

## Life histories and abundance patterns of snag-dwelling mayflies in a blackwater Coastal Plain river

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**Abstract.** A diverse mayfly community (28 species) was found in the Ogeechee River, a blackwater river in the Georgia Coastal Plain. Quantitative samples of snag habitat, where most species (22) were found, were collected at 2-4 wk intervals in 1982 to investigate life history characteristics, and at monthly intervals in 1983 to determine consistency of seasonal and annual abundance patterns. Baetidae and Heptageniidae were abundant throughout each year with average densities of 1553-5981/m<sup>2</sup> (1982-1983) and 1498-1828/m<sup>2</sup> of snag surface, respectively. Field data for the most common species of Baetidae (*Baetis ephippiatus*, *B. intercalaris*) and Heptageniidae (*Stenonema exiguum*, *S. integrum*, *S. modestum*) showed no recognizable pattern of cohort development. This developmental asynchrony and long emergence periods for *S. exiguum* and *S. modestum* are consistent with previously published growth studies indicating multivoltinism. Ephemerellidae (551-719/m<sup>2</sup>), Oligoneuriidae (206-469/m<sup>2</sup>), Tricorythidae (721-1599/m<sup>2</sup>) and Caenidae (114-110/m<sup>2</sup>) were also commonly found on snags, but were seasonal in abundance. The major species of Ephemerellidae (*Ephemerella argo*, *E. dorothea*, *Eurylophella* sp.) showed distinct single cohorts developing primarily during winter/spring. *Isonychia* spp. (Oligoneuriidae) also showed a well-defined winter cohort, but had as many as two weakly defined cohorts during warm months. *Caenis* spp. (Caenidae) and *Tricorythodes* sp. (Tricorythidae) occurred primarily in summer months, during which time they were able to pass through multiple generations, as substantiated by either long emergence periods or independent growth studies. Major differences in life histories occurred between rather than within families. Relative abundance and seasonality at the family level were very consistent between years. The high degree of life history overlap in this diverse mayfly assemblage raises questions about the relationship between phenology and community structure, as well as latitudinal patterns of species richness.

**Key words:** Ephemeroptera, stream, seasonality, life history overlap, species richness, voltinism, generation time, coexistence.

Determination of life history patterns among closely related members of the same community or between communities along environmental gradients is critical to understanding basic ecological relationships (Hynes 1970, Butler 1984). Life history analyses of aquatic invertebrates have permitted investigations into strategies of coexistence through temporal separation of closely related species (e.g., Benke and Benke 1975, Sweeney and Vannote 1981, Brittain 1982), how species modify their synchrony and voltinism along latitudinal or temperature gradi-

ents (e.g., Clifford 1982, Smock 1988), how life history patterns or development times are affected by temporary drying of habitat (e.g., Gray 1981, Delucchi and Peckarsky 1989), and how life history variation allows species to avoid low pH (Giberson and Mackay 1991). Knowledge of life history is also fundamental for estimating secondary production among coexisting populations and distribution of this production through time (e.g., Vannote and Sweeney 1980, Georgian and Wallace 1983, Rader and Ward 1989a, 1989b). Regardless of the reason for initiating life history studies, they are clearly most useful if all members of a community, assemblage of closely related species, or functional group are considered simultaneously (e.g., Mackay 1969, Huryn and Wallace 1987a, Bunn 1988, Smock 1988).

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Mayflies (Ephemeroptera) are among the most-studied of any order of aquatic insects in terms of their life histories (see review of Clifford 1982). Although several hundred such studies have been conducted over the past three decades, most have examined species from cool-water streams at high latitudes ( $>40^{\circ}\text{N}$ ) of the Northern Hemisphere, where development is often relatively synchronous, and well-defined cohorts can be followed from field data (e.g., Lauzon and Harper 1988). Such developmental synchrony makes secondary production analysis a straightforward matter (e.g., Waters and Crawford 1973), and also allows for easy comparisons of temporal separation among species (e.g., Brittain 1982). Far fewer life-history studies of mayflies from warmwater streams in south-temperate to tropical regions have been published (Gray 1981, Smock 1988), even though much has been hypothesized about the importance of temperature to life history (e.g., Vannote and Sweeney 1980, Ward and Stanford 1982, Sweeney 1984). In these regions, where water temperatures may exceed  $20^{\circ}\text{C}$  for  $>6$  mo of the year, larval development often becomes less synchronous and emergence periods more extended, making clarification of life histories extremely difficult from field data alone (e.g., Bishop 1973, Wolda and Flowers 1985, Berner and Pescador 1988). Little attention has been given to how such shifts in life history patterns might affect coexistence of closely related taxa and mayfly richness.

The objectives of this paper are to describe and compare life history and abundance patterns of a diverse assemblage of mayflies coexisting on the snag (submerged woody debris) habitat in a warmwater river of the southeastern USA, to compare family-level patterns of abundance over two consecutive years, and to explore the community-level implications of these results. This work is part of an ecosystem study in which we have attempted to assess the distribution of energy flow, including invertebrate production, through space and time (e.g., Benke and Meyer 1988, Benke and Parsons 1990). Owing to widespread asynchrony in development among most of our mayfly species, interpretation of life history patterns required a combination of larval size-frequency and emergence data, as well as independently derived growth rates (Benke and Jacobi 1986).

### Study Site and Habitat

The Ogeechee River is a blackwater river that meanders southeasterly through adjoining floodplain swamps ( $\approx 1$  km in width) in the Coastal Plain of Georgia. At our study site near Meldrim, Georgia ( $32^{\circ}8'\text{N}$  latitude), the Ogeechee is a 6th-order, low-gradient (0.02%) river, with the main channel averaging about 33 m in width. During most years the river inundates the swamps for several weeks at a time, increasing the functional width of the river by  $\approx 40\times$ . Discharge over a 47-yr period of record averaged  $66.8\text{ m}^3/\text{s}$ . During the first year of our study (1982) mean discharge was relatively low ( $50.7\text{ m}^3/\text{s}$ ) and during the second year (1983), it was relatively high ( $79.1\text{ m}^3/\text{s}$ ) (Benke and Parsons 1990). Mean water temperature was  $19.5^{\circ}\text{C}$  in 1982 and  $19.2$  in 1983 with summer temperatures usually fluctuating between  $25$  and  $30^{\circ}\text{C}$  and winter temperatures rarely falling below  $10^{\circ}\text{C}$  (Benke and Parsons 1990). Thus, temperature conditions exist that would allow growth and emergence for a major portion of the year. Water quality is generally very good, although naturally low levels of dissolved oxygen ( $<5\text{ mg/L}$ ) can be found during warm months when discharge is low (Benke and Meyer 1988, Meyer, in press).

Snags are a major habitat type in the Ogeechee River and typically contribute 30–40% as much habitat surface as benthic areas (Wallace and Benke 1984). Snags along the main river channel are very stable (Benke and Wallace 1990) and provide the major site of colonization by most species of macroinvertebrates in these types of lotic environments (Benke et al. 1984). Mayflies are the third most abundant insect order on snags in the Ogeechee River, exceeded only by Diptera and Trichoptera.

### Methods

Samples of snags were collected every 2 wk (April through September) or monthly from December 1981 through December 1982 along a 1-km stretch of river to obtain detailed life history information and annual patterns of abundance. Monthly samples were collected from January through November 1983 to assess the consistency of family-level patterns of abundance. Twenty cut sections (about 40 cm length) of attached submerged snags, along with any associated leaf packs, root masses, or aquatic

macrophytes, were collected from a small boat or by wading on each date in the first year. Ten snag samples per date were collected in the second year. Samples were placed in polyethylene bags with water and a small amount of formalin for transport to the laboratory. After staining with rose bengal, samples were sorted in a white porcelain pan or under a microscope and preserved in Kahle's solution for later enumeration, identification, and measurement. Head widths and body lengths were measured to the nearest 10  $\mu\text{m}$  with an ocular micrometer in a dissecting microscope.

We identified larvae to species whenever possible, depending on development stage of individuals and adequacy of keys (i.e., Edmunds et al. 1976, Unzicker and Carlson 1982). To help verify species identifications and obtain some idea of emergence patterns, we collected black light samples at irregular intervals (averaging every 6 d) from late February to early October 1982. Because not all species would be attracted to a black light at a single location, the distribution of adults for any species throughout the year must be considered conservative. For example, *Baetis* species were observed emerging throughout the year but were rarely attracted to the black light. All adults were identified by Jan Peters and Manuel Pescador (Florida A&M University).

Surface area of each snag sample was determined after all animals were removed, and numbers were initially expressed per  $\text{m}^2$  of snag (see Benke et al. 1984 for a more complete description of procedure). Surface area for a single snag section was typically about  $250 \text{ cm}^2$ . Snag densities were then converted to number per  $\text{m}^2$  of channel bottom according to equations developed by Wallace and Benke (1984), in which amount of snag surface inundated is a function of water height (see Benke and Parsons 1990 for the pattern predicted during 1982-1983).

### Results and Discussion

At least 28 species of mayflies were collected as larvae or adults, of which 22 or more were found on snags or would be expected to occur there (Appendix 1). In some cases it was possible to identify taxa to species from both larvae and adults (e.g., *Stenonema modestum* and *Baetis ephippiatus*). In other cases, species could be identified only from larvae (e.g., *Ephemerella*

*argo*), or only from adults (e.g., *Caenis diminuta*). Of those species not found on snags, some such as *Macdunnoa brunnea* were probably too rare to be found as larvae. Some taxa such as *Baetisca carolina* (shallow floodplain or sandbar), *Tortopus incertus* (clay banks), and *Brachycercus* sp. (sand) are found in their own distinct habitats and were not quantitatively sampled as larvae. The specific habitats of *Siphloplecton* spp. and *Siphonurus* sp. in the Ogeechee River were unknown.

Thirteen taxa were sufficiently abundant to allow an assessment of temporal patterns of size-frequency distributions. It was possible to identify seven species of *Baetis*, *Stenonema*, and *Ephemerella*. In four genera (*Heptagenia*, *Eurylophella*, *Pseudocloeon*, and *Tricorythodes*) there appeared to be a single species, but it could not be identified with certainty. Although *Pseudocloeon* is no longer considered a valid genus (McCafferty and Waltz 1990), we continue to use this designation for an unknown species of Baetidae. Since most species previously considered as *Pseudocloeon* have been placed in *Baetis*, our unknown species is probably in this genus. For *Caenis* and *Isonychia* (2-3 species each), identification at the species level was not feasible, so congeners were combined in size-frequency distributions.

Size-frequency distributions for species or genera were based only on those individuals that could be identified with a reasonable degree of certainty. Relatively high fractions of Ephemerellidae (57%), Baetidae (36%) and Heptageniidae (54%) consisted of very small individuals only identified to family. Thus, the smallest size classes of all species from these families are underrepresented in the histograms presented below. Nonetheless, patterns of synchrony or asynchrony are still reasonably clear for most taxa.

Our interpretations of life histories rely on observations of shifts in size-frequency distributions, temporal abundance patterns of larvae, emergence patterns, and previously published growth rates of *Stenonema* spp., *Baetis* spp., and *Tricorythodes* sp. (Benke and Jacobi 1986). When interpreting size-frequency distributions, it is important to distinguish between our usage of the terms cohort and generation. If size distributions show a reasonably consistent shift from smaller to larger classes through time (i.e., developmental synchrony), we refer to this group of growing individuals as a larval cohort. Often

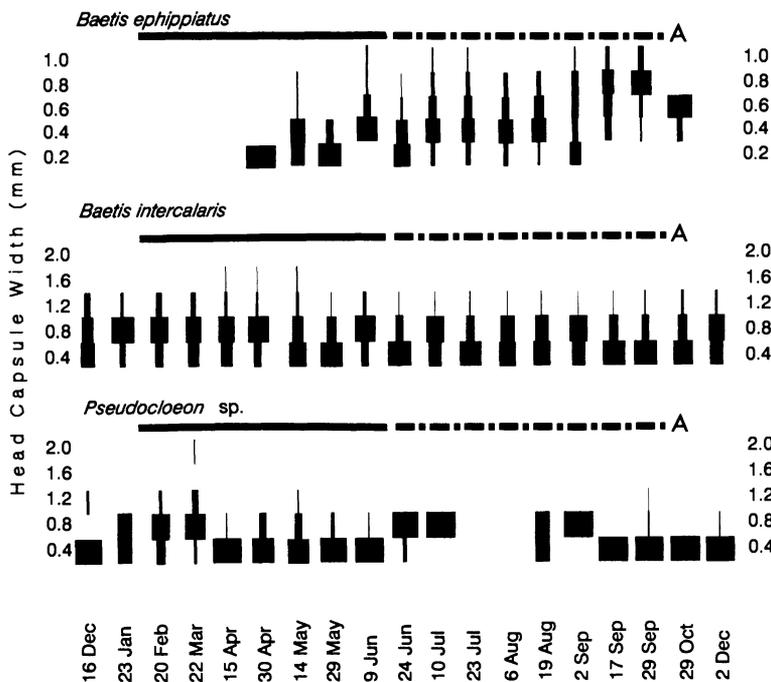


FIG. 1. Size-frequency distributions for baetid larvae on snags in the Ogeechee River during 1982. Width of bar indicates relative abundance of each size class on each date. Horizontal lines designated with A show periods of activity for adult Baetidae (not differentiated to species). Solid line shows actual (documented) activity, and dashed line shows probable (undocumented) activity based on larval size-frequency distributions and growth rates.

a well-defined cohort represents an entire generation, but it is possible for a single generation of adults to produce more than one cohort of offspring, and successive larval cohorts within the same year may not represent successive generations.

#### Baetidae

Life histories of baetid mayflies were difficult to interpret from larval size distributions alone (Fig. 1). *Baetis intercalaris* was by far the most abundant of the baetid species throughout the year (Fig. 2) and maintained a mixed size distribution with no cohort synchronization (Fig. 1). *Baetis ephippiatus* first appeared at the end of April and rapidly achieved a mixed size distribution, again with little indication of cohort synchronization; it was most abundant from June through late fall. *Pseudocloeon* sp. seemed to have at least one distinct winter cohort that hatched in late fall and emerged in early spring; it was most abundant during April–May when it displayed a mixed size distribution. Few adult baetids were collected in black lights, but were

found as early as February and as late as June. However, adult baetids were observed later in the summer, and probably emerge well into the fall. Although mixed size distributions, asynchronous development, and long emergence periods are suggestive of a multivoltine life history, they are insufficient in themselves to prove it. In the case of *Baetis*, independently determined summer growth rates of about  $0.26 \text{ mg mg}^{-1} \text{ d}^{-1}$ , which suggests a developmental time of  $<20 \text{ d}$  (Benke and Jacobi 1986), strongly support the interpretation of many generations per year. The life history of *Pseudocloeon* sp. is less certain (Fig. 1), but based on its mixed size distributions much of the time (Fig. 2), it also seems to be multivoltine.

More life history studies have been conducted for species of *Baetis* than any other mayfly genus, and members of the Baetidae have a wide degree of flexibility in their life histories that is strongly mediated by temperature (Clifford 1982). Except in the northernmost part of the temperate zone and beyond, most Baetidae are multivoltine, typically with 2–3 generations per year (e.g., Ciborowski and Clifford 1983). The

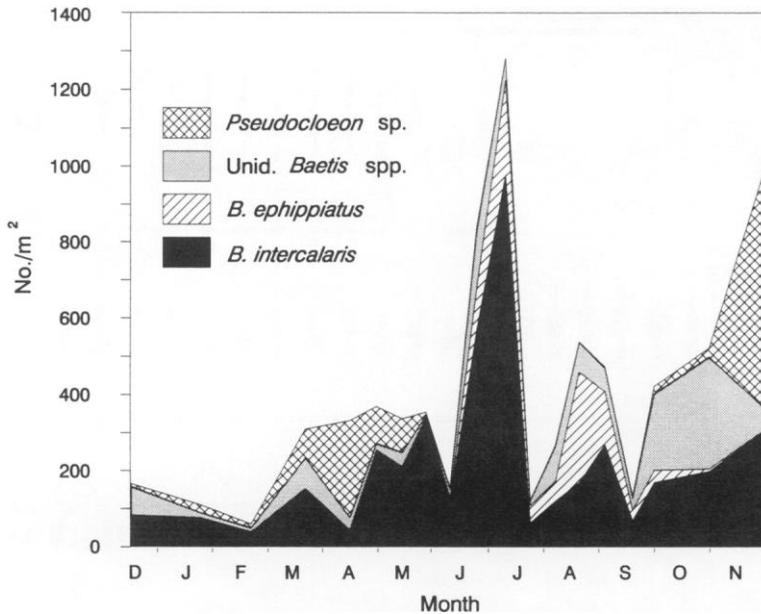


FIG. 2. Abundance patterns for baetid larvae on snags in the Ogeechee River during 1982. Units are number per m<sup>2</sup> of channel bottom.

question in south-temperate to tropical regions is not whether baetids are multivoltine, but on average how fast do they complete their larval development and entire life cycle. Growth rates measured by Benke and Jacobi (1986) and larval development times of <2 wk for *Baetis quilleri* in a southwestern USA desert stream (Gray 1981) suggest that the equivalent of at least 10 generations per year are possible in warmwater environments, assuming non-larval stages represent a relatively small portion of total generation time.

#### Ephemerellidae

In contrast to the baetids, each ephemerellid was univoltine with a distinct winter cohort. The two *Ephemerella* species (*E. argo* and *E. dorrothea*) apparently spent the summer in an egg diapause and were first found as early instars (Fig. 3) at low densities (Fig. 4) in September. By early winter, densities increased, apparently through delayed hatching. Growth occurred rapidly throughout the winter, and the last larvae (late instars) were sampled on 30 April. Early instar *Eurylophella* sp. (possibly *doris*) appeared in late summer, but densities increased throughout the fall, again through delayed

hatching (Fig. 4). In their case, however, growth clearly occurred during fall. Unfortunately, relatively low densities of late instars in the winter of 1982 (the previous generation) prevented a clear picture of the remainder of their development, but they probably emerged earlier than the *Ephemerella* species. Adults could only be identified to subfamily because black light samples were limited to collections of subimagos. Emergence began as early as 4 March and continued through April.

Results for these three ephemerellids are consistent with many previous studies of this family. With few exceptions, they have been univoltine (see Clifford 1982), even in the southeastern USA (e.g., Berner and Pescador 1988, Smock 1988). Winter cohorts (larvae) have been found more frequently than summer cohorts, but both are common (Clifford 1982). Unlike its effect on many mayfly families, temperature seems to have relatively little effect on voltinism in ephemerellids, but temperature probably determines whether winter or summer cohorts (and in rare instances, both) are found. Several months of egg dormancy appear to be common for this family, and in the case of Ogeechee mayflies, this occurred during the summer.

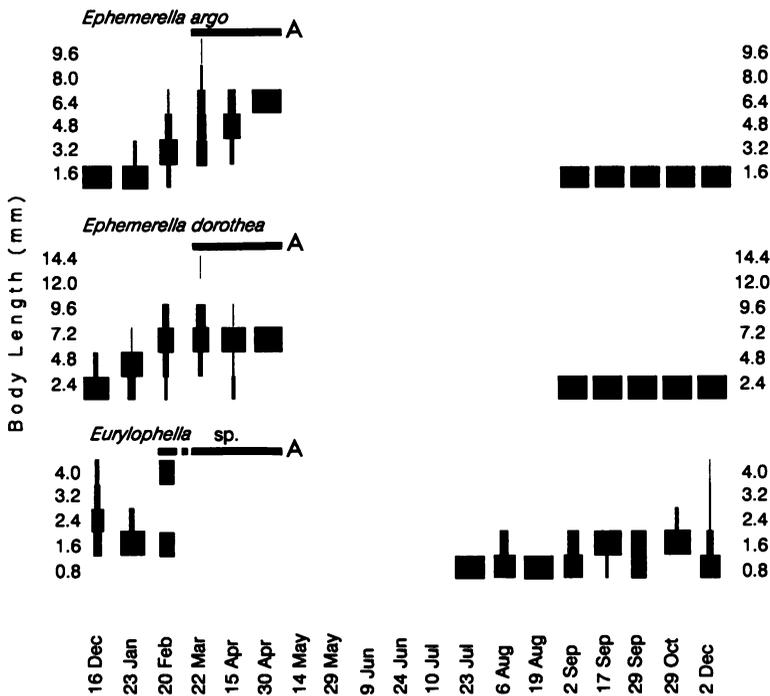


FIG. 3. Size-frequency distributions for ephemereid larvae on snags in the Ogeechee River during 1982. Width of bar indicates relative abundance of each size class on each date. Horizontal lines designated with A show periods of activity for adult Ephemerellidae (not differentiated to species). Solid line shows actual (documented) activity, and dashed line shows probable (undocumented) activity based on larval size-frequency distributions.

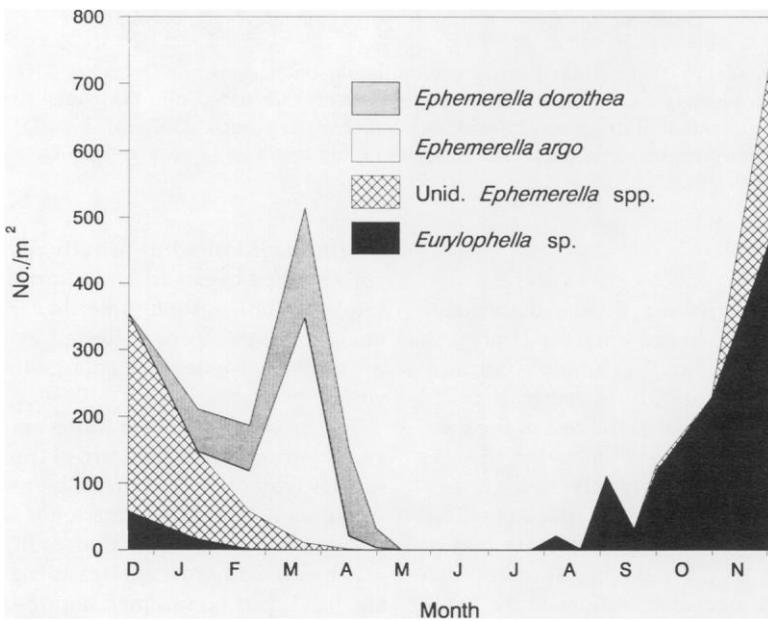


FIG. 4. Abundance patterns for ephemereid larvae on snags in the Ogeechee River during 1982. Units are number per m² of channel bottom.

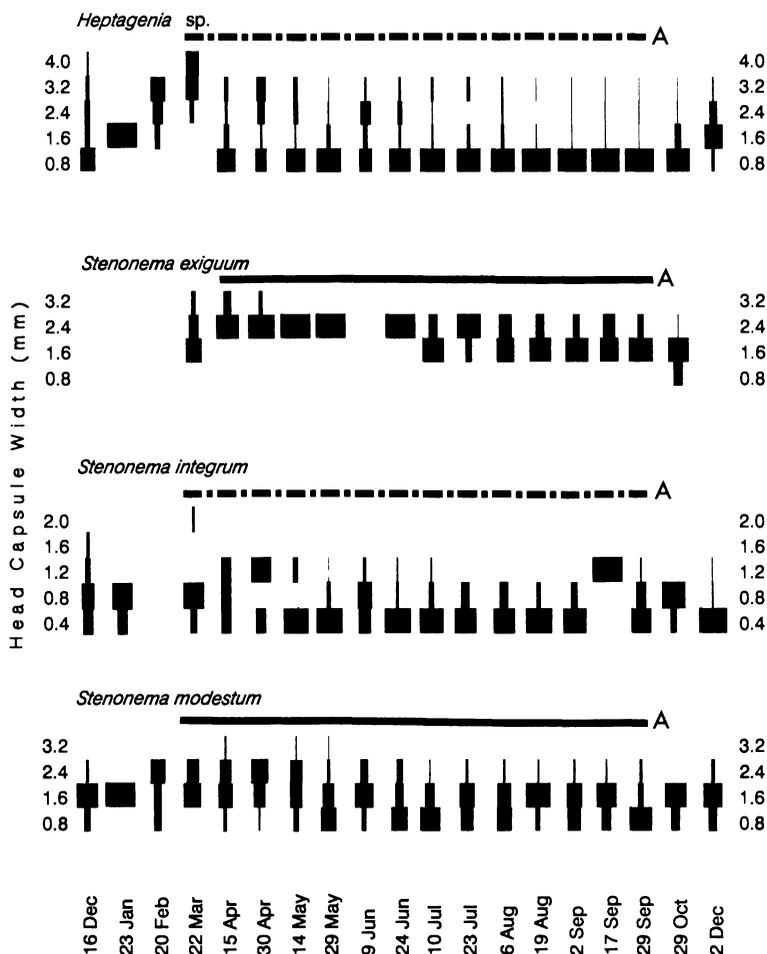


FIG. 5. Size-frequency distributions for heptageniid larvae on snags in the Ogeechee River during 1982. Width of bar indicates relative abundance of each size class on each date. Solid horizontal lines designated with A show documented adult activity periods for *Stenonema exiguum* and *S. modestum*. Dashed lines for *Heptagenia* and *S. integrum* show probable adult activity period based on larval size-frequency distributions.

### Heptageniidae

Of the heptageniid mayflies, a discernable pattern could be observed only for *Heptagenia* sp. (possibly *julia*) (Fig. 5). A single cohort developed over the winter, followed by a mixed size distribution for most of the rest of the year. For *Stenonema modestum* and *S. integrum*, the other two heptageniids with relatively high densities (Fig. 6), mixed size distributions persisted throughout the year. When *S. exiguum* had its highest density in the fall (Fig. 6), it too displayed a mixed size distribution. Only for *S. modestum* and *S. exiguum* did we obtain a con-

sistent record of adult activity; emergence for both species began in early spring and lasted into early fall. Although neither *Heptagenia* sp. nor *S. integrum* were collected as adults, they probably had extended emergence periods as well.

The mixed size distributions and long emergence periods for at least two of the heptageniid species from the Ogeechee River suggest multivoltinism. This interpretation is strongly supported by independent studies in which *Stenonema* spp. had growth rates as high as  $0.12 \text{ mg mg}^{-1} \text{ d}^{-1}$  during summer months (Benke and Jacobi 1986). Such growth rates are not es-

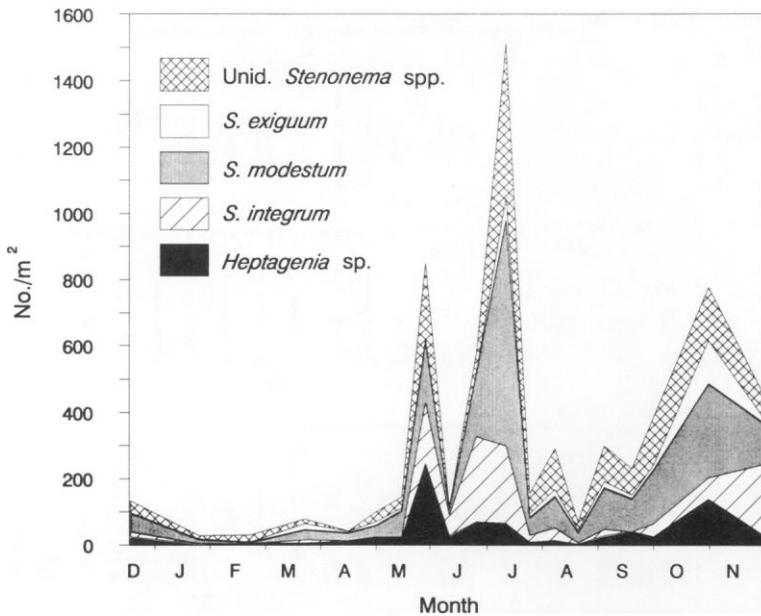


FIG. 6. Abundance patterns for heptageniid larvae on snags in the Ogeechee River during 1982. Units are number per  $m^2$  of channel bottom.

pecially high in comparison with those found for smaller mayflies (e.g., *Baetis*), but they are high enough to imply multivoltine life histories.

Many life history studies have been done on Heptageniidae and most species (particularly *Stenonema*) are univoltine (Clifford 1982). In some warmwater streams of the southeastern USA, it is possible to observe from field data at least two generations per year, as in Virginia (Kondratieff and Voshell 1980) and South Carolina (Smock 1988). However, cohort distinctions become obscured farther south in the Ogeechee River as an additional generation appears to be added. Reports of long emergence periods for *Stenonema* species in the southeast further support the relationship between number of generations and latitude/temperature (Unzicker and Carlson 1982, Berner and Pescador 1988).

#### *Tricorythidae, Caenidae, and Oligoneuriidae*

Among the remaining mayfly taxa, *Tricorythodes* sp. (possibly *allectus*) (Tricorythidae), *Caenis* spp. (Caenidae), and *Isonychia* spp. (Oligoneuriidae) were the most common on snags.

*Tricorythodes* and *Caenis*, although only distantly related, are similar in size and morphological features, are very difficult to identify to species as larvae, and are often found coexisting in river habitats (Corkum 1989).

*Tricorythodes* larvae first appeared in the samples on 14 May as early instars (Figs. 7, 8). They rapidly developed to emergence size, increased in density, and maintained a mixed size distribution from June through fall. By late fall, densities had declined sharply. Although our adult activity data for *Tricorythodes* are sparse, adults emerge throughout most of the year in Florida (Berner and Pescador 1988), and probably did so in the Ogeechee River as well. These field data, along with independent studies documenting summer growth rates of  $0.16 \text{ mg mg}^{-1} \text{ d}^{-1}$  (or larval development time of about 30 d) (Benke and Jacobi 1986) for Ogeechee River populations, suggest the equivalent of as many as 4–5 generations from early May through late October.

*Caenis* spp. appeared to follow a life history and abundance pattern similar to *Tricorythodes*, although at least some *Caenis diminuta* may have overwintered as late instars (densities became too low to detect them on most dates) (Fig. 7).

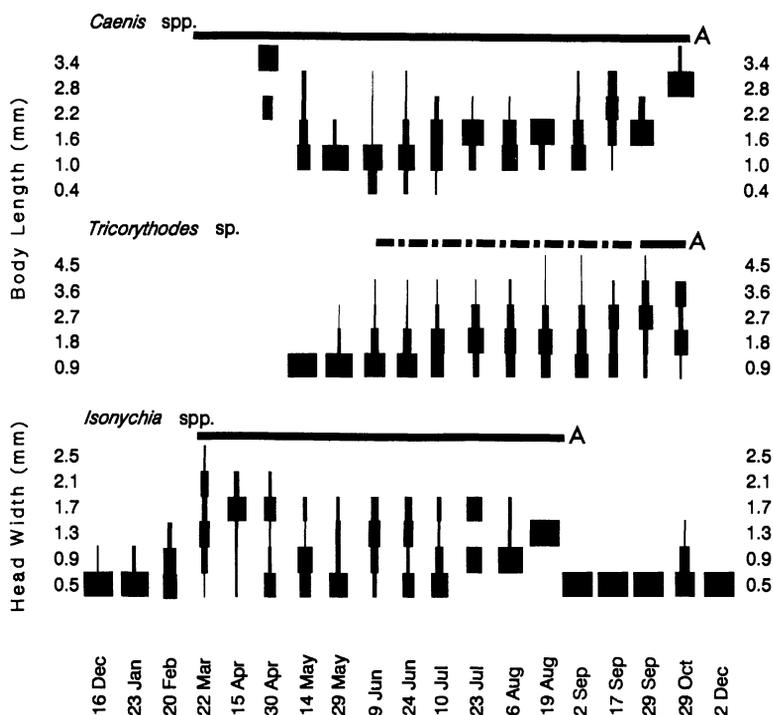


FIG. 7. Size-frequency distributions for *Tricorythodes* sp., *Caenis* spp., and *Isonychia* spp. in the Ogeechee River during 1982. Width of bar indicates relative abundance of each size class on each date. Solid horizontal lines designated with A show documented adult activity periods. Dashed line suggests probable adult activity period for *Tricorythodes* based on size-frequency distribution and growth rates.

*Caenis diminuta* adults were found from 18 March through 5 October and *C. hilaris* from 22 June through 16 October. Although we do not have independent verification of high growth rates for *Caenis*, their extended emergence period and mixed size distribution (Fig. 7) strongly suggests multivoltinism. A multivoltine life history for both *Caenis* and *Tricorythodes* in the Ogeechee River is not surprising since it has frequently been reported for both genera in cool-water environments (Clifford 1982). For example, Newell and Minshall (1978) showed the effect of temperature on voltinism of *Tricorythodes minutus* in an Idaho stream. Furthermore, Gray (1981) reported development times of <2 wk for *Tricorythodes dimorphus* in a southwestern stream.

Size-frequency distributions of large filter-feeding *Isonychia* species in the Ogeechee River are difficult to interpret owing to lack of criteria for separating early instars into species (e.g., Berner and Pescador 1988). What appeared to be a well-defined cohort began growth in late fall and emerged in early spring (Fig. 7). How-

ever, black light collections showed that this "cohort" actually included two species, with *I. georgiae* adults found throughout March and *I. sayi* in late April through at least early May. Although the winter cohort (or cohorts) consisted of high numbers, interpretation of spring/summer patterns was hindered by low densities (Fig. 8). An apparent cohort of unknown species appeared in late April, reaching late instars by early June, followed by another cohort in mid-summer. Emergence of unknown species of *Isonychia* (possibly including *sicca*) occurred from late April through early August. Thus, either multivoltinism or alternation of species is possible.

Grant and Stewart (1980) described the life history of *Isonychia sicca* in a Texas stream where the size-frequency pattern is similar to the multi-species group from the Ogeechee River. They interpreted their data as evidence that an early winter cohort was followed by a late-hatching spring cohort, both of which produced eggs for a summer cohort. Sweeney (1978) found that *I. bicolor* was bivoltine in a cool-water stream in

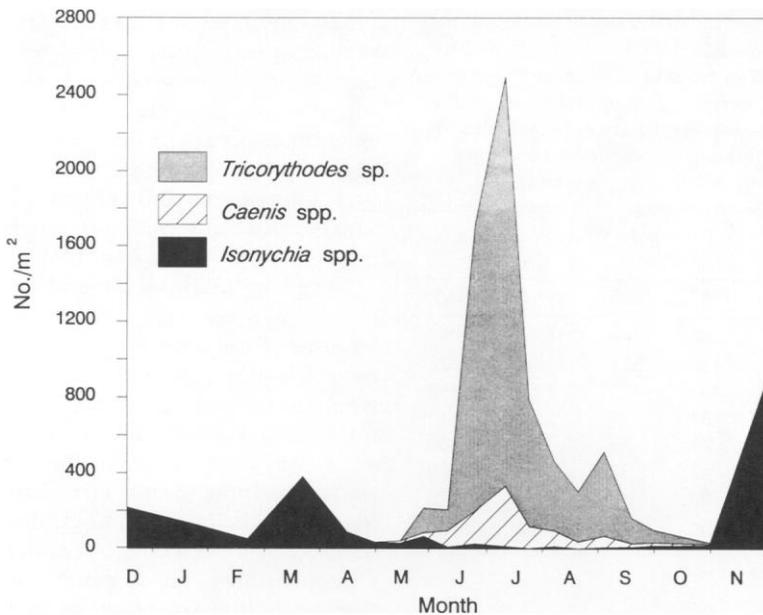


FIG. 8. Abundance patterns for *Tricorythodes* sp., *Caenis* spp., and *Isonychia* spp. in the Ogeechee River during 1982. Units are number per m<sup>2</sup> of channel bottom.

Pennsylvania. Furthermore, Berner and Pescador (1988) reported that adults of *I. sayi* have been found throughout the year in Florida. Regardless of the number of generations per year for each species, larval development time of individual *Isonychia* species is very rapid for such a large mayfly, and is probably a function of temperature.

#### Abundance and seasonality by family

Of the 12 mayfly families found in the Ogeechee River (Appendix 1), six were commonly found on the snag habitat. The relative abundance of these six families was consistent for two consecutive years (Baetidae > Heptageniidae > Tricorythidae > Ephemerellidae > Oligoneuriidae > Caenidae) (Table 1). Relative abundance of mayfly families on snags was also consistent with mean annual drift densities for 1982–1983, except that Tricorythidae in the drift were last in abundance rather than third (Benke et al. 1991). With the exception of Caenidae, densities for all other families were highest in the second year, regardless of whether snag surface or channel bottom densities were considered. Total mayfly densities were about twice as high in 1983 as in 1982, primarily due to the almost 4-fold increase in Baetidae.

Total mayfly densities of 4758 (1982) to 10,725/m<sup>2</sup> (1983) of snag surface are extremely high values for a habitat surface area (Table 1). In comparison with snags from the Satilla River, another blackwater river in the Georgia Coastal Plain (Benke et al. 1984), heptageniids were more than three times as high and total mayfly densities about an order of magnitude higher in the Ogeechee River. Our ephemereiid and heptageniid densities were also about an order of magnitude higher than Smock (1988) found for those families on snags in a small Coastal Plain stream in South Carolina.

In order to compare our mayfly densities with those found in most other streams, conversion to densities per area of stream bottom are necessary, resulting in a reduction to roughly 30% of the habitat surface values (Table 1). The densities shown in Table 1 can be put in context by reference to Clifford (1980), who conducted an extensive literature review of mayfly abundance and found that mean annual density was only 375/m<sup>2</sup> and that 93% of the estimates were <700/m<sup>2</sup>. Recent studies have shown that mean annual densities >1000/m<sup>2</sup> are more common than suggested by Clifford's review (e.g., Huryn and Wallace 1987a, 1987b), and in some systems may exceed 10,000/m<sup>2</sup> (e.g., Lauzon and Harper 1988). Nonetheless, our channel bottom den-

TABLE 1. Annual mean densities (no./m<sup>2</sup>) of mayflies on the snag habitat in the Ogeechee River during 1982–1983. Listed in order of abundance. "Other" includes Neophemeridae, Leptophlebiidae, and unidentified ephemeroptera. Channel bottom densities are calculated from snag surface densities using equations developed by Wallace and Benke (1984).

Family	Channel bottom		Snag surface	
	1982	1983	1982	1983
Baetidae	487	1704	1553	5981
Heptageniidae	433	521	1498	1828
Tricorythidae	250	420	721	1599
Ephemerellidae	184	265	551	719
Oligoneuriidae	78	176	206	469
Caenidae	40	28	114	110
Other	33	6	116	20
Total	1505	3120	4758	10,725

sities of 1505–3120/m<sup>2</sup> should be considered high in comparison with most streams.

The somewhat variable annual patterns of species abundance (Figs. 2, 4, 6, 8) produce distinct seasonal patterns of relative abundance when combined into family-level groupings (Fig. 9). Furthermore, a second year of sampling shows that these family patterns are quite repeatable. Baetidae and Heptageniidae, the most abundant families (Table 1), were also the only two families consistently found throughout the year (Fig. 9). Abundance peaks seemed to appear consistently for heptageniids in late spring and mid-fall. In contrast, the other four families were highly seasonal. Ephemerellidae and Oligoneuriidae formed a significant fraction of the mayfly assemblage only in the cooler months, whereas Tricorythidae and Caenidae were restricted primarily to summer and early fall. Although Tricorythidae and Ephemerellidae were only third and fourth in annual mean densities (Table 1), the former tended to dominate total abundance in summer and the latter in winter (1982 only). These family-level patterns of seasonality on the snag habitat were confirmed by seasonal drift patterns during both 1982 and 1983 (Benke et al. 1991).

### General Discussion

Aquatic insects in general, and mayflies in particular, have often been classified into various life history types (e.g., Hynes 1970, Clifford

1982). On Ogeechee River snags, mayflies exhibited at least three basic types: (1) seasonal-univoltine-winter, where a single well-defined cohort is seen growing over the winter months, emergence occurs in the spring, and a resting egg stage apparently persists through at least part of the summer (all Ephemerellidae); (2) seasonal-multivoltine-summer, where either resting eggs or very few late instars in winter are followed by multiple generations and almost continuous emergence through the warm months (*Tricorythodes* sp., *Caenis* spp., *Baetis ephippiatus*); and (3) non-seasonal-multivoltine, where mixed size classes are found throughout the year, and growth and emergence may occur almost anytime, except for the very coldest periods of winter (*Baetis intercalaris*, Heptageniidae, and possibly Oligoneuriidae). Additional variations of these categories are possible (e.g., Oligoneuriidae), but in general, our data show that with the exception of a single family (Ephemerellidae), all other snag-dwelling mayflies are multivoltine. Of course it is possible that rarer species (e.g., *Leptophlebia* sp.) or species from other habitats (e.g., *Tortopus incertus*) in the Ogeechee River are univoltine.

This picture of extensive multivoltinism for stream mayflies is a substantial departure from hundreds of previous studies, most of which were conducted in northern parts of the temperate zone where mean annual temperatures are often <12°C. It seems likely that as more studies are conducted at latitudes <35°, we will find an increase in the incidence of multivoltinism. This will be caused by two factors. Those species capable of multivoltinism will shift from univoltine to bivoltine to polyvoltine as mean annual temperature increases. Alternatively, univoltine species requiring cooler temperatures will disappear when winter temperatures become too warm for their larval development; for example, ephemerellids disappear south of ~30°N in Florida (Berner and Pescador 1988). The extent to which univoltine species found in strictly warmwater environments enter mayflies assemblages at lower latitudes is unknown.

An increase in multivoltinism with decreasing latitude (or increasing temperature) raises questions regarding the relationship between phenology and community structure. Hynes (1970), Brittain (1982) and many others have pointed to the extensive documentation of temporal separation among coexisting species in attempts to explain community structure and

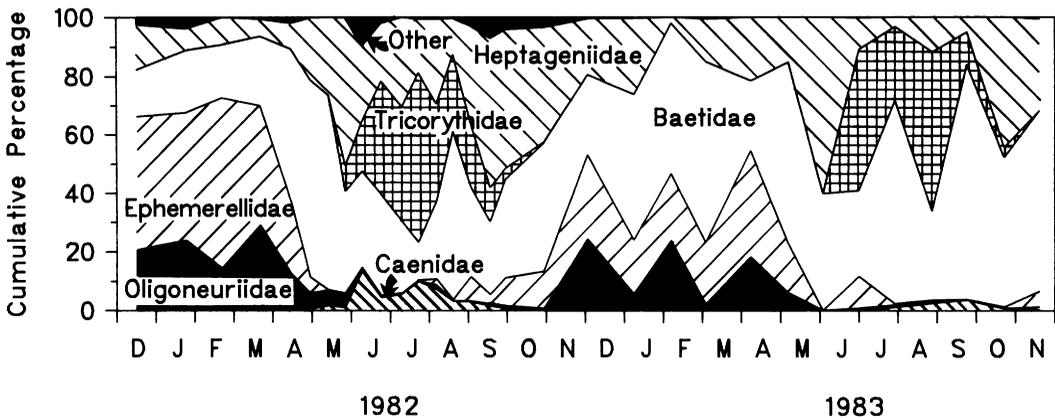


FIG. 9. Relative abundance patterns for major families of mayflies in the Ogeechee River during 1982 and 1983.

richness. Many authors have suggested that temporal separation, particularly among species with synchronous development, represents evidence for avoidance of competition (e.g., Mackay 1969, Sweeney and Vannote 1981, Hawkins 1990), although other explanations are possible (Butler 1984). Among Ogeechee River mayflies, temporal separation of summer and winter families undoubtedly reduces overlap at this higher taxonomic level, and slight degrees of temporal separation among species within families (e.g., Ephemerellidae and *Isonychia* spp.) may reduce overlap as well. However, extensive overlap was found among most species due to multivoltinism and broad size distributions occurring throughout most of the year. For example, *Caenis* spp. and *Tricorythodes* are functionally very similar (Corkum 1989), yet occur with greatly overlapping size classes at exactly the same time of the year. Furthermore, most species of baetids and heptageniids coexist through time with overlapping size distributions.

Over 50 years ago, Ide (1935) found a strong positive relationship between mayfly species richness and temperature (or annual temperature range) along a longitudinal gradient of an Ontario stream system. Ide suggested that more species are capable of surviving in an environment with a broad temperature range than in a narrow one. Our study suggests that as temperature increases beyond the highest mean annual temperature in Ide's study (probably  $<12^{\circ}\text{C}$ ), multivoltinism increases with a corresponding increase in temporal overlap among coexisting species. If temporal overlap increases competition, as others have suggested, then one

might predict a decline in species richness with decreasing latitude due to competitive exclusion. However, examination of mayfly richness per stream along a latitudinal (or temperature) gradient does not support this prediction. Wolda and Flowers (1985) reviewed a portion of the mayfly literature and found no relationship between latitude and mayfly richness per stream site. Additional studies of the more species-rich streams at various latitudes tend to confirm their conclusions. North-temperate streams can have many species, e.g., 24–34 species in Ontario (Ide 1935, Sprules 1947), 24 in Manitoba (Flannagan et al. 1990), 22 in Quebec (Harper and Harper 1982), and 21 in Czechoslovakia (Zelinka et al. 1977). Richness is at least as high in subtropical streams, viz: 32 in South Carolina (Morse et al. 1980) and 36 in Florida (Peters and Jones 1973), and in tropical streams: 44 in Malaysia (Bishop 1973), and 30 in Panama (Wolda and Flowers 1985).

Species richness (28) in the Ogeechee River compares favorably with other subtropical and tropical streams, even though we did not make a major effort to determine the total number of species by sampling multiple sites with multiple emergence traps as did Morse et al. (1980) and Flannagan et al. (1990). The Ogeechee River fauna is unusual in that at least 13 species were sufficiently abundant for life history analyses. Most mayfly assemblages are limited to only a few common species (e.g., Flannagan et al. 1990), and rarely are more than eight species available for life history analyses (e.g., Huryn and Wallace 1987a, Lauzon and Harper 1988, Giberson and Mackay 1991).

Examination of feeding habits of several snag-dwelling mayflies (*Baetis*, *Heptagenia*, *Stenonema*, *Ephemerella*, *Eurylophella*, *Isonychia*) from the Ogeechee River does little to resolve the issue of how so many species can coexist (Wallace et al. 1987). Although *Isonychia* spp. are filtering collectors whose diet is restricted almost entirely to amorphous detritus (98%), the other taxa are gathering collectors and consume >60% amorphous detritus in addition to vascular plant detritus and diatoms. Dietary overlap (proportional similarity) among mayfly gathering collectors was always >0.6 and usually >0.8. Because all mayflies analyzed in detail were from a single habitat (snags), possibilities for resource partitioning along the space dimension were limited too. However, some possibilities for partitioning occur from variation in current velocity or microhabitat.

In conclusion, a high fraction of mayfly species found on Ogeechee River snags were multivoltine (Baetidae, Heptageniidae, Caenidae, Tricorythidae, Oligoneuriidae), the result of a high mean annual temperature. Although some degree of seasonality occurred at both family and species levels, multivoltinism and common use of food and space in this species-rich mayfly assemblage implies high overlap along the major niche dimensions. In spite of this, community structure, as reflected in relative abundance of mayfly families and their seasonal patterns, was very consistent between two consecutive years, suggesting a high degree of stability in the snag mayfly assemblage. This richness and consistency is probably due to at least two environmental factors. First, mayflies on snags have access to abundant food (amorphous detritus) that is enriched by a large bacterial component and continuously replenished from the seston (Edwards and Meyer 1990). Second, in addition to a seemingly inexhaustible food supply, the snag habitat shrinks and expands, as fluctuating water levels cause either habitat desiccation or inundation. Newly inundated snags can be recolonized by drift (Benke et al. 1991) and by reproduction throughout much of the year. Perhaps this combination of a variable habitat space, abundant food, and extended periods of reproduction offers continuing opportunities for species invasion and enhancement of richness.

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### Literature Cited

- BENKE, A. C., AND S. S. BENKE. 1975. Comparative dynamics and life histories of coexisting dragonfly populations. *Ecology* 56:302-317.
- BENKE, A. C., AND D. I. JACOBI. 1986. Growth rates of mayflies in a subtropical river and their implications for secondary production. *Journal of the North American Benthological Society* 5:107-114.
- BENKE, A. C., AND J. L. MEYER. 1988. Structure and function of a blackwater river in the southeastern U.S.A. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 23:1209-1218.
- BENKE, A. C., AND K. A. PARSONS. 1990. Modelling black fly production dynamics in blackwater streams. *Freshwater Biology* 24:167-180.
- BENKE, A. C., K. A. PARSONS, AND S. M. DHAR. 1991. Population and community patterns of invertebrate drift in an unregulated Coastal Plain river. *Canadian Journal of Fisheries and Aquatic Sciences* 48:811-823.
- BENKE, A. C., T. C. VAN ARSDALL, D. M. GILLESPIE, AND F. K. PARRISH. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. *Ecological Monographs* 54:25-63.
- BENKE, A. C., AND J. B. WALLACE. 1990. Wood dynamics in Coastal Plain blackwater streams. *Canadian Journal of Fisheries and Aquatic Sciences* 47:92-99.
- BERNER, L., AND M. L. PESCADOR. 1988. The mayflies of Florida. Revised edition. University Presses of Florida.
- BISHOP, J. W. 1973. *Limnology of a small Malayan river, Sungai Gombak*. Dr. W. Junk B.V., Publishers, The Hague.
- BRITAIN, J. E. 1982. Biology of mayflies. *Annual Review of Entomology* 27:119-147.

- BUNN, S. E. 1988. Life histories of some benthic invertebrates from streams of the northern jarrah forest, Western Australia. *Australian Journal of Marine and Freshwater Research* 39:785-804.
- BUTLER, M. G. 1984. Life histories of aquatic insects. Pages 24-55 in V. H. Resh and D. M. Rosenberg (editors). *The ecology of aquatic insects*. Praeger, New York.
- CIBOROWSKI, J. J. H., AND H. F. CLIFFORD. 1983. Life histories, microdistribution and drift of two mayfly (Ephemeroptera) species in the Pembina River, Alberta. *Holarctic Ecology* 6:3-10.
- CLIFFORD, H. F. 1980. Numerical abundance values of mayfly nymphs from the Holarctic region. Pages 503-509 in J. F. Flannagan and K. E. Marshall (editors). *Advances in Ephemeroptera biology*. Plenum, New York.
- CLIFFORD, H. F. 1982. Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. *Quaestiones Entomologicae* 18:15-90.
- CORKUM, L. D. 1989. Habitat characterization of the morphologically similar mayfly larvae, *Caenis* and *Tricorythodes* (Ephemeroptera). *Hydrobiologia* 179:103-109.
- DELUCCHI, C. M., AND B. L. PECKARSKY. 1989. Life history patterns of insects in an intermittent and a permanent stream. *Journal of the North American Benthological Society* 8:308-321.
- EDMUNDS, G. F., S. L. JENSEN, AND L. BERNER. 1976. *The mayflies of North and Central America*. University of Minnesota Press, Minneapolis.
- EDWARDS, R. T., AND J. L. MEYER. 1990. Bacterivory by deposit-feeding mayfly larvae (*Stenonema* spp.). *Freshwater Biology* 24:453-462.
- FLANNAGAN, J. F., D. G. COBB, AND M. K. FRIESEN. 1990. The relationship between some physical factors and mayflies emerging from South Duck River and Cowan Creek, Manitoba. Pages 233-242 in I. C. Campbell (editor). *Mayflies and stoneflies: life histories and biology*. Kluwer, Boston.
- GEORGIAN, T., AND J. B. WALLACE. 1983. Seasonal production dynamics in a guild of periphyton-grazing insects in a southern Appalachian stream. *Ecology* 64:1236-1248.
- GIBERSON, D. J., AND R. J. MACKAY. 1991. Life history and distribution of mayflies (Ephemeroptera) in some acid streams in south central Ontario, Canada. *Canadian Journal of Zoology* 69:899-910.
- GRANT, P. M., AND K. W. STEWART. 1980. The life history of *Isonychia sicca* (Ephemeroptera: Oligoneuriidae) in an intermittent stream in north central Texas. *Annals of the Entomological Society of America* 73:747-755.
- GRAY, L. J. 1981. Species composition and life histories of aquatic insects in a lowland Sonoran desert stream. *American Midland Naturalist* 106:229-242.
- HARPER, P. P., AND F. HARPER. 1982. Mayfly communities in a Laurentian watershed (Insecta: Ephemeroptera). *Canadian Journal of Zoology* 60:2828-2840.
- HAWKINS, C. P. 1990. Relationships between habitat dynamics, food availability, and growth patterns of ephemeroptid mayflies from western North America. Pages 35-42 in I. C. Campbell (editor). *Mayflies and stoneflies: life histories and biology*. Kluwer, Boston.
- HURYN, A. D., AND J. B. WALLACE. 1987a. The exopterygote insect community of a mountain stream in North Carolina, USA: life histories, production, and functional structure. *Aquatic Insects* 9:229-251.
- HURYN, A. D., AND J. B. WALLACE. 1987b. Local geomorphology as a determinant of macrofaunal production in a mountain stream. *Ecology* 68:1932-1942.
- HYNES, H. B. N. 1970. *The ecology of running waters*. University of Toronto Press, Toronto.
- IDE, F. P. 1935. The effect of temperature on the distribution of the mayfly fauna of a stream. *University of Toronto Studies, Biological Series* 39:1-76.
- KONDRATIEFF, B. C., AND J. R. VOSHELL. 1980. Life history and ecology of *Stenonema modestum* (Banks) (Ephemeroptera:Heptageniidae) in Virginia, USA. *Aquatic Insects* 2:177-189.
- LAUZON, M., AND P. P. HARPER. 1988. Seasonal dynamics of a mayfly (Insecta:Ephemeroptera) community in a Laurentian stream. *Holarctic Ecology* 11:220-234.
- MACKAY, R. J. 1969. Aquatic insect communities of a small stream on Mont St. Hilaire, Quebec. *Journal of the Fisheries Research Board of Canada* 26:1157-1183.
- MCCAFFERTY, W. P., AND R. D. WALTZ. 1990. Revisionary synopsis of the Baetidae (Ephemeroptera) of North and Middle America. *Transactions of the American Entomological Society* 116:769-799.
- MEYER, J. L. In press. Seasonal patterns of water quality in blackwater rivers of the southeastern U.S. Coastal Plain. In C. D. Becker and D. A. Neitzel (editors). *Water quality of North American river systems*. Battelle Press, Richland, Washington.
- MORSE, J. C., J. W. CHAPIN, D. D. HERLONG, AND R. S. HARVEY. 1980. Aquatic insects of Upper Three Runs Creek, Savannah River Plant, South Carolina. Part I: orders other than Diptera. *Journal of the Georgia Entomological Society* 15:73-101.
- NEWELL, R. L., AND G. W. MINSHALL. 1978. Life history of a multivoltine mayfly, *Tricorythodes minutus*: an example of the effect of temperature on the life cycle. *Annals of the Entomological Society of America* 71:876-881.

- PETERS, W. L., AND J. JONES. 1973. Historical and biological aspects of the Blackwater River in northwestern Florida. Pages 241-253 in W. L. Peters and J. G. Peters (editors). Proceedings of the First International Conference on Ephemeroptera. E. J. Brill, Leiden.
- RADER, R. B., AND J. V. WARD. 1989a. Influence of impoundments on mayfly diets, life histories, and production. *Journal of the North American Benthological Society* 8:64-73.
- RADER, R. B., AND J. V. WARD. 1989b. The influence of environmental predictability/disturbance characteristics on the structure of a guild of mountain stream insects. *Oikos* 54:107-116.
- SMOCK, L. A. 1988. Life histories, abundance and distribution of some macroinvertebrates from a South Carolina, USA coastal plain stream. *Hydrobiologia* 157:193-208.
- SPRULES, W. M. 1947. An ecological investigation of stream insects in Algonquin Park, Ontario. *University of Toronto Studies, Biological Series* 56:1-81.
- SWEENEY, B. W. 1978. Bioenergetic and developmental response of a mayfly to thermal variation. *Limnology and Oceanography* 23:461-477.
- SWEENEY, B. W. 1984. Factors influencing life-history patterns of aquatic insects. Pages 56-100 in V. H. Resh and D. M. Rosenberg (editors). *The ecology of aquatic insects*. Praeger, New York.
- SWEENEY, B. W., AND R. L. VANNOTE. 1981. *Ephemere*lla mayflies of White Clay Creek: bioenergetic and ecological relationships among six coexisting species. *Ecology* 62:1353-1369.
- UNZICKER, J. D., AND P. H. CARLSON. 1982. Ephemeroptera. Pages 3.1-3.97 in A. R. Brigham, W. U. Brigham, and A. Gnilka (editors). *Aquatic insects and oligochaetes of North and South Carolina*. Midwest Aquatic Enterprises, Mahomet, Illinois.
- VANNOTE, R. L., AND B. W. SWEENEY. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist* 115:667-695.
- WALLACE, J. B., AND A. C. BENKE. 1984. Quantification of wood habitat in subtropical Coastal Plain streams. *Canadian Journal of Fisheries and Aquatic Sciences* 41:1643-1652.
- WALLACE, J. B., A. C. BENKE, A. H. LINGLE, AND K. PARSONS. 1987. Trophic pathways of macroinvertebrate primary consumers in subtropical blackwater streams. *Archiv für Hydrobiologie, Supplementbande* 74:423-451.
- WARD, J. V., AND J. A. STANFORD. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* 27:97-117.
- WATERS, T. F., AND G. W. CRAWFORD. 1973. Annual production of a stream mayfly population: a comparison of methods. *Limnology and Oceanography* 18:286-296.
- WOLDA, H., AND R. W. FLOWERS. 1985. Seasonality and diversity of mayfly adults (Ephemeroptera) in a "nonseasonal" tropical environment. *Biotropica* 17:330-335.
- ZELINKA, M., AND WORKING TEAM. 1977. Production conditions of the polluted trout brook. *Folia Facultatis Scientiarum Naturalium Universitatis Purkynianae Brunensis, Biologia* 18:5-105.

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APPENDIX 1. Mayflies collected as larvae from snags or as adults (imago or subimago) from black light traps at the Ogeechee River from 1981-1983. Unless otherwise indicated, taxa not collected as larvae probably occur on snags. Identification: \*\* to the species level, \* to genus, † to family.

	Larvae	Adults
<b>Heptageniidae</b>		
<i>Stenonema modestum</i>	**	**
<i>Stenonema exiguum</i>	**	**
<i>Stenonema integrum</i>	**	
<i>Heptagenia</i> sp. (poss. <i>julia</i> )	**	
<i>Macdunnoa brunnea</i>		**
<i>Epeorus</i> sp. (poss. <i>dispar</i> )		**
<b>Caenidae</b>		
<i>Caenis diminuta</i>	*	**
<i>Caenis hilaris</i>	*	**
<i>Caenis maccafferti</i>	*	**
<i>Brachycercus</i> sp. (near <i>prudens</i> )	sand	**
<b>Baetidae</b>		
<i>Baetis ephippiatus</i>	**	**
<i>Baetis intercalaris</i>	**	**
<i>Pseudocloeon</i> sp.	*	*
<b>Ephemerellidae</b>		
<i>Ephemerella argo</i>	**	†
<i>Ephemerella dorothea</i>	**	†
<i>Eurylophella</i> sp. (poss. <i>doris</i> )	**	†
<i>Danella simplex</i>	**	†
<b>Tricorythidae</b>		
<i>Tricorythodes</i> sp. (poss. <i>allectus</i> )	*	**
<b>Neophemeridae</b>		
<i>Neophemera youngi</i>	**	
<b>Oligoneuriidae</b>		
<i>Isonychia georgiae</i>	*	**
<i>Isonychia sayi</i>	*	**
<i>Isonychia</i> sp. (poss. <i>sicca</i> )	*	**
<b>Leptophlebiidae</b>		
<i>Leptophlebia</i> sp. (poss. <i>intermedia</i> )	*	**
<b>Metretopodidae</b>		
<i>Siphloplecton simile</i>	unknown	**
<i>Siphloplecton basale</i>	unknown	**
<b>Baetiscidae</b>		
<i>Baetisca carolina</i>	flood-plain or sand bar	**
<b>Polymitarcyidae</b>		
<i>Tortopus incertus</i>	clay banks	**
<b>Siphonuridae</b>		
<i>Siphonurus</i> sp. (poss. <i>quebecensis</i> )	unknown	**