–6 cm diameter; 20–30 cm length) were collected from mid-depth in the main channel by placing a bucket around, and then cutting, the wood. Natural leaf packs (10–20 leaves per pack) caught on snags in midstream were collected by placing a bucket around a pack and lifting it from the water. Each sample of *Sparganium* consisted of a 30–45 cm leaf blade collected by slipping a polyethylene corer around a blade, placing a stopper in the bottom of the corer and cutting the blade. Intensive qualitative sampling was performed in all habitats using a dip net in order to provide sufficient individuals to develop life histories of the more abundant species.

All samples were washed through a 0.15 mm pore-size sieve. Individuals were sized according to head capsule width using an ocular micrometer. Densities of macroinvertebrates are based on the means of 3–5 replicate samples from each of the major habitats. Surface areas used for the density calculations for the snags were calculated using the mean diameter and length of the sampled wood. Surface areas of the *Sparganium* leaves were determined by direct measurement of leaf length and width, while the surface areas of leaves in leaf packs were determined planimetrically. The mean monthly densities of each species in each habitat were then weighted according to the relative abundance of each habitat at each site in order to calculate the densities of each species in an average stretch of stream. Only the weighted densities from the site at which a species was most abundant are presented.

Results and discussion

Ephemeroptera

Eurylophella temporallis (McDunnough) (Ephemerellidae) was univoltine in Cedar Creek, similar to the voltinism of nearly all Ephemerellidae (Clifford, 1982). Recruitment occurred mainly in October, although early instars were present every month from October through April (Fig. 1). This may be due to either continuous recruitment or slow growth of some individuals. Adult emergence occurred predominately in April. The eggs probably

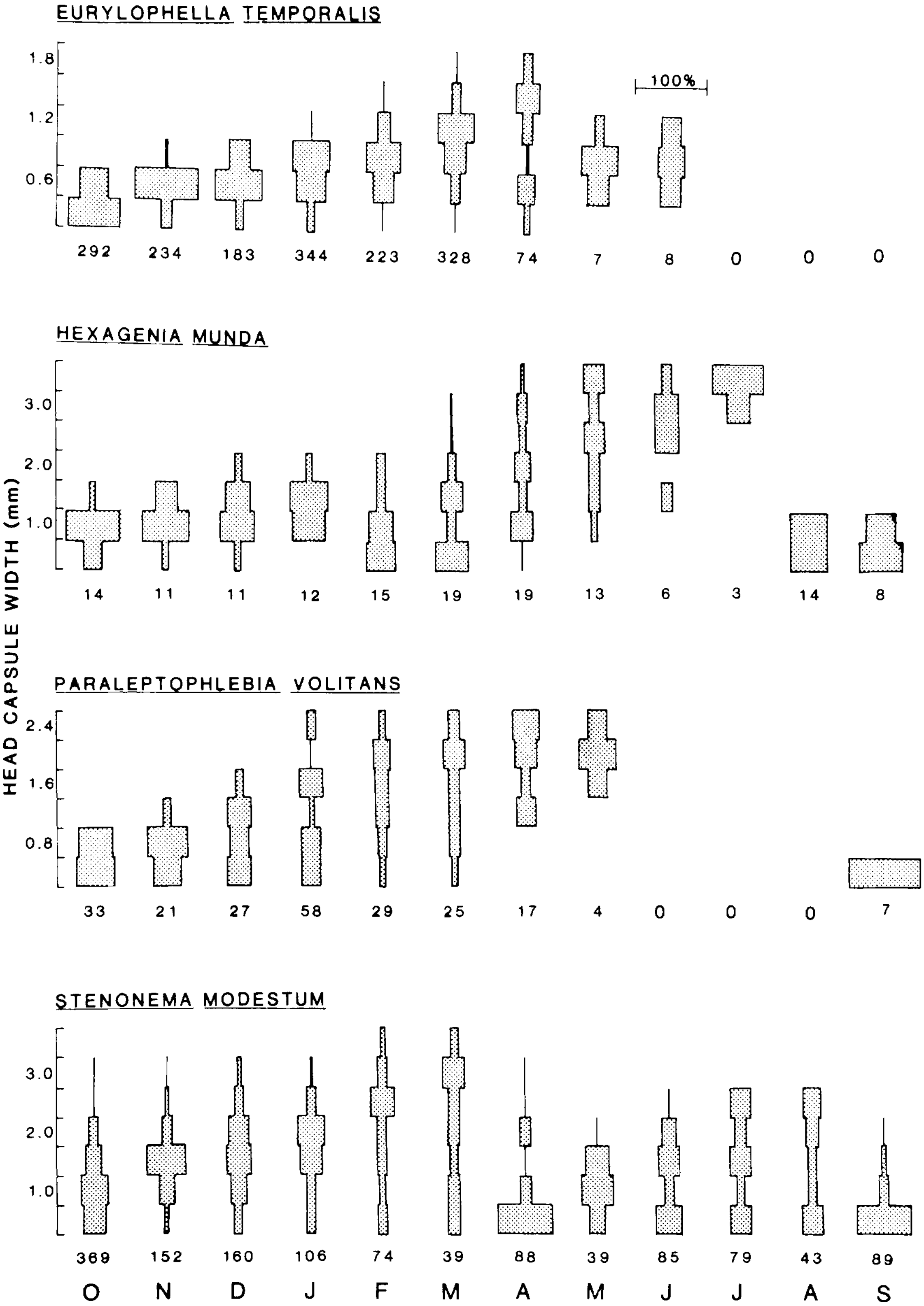

Fig. 1. Life histories of Ephemeroptera in a South Carolina Coastal Plain stream.

underwent a long summer diapause since no first instars were present from May through September. Coleman & Hynes (1970) noted that several species of Ephemerellidae in Ontario and Europe also are known to have long egg diapause periods.

Weighted densities of this species were highest at the swamp site, reaching $70/m^2$ in November and remaining relatively high until adult emergence the following spring (Fig. 2). A late February flood had little effect on densities at the swamp site, but did decrease weighted densities from over $10/m^2$ to less than $1/m^2$ at the higher gradient upstream site. This species was common in all habitats in the stream except for the sandy stream sediments, with densities reaching $354/m^2$ of snag surface area at the swamp site in November.

Hexagenia munda Eaton (Ephemeridae) was univoltine, with recruitment beginning in August/September and continuing at least through the fall (Fig. 1). Early instars were present from August through April. Emergence began in early summer and was completed by August. Morse *et al.* (1980) collected adults of this species from June through September at the Savannah River Plant in South Carolina. Growth of individuals was slow until the spring months, with no final instars being present until April. This species was collected almost exclusively from the silty main channel sediments at the swamp site. Weighted densities were highest in January and February, reaching $27/m^2$, and decreased steadily thereafter (Fig. 2).

Paraleptophlebia volitans (McDunnough) (Leptophlebiidae) was univoltine, recruitment beginning in September and emergence being completed by June (Fig. 1). It probably then undergoes a long summer egg diapause, similar to that of *P. moerens* McDunnough in Ontario (Coleman & Hynes, 1970), since no individuals were collected from May until September. While this development period is consistent with that found for this genus in Florida by Berner (1959), Morse *et al.* (1980) present data on adult *P. volitans* that suggest that this species may be bivoltine at the Savannah River Plant, with distinct emergence periods occurring in both May/June and September. Adults from a univoltine cohort of this species were found from June though August in Quebec (Harper & Harper, 1982).

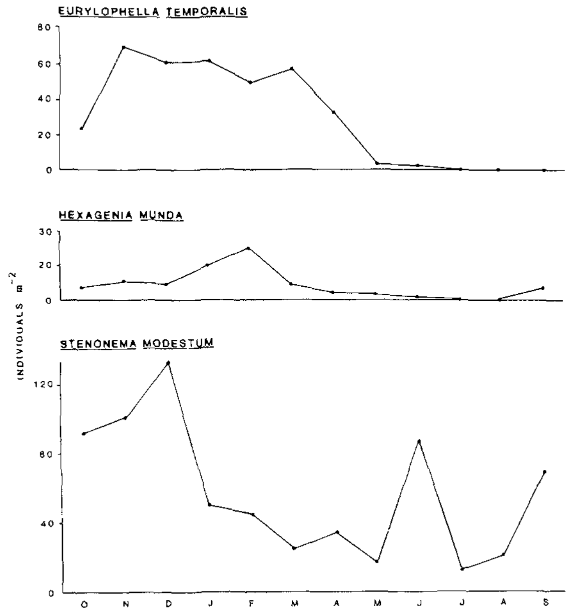

Fig. 2. Densities of Ephemeroptera in a South Carolina Coastal Plain stream. Densities were calculated from habitat-specific densities weighted according to the abundance of each habitat. *E. temporalis* and *H. munda* densities are from the swamp site; *S. modestum* densities are from the upstream site.

This species was most abundant at the downstream site, but weighted densities were never greater than $6/m^2$, being highest during recruitment in October. It was found in all habitats where detritus accumulations occured. However, Harper & Harper (1982) indicate that, while occurring in most stream habitats in Quebec, this species preferred faster-flowing areas. Occurence of potentially suboptimal low-flow conditions during the summer in Cedar Creek, versus the relatively faster flow of Upper Three Runs Creek at the Savannah River Plant (W. R. English, personal communication), may preclude bivoltinism at Cedar Creek and cause a shorter late-spring emergence period rather than the extended period found in Ontario.

Stenonema modestum (Banks) (Heptageniidae) was the most abundant mayfly in Cedar Creek, with weighted densities reaching $132/m^2$ in December (Fig. 2). It was collected almost entirely from the snag and leaf pack habitats, mainly at the upstream site. While most studies have shown a univoltine life history for many species of *Stenonema* (e.g. Lyman, 1955; Coleman & Hynes, 1970; Flowers & Hilsenhoff, 1978; Clifford, 1982), the size-frequency analysis suggests that this species is at least bivoltine (Fig. 1), emergence peaks occurring in March/April and again in August/September, and with heavy first instar recruitment occurring in April and September. However, early instars were present during all months of the year. Kondratieff & Voshell (1980) found a similar pattern for this species in a Virginia river, with the winter generation emerging in April and the summer generation emerging in mid-August but with fairly continuous emergence occurring throughout the year due to stragglers. Other studies similary have shown a prolonged emergence period for *S. modestum* and closely related species (Lyman, 1955; Harper & Harper, 1982; Morse *et al.*, 1980).

That *S. modestum* may have more than two generations per year is very possible since Benke & Jacobi (1986) found that the cohort production interval for *Stenonema* spp. is 41 days at the water temperatures found in Cedar Creek during the summer. Also, although this species was very rare at the swamp site during most of the year, early instars were abundant in April, June and September. This suggests that eggs from three distinct generations may have been swept in from upstream sites or were laid by ovipositing females. Later instars probably then experienced high mortality due to unfavorable environmental conditions at this site.

Odonata

The life histories of six species of Odonata were determined, although some are based on a relatively low number of individuals. *Epitheca cynosura* (Say) (Corduliidae), *Calopteryx dimidiata* Burmeister (Calopterygidae), and *Enallagma divagans* Selys (Coenagrionidae) were univoltine (Fig. 3). Recruitment of first instars began in June and continued through August. Most *E. cynosura* overwintered in the final or F-1 instar, while most *C. dimidiata* overwintered as F-1 or F-2 instars. The instars in which *E. divagans* overwintered were much more variable. Emergence of *E. cynosura* and *C. dimidiata* was completed by May, while that of *E. divagans* was completed by June. Paulson & Jenner (1971) reported overwintering instars and adult flight periods for these species in North Carolina that are similar to these findings. Benke & Benke (1975) also reported similar results for *Epitheca* spp. in a pond in South Carolina, although the summer rate of development for the pond population was somewhat higher than that of the Cedar Creek population. This may have been due to a potentially greater food supply present in the pond during the summer months.

Boyeria vinosa (Say) (Aeshnidae), *Gomphus lividus* Selys (Gomphidae), and *Macromia georgina* (Selys) (Macromiidae) were all semivoltine with two-year life histories (Fig. 3). Adult emergence was probably completed by late spring/early summer for these species. First instar recruitment occurried in November and December of *B. vinosa*, in August through December for *M. georgina*, and throughout the summer and fall for *G. lividus.*

Weighted densities of all species except *G. lividus* were typically $0.1-0.5/m^2$ at times other than during first instar recruitment. *G. lividus* was the most abundant odonate in Cedar Creek, with an annual mean weighted density of $2.9/m^2$ at the upstream site. Some degree of habitat partitioning among the six species was noted. *C. dimidiata* and *B. vinosa* were found almost exclusively on snags at the upstream and downstream sites while *G. lividus* was found only in the sandy sediments at those two sites. *E. divagans*, *E. cynosura* and *M. georgina* were found only in the mud sediments at all three sites.

Coleoptera

Three species of Elmidae were commonly encountered in Cedar Creek. They were all univoltine (Fig. 4). Although early instars were present during most months, the main periods of recruitment were April–June for *Ancyronx variegata* (Germar), June–July for *Macronychus glabratus* Say, and August–October for *Dubiraphia quadrinotata* (Say). This suggests possible resource partitioning by at least the early instars of these species. Adult *A. variegata* and *M. glabratus* were found during nearly all months, supporting Brown's (1972) observation that adults may have extended life spans. Nearly all *D. quadrinotata* adults, however, were found during the summer and fall months just prior

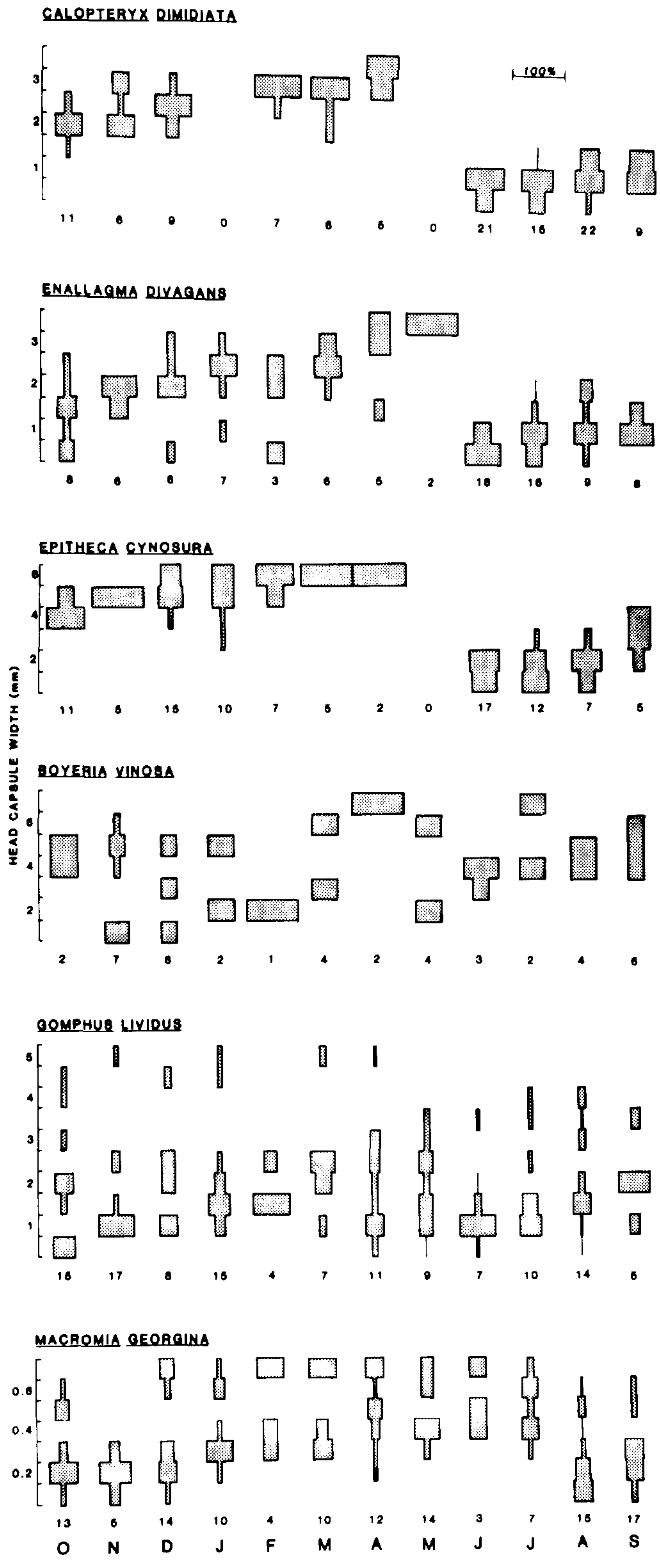

Fig. 3. Life histories of Odonata in a South Carolina Coastal Plain stream.

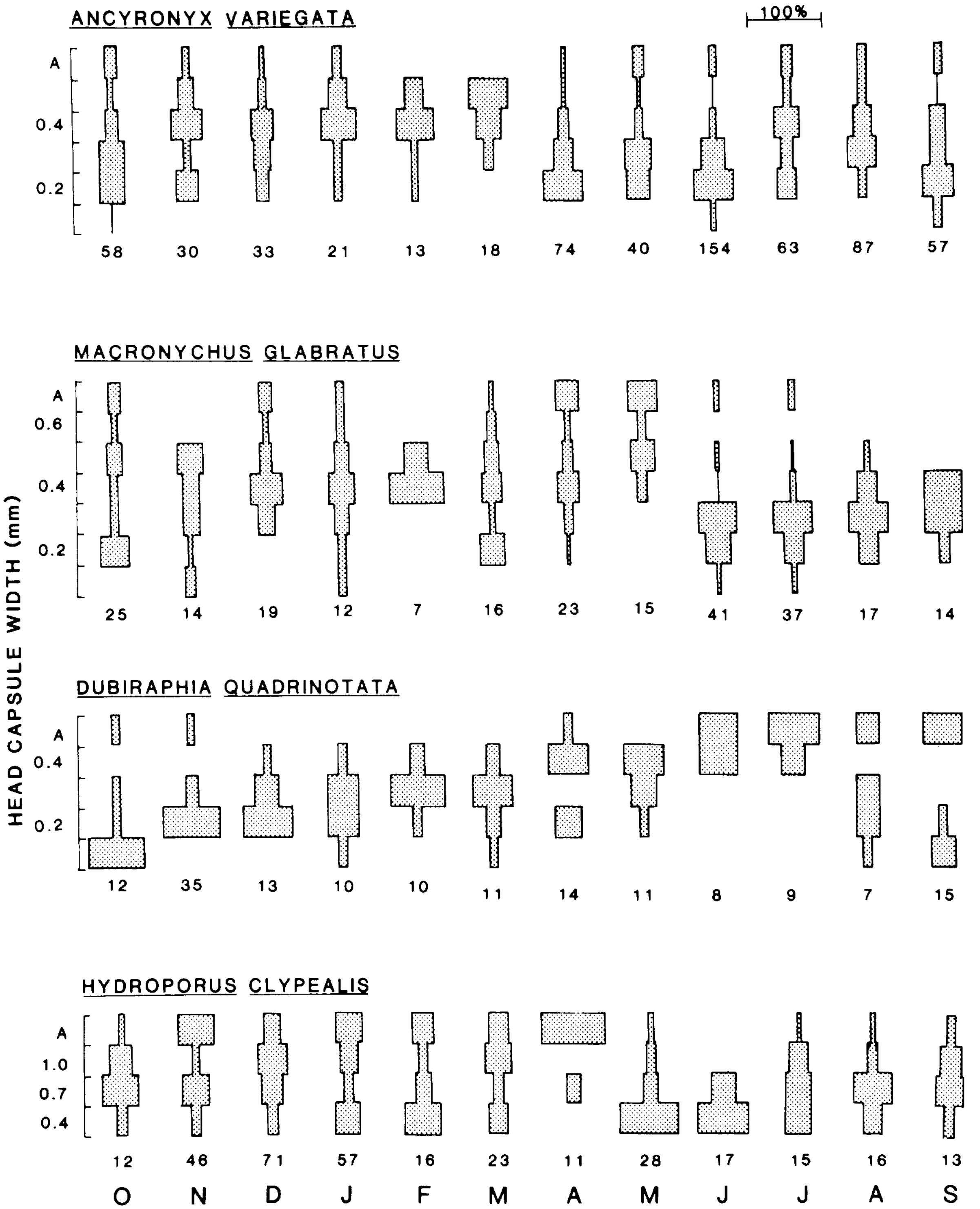

Fig. 4. Life histories of Coleoptera in a South Carolina Coastal Plain stream.

to and coinciding with the appearance of first instars. They therefore may not have an extended life span.

A. variegata was the most abundant elmid in Cedar Creek, with weighted densities reaching 74/m^2 in the stream in June following first instar recruitment (Fig. 5). Weighted densities of adults, however, were never greater than 3/m^2. Larvae and adults of both *A. variegata* and *M. glabratus* were found almost entirely on snags, with *A. variegata* densities reaching 652/m^2 of snag surface in June at the downstream site. *D. quadrinotata* larvae were found mainly in the sediments rather than on snags, similar to the findings of Smock (unpublished data) for a first-order stream in Virginia and to the findings of Benke *et al.* (1984) for *Stenelmis* in the Satilla River in Georgia. Adults were found both in the sediments and on snags.

Hydroporus clypeales Sharp (Dytiscidae) was the only other commonly encountered Coleoptera in Cedar Creek. It is probably univoltine, with the majority of the population in April consisting of adults and the main period of recruitment occurring during May and June (Fig. 4). It was most abundant

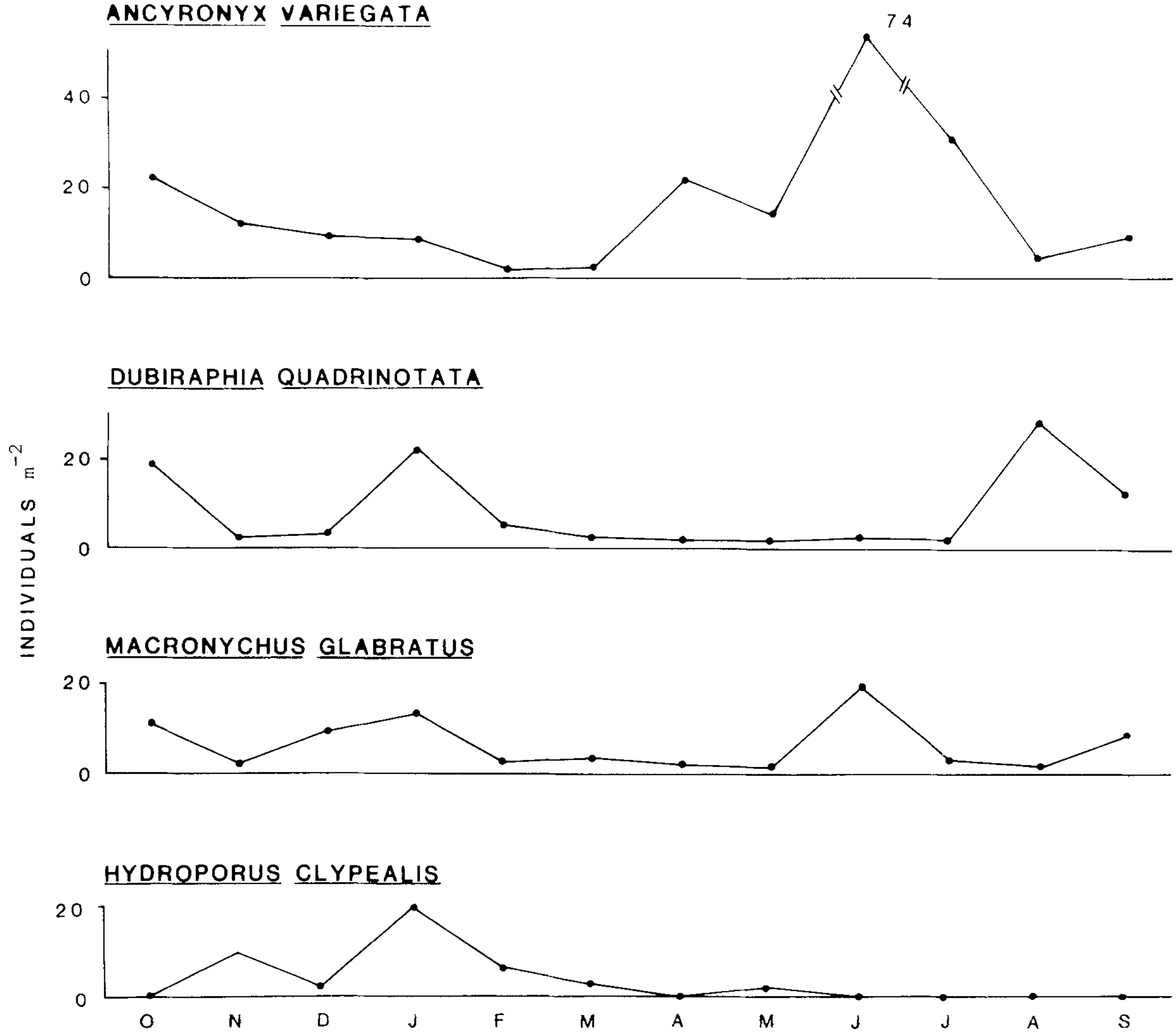

Fig. 5. Densities of Coleoptera in a South Carolina Coastal Plain stream. Densities were calculated from habitat-specific densities weighted according to the abundance of each habitat. *A. variegata* and *D. quadrinotata* densities are from the upstream site; *H. clypealis* densities are from the swamp site; *M. qlabratus* densities are from the downstream site.

at the swamp site, with most adults occurring in the bank areas but with the larvae occurring in all habitats.

Megaloptera

Sialis aequalis Banks (Sialidae) was univoltine in Cedar Creek (Fig. 6), having a life history similar to that found for most species of *Sialis* (Minshall, 1965; Azam & Anderson, 1969; Woodrum & Tarter, 1973). First instar recruitment occurred in April and May, and adult emergence probably occurred the following March and April. Woodrum & Tarter (1973) found that in West Virginia this species pupated in March and April and that adults were present in April and early May. *S. aequalis* was most abundant in the muddy sediments along the bank at the swamp site. Weighted densities peaked in September at nearly $7/m^2$ (Fig. 6).

Trichoptera

Macrostemum carolina Banks was the only commonly occurring univoltine Hydropsychidae (Fig. 7). Recruitment of first instars extended from June through October. However, pupae of this species were found only during May. Most individuals were collected at the upstream site, with weighted densities reaching $308/m^2$ in July (Fig. 8). This species was common at the other two sites only during first instar recruitment, with weighted densities of only 27 and $84/m^2$ in June at the swamp and downstream sites, respectively. Densities decreased rapidly after this month at these two sites, with no individuals being present after October at the swamp site and with densities being less than $1/m^2$ after September at the downstream site. Low flow rates, making filter-feeding inefficient, probably account for the high mortality of this species at the swamp site. The reason for the low densities at the down-

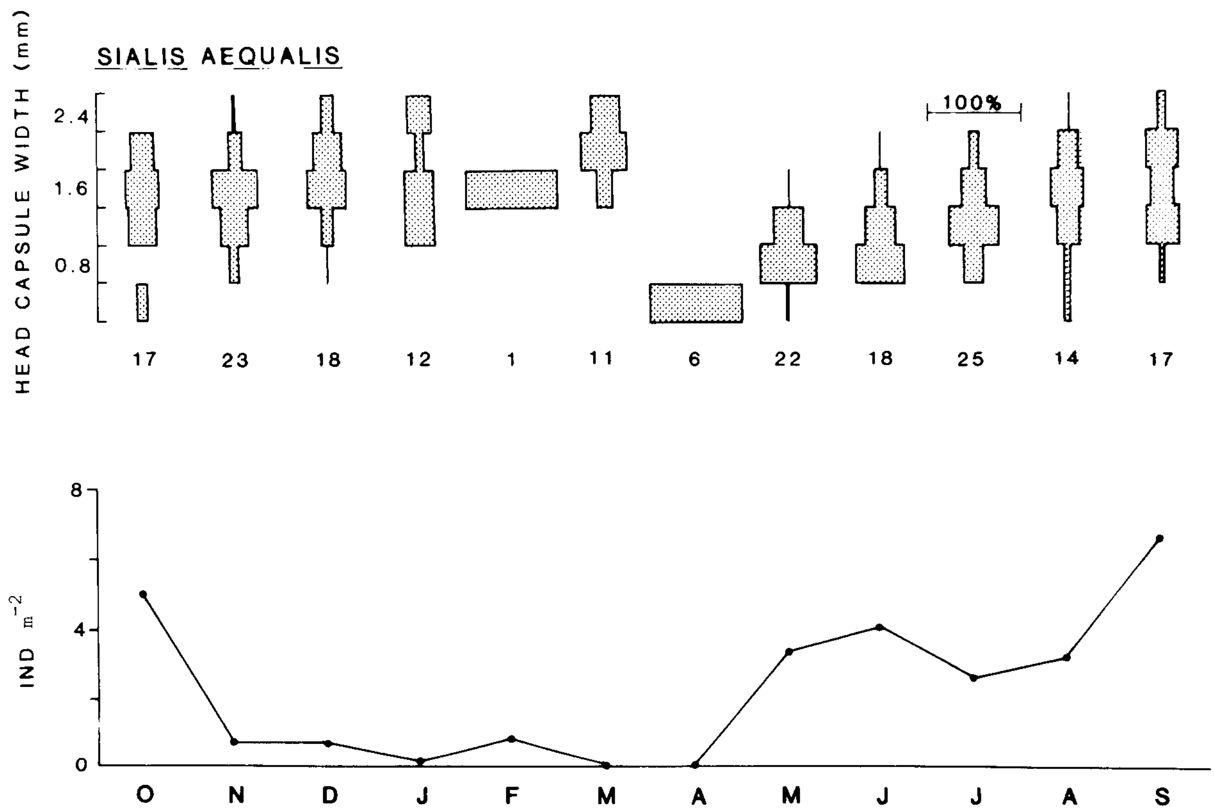

Fig. 6. Life history and densities of *Sialis aequalis* (Sialidae: Megaloptera) in a South Carolina Coastal Plain stream. Densities were calculated from habitat-specific densities weighted according to the abundance of each habitat at the swamp site.

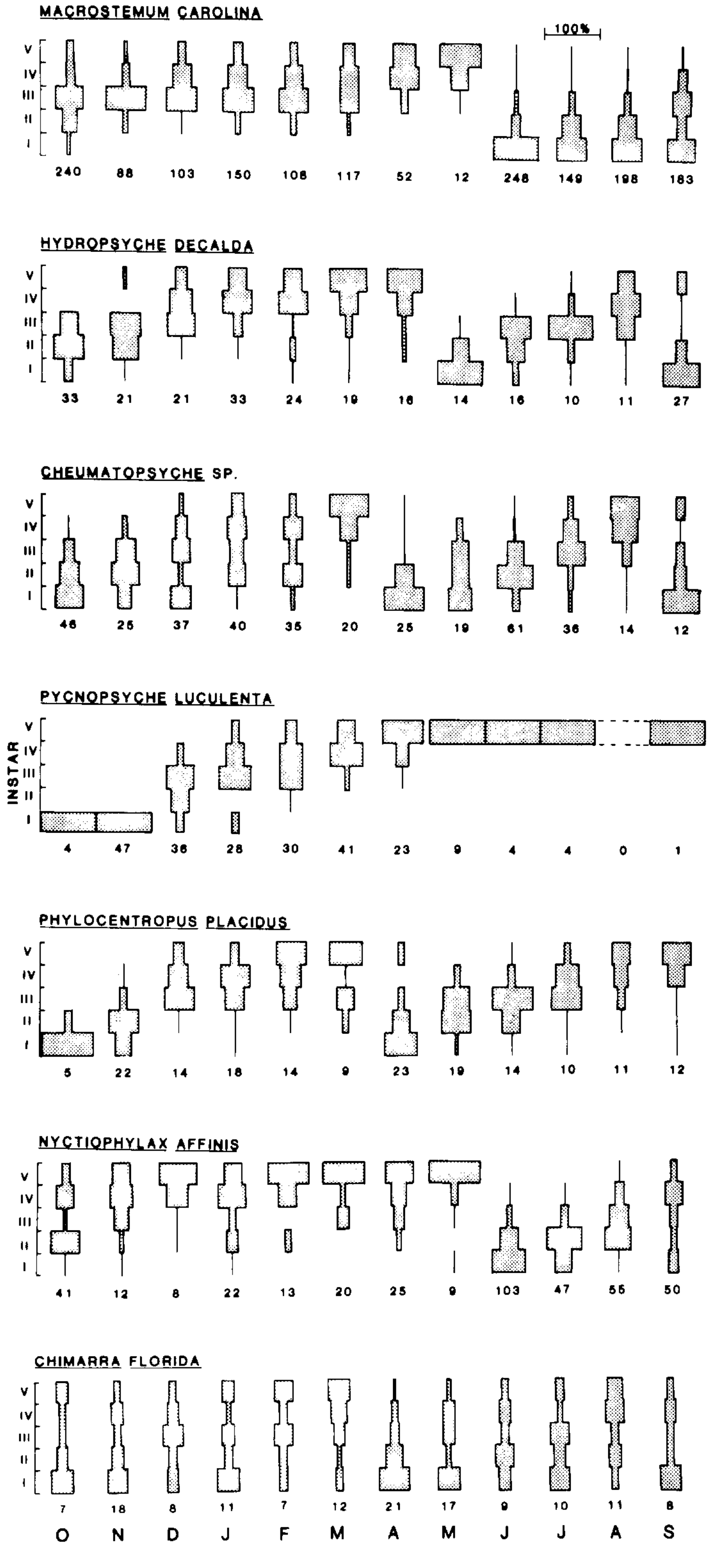

Fig. 7. Life histories of Trichoptera in a South Carolina Coastal Plain stream.

stream site is unknown, since flow rates and habitat type and availability were similar at the up and downstream sites. The answer may lie in the type and/or nutritional quality of seston being transported out of the swamp to the downstream site.

Snags were the main habitat for this species, with densities of $739/m^2$ of snag surface during June at the upstream site. Densities remained over $130/m^2$ of snag surface until the following April. Considerable oviposition occurred on the leaves of *Sparganium*, with densities reaching $3701/m^2$ of leaf surface in July, nearly all of these individuals being first or second instars. However, no individuals were found on *Sparganium* after October, indicative of this species' use of crevices in snags as the site for constructing its retreat and capture net (Wallace & Sherberger, 1974).

Hydropsyche decalda Ross (Hydropsychidae) was collected only at the upstream site. It was bivoltine, with both a short summer generation and a longer winter generation. (Fig. 7). Recruitment occurred mainly during May and September. Weighted densities were much lower than those of *M. carolina*, with a maximum of only $9/m^2$ following recruitment of the winter generation (Fig. 8). This species was most abundant on snags, but was also commonly encountered on *Sparganium*. Unlike *M. carolina*, all instars of *H. decalda* were present on *Sparganium*, although it appeared that most of the last instars were free-living rather than associated with capture nets.

Cheumatopsyche sp. (Hydropsychidae) was also bivoltine (Fig. 7), with recruitment occurring mainly during April and September. This species was

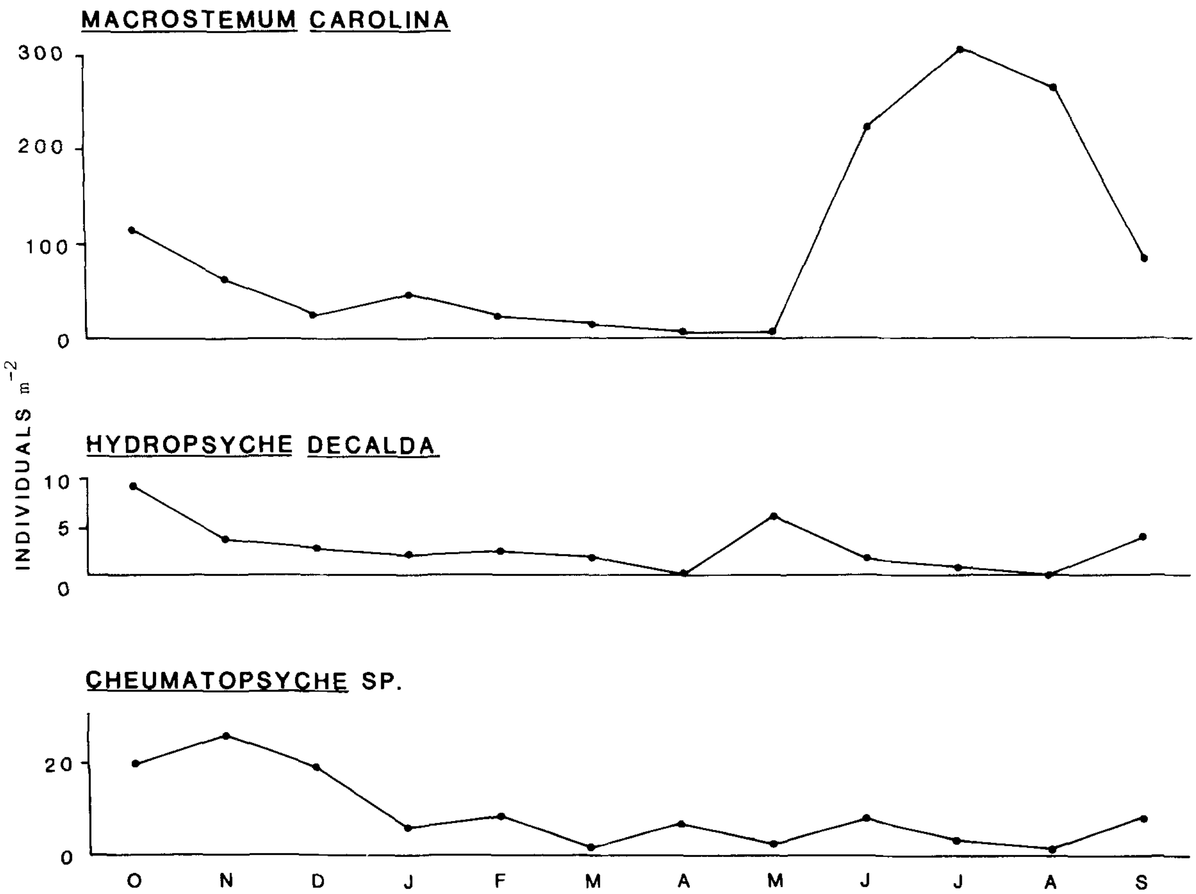

Fig. 8. Densities of Trichoptera in a South Carolina Coastal Plain stream. Densities were calculated from habitat-specific densities weighted according to the abundance of each habitat. Densities of all species are from the upstream site.

found mainly on the snags and in the leaf packs at both the upstream and downstream site. It was more abundant than *H. decalda*, but still far less abundant than *M. carolina* (Fig. 8).

The life histories of the three species of Hydropsychidae in Cedar Creek are consistent with those reported for these and closely related species from the southeastern USA (Cudney & Wallace, 1980; Ross & Wallace, 1983; Benke *et al.*, 1984), although trivoltinism for species of *Hydropsyche* and *Cheumatopsyche* has been reported from Virginia (Parker & Voshell, 1982) and Georgia (Freeman & Wallace, 1984). Species of *Macrostemum* seem to be consistently univoltine, with the only reported instance of bivoltinism in a species of *Macrostemum* being for *M. zebratum* in Virginia (Parker & Voshell, 1982). Partial or complete bivoltinism of species of *Hydropsyche* and *Cheumatopsyche* also has been reported from colder northern streams (e.g. Oswood, 1976; Mackay, 1979; Rutherford & Mackay, 1986; Schmude & Hilsenhoff, 1986). Many of these instances of multivoltinism occur below impoundments where food quantity and especially quality are considerably enhanced. Warmer water temperature seems to be sufficient to cause bivoltinism in southern streams.

The summer recruitment periods of the three species of hydropsychids were staggered by one month, with *Cheumatopsyche, Hydropsyche* and *Macrostemum* recruitment occurring mainly in April, May and June, respectively. Less temporal separation occurred in the recruitment of the winter generation, with both *Cheumatopsyche* and *Hydropsyche* first instars appearing mainly in September, a month when 50% of the *Macrostemum* present are also first instars. This suggests a greater need for temporal separation during the summer months.

Pycnopsyche laculenta (Betten) (Limnephilidae) was the only abundant shredder in Cedar Creek. It was univoltine, with first instars appearing in October and especially November (Fig. 7). Most of the individuals passed the winter months as third and fourth instars, with the majority of the population completing the final moult to the fifth instar in late March and April. Fifth instars attached themselves to the undersides of logs during April/May and remained there in a quiescent state until pupation up to six months later. A similar life history for this species was reported by Roeding (1986) in Virginia and Mackay (1972) in Ontario, although in Ontario the larval growth period is much longer and the aestivation period shorter (4–6 weeks). This most likely is due to faster growth rates in the warmer South Carolina water.

Pupae were found in October in Cedar Creek, and Morse *et al.* (1980) reported an October-November flight period for adults of the species at the Savannah River Plant in South Carolina. Early instars were found predominately in leaf packs, but later instars were found mainly along the bank areas. Weighted densities were low, reaching a maximum of only $5/m^2$ in November at the upstream site.

Phylocentropus placidus (Banks) (Polycentropodidae) was bivoltine, with the winter generation being present from October/November through March/April and the summer generation occurring from April through September (Fig. 7). Adult flight periods for this species in South Carolina have been reported as March through June and again from August through October (Morse *et al.*, 1980). Nearly all individuals were collected in the muddy bank areas where they construct their subsurface tubes. Weighted densities were low, with a maximum of $3.5/m^2$ at the swamp site in April (Fig. 8).

The life history analysis of *Nyctiophylax affinis* (Banks) (Polycentropodidae) suggests split-cohort development, with the majority of the population being univoltine, but with some individuals also completing a summer generation (Fig. 7). The majority of first instar recruitment occurred in June and July, but the rapid development to the fifth instar by some individuals, the renewed presence of first instars in September, and the collection of a few pupae during that month indicate that a small summer generation occurred. Partial bivoltinism has been commonly observed in other trichopterans (e.g. Dall *et al.*, 1984; Kreuger & Cook, 1984; Rutherford & Mackay, 1986). The majority of the population overwintered as a fifth instar, with pupation and emergence occurring during May and especially June. Morse *et al.* (1980) reported a May through September adult flight period for this species.

All individuals were collected on snags, with densities reaching $356/m^2$ of snag surface area in June at the downstream site. The annual mean weighted density, however, was only $4/m^2$.

Chimarra florida Ross (Philopotamidae) was at least bivoltine, but with first instars constituting a significant proportion of the population during all months (Fig. 7). Cudney & Wallace (1980) and Parker & Voshell (1982) reported bivoltinism for species of *Chimarra* in Georgia and Virginia, respectively. The identification to species is based on only two adults captured during April; other species of this genus may have been present, obscuring the life history of this species. Heaviest first instar recruitment occurred in April, and Morse *et al.* (1980) reported an adult flight period of March through September. All individuals were collected from snags or leaf packs caught on snags. Weighted densities were generally less than $1/m^2$.

Diptera

Similium taxodium Snoddy & Beshear (Simuliidae) was by the most abundant blackfly in Cedar Creek. It had a minimum of six generations during a one-year period (Fig. 9); other generations may have been missed between the monthly sampling trips due to the potentially rapid development of blackflies at the warm summer water temperatures. Stone & Snoddy (1969) reported up to seven generations per year for several species of blackflies in Alabama. Pupae were found during all winter and spring months, but were far less abundant during the summer, reflecting the decreased abundance of this species (Fig. 9). Most individuals were collected from the snags, leaf packs and *Sparganium* leaves.

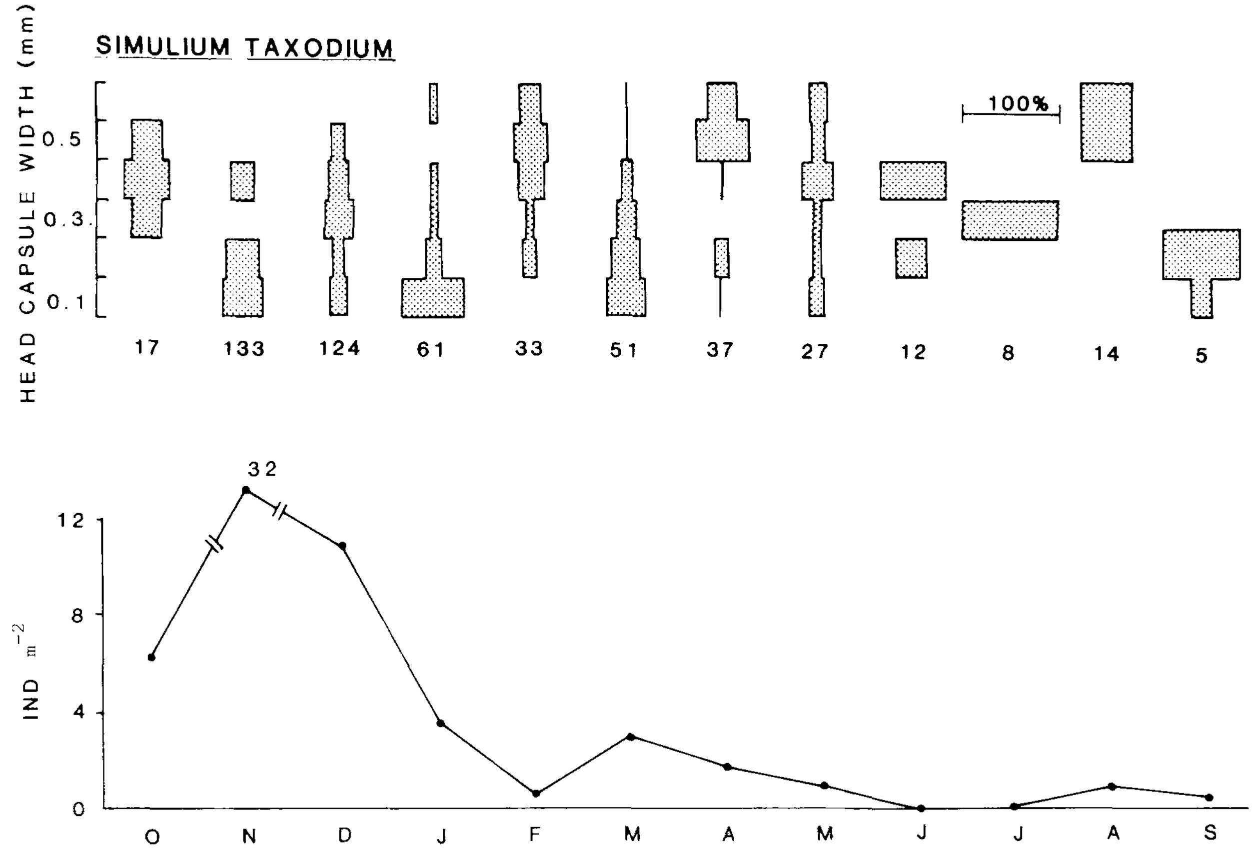

Fig. 9. Life history and densities of *Simulium taxodium* (Simuliidae: Diptera) in a South Carolina Coastal Plan stream. Densities were calculated from habitat-specific densities weighted according to the abundance of each habitat at the downstream site.

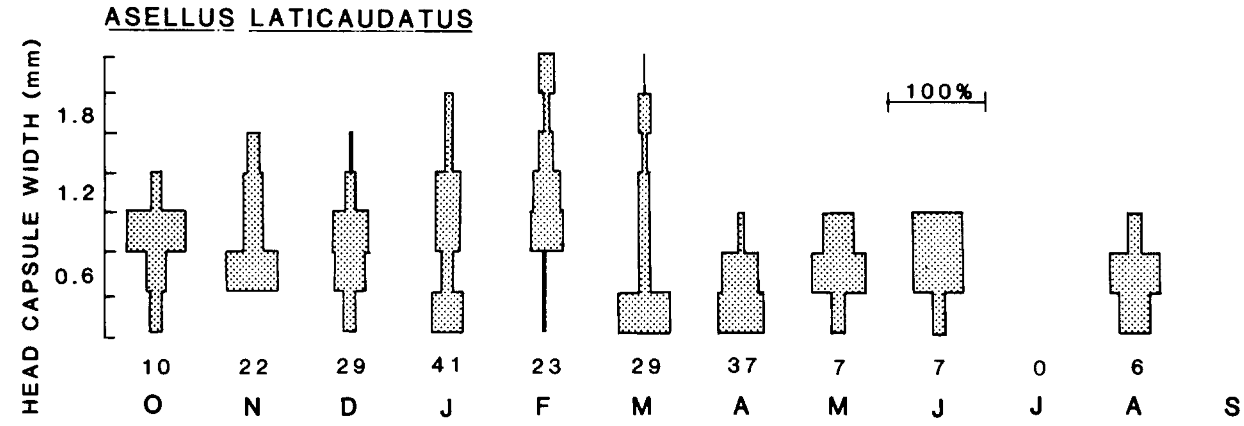

Fig. 10. Life history of *Asellus laticaudatus* (Asellidae: Isopoda) from a South Carolina Coastal Plain stream.

Isopoda

The size-frequency distribution of *Asellus laticaudatus* Williams (Asellidae) (Fig. 10) and the observation that gravid females were collected only in January through April suggest that this species is univoltine. However, gravid females of this species have been collected throughout the year at a nearby site on the South Carolina coast (LA Smock, unpublished data). Also, early instars were found during much of the year at Cedar Creek, suggesting that more than one generation may actually occur at this location. Bivoltinism is common among ispods, with both partial and complete bivoltine life histories having been reported for lotic populations of the European species *A. aquaticus* (L.) (Steel, 1961; Aston & Milner, 1980; Murphy & Learner, 1982), while *A. intermedius* Forbes was partially bivoltine in Michigan (Ellis, 1961). *A. laticaudatus* was most common at the swamp site in Cedar Creek, occurring mainly on snags and in the muddy bank areas, with an annual mean weighted density of $8/m^2$.

Overview

The life histories reported here for the predominant macroinvertebrates (exclusive of chironomids and oligocheates) in Cedar Creek are similar to those reported for the same or closely related species from the warm-water streams and rivers of the southeastern USA. For some species, however, this is the first documentation of their life history in this geographical area.

While there is a general similarity in the life history of the Cedar Creek population of a given species with that of populations from streams in colder climates, the specific timing of such events as egg hatching, pupation and emergence often differ. These differences probably reflect differences in development time as affected mainly by water temperature and possibly nutritional quality of available food resources. For some species the more rapid development time allows added generations to occur over a year. Besides being of inherent interest to the biology and ecology of these species, this life history information is critical to the estimation of macroinvertebrate secondary production (Benke, 1979; Waters, 1979), especially given the paucity of information on life histories of macroinvertebrates from the relatively warmwaters of the southeastern USA.

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