

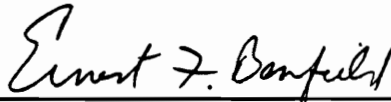
**Effects of Forest Disturbance on
Shredder Production in Headwater Streams**

by

Benjamin Mortimer Stout III

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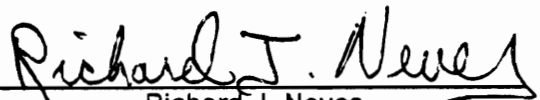
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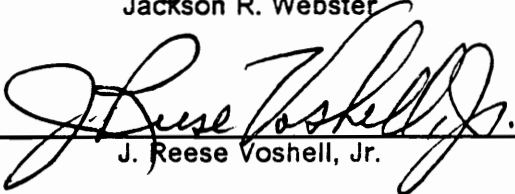
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(ABSTRACT)

Effects of forest disturbance on leaf shredding aquatic insects were investigated by comparing leaf biomass and shredder production in disturbed versus reference forest streams. Benthic samples were collected monthly in 3 streams in a mature hardwood reference forest and 3 streams in an 11-year-old clearcut. Reference forest streams had significantly greater total leaf biomass and significantly more slow-processing leaf material than disturbed forest streams. Disturbed forest streams had significantly greater fast-processing leaf biomass than did reference streams.

The leaf shredding insects *Tipula abdominalis*, *Pycnopsyche* sp., and *Tallaperla maria* comprised over 90% of the shredder biomass in all streams. Total shredder production was significantly greater ($p < 0.05$) in disturbed versus reference streams. Production of *Pycnopsyche* and *T. maria* was significantly greater ($p < 0.10$) in disturbed versus reference streams, but *T. abdominalis* production was not significantly different ($p = 0.28$). Greater *T. maria* production was attributed mostly to better survivorship in disturbed versus reference streams. Greater total shredder production in disturbed streams was attributed mostly to greater production by *Pycnopsyche*, which was due mostly to better survivorship and growth of early instar larvae in disturbed streams.

T. maria and *T. abdominalis* were studied under laboratory conditions to determine whether feeding on various types of leaf material would affect growth. Shredder growth rates were affected more by length of instream conditioning of leaves than leaf species or leaf exposure site. Each shredder species had different patterns of growth and survivorship relative

to leaf species and conditioning. There was no difference in shredder growth patterns between early versus late successional leaf species.

Pycnopsyche growth was not studied, but *Pycnopsyche* may be more capable than the other shredders of exploiting fast-processing, early successional leaf species. *Pycnopsyche* production was greatest in streams having the greatest quantities of early successional leaf biomass. *Pycnopsyche* biomass correlated significantly with fast-processing leaf biomass typical of the early successional forest, whereas other shredders did not.

Shredder production was significantly greater in disturbed versus reference forest streams, even though total leaf biomass was significantly greater in reference streams. Providing that forest clearcutting is accomplished with minimal physical disturbance to streams, shredder populations may exhibit greater production in streams 11-years after forest clearcutting than in reference forest streams.

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Introduction

Organic carbon is a regulating component for carbon metabolism in aquatic ecosystems (Wetzel, *et al.*, 1972; Rich & Wetzel, 1978) and an energy reserve that supports microbial regeneration of nutrients, providing a basis for metabolic stability (Wetzel, 1984). Forested headwater streams throughout the world depend largely on terrestrial particulate organic carbon as a primary energy source (Nelson & Scott, 1962; Minshall, 1967; Coffman, *et al.*, 1971; Fisher & Likens, 1973; Mann, 1975; Davis & Winterbourne, 1977), and up to 99% of the energy available in first and second order streams may be of allochthonous origin (Fisher & Likens, 1973).

Aquatic macroinvertebrates are the major macroconsumers in headwater streams (Cummins, 1974), and their ecological roles are indicative of the energy resources available in an ecosystem (Wiggins & Mackay, 1978; Cummins & Klug, 1979; Cushing, *et al.*, 1983). Headwater streams are characterized as having a relatively high proportion of organisms that consume coarse particulate organic matter (CPOM). Middle order reaches of rivers are characterized by organisms that filter and collect fine particulate organic matter (FPOM), and it has been hypothesized that a substantial portion of the organic matter consumed by collectors originates upstream as detritus (Vannote, *et al.*, 1980). Mean particle size of detritus

decreases downstream through a stepwise progression of physical and biological processes (Boling, *et al.*, 1975; Minshall, *et al.*, 1983). Organic matter is recycled as it is processed downstream, including reingestion of fecal materials (Wotton, 1980; Fisher & Gray, 1983), and less than 10% of the carbon inputs to oceans are of potamon origin (Schlesinger & Melack, 1981; Wetzel, 1984). Transformation of CPOM to FPOM by shredders in forested headwater streams provides an energy source to organisms inhabiting larger streams and rivers.

Benthic macroinvertebrates in forested headwater streams depend largely on leaves as a source of food and cover (Cummins, 1974). Leaf-shredding aquatic invertebrates (shredders) reduce coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM) through feeding activities (Cummins & Klug, 1979). The importance of shredders to leaf breakdown has been demonstrated for streams throughout the world (*e.g.*, Cummins, 1973; Grafius & Anderson, 1979; Winterbourne & Davis, 1976; Iversen, *et al.*, 1982; Benfield & Webster, 1985). Shredders have relatively low growth and assimilation efficiencies (McDiffett, 1970; Iversen, 1974; Winterbourn & Davis, 1976; Grafius & Anderson, 1980), and individual species have been shown to process large amounts of the leaf material available in aquatic systems (Minshall, 1967; Coffman, *et al.*, 1971; Richardson & Mackay, 1984). Shredders make FPOM available to collectors through CPOM fragmentation and seston generation (Short & Maslin, 1977; Grafius & Anderson, 1980; Mulholland, *et al.*, 1985). Elimination of shredders from a headwater stream in North Carolina resulted in a significant reduction in the amount of seston transported downstream (Cuffney, *et al.*, 1984).

Vegetational differences stemming from forest management practices have been cited as a major factor determining invertebrate community composition in streams (Woodall & Wallace, 1972). Quality and quantity of leaves available to shredders in streams depend on the relative stage of forest succession. Because of their inherent chemical nature (*e.g.*, Suberkropp, *et al.*, 1976), leaves of different species appear to provide a spectrum of food quality to shredders (Petersen & Cummins, 1974), and leaf quality seems to be related to growth and survivorship of shredders (Anderson & Cummins, 1979; Sweeney, *et al.*, 1986). Eastern deciduous forests in late successional stages are dominated by mature hardwoods,

and leaves from most of these species are processed slowly in streams (Petersen & Cummins, 1974; Webster, *et al.*, 1983). Leaves from many early successional plants, such as dogwood, basswood, and alder are processed rapidly in streams (Hart & Howmiller, 1975; Benfield & Webster, 1985), in fact, alder has been used repeatedly as a reference for good food quality in detritivore nutrition studies (Anderson & Cummins, 1979).

Secondary production in streams

Animal production is tissue elaboration per unit area over time (Waters, 1977). Production is the most direct estimate of the ability of invertebrates to use available resources (Benke, *et al.*, 1984). Caloric equivalents of production have been used to measure relationships between primary and secondary consumers in streams by showing potential energy transfer between trophic levels (Neves, 1979; Mortensen and Simonsen, 1983). Production is an important property for evaluating ecosystems because it incorporates measures of growth and survivorship of a population (Benke, 1984). Combined with knowledge of feeding habits, production gives a measure of ecosystem function that is superior to traditional abundance and biomass estimates (O'Hop, *et al.*, 1984; Benke, 1984).

Prior to 1970, few production studies were undertaken in streams. This was due partly to the difficulty in sorting large quantities of samples (Waters, 1977), and partly to the high costs involved in measuring and weighing individuals (Sheldon, 1984). With the advent of the Hynes and Coleman (1968) "size/frequency" method and initiation of studies by the International Biological Program, secondary production has become a more popular approach to stream ecology (Benke, 1984).

In recent years production studies have been used to compare natural habitats or evaluate disturbance of stream ecosystems. Krueger and Waters (1983) compared three streams and found that higher alkalinity and nitrate levels positively influenced macroinvertebrate

production. In one case, siltation caused production to decline (Waters & Hokenstrom, 1980). Studies estimating production in different habitats within streams have shown that certain habitats (e.g., snags) support very high production (Benke, *et al.*, 1984; Smock, *et al.*, 1985), while others (e.g., shifting sands) appear to be less productive due to frequent disturbance or limited food resources (Soluk, 1985). Production of two collector-filterer species was greater in a clearcut versus a reference forest stream due to higher food quality and availability of suitable substrate (Haefner & Wallace, 1981b). Availability of space has been implicated as a limiting resource in other production studies (Cudney & Wallace, 1980; Benke, *et al.*, 1984). Production by the grazer *Baetis sp.* increased following clearcutting because of life history features that allowed it to exploit newly available autochthonous food resources (Wallace & Gurtz, 1986).

Production of aquatic invertebrates is temperature dependent, and individual species appear to have temperature optima for growth (Anderson & Grafius, 1975; Merritt, *et al.*, 1982; Perry, *et al.*, 1988). Interactions of temperature and food quality have been shown to affect growth rates and adult fecundity of several species (Ward & Cummins, 1979; Sweeney & Vannote, 1984). Temperature controls important life history features, such as the amount of time spent in the larval stage, or cohort production interval, by dictating timing of egg hatching and adult emergence (Rupprecht, 1975; Elliott, 1984; Wright & Mattice, 1985). It has been hypothesized that species have optimal temperature regimes that influence cohort production interval such that adult body weight and fecundity will be maximal, and thermal constraints may limit the range and geographic distribution of species (Sweeney & Vannote, 1978).

Leaf quality in streams

Food quality has been implicated as limiting growth in production of many stream invertebrates (Winterbourn, 1971; Iversen, 1974; Anderson, 1976; Herbst, 1980; Fuller &

Mackay, 1981; Hanson, *et al.*, 1983; Frankenhuyzen, *et al.*, 1985). Food quality for aquatic insects has been characterized from the perspectives of feeding preference, foregut contents, and insect growth and assimilation efficiencies when consuming various tissues. A nutritional gradient proposed by Anderson and Cummins (1979) ranked foods available to stream consumers from greatest to least food quality as follows: animal > algae > aquatic vascular plants > FPOM > terrestrial vascular plants > wood. Tree leaves rank low in nutritional hierarchies, but their food quality may be enhanced to some degree by microbial colonization (Barlocher & Kendrick, 1975). Bacterial and fungal microbes may be important in supplying essential nutrients for detritivore growth (Phillips, 1984), but their caloric contributions are clearly insufficient to meet the energy requirements of some detritivores (Baker & Bradnam, 1976; Findlay, *et al.*, 1984).

Lignin and cellulose compounds constitute the greatest portion of potential energy of terrestrial vegetation, and these compounds may provide energy for detritivore growth. Some shredders apparently have the ability to digest cellulose (Sinsabaugh, *et al.*, 1985). The stonefly *Pteronarcys proteus* may acquire microbial cellulolytic enzymes through feeding. The crane fly *Tipula abdominalis* has an efficient protein digesting system (Martin, *et al.*, 1980) and probably harbors cellulase producing endosymbionts (Sinsabaugh, *et al.*, 1985). In addition, *T. abdominalis* may be able to maintain normal growth on poor quality food by increasing ingestion rates (Anderson & Cummins, 1979). Crane fly larvae seem to require leaves with some degree of microbial conditioning (Golladay, *et al.*, 1983) and grow best on leaves that have been conditioned in streams for a few weeks (Lawson, *et al.*, 1984).

Recent work has shown that certain molecules may be of particular importance in shredder nutrition. Protein may be important in the nutrition of *T. abdominalis* but may not limit growth of limnephilid caddisflies (Cargil, *et al.*, 1985). Lipid anabolism may be important in the final instars of some caddisfly species (Otto, 1974; Hanson, *et al.*, 1983). For *Clistoronia magnifica*, triglycerides are of particular importance with reference to fecundity, and this may be the reason for a shift to higher quality food during final instars for some shredders (Anderson & Cummins, 1979; Cargil, *et al.*, 1985). Preference for higher quality food resources

may be common among shredders, but each shredder species may exhibit different food preference at various life history stages.

Stream community response to watershed disturbance

A typical stream response to forest clearcutting is an increase in autochthonous production due to opening of the canopy (Webster, *et al.*, 1983; Duncan & Brusven, 1985). Stream macroinvertebrate communities respond to increased primary production with increased abundances of grazers, but shredder biomass may decrease in response to reduced leaf litter in streams (Haefner & Wallace, 1981a; Newbold, *et al.*, 1980; Wallace & Gurtz, 1986; Woodall & Wallace, 1972). Density of collector-gatherers and algal grazers in streams increased, while density of leaf shredding invertebrates declined during the first year of logging in streams at Coweeta Hydrologic Lab (Gurtz & Wallace, 1984). Autochthonous production in a Coweeta stream declined to near pre-disturbance levels 4 years after forest clearcutting, and allochthonous inputs increased significantly as riparian vegetation regrew (Webster, *et al.*, 1983). Increased solar influx and higher nitrogen levels resulted in greater algal biomass, thus higher grazer density in a Coweeta stream ten years after clearcutting (Woodall & Wallace, 1972), however, 20 years later grazer density had returned to pre-disturbance levels (Haefner & Wallace, 1981a). New leaf input from the early successional forest caused shredder density to increase, but to levels somewhat less than an undisturbed reference stream.

Recovery of macroinvertebrates in headwater streams following clearcutting appears to be closely aligned with recovery of the surrounding forest (Gurtz, *et al.*, 1980). Recovery of shredders may depend on the quality and availability of leaf material reaching disturbed streams. Lower density of the leaf shredding stonefly *Tallaperla maria* was the result of a significant reduction in smaller nymphs following clearcutting (Gurtz, 1981). Density of *T. maria* was 2 times greater in a reference than in a disturbed stream, but production was not

significantly different because nymphs in the disturbed stream were larger (O'Hop, *et al.*, 1984). Growth rates of the leaf-shredding stonefly *Soyedina carolinensis* (Claassen) differed with leaf diet (Sweeney, *et al.*, 1986). In general, relatively fast-processing leaf species (yellow poplar, sugar maple) provided good growth but only moderate survival of *S. carolinensis*, while slow-processing leaf species (red oak, chestnut oak) resulted in slower growth but increased survival.

The purpose of this study was to determine whether forest clearcutting influences production by leaf shredding insects in forest streams. I hypothesized that there would be no significant difference in shredder production between early versus late successional forest streams, because higher food quality of early successional leaves would compensate for lower availability of leaf material in disturbed forest streams. Shredder production, quality, and quantity of leaf material available to shredders were measured in 3 streams in a reference forest and 3 streams in an 11-year-old clearcut forest. Shredder growth on various leaf material was measured under laboratory conditions to determine whether differences in growth could be attributed to leaf quality.

Materials and Methods

This research was conducted in two projects. Project I was a field study designed to measure shredder production and leaf standing crop in 3 streams within a successional forest and 3 streams within a mature forest. Project II consisted of short-term laboratory growth bioassays of 2 shredder species fed leaf material exposed in 4 streams draining forests of different successional stages.

Site description

Fieldwork was conducted in 2 watersheds at Coweeta Hydrologic Laboratory (lat. 35°03'N, long. 83°27'W), a U. S. Forest Service facility in southwestern North Carolina, USA. Big Hurricane Branch, which drains Watershed 7 (WS 7), and Hugh White Creek, which drains WS 14, were selected for shredder production studies based on similarities in geomorphology but contrasting stages of forest succession (Table 1). WS 14 is a long-term reference watershed that has not been disturbed since selective logging more than 60 years ago and the chestnut blight in the early part of this century. Overstory vegetation in the reference forest

is dominated by chestnut oak (*Quercus prinus* L.), white oak (*Quercus alba* L.), red oaks (*Quercus spp.*), beech (*Fagus grandifolia* Ehrh.), and hickory (*Carya glabra* (Mill.) Sweet). The disturbed forest (WS 7) was clearcut and cable-logged in 1976-77. Present vegetation includes rapidly sprouting species such as dogwood (*Cornus florida* L.) and basswood (*Tilia sp.*) and many early successional species such as sassafras (*Sassafras albidum* (Nutt.) Nees), blackberry (*Rubus spp.*), and a variety of vines and shrubs. Species common in both watersheds include yellow poplar (*Liriodendron tilipifera* L.), red maple (*Acer rubrum* L.), and black birch (*Betula lenta* L.) in the overstory and *Rhododendron maximum* L. in the understory (Boring, *et al.*, 1984).

Sawmill Branch (WS 6) and Carpenter Branch (WS 13) were used in addition to WS 7 and WS 14 as leaf exposure sites for shredder growth studies. Watershed 6 was clearcut and converted to grass in 1958. After herbicide treatment in 1967 the forest was allowed to regrow, and forest regrowth at the time of this study was mostly successional species such as black locust, yellow poplar, vines, and shrubs. WS 13 is a coppice forest, *i.e.*, trees were felled and left in place, and forest regrowth consists mostly of yellow poplar stump sprouts. WS 13 has dense rhododendron in much of the understory, and WS 6 has rhododendron in patches along the stream.

Project I - Field Studies

In Project I, 3 first-order (first perennial) tributary streams were selected as independent replicates for monthly sampling within the disturbed and the reference forest. Samples were collected monthly beginning at least 10 m above the junction with other streams.

Table 1. Selected morphometric characteristics of the study basins.

parameter	WS 7	WS 14	WS 6	WS 13
basin area (ha)	59.5	61.1	8.9	16.1
mainstream length (m)	1225	1077	450	604
gradient (m/m)	0.19	0.16	0.24	0.19
mean annual discharge (l/sec)	17.7	19.0	2.30	4.70
maximum watershed elevation (m)	1060	996	919	965
minimum watershed elevation (m)	724	708	742	774
basin orientation	S	N	NW	E
successional stage	recently disturbed	mature forest	grass to forest	coppice forest

Benthic samples

Five random benthic samples were collected monthly from each stream using a 30-cm diameter corer (0.071 m²), which was large enough to include large cobbles (Cummins, 1962). The sample area was enclosed by pushing the corer into the stream bottom. A towel was wrapped around the base of the corer to create a water-permeable seal. Large rocks were examined and removed from the sample area, and coarse organic debris was saved. Substratum in the sample area was stirred to a depth of 10 cm to dislodge organisms and fine debris. Using a Guzzler® pump water, organisms, and debris were pumped from the sample area into a 100- μ m nitex® net supported by a 20-l bucket. After the initial stirring and drawdown, stream water was allowed to seep through the towel into the sample area. The stirring and drawdown process was repeated 4 additional times. The pump and hoses were flushed with water from the bucket. The sample was removed from the mesh bag, placed in a heavy-duty zip-top bag, and concentrated formaldehyde was added to preserve the sample at a concentration of approximately 5% formalin.

Prior to benthic sampling, stream temperature was measured to the nearest 0.1 °C with a mercury thermometer. Hourly stream temperatures were recorded by personnel at Coweeta Hydrological Laboratory using digital recording thermometers placed about 100 m above weir ponds in the main stream draining each watershed. Degree-day accumulation was calculated by summing daily average stream temperatures from recording thermometers beginning at various times during the study period.

In the laboratory, benthic samples were emptied into 102- μ m sieves and rinsed to remove preservative. Samples were rinsed into a series of nested sieves (mesh sizes: 600, 250, and 102 μ m). Leaf material from the largest sieve was washed to remove debris and invertebrates, placed in paper bags, dried at 50°C for 48 hrs., and stored at room conditions. Contents of each sieve were preserved and stored, and shredders were later hand sorted from debris, stored in vials, and preserved with 5% formalin. Samples from the 102- μ m sieve were sorted under a 40X dissecting microscope.

Sampling efficiency

A series of samples was collected to test the adequacy of the sampling technique. Two samples were taken from a reference stream in July, and samples were taken from each of the 6 streams in both August and March. Each sample was collected as described previously, except that samples from successive stirring and drawdown cycles were placed in separate containers and analyzed separately. Linear regressions of insect number and number of successive drawdowns were used to predict the number of drawdowns required to capture all individuals in the sample area.

Leaf quantity and quality

Dry leaf material from benthic samples was sorted to species when possible and weighed to the nearest 0.01 g. Leaf material that could not be identified, particularly shrubs and pieces <3cm diameter, was designated as miscellaneous. Total leaf mass, as well as slow, medium, and fast-processing leaf mass were calculated for each sample. Assignment of species to slow, medium, and fast-processing classes was based on literature values (Webster & Benfield, 1986).

Mean leaf mass in each stream was calculated monthly from the 5 replicate samples. Mean leaf mass in each of 3 streams was calculated for each forest type, and each point in the figures represent the mean and 1 standard deviation of the mean of 3 streams. Log-transformed mean leaf mass in streams within each forest type were compared monthly and annually using ANOVA with the variable "streams" nested within forest type (Kleinbaum & Kupper, 1978).

Shredder life history and production

Headcapsule width and total length of preserved *Tallaperla maria* (Stewart & Stark)(Plecoptera: Peltoperlidae) and *Pycnopsyche* sp. (Trichoptera: Limnephilidae) were measured using a camera lucida and digitizing tablet. Total length of *Tipula abdominalis* Say (Diptera: Tipulidae) was measured to the nearest mm using a ruler. Headcapsule width was

used to produce size frequency histograms of *T. maria* and *Pycnopsyche* sp.. Size-frequency of *T. abdominalis* was based on dry weights of preserved specimens.

Dry weight (DW) of *T. maria* was estimated for each individual based on the relationship between total length (TL) and DW of 289 fresh specimens ($\ln DW = \ln TL(2.6) - 11.2$, $R^2 = 0.89$). Dry weights for *Pycnopsyche* sp. were obtained using a regression ($\ln DW = \ln TL(2.7) - 11.6$, $R^2 = 0.89$, $N = 300$) developed for *Platycentropus radiatus* Say, a similar size species belonging to the same family (Figure 1). *P. radiatus* was substituted for *Pycnopsyche* because fresh *P. radiatus* specimens were readily obtainable near Blacksburg. Dry weight of *T. abdominalis* was measured by drying each preserved specimen at 50°C for 24 hrs., desiccating for 24 hrs., and weighing to the nearest 0.01mg.

Analysis of field data

Mean individual weight (MIW) of each shredder species within each forest type was calculated by first calculating the mean of individuals per sample, secondly calculating the mean of the 5 samples within a stream, and finally calculating the mean of the three streams within each forest type. Mean density in each stream was calculated monthly from 5 samples, and mean density within each forest type was calculated from 3 streams. Error bars on all figures equal 1 standard deviation of the means of 3 streams. Mean individual weight, mean density, and mean biomass of each shredder species and the combined shredders in WS 7 and WS 14 were log transformed when necessary to meet assumptions of ANOVA, and compared using ANOVA with streams nested within each forest type, followed by Least Squares Means procedure.

Annual shredder production was calculated for each species in each stream using the instantaneous growth method (Waters, 1977). Production by *T. maria* was calculated separately for each of the 2 cohorts in each stream and summed to obtain annual production. Production was calculated 2 different ways for *T. abdominalis* and *Pycnopsyche*. First, production was calculated assuming a single recruitment period for the cohort of each species. However, there appeared to be 2 subsequent, relatively distinct recruitment periods for *T.*

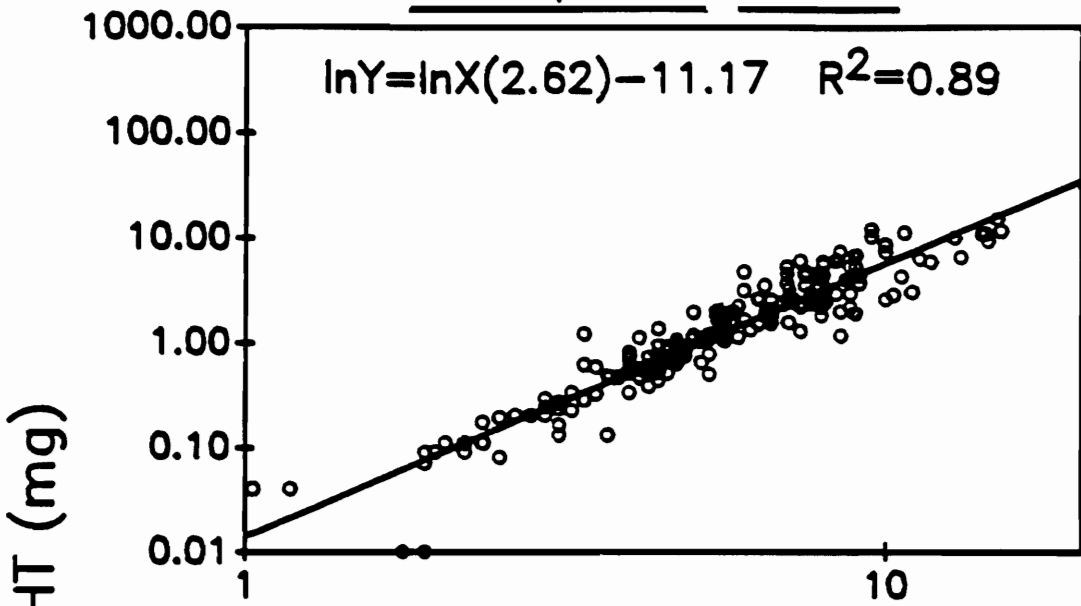
abdominalis and *Pycnopsyche* as identified from density and weight data. Production was then recalculated for each of the 2 recruitment periods within the cohorts of each species. Calculating production for 2 subsequent recruitment periods and summing these values for each species in each stream resulted in 5 - 12% greater production compared with calculating production for a single recruitment period. It was felt that the second method was more accurate because it avoided negative production that occurred when early instar recruits joined the already established populations. Mean production of each species and the combined shredders in streams within each watershed was compared using student's t-test.

Data from the benthic samples included: biomass of identifiable leaf taxa, total leaf biomass, biomass of fast, medium, and slow-processing leaves, biomass of each shredder species, and biomass of all shredders. Multiple correlations were used to look for significant relationships between leaf and shredders biomass in samples. Correlations were performed on all samples, samples within each forest type, and samples from each sampling date.

Project II: Shredder Growth Studies

Growth studies were used to assay the quality of leaf resources available to shredders in Coweeta watersheds and to provide supportive evidence for field production studies (Benke, 1984). The stonefly *T. maria* and the crane fly *T. abdominalis* were selected for growth bioassays because they represented different orders of insects that have different modes of feeding and digestion, and because they are 2 of the dominant shredders in Coweeta streams. Leaf treatments were designed to determine if shredder growth was affected by leaf species, conditioning, and site. Seven leaf species ranging from early to late successional plants were placed in 4 Coweeta streams beginning shortly after leaf-fall and retrieved at 6 time intervals over the ensuing 9 months (Table 2).

Talloperla maria



Platycentropus radiatus

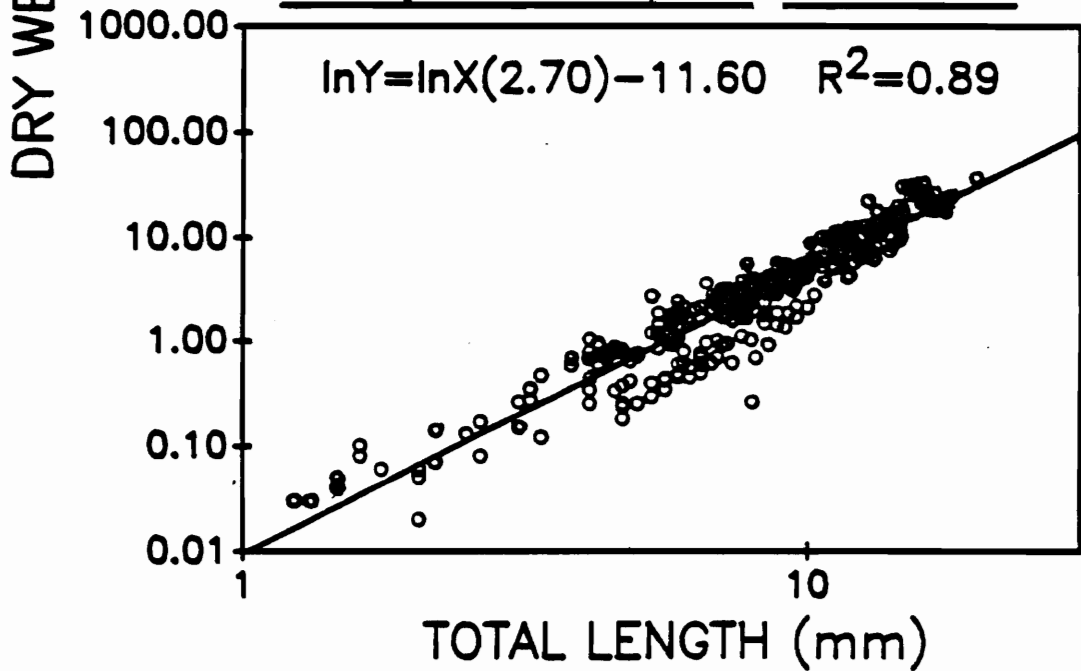


Figure 1. Regression of unpreserved dry weight and total length of insects.

Growth Chambers

Growth chambers used for rearing *T. maria* were modified 200-ml plastic funnels. Air was supplied to each chamber via a plastic pipette tip fitted through the wall of the funnel at an angle such that air bubbles created circular flow of water within each chamber. Chambers had screening at the top and above the funnel neck to prevent animals from escaping. Growth chambers used for rearing *T. abdominalis* were 6 by 8 by 20-cm clear acrylic boxes with removable tops. Boxes were filled with water to 3-cm depth, and no air was supplied.

Water for the experiments was 1 part tapwater and 3 parts distilled water which had been aerated for 24 hrs. and brought to thermal equilibration inside the environmental cabinet. Temperature within the environmental cabinet was maintained at 10°C for all experiments. Air supply to growth chambers was constant, and lights were used in the cabinet only during servicing.

Growth study design

Leaf species and exposure site were selected to cover a spectrum of leaf quality and forest disturbance. Leaves were picked from plants in Coweeta watersheds just prior to autumn abscission and dried at room temperature. Ten-gram packs of each species were placed in plastic mesh bags (mesh size = 1.5 cm). Five bags of each leaf species were attached by nylon strings tethered to gutter nails in the streambed on November 30, 1987, and retrieved at time intervals according to the schedule (Table 2). Leaf bags were collected, placed individually in plastic bags, and put on ice for return to the lab where they were rinsed of debris and frozen at -10°C until needed.

Shredders were collected near the White Rocks Recreation Area in Big Stoney Creek Giles Co., Virginia, and in an adjacent watershed near the Cascades Recreation Area in Little Stoney Creek (elev. 700-850 m, lat. 37°26'N, long. 80°36'W). Shredders were placed in plastic bags with streamwater and returned to the lab within a few hours.

For each shredder species, each leaf treatment was replicated in 5 randomly assigned growth chambers during the first month and 7 replicate chambers thereafter. Chambers were

drained, rinsed, and water and leaf material were replaced 7 days into each experiment. Growth experiments were conducted for 14 days.

Growth analysis

Relative growth rates (RGR) of shredders were calculated as mg dry weight gained per g average body weight per day. Growth was linear within the size range of animals used in this study, so average body weight was calculated as the the mean weight of an individual before and after each experiment. Live blotted wet weights before and after each experiment were converted to dry weight using a wet weight/dry weight ratio developed for each species. Mean RGR was calculated for each replicate of shredder, leaf species, length of instream conditioning, and site. For each shredder, mean RGR was compared between leaf treatments using Least Squares Means. Effects of leaf species, conditioning, and site on shredder RGR was determined using one-way ANOVA followed by Least Squares Means procedure. Effects of conditioning and site of exposure of yellow poplar were tested for each shredder species using 2-way ANOVA.

Table 2. Schedule for retrieval of leaves placed in Coweeta watersheds 6, 7, 13, and 14 on November 30, 1987.

date retrieved	yellow poplar	dogwood	red maple	black-berry	black locust	chestnut oak	rhododendron
19 DEC 87	6, 7, 13, 14	6, 14	6, 14	7	6, 7		
23 JAN 88	6, 7, 13, 14	6, 14		7	6, 7	14	6, 14
24 FEB 88	6, 7, 13, 14	6, 14	6, 14	7*	6, 7		
27 MAR 88	6, 7*, 13, 14		6, 14*		7	14	6, 14
23 APR 88							
05 AUG 88						14	6, 14

*little or no leaf material remaining.

Results

Physical variables

Basin morphology

Basins containing disturbed and reference forests were morphological similar (Table 1). Morphological attributes of sub-basins containing streams within disturbed and reference forests were compared using student's t-test. Mean basin area, main stream length, gradient, and minimum elevation (range 807 to 853 m) of sub-basins within disturbed versus reference forests were not significantly different. Substratum in all streams was characterized by observation as mostly medium cobble > pebbles > coarse sand (Cummins, 1962).

Stream temperature

Average daily stream temperatures were higher in the reference forest than in the disturbed forest during the summer and lower in the reference forest during the winter (Figure 2). Daily minimum and maximum stream temperatures for the period beginning 5 months prior to the first sampling date and continuing over the duration of the study ranged from 3.5 to 20.5°C in the disturbed forest, and 2.5 to 19.5°C in the reference forest. Average daily

stream temperature in the reference forest was as high as 17°C in early May, but average daily stream temperature did not reach 17°C in the disturbed forest until early July.

Monthly temperature taken with a hand-held thermometer at the time of sampling verified the trend of more extreme seasonal temperature in reference versus disturbed forest streams. Based on student's t-test, monthly mean temperature of reference forest streams was significantly greater in the summer and significantly lower in the winter than mean temperature in disturbed forest streams ($p < 0.05$).

Differences in degree-day accumulation in main streams draining each forest type were most apparent in late summer and mid-winter (Figure 3). The main stream draining the disturbed forest accumulated 350 more degree-days than the reference forest main stream during winter. The disturbed forest main stream was approximately 40 days ahead of the reference forest main stream at the point of maximum difference in degree-day accumulation during the winter. The reference forest main stream accumulated 202.5°C more degree-days than the disturbed forest during the summer and was approximately 20 days ahead of the disturbed forest at the point of maximum difference in degree-day accumulation during the summer. Because of differences in seasonal degree-day accumulation, there was little difference in degree-day accumulation between forest types on an annual basis.

Major physical differences that might affect temperature in disturbed and reference forest streams included basin orientation and forest canopy. The disturbed forest was in a south-facing basin, while the reference forest was in a north-facing basin. Basin orientation may have been an important factor causing disturbed forest streams to be somewhat warmer during the winter. However, if basin orientation was the major determinant of water temperature it would be expected that summer stream temperature would also be higher in the disturbed forest, when in fact summer stream temperature was higher in the reference forest. Based on forest cover, it would be expected that seasonal temperature in disturbed forest streams would be more extreme than in the reference forest streams, when in fact the opposite was true. Differences in stream temperature profiles between basins appeared to be the result of geomorphological differences. In all likelihood, groundwater retention time was

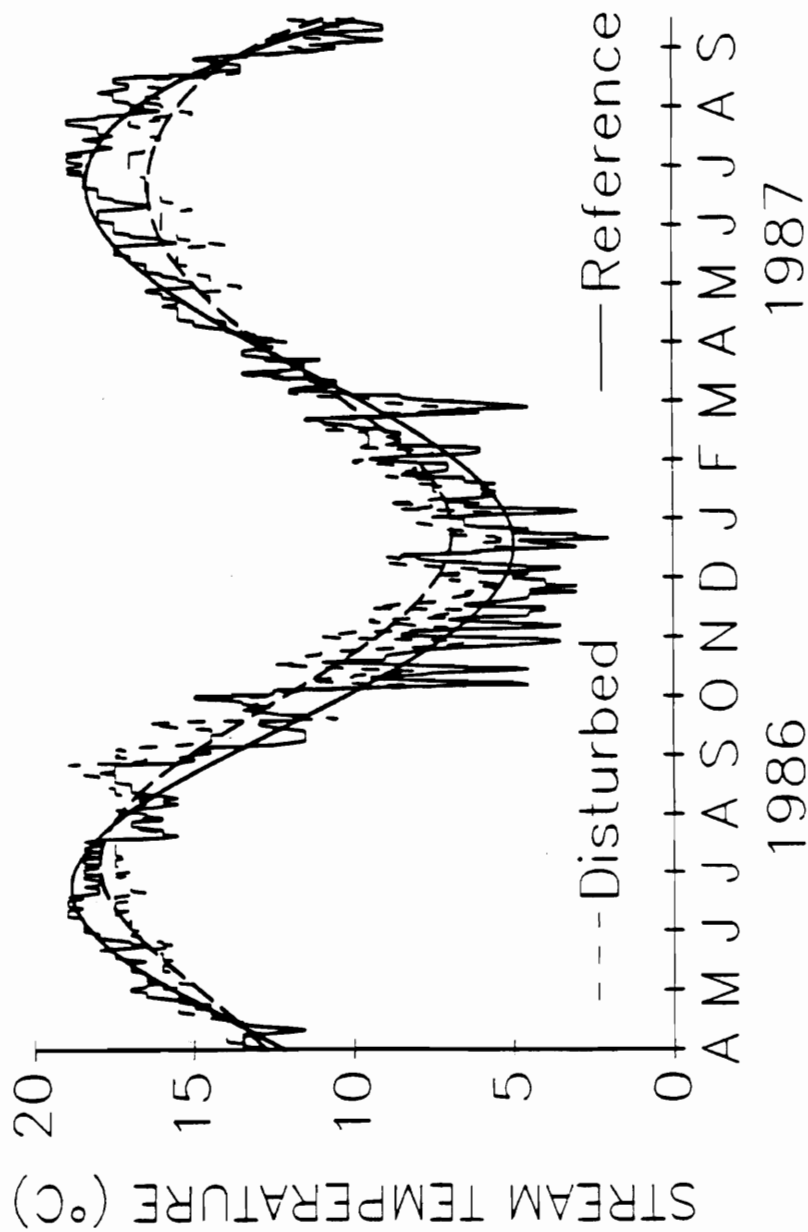


Figure 2. Mean daily stream temperature (thin lines) in the main stream draining disturbed and reference forests. Thick lines fitted by eighth-order polynomial regression.

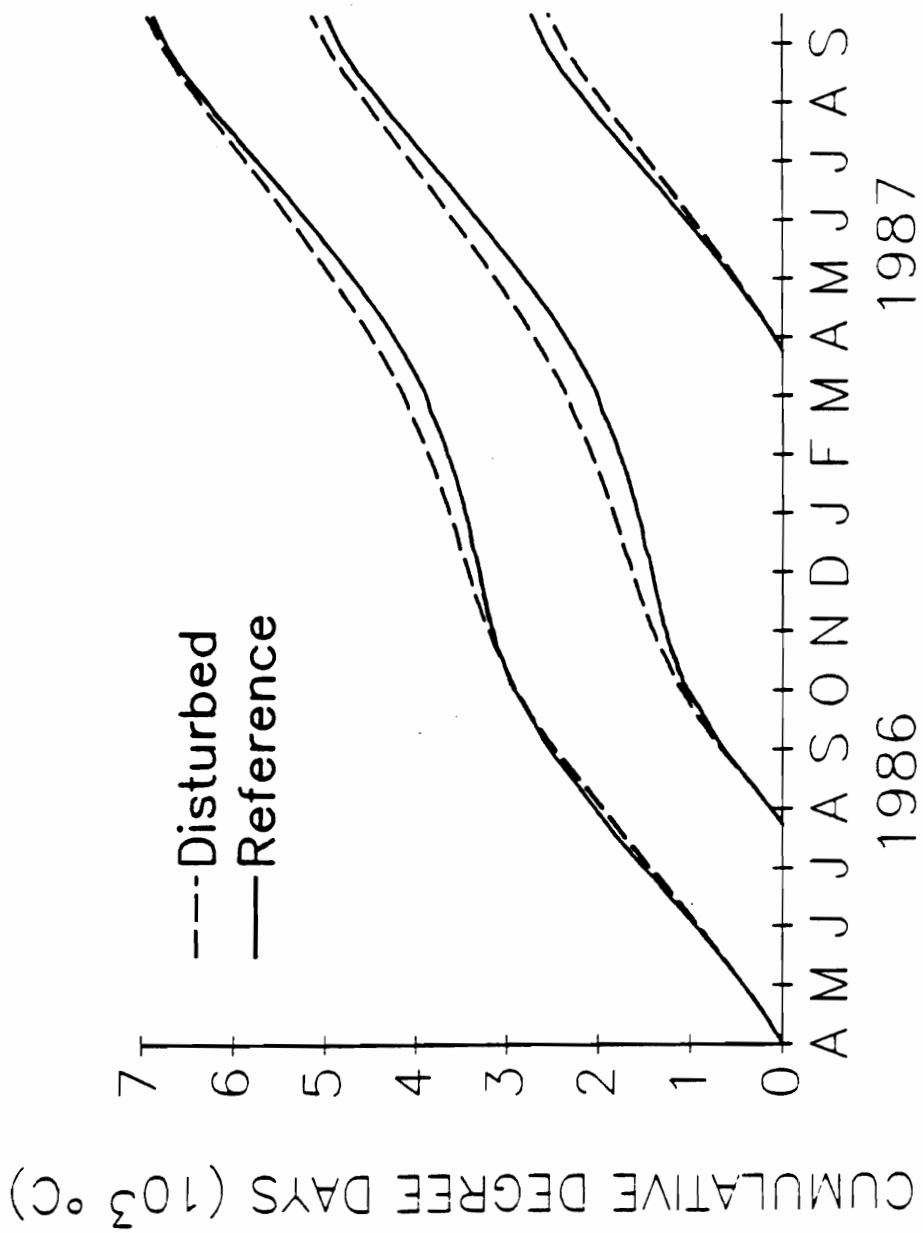


Figure 3. Accumulation of degree-days above 0°C in the main stream draining the disturbed and reference forest.

greater in the disturbed versus the reference forest, so that disturbed forest stream temperature most closely approximated mean annual temperature (J.R. Webster, personal communication).

Efficiency of sampling benthic invertebrates

The benthic sampler was tested to determine the number of successive stirring/drawdown cycles required to capture 95% of the organisms in the sample area. The number of drawdowns required was determined by the X-intercept of the linear regression comparing the mean number of organisms captured in each of 5 successive stirring/drawdown cycles (Figure 4).

For all groups of organisms, more individuals were captured in the first drawdown than in any subsequent drawdown. The regression lines intercepted the X-axis between 4 and 5 drawdowns for all groups of organisms. Slightly more than 4 successive drawdowns were required to capture over 95% of the total number of organisms collected.

For most groups, few if any animals were captured in the fifth drawdown. However, there was a 40% likelihood that a tipulid would be captured in the fifth drawdown. In contrast, over 90% of peltoperlids were captured in only 3 drawdowns. Nearly 99% of the limnephilids and small peltoperlids were captured in 3 drawdowns. Tipulids required the greatest sampling effort of any group of organisms, suggesting that they were deep in the substrata. Limnephilids and small peltoperlids appear to have resided in the superficial sediments.

From these sampler tests it was determined that 5 successive drawdowns were sufficient to capture 95% of the organisms in the sample area. For all subsequent benthic samples collected in this study I used 5 successive drawdowns.

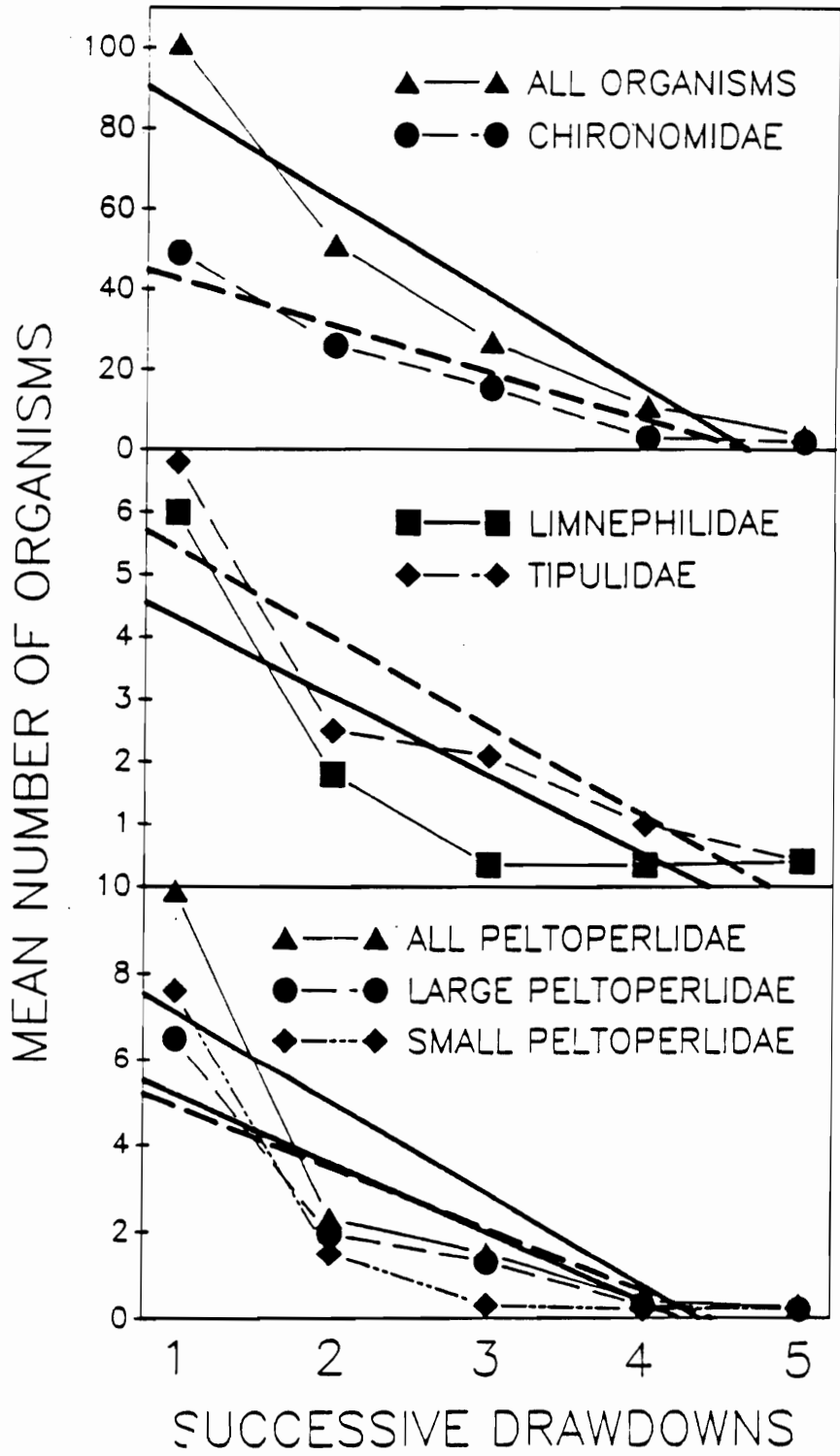


Figure 4. Mean number of organisms captured within a sample area during each of 5 successive stirring and drawdowns (N=14).

Leaf quantity and quality

Mean annual biomass of all leaf material was significantly greater ($p < 0.05$) in reference than in disturbed forest streams (Table 3). Mean monthly biomass of leaf material was significantly greater in reference versus disturbed streams from March through June but was not significantly different during the 4-month period (November - February) following leaf abscission (Figure 5).

Maximum leaf input to streams occurred mostly in September and October, and leaf biomass generally declined gradually thereafter. One exception was in February, when there appeared to be a slight increase in total leaf biomass in streams in each forest, possibly due to blow-in or transport from upstream. In August 1987 total leaf biomass was similar in all streams, but in August 1988, leaf biomass was significantly greater in disturbed versus reference forest streams. Early input of leaf material (mostly rhododendron, birch, and shrubs) in August 1988 may have been due to the combined effects of drought and southern exposure resulting in early leaf abscission in the disturbed forest.

Leaf quality differed considerably between disturbed and reference streams. Mean annual biomass of slow-processing leaf species was significantly greater in reference versus disturbed forest streams (Table 3), and mean biomass of slow-processing species in late October was more than twice as high in reference streams (Figure 5). Reference forest streams had 50% higher biomass of medium-processing species than disturbed streams in October (Figure 6), and annual differences were significant at $p < 0.10$ (Table 3). Disturbed streams had 7.5 times more fast-processing leaf biomass than reference streams in October, and biomass of fast-processing leaves was significantly greater in disturbed streams on an annual basis (Table 3). Fast-processing species accounted for approximately 20% of the biomass of all identifiable leaf material in disturbed streams after leaf-fall, but less than 2% of the post-abscission biomass in reference streams. Slow-processing leaf biomass, over 90% of which was rhododendron, made up 43% of total leaf biomass in disturbed streams.

Table 3. Mean annual leaf biomass (g/m²) in disturbed and reference forest streams (asteriks indicate significant differences between means: *p < 0.10, **p < 0.05, ***p < 0.01).

	all leaf species	slow decay	medium decay	fast decay
disturbed forest streams				
Stream 1	58.65	14.24	22.31	7.20
Stream 2	72.93	42.35	13.33	4.20
Stream 3	48.17	19.97	10.35	7.13
reference forest streams				
Stream 4	113.11	78.15	19.82	1.25
Stream 5	120.06	73.73	31.96	0.69
Stream 6	74.26	42.90	22.34	0.49
mean of streams				
disturbed forest	59.91	25.52	15.34	6.17***
reference forest	102.48**	64.93**	24.70*	0.82

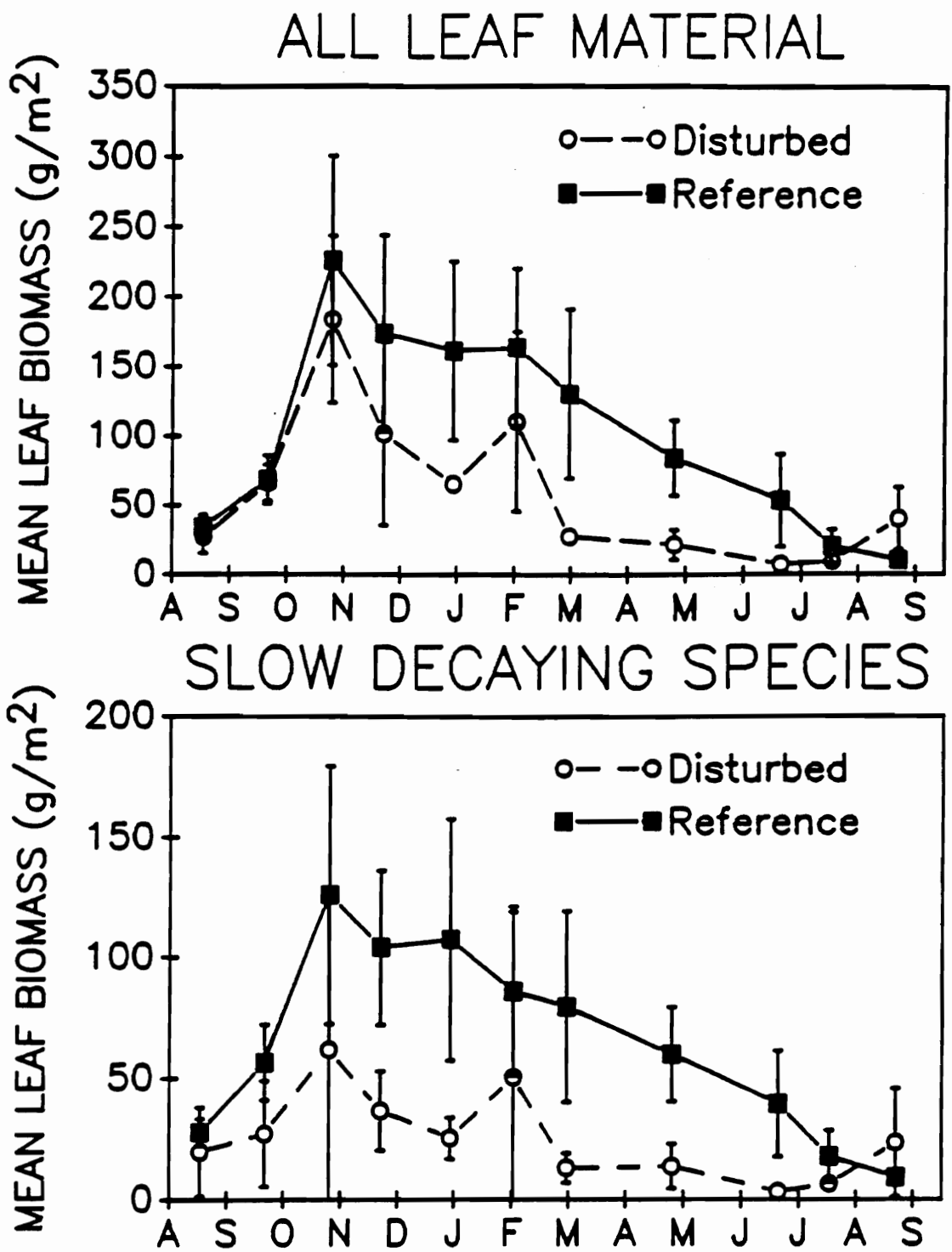


Figure 5. Mean leaf biomass (and 1 S.D.) in disturbed and reference forest streams.

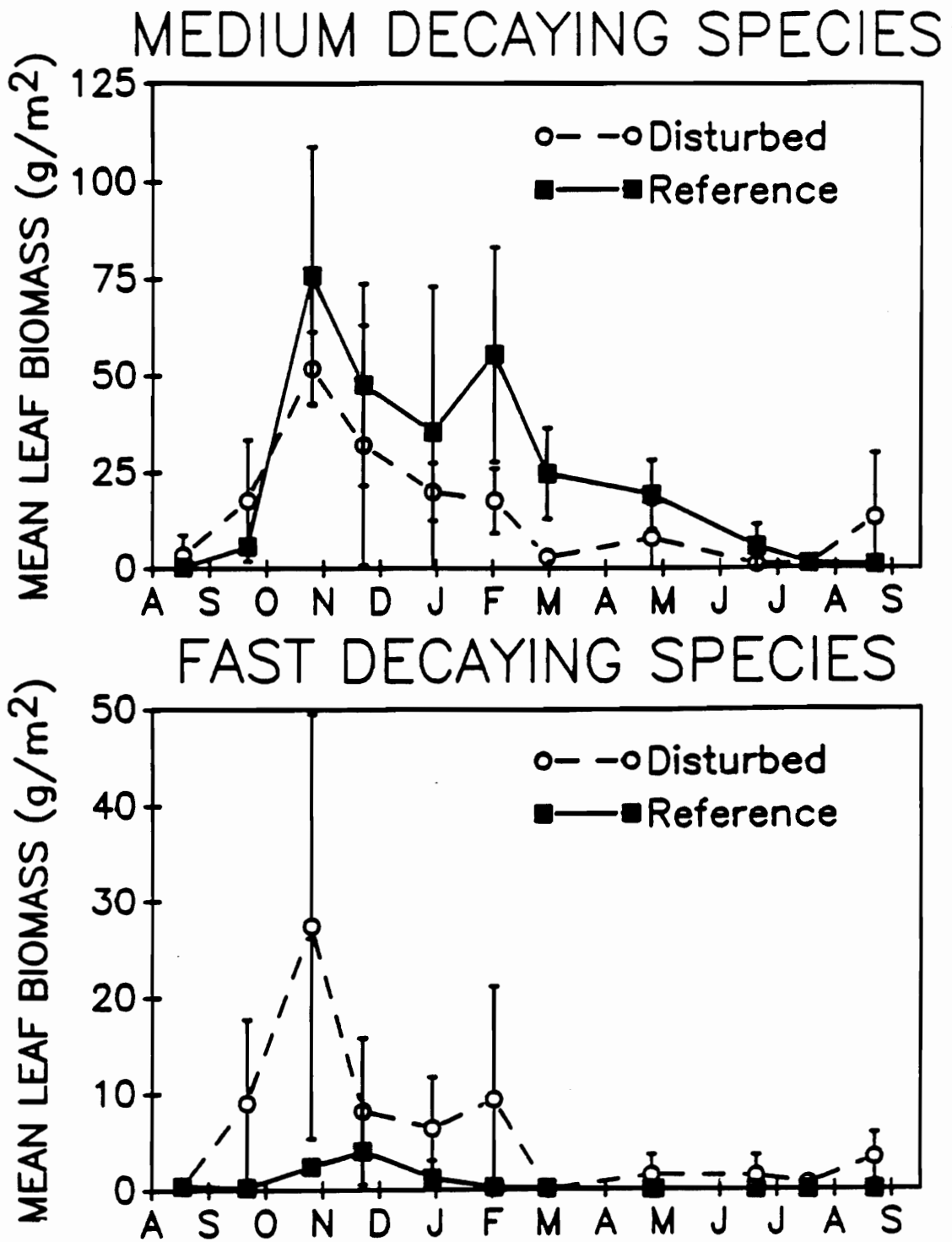


Figure 6. Mean leaf biomass (and 1 S.D.) in disturbed and reference forest streams.

Unidentifiable leaf material generally accounted for less than 20% of the total leaf biomass on any given date, and there were no significant differences in biomass of unidentifiable leaf material between stream types (Table 4). Biomass of identifiable leaves was representative of the contrasting types of vegetation in each forest. Rhododendron and white oaks (mostly chestnut oak), slow-processing species, dominated the leaf biomass of reference forest streams. Rhododendron was the only slow-processing species of any significance in disturbed forest streams and constituted approximately one-third of the leaf biomass in all streams.

Leaf species characterized as having medium decay rates (black birch, yellow poplar, red maple) were common in both forests. Yellow poplar had significantly greater mean annual biomass in reference versus disturbed forest streams. Black birch had generally greater biomass in reference forest streams, but red maple had somewhat greater biomass in disturbed forest streams (Table 4).

Fast-processing leaf species were understory or early successional plants such as dogwood, basswood, sassafras, greenbrier, and a variety of shrubs. Herbaceous plants important in the disturbed forest but rarely detected in benthic samples included blackberry (*Rubus sp.*), grape (*Vitis sp.*), and sedge (*Carex sp.*). Leaves of one herbaceous species, blackberry, had greater instream decay rates than woody species in the disturbed forest (E.F. Benfield, unpublished data). Herbaceous species may have been underrepresented in samples because of their rapid decay rates in streams.

Shredder life histories

Life history patterns of the 3 dominant shredders varied considerably. *Pycnopsyche sp.* and *T. abdominalis* were univoltine, but recruitment of early instar individuals was asynchronous, occurring in 2 peak recruitment periods separated by 3-4 months. *T. maria* was

Table 4. Mean annual leaf biomass (g/m²) in disturbed and reference forest streams (asteriks indicate significant differences between streams: *p < 0.10, **p < 0.05, ***p < 0.01).

	Rhodo- dendron	White Oaks	Red Oaks	All Oaks	Red Maple	Black Birch
disturbed forest streams						
Stream 1	12.99	0.46	0.03	0.49	8.82	10.92
Stream 2	40.49	0.54	0.72	1.25	2.76	7.55
Stream 3	16.34	2.48	0.79	3.35	7.20	0.93
reference forest streams						
Stream 4	38.87	27.97	8.07	35.03	6.89	1.51
Stream 5	55.45	7.25	7.69	14.93	6.23	17.06
Stream 6	24.92	6.85	8.48	15.31	1.69	11.39
mean of streams						
disturbed forest	23.27	1.15	0.51	1.68	6.25	6.46
reference forest	39.75	13.67	8.07***	21.76**	13.08	9.99
	Dog- wood	Beech	Yellow Poplar	*Other Fast spp.	Green- brier	Unident- ifiable
disturbed forest streams						
Stream 1	4.30	0.44	2.59	2.85	0.06	14.34
Stream 2	1.34	0.18	0.85	1.21	1.66	12.70
Stream 3	2.87	0.18	2.23	3.63	0.62	12.45
reference forest streams						
Stream 4	0.87	2.04	12.41	0.37	0.03	13.83
Stream 5	0.66	3.23	8.68	0.03	0.00	14.37
Stream 6	0.35	2.00	9.24	0.13	0.00	8.66
mean of streams						
disturbed forest	2.83*	0.27	2.62	2.56**	0.77	1.11
reference forest	0.63	2.42***	9.79***	0.17	0.01	12.28

*includes: sassafras, basswood, greenbrier, blackberry, grape, shrubs.

hemivoltine with 2 relatively distinct cohorts present, each of which appeared to represent a separate year class. Little difference was observed between disturbed and reference forest streams in terms of chronology of *T. maria* and *Pycnopsyche* sp. life cycles, however, the life cycle of *T. abdominalis* in reference forest streams preceded that of disturbed forest streams by approximately 4 months.

Life history of *Tallaperla maria*

Adult *T. maria* were collected from streamside vegetation in the disturbed forest beginning in early May, reached a peak by late May, and were absent by late June. Flights were observed only during the day, and *T. maria* was never present in light traps. Approximately 16 occurrences of upstream flight were observed in the disturbed forest during a 1-hr. period on May 16. A few additional upstream and 2 downstream flights were observed while sampling in May. Adults appeared to spend the majority of time resting on vegetation 1-4 m above stream level.

Individual eggs of *T. maria* were collected occasionally in benthic samples. Eggs were 0.5×0.9 mm ovoids weighing an average 8 μ g. Viable eggs obtained from benthic samples contained fully developed first instar larvae. Empty egg shells had lengthwise slits where larvae had escaped. Egg dimensions were 4-6 times larger than dimensions reported for eggs collected from gravid females (Stark & Stewart, 1981), suggesting that enlargement occurs during embryonic stages. Viable eggs were collected in July and August in all streams at densities ranging from 5-16 eggs/m². Less than 3 viable eggs/m² were collected in September in disturbed streams. No additional viable eggs were found until January and February in reference streams, when <2 eggs/m² were collected. Although the total number of eggs collected in either watershed could account for <8% of early instar larvae, egg densities coincided well with the recruitment period for early instar larvae. Peak egg hatching and subsequent recruitment of early instar larvae in disturbed streams appeared to precede that in reference streams by 2 to 3 months.

Early instar nymphs (Cohort I) began appearing in late August in all streams (Figure 7). December mean density of Cohort I was significantly greater in disturbed versus reference streams. Cohort I peak density occurred in January in disturbed streams and February in reference streams. Cohort I survivorship from the period January through September was 30% in reference streams, and 70% in disturbed streams. Cohort II mortality was greatest during the period September through December, when mortality was approximately 70% in disturbed streams, and 40% in reference streams. On an annual basis, mean density of Cohort I, Cohort II, and total mean density was significantly greater in disturbed versus reference streams for *T. maria* (Table 5). Similar mean density patterns of the 2 cohorts on consecutive annual dates indicated that forest type had a consistent effect on density of each year class.

Nymphal development in each *T. maria* cohort was relatively synchronous, and little difference was observed between forest types in terms of frequency distribution of size classes on any sampling date (Figures 9 & 10). Size class 1 individuals were first and possibly second instar larvae, and were present from August through March in all streams. The relative proportion of size 1 individuals decreased gradually in streams during the period August through March. In March the proportion of Cohort I size 1 individuals appeared to increase in reference streams (Figure 9). The apparent increase in size 1 individuals in March, however, coincided with a very low March density estimate, thus a limited number of individuals was measured (Figure 7). Small sample size of Cohort II individuals in reference forest streams in March also resulted in an apparently smaller size distribution (Figure 9), and low estimated density in disturbed streams in February resulted in apparently smaller size distribution of both cohorts (Figure 8). Occurrence of size 1 individuals coincided with the recruitment period identified from larval and egg density data. There was little difference in size distribution of either cohort of *T. maria* between disturbed and reference streams.

Size distribution of *T. maria* was based on headcapsule width, a measure in which each instar has a theoretical maximum size, thus increases in size occurs mostly during molting. In contrast, total length includes abdominal segments that have more soft tissue than head

and thoracic integument. Continuous growth of soft tissue during intermolt periods resulted in dry weight of fresh specimens correlating more closely with total length ($R^2=0.89$) than with headcapsule width ($R^2=0.83$). Dry weight of preserved specimens was estimated from total length, and differences in dry weight of *T. maria* in streams within the 2 forest types were independent of size class distribution.

Although nymphal development was similar in disturbed and reference streams, monthly Mean Individual Weight (MIW) was generally greatest in disturbed streams (Figure 10). Annual MIW of Cohort I was significantly greater in disturbed versus reference streams (Table 5). Cohort II MIW was significantly greater in disturbed versus reference streams in winter, but there was no significant difference in Cohort II MIW on an annual basis. Lower Cohort II MIW in reference streams during winter was compensated for by rapid growth prior to emergence in May, and pre-emergence MIW was not significantly different between disturbed and reference streams.

Mean annual biomass of *T. maria* was significantly greater in disturbed versus reference streams (Table 5). Cohort II annual mean density and annual MIW were lower in Stream 1 than Streams 2 and 3. Cohort I annual mean density was highest in Stream 1, but annual MIW was moderate, thus biomass was comparatively low. Biomass of both cohorts in Stream 1 appeared to resemble reference streams more closely than other disturbed streams.

Life history of *Tipula abdominalis*

Late instar *T. abdominalis* were absent from reference streams after March. In April, larvae were found under moss and litter covering mid-stream and streamside rocks and logs in reference streams. Larvae emigrating from reference streams were dark and had dried epidermal tissue, were relatively immobile, and appeared to have begun pupal metamorphosis. Larvae were present in disturbed streams until July, thus *T. abdominalis* pupated about 4 months earlier in reference versus disturbed forest streams.

Mean individual weight (MIW) of *T. abdominalis* in reference streams in February was not significantly different than MIW in disturbed streams during the summer, suggesting that

Table 5. Mean annual density, mean individual weight (MIW), and biomass of *Tallaperla maria* in streams (astriks indicate significant differences between means: * $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$).

	Density (number/m ²)			MIW (mg)		Biomass (mg/m ²)		
	Cohort I	Cohort II	TOTAL	Cohort I	Cohort II	Cohort I	Cohort II	TOTAL
disturbed forest streams								
Stream 1	154.5	49.0	203.5	0.127	0.528	18.0	33.8	51.8
Stream 2	136.6	80.3	216.9	0.118	0.975	26.0	68.4	94.4
Stream 3	129.7	92.3	222.0	0.158	0.994	23.3	103.8	127.1
reference forest streams								
Stream 4	97.5	37.7	135.2	0.076	0.722	15.9	31.3	47.2
Stream 5	90.1	34.8	124.9	0.090	0.475	8.5	33.2	41.7
Stream 6	105.6	40.1	145.8	0.089	0.654	10.7	32.1	42.8
mean of streams								
disturbed	140.3***	73.8***	214.1***	0.134**	0.83	22.4***	68.7**	91.1*
reference	97.7	37.6	135.3	0.085	0.62	11.7	32.2	43.9

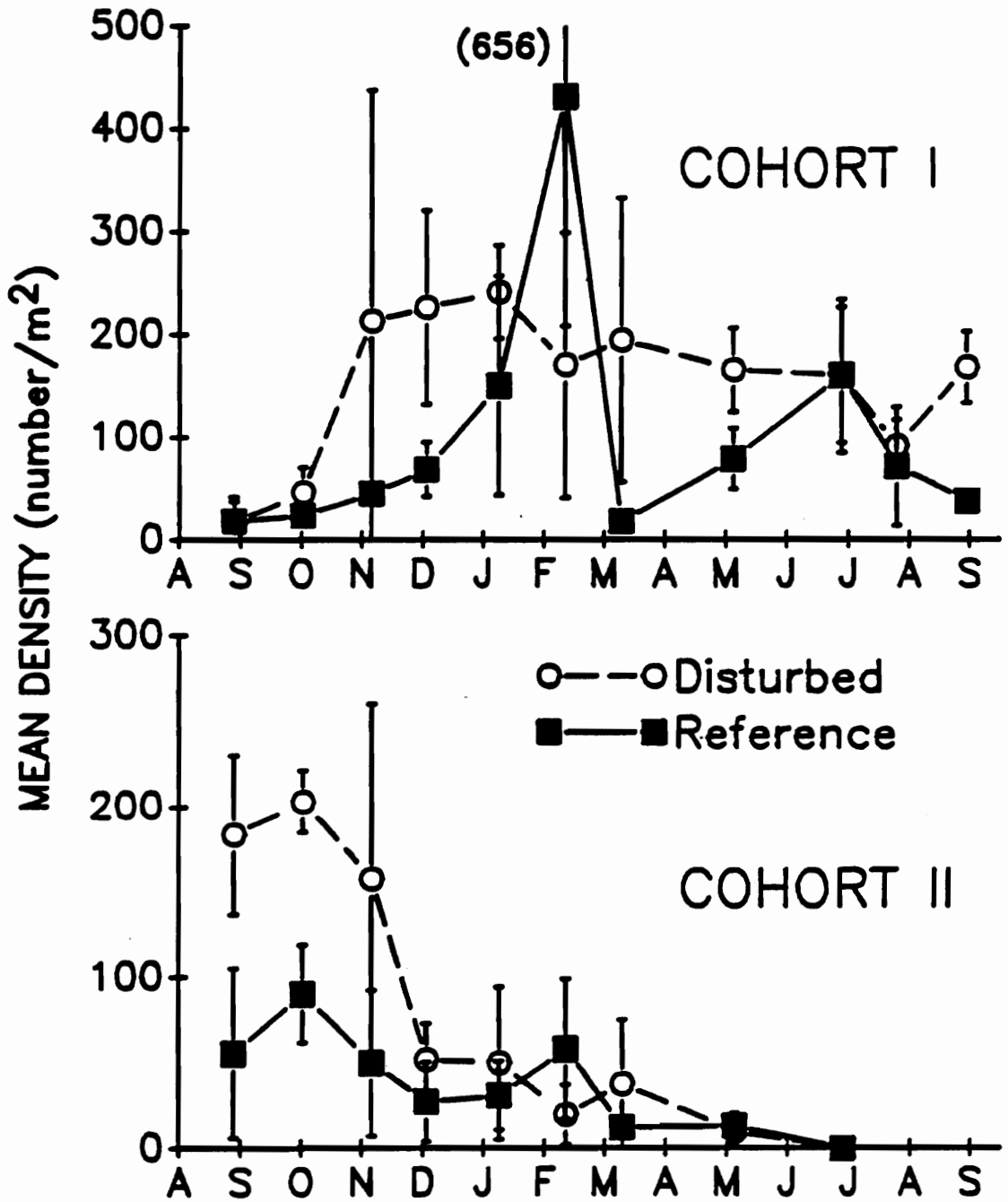


Figure 7. Mean density (and 1 S.D) of *Tallaperla maria* in disturbed and reference forest streams.

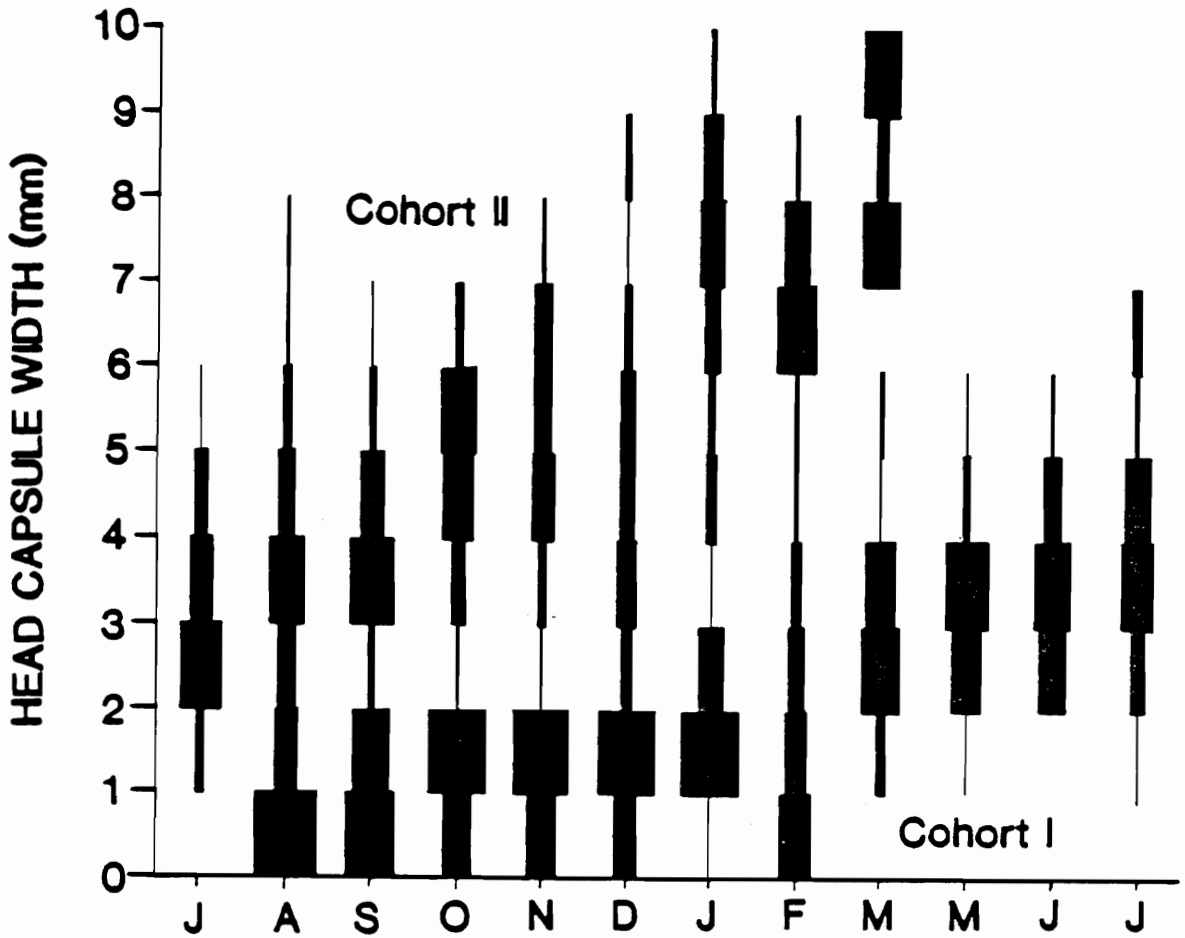


Figure 8. Annual frequency distribution of *Tallaperla maria* size classes in disturbed forest streams. Width of bars represent percent of cohort in each size class.

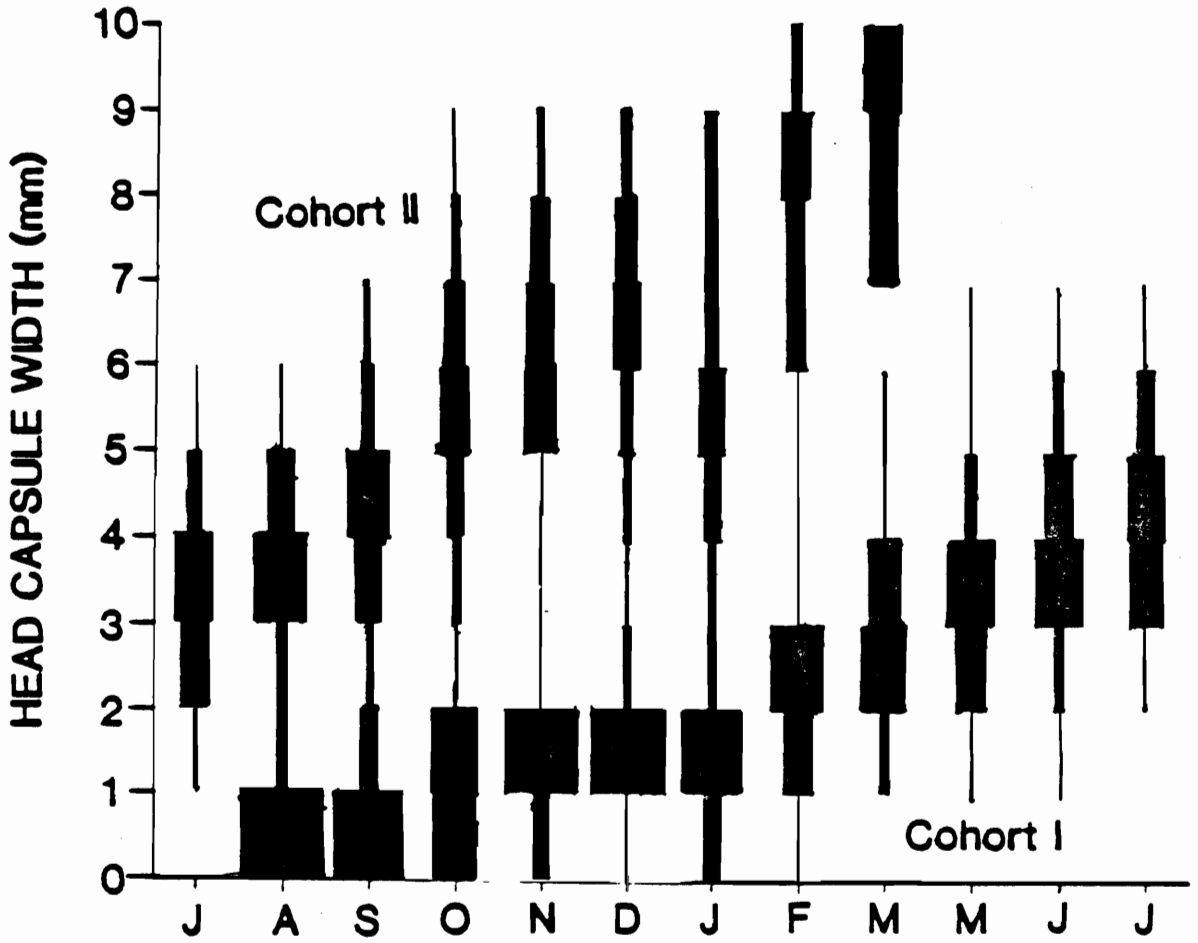


Figure 9. Annual frequency distribution of *Tallaperla maria* size classes in reference forest streams. Width of bars represent percent of cohort in each size class.

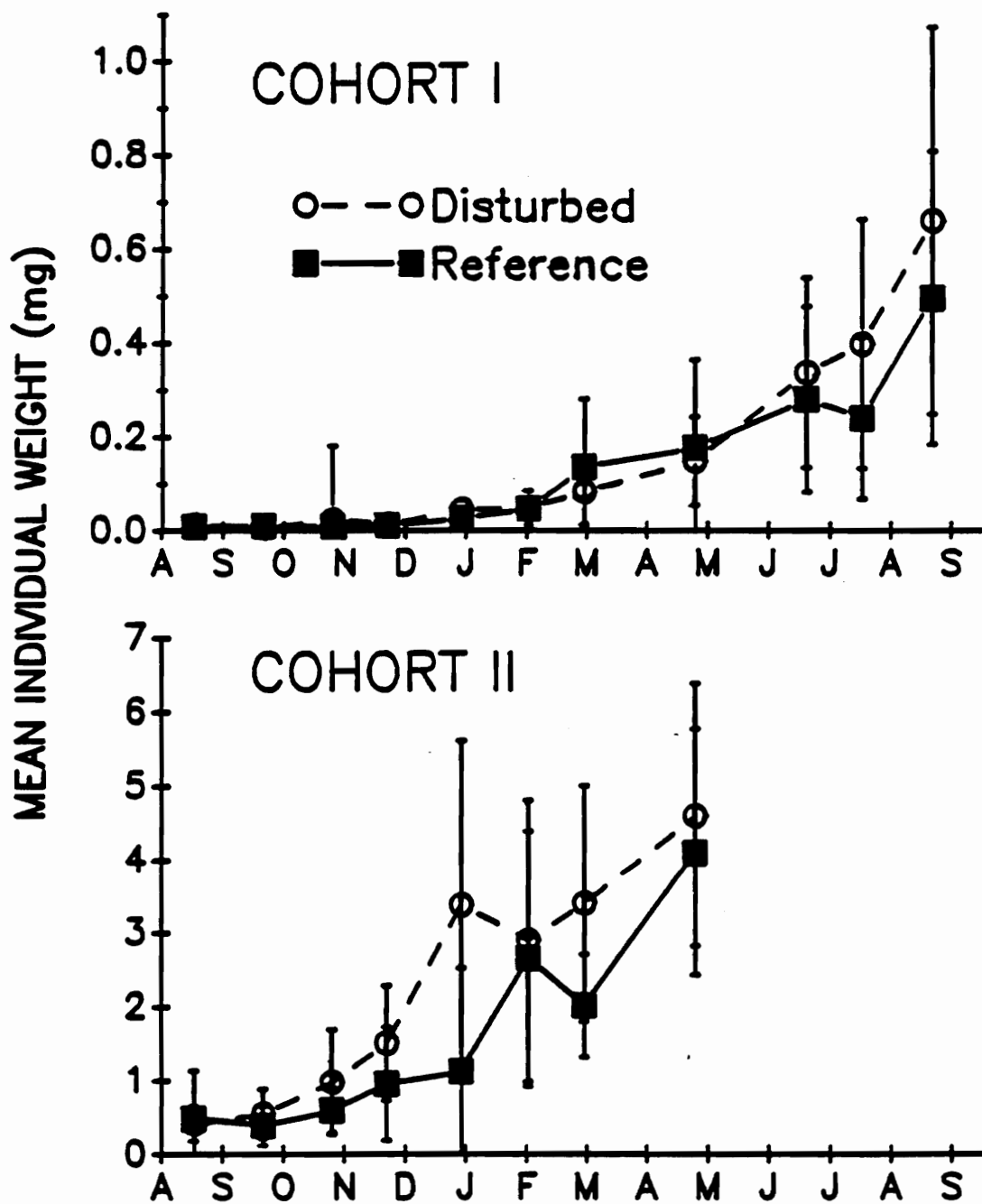


Figure 10. Mean individual weight (and 1 S.D.) of *Tallaperla maria* in disturbed and reference forest streams.

critical mass required for emergence was obtained in all streams by early spring. Early emergence from reference streams may have been temperature related. Daily main stream temperature was consistently higher in reference than in disturbed streams from April through August (Figure 2). The main stream of the reference forest accumulated more degree-days than the main stream of the disturbed forest during the summer (Figure 3), but differences in degree-day accumulation were sufficient to explain only 1-2 month differences in life cycle features of *T. abdominalis*.

Early instar larvae first appeared in late June in all streams (Figure 11). Larval recruitment was asynchronous in all streams, with early instars present from June through November (Figure 12). Recruitment appeared to peak in June in reference streams and September through October in disturbed streams. Some early instar larvae were present in each stream during each of the 2 peak recruitment periods. The occurrence of 2 peak recruitment periods could have been caused by misidentification of early instar larvae, however, mistaken identity would have been consistent for streams within both forests, and density of early instar *T. abdominalis* would undoubtedly have peaked twice in each forest rather than differentially as shown by density data. Several species of tipulids occur in all streams, but most are *Hexatoma*, which are relatively easy to distinguish from *Tipula*. Early versus late recruits of *T. abdominalis* may represent 2 closely related species or genotypes.

Monthly mean densities of *T. abdominalis* were not significantly different when comparing disturbed and reference streams, except during the period March through July when late instar larvae were absent from reference streams. Monthly MIW of were not significantly different between disturbed and reference streams (Figure 11). Annual mean density, MIW, and biomass of *T. abdominalis* in streams were not significantly different between forest types (Table 6).

Life history of *Pycnopsyche* sp.

Several species of *Pycnopsyche* occur in Coweeta streams, the most common of which is *Pycnopsyche gentilis* (J. B. Wallace and A. Huryn, personal communication). All larvae in-

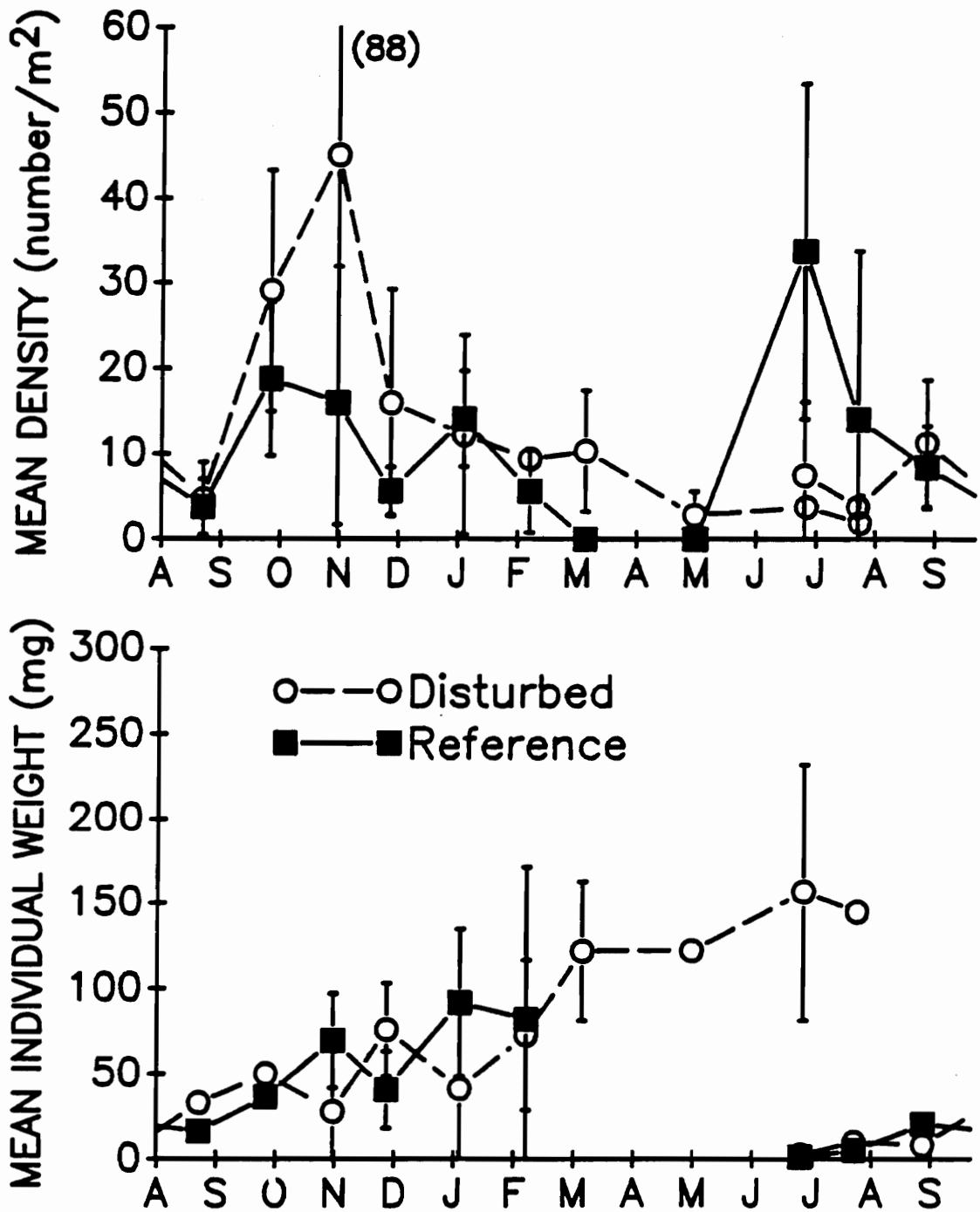


Figure 11. Mean density and mean individual weight (and 1 S.D.) of *Tipula abdominalis* in disturbed and reference forest streams.

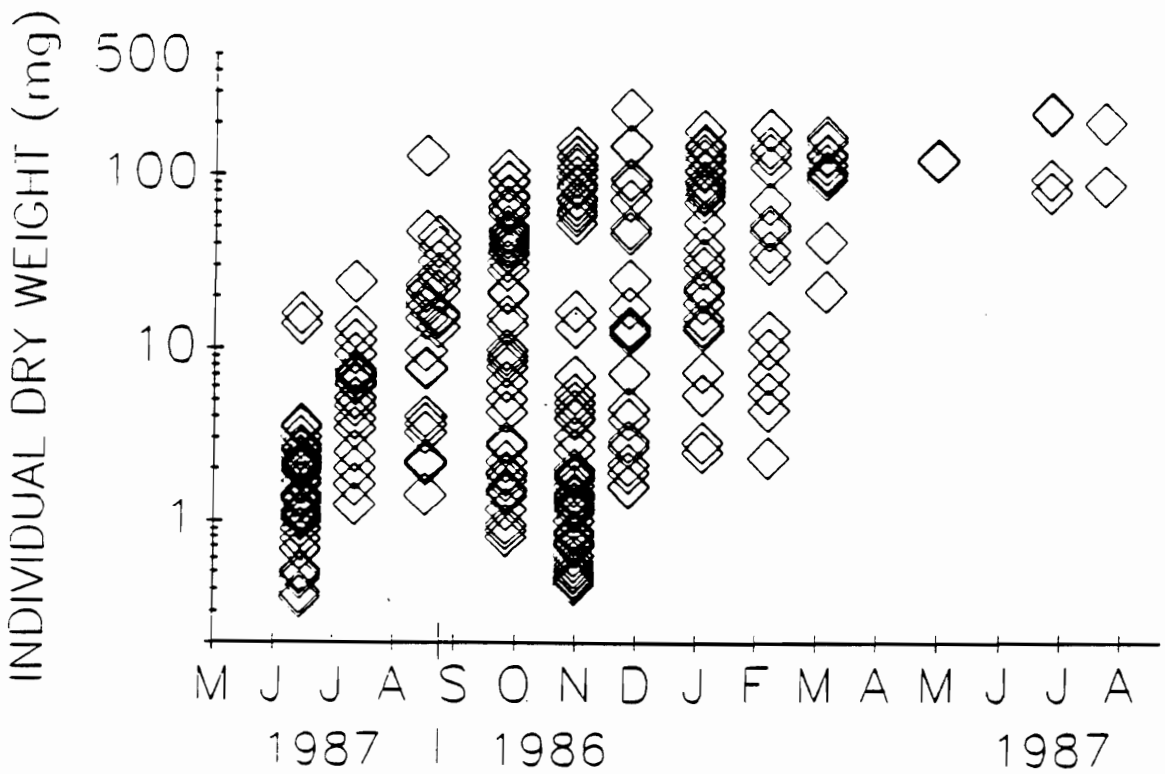


Figure 12. Annual distribution of individual *Tipula abdominalis* dry weight measurements in all streams. Due to the presence of 2 year classes, small individuals from June through August 1987 were placed at the beginning of the figure.

Table 6. Mean annual density, mean individual weight (MIW), and mean biomass of *Tipula abdominalis* in streams (means not significantly different).

	Density (number/m²)	MIW (mg)	Biomass (mg/m²)
disturbed forest streams			
Stream 1	23.55	63.22	1156.35
Stream 2	10.76	62.21	1138.63
Stream 3	8.71	50.57	825.02
reference forest streams			
Stream 4	15.11	49.10	1183.57
Stream 5	10.24	32.43	909.60
Stream 6	7.43	35.02	859.79
mean of streams			
disturbed forest	14.34	58.66	1040.00
reference forest	10.93	38.85	984.32

cluded in this study had morphology and case architecture characteristic of *P. gentilis* (Flint, 1960; Mackay, 1972; Wiggins, 1977; Huryn & Wallace, 1988). Early instar larvae constructed cases of leaf disks arranged in triangular cross-section. Intermediate instars constructed transitional cases in which the posterior portion was mostly leaf disks and the anterior portion small gravel. Fifth instar larvae had gravel cases that were circular in cross-section.

Early instar *Pycnopsyche* first appeared in streams of both forests in late September. Peak larval density occurred in November in disturbed streams and February in reference streams. Mean density in disturbed streams decreased significantly from January to February (Figure 13). In reference streams, *Pycnopsyche* was present in November at very low density, appeared to increase somewhat in January, and declined through May.

Mean individual weight (MIW) of *Pycnopsyche* in disturbed streams increased gradually from October through January but decreased significantly in February. Decreased MIW in February followed an influx of small individuals, apparently the result of a second major recruitment as shown by size/frequency distribution (Figure 14). MIW increased significantly in reference streams in February but decreased significantly in March (Figure 13). Variability in MIW of reference stream populations in January through March coincided with variability in population density measurements, so that MIW measurements were lowest when sample size was small. In addition, variability in density and MIW in all streams appeared to be the result of an extended recruitment period, with peak recruitment occurring in September and January.

The timing of peak density of *Pycnopsyche* was different for disturbed and reference streams, and there were differences in the relative proportion of first or second recruitment period larvae in streams within each forest. Most early instar larvae in disturbed streams were present in late September, whereas most early instar larvae in reference streams were present in January. Individuals originating from the first recruitment period developed rapidly, reaching fifth instar by late November. Individuals from the second recruitment developed less rapidly, reaching fifth instar by May. Individuals collected in July and August were pupae or fifth instar larvae. Patterns of *Pycnopsyche* peak recruitment between streams were similar

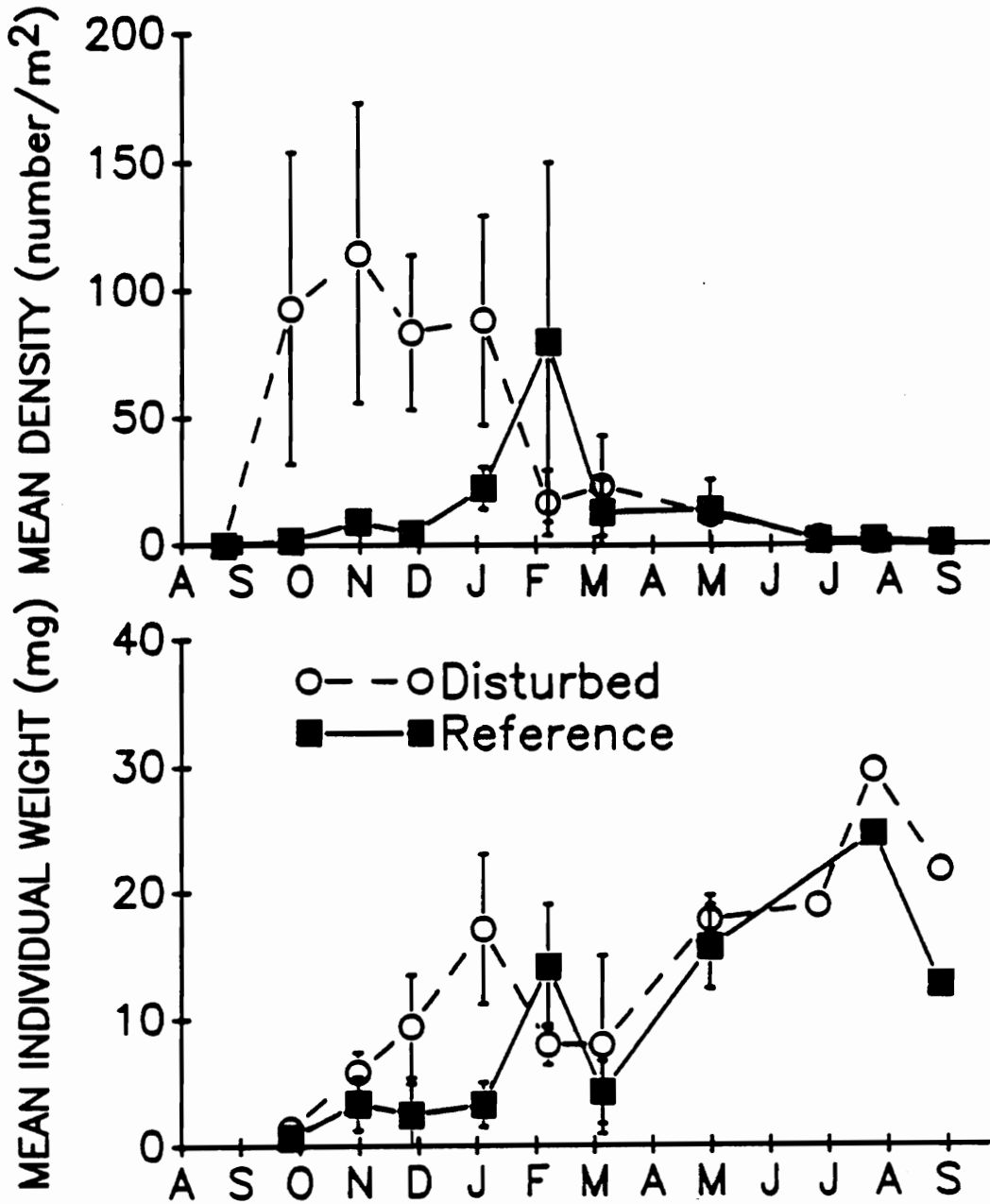


Figure 13. Mean density and mean individual weight (and 1 S.D.) of *Pycnopsyche* in disturbed and reference forest streams.

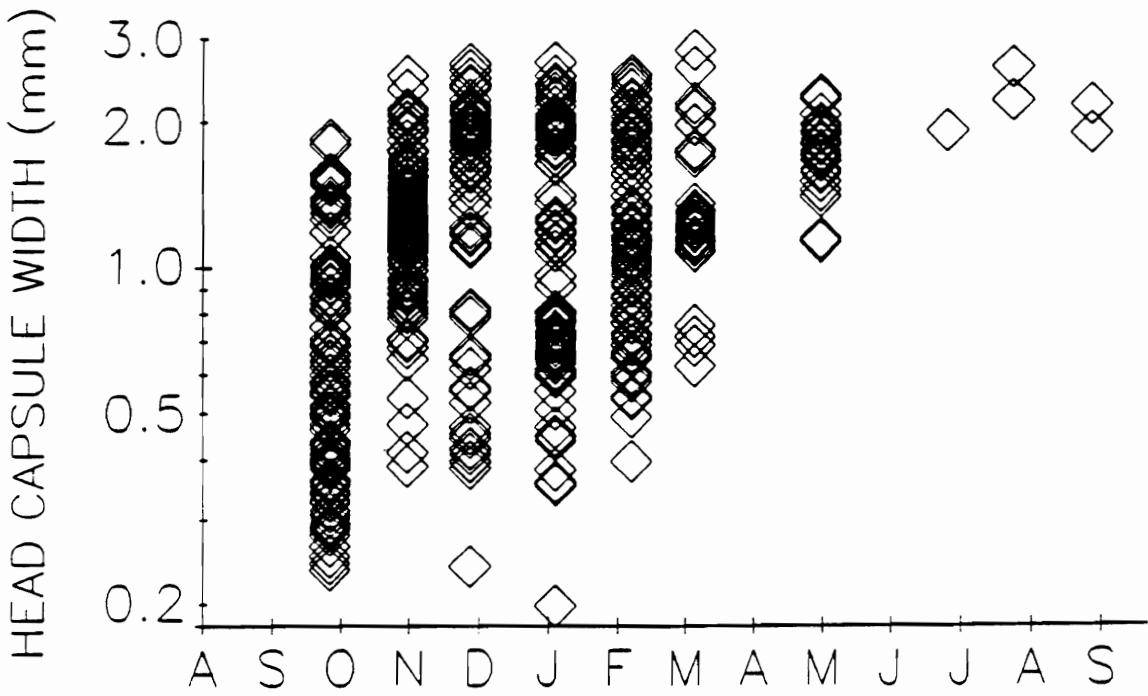


Figure 14. Annual distribution of individual *Pycnopsyche* headcapsule measurements in all streams.

Table 7. Mean annual density, mean individual weight (MIW), and mean biomass of *Pycnopsyche* in streams (astriks indicate significant differences between means: * $p < 0.10$, ** $p < 0.05$).

	Density (number/m ²)	MIW (mg)	Biomass (mg/m ²)
disturbed forest streams			
Stream 1	50.96	11.17	810.94
Stream 2	28.43	7.99	550.80
Stream 3	39.69	10.75	835.19
reference forest streams			
Stream 4	5.89	7.81	188.12
Stream 5	21.51	7.40	589.74
Stream 6	13.57	8.01	428.96
mean of streams			
disturbed forest	39.69**	9.97*	732.31**
reference forest	13.66	7.74	402.27

to that observed for *T. abdominalis*. Unlike *T. abdominalis*, however, *Pycnopsyche* apparently emerged from all streams over the same time interval.

Mean annual density, MIW, and biomass of *Pycnopsyche* were significantly greater in disturbed versus reference streams (Table 7). Mean annual density was 3 times greater, MIW was 22% greater, and biomass was 45% greater in disturbed streams.

Shredder production

Total production of the 3 dominant shredders was significantly greater in disturbed than in reference streams (Table 8). The majority of shredder production in all streams was by *T. abdominalis*, however, *T. abdominalis* production was not significantly different between stream types. Greater total shredder production in disturbed versus reference streams was due to significantly greater production by *Pycnopsyche* and *T. maria*, and somewhat greater production by *T. abdominalis*.

T. maria was the most abundant shredder, but because of relatively low individual mass it accounted for only 7-8% of total shredder production in streams. Production by Cohorts I and II was significantly greater in disturbed than in reference streams, and total production was 2 times greater in disturbed streams. This difference was the result of significantly greater density and generally greater mean individual weight in disturbed streams (Table 5). Peak density of Cohort I was greatest in reference streams, but survivorship of early instar larvae was much better in disturbed streams (Figure 7). Greater Cohort I survivorship in disturbed versus reference streams promoted greater biomass growth in disturbed streams. Cohort II density was significantly higher in disturbed versus reference streams prior to leaf fall. Highest Cohort II mortality in disturbed streams occurred in October and November. Greater mean individual weight suggested somewhat better growth in disturbed versus ref-

Table 8. Mean annual production (mg/m²/yr) by shredders in disturbed and reference forest streams (astriks indicate significant differences between means: *p < 0.10, **p < 0.05).

	<i>Tallaperla maria</i>		<i>Tipula abdominalis</i>	<i>Pycnopsyche sp.</i>	total shredder production	
	Cohort I	Cohort II				total
disturbed forest streams						
Stream 1	84	255	339	4098	3577	8014
Stream 2	112	389	501	2982	2178	5661
Stream 3	130	536	666	2252	3125	6043
reference forest streams						
Stream 4	67	152	219	3355	272	3856
Stream 5	37	252	289	1578	2123	3990
Stream 6	59	127	186	1143	1118	2447
mean of streams						
Disturbed	109**	393*	502*	3111	2960*	6573**
Reference	54	177	231	2025	1171	3428

erence streams, but higher production can be attributed mostly to better survivorship in disturbed streams.

Production by *T. abdominalis* appeared to be 54% greater in disturbed versus reference streams, but mean production in streams between forest types was not significantly different ($p=0.28$). Growth and survivorship of *T. abdominalis* appeared to follow similar patterns in disturbed and reference streams, even though pupation, emergence, and subsequent peak larval density in reference streams preceded disturbed streams by about 4 months (Figure 11). Production by *T. abdominalis* was 6.2 and 8.8 times greater than total production of *T. maria* in disturbed and reference streams, respectively (Table 8). Production by *T. abdominalis* was 1.07 and 1.80 times greater than total production of *Pycnopsyche* in disturbed and reference streams, respectively. *T. abdominalis* production accounted for 47% of total shredder production in disturbed streams, and 60% of total shredder production in reference streams.

Pycnopsyche production was significantly greater in disturbed streams due to significantly greater density and mean individual weight. Production by *Pycnopsyche* accounted for 45% of total shredder production in disturbed streams and 33% of total shredder production in reference streams.

Shredder mean production/biomass ratios ($\overline{P/B}$) ranged from 2.6 to 5.7 for shredders in each forest type (Table 9). Disturbed streams produced the highest $\overline{P/B}$ for each shredder species and for all shredders combined. Production/biomass ratios (P/B) for shredders in each stream ranged from 1.3 to 6.9. Annual mean biomass of all shredders in reference streams was 77% of shredder biomass in disturbed streams.

Table 9. Annual production/biomass ratios, and mean annual shredder biomass (mg/m²).

	<i>Tallaperla maria</i>		<i>Tipula abdominalis Pycnopsyche sp.</i>			shredder biomass
	Cohort I	Cohort II	total			
disturbed forest streams						
Stream 1	4.7	7.5	6.5	3.5	4.4	2019.1
Stream 2	4.3	5.7	5.3	2.6	4.0	1783.8
Stream 3	5.6	5.2	5.2	2.7	3.7	1787.3
reference forest streams						
Stream 4	4.2	4.9	4.6	2.8	1.4	1418.9
Stream 5	4.4	7.6	6.9	1.7	3.6	1541.0
Stream 6	5.5	4.0	4.3	1.3	2.6	1331.6
mean of streams						
Disturbed	4.9	5.7	5.5	3.0	4.0	1863.4
Reference	4.6	5.5	5.3	2.6	2.8	1430.5

Shredder and leaf biomass correlations

Correlations between shredder and leaf biomass were performed to determine whether shredder biomass could be predicted from quantity and quality of leaf biomass. There was a significant positive relationship between total leaf biomass and total shredder biomass in 330 samples (Table 10). Biomass of each of the 3 dominant shredders correlated significantly with total leaf biomass, and total shredder biomass correlated significantly with leaf biomass in each of 3 leaf decay categories. The relationships were not close enough to provide predictive power ($r < 0.30$), thus less than 10% of the variability associated with shredder biomass could be explained by differences in leaf biomass in 330 samples.

Despite the significant positive relationship between total leaf biomass and total shredder biomass, some relationships between specific shredders and certain leaf processing categories were not significant. *T. maria* biomass was significantly correlated with biomass of slow and medium-processing leaf species but not with fast-processing leaf species. *T. abdominalis* biomass was significantly correlated only with slow-processing leaf biomass. *Pycnopsyche* biomass was significantly correlated with medium and fast-processing leaf biomass but not with slow-processing leaf biomass.

Total shredder biomass was significantly correlated with biomass of 6 of the 9 most abundant leaf taxa on an annual basis, but correlation coefficients were low (Table 11). Red oak, black birch, and biomass of mixed fast-processing leaf species did not correlate significantly with total shredder biomass. Shredders varied considerably in their significant relationships with various leaf taxa. Red oak and black birch biomass did not correlate well with biomass of any of the 3 dominant shredders, but the relationship between mixed fast-processing leaf biomass and *Pycnopsyche* biomass was significant. Biomass of *T. abdominalis* and *T. maria* correlated significantly with rhododendron and white oak biomass, but *Pycnopsyche* biomass did not. Biomass of *Pycnopsyche* correlated significantly with

biomass of red maple and dogwood. Biomass of *T. maria* correlated significantly with red maple biomass, and *T. abdominalis* biomass correlated significantly with beech.

Monthly leaf and *Pycnopsyche* biomass correlation coefficients in the disturbed forest were much greater than annual coefficients calculated for both forests (Table 12). Correlations with disturbed forest leaf taxa during certain months provided adequate information to explain over 80% of the variation in *Pycnopsyche* biomass. Significant correlations with dogwood and other fast-processing species occurred early in the seasonal cycle of leaf processing, during a time when mostly early instar *Pycnopsyche* were present. Fast processing leaves had disappeared by January, and *Pycnopsyche* correlated well medium and slow-processing species from January through May. Even though rhododendron was the most abundant leaf material in disturbed forest streams, *Pycnopsyche* biomass did not correlate significantly with rhododendron except in July when mostly pupae were present. *Pycnopsyche* exhibited few significant correlations with leaf species in the reference forest (not shown).

Unlike *Pycnopsyche*, correlations of *T. abdominalis* and *T. maria* biomass with fast processing species were rarely significant in either forest (not shown). In addition, both species exhibited significant correlations with rhododendron on several dates in both forests, and annual biomass of both species correlated significantly with rhododendron biomass in the disturbed forest. *T. maria* biomass correlated well with most leaf taxa except fast processing species, and there was no monthly trend toward fast to slow processing species as seen in *Pycnopsyche*. Significant correlations of *T. abdominalis* biomass with various leaf taxa were scattered across monthly dates within each forest type and no patterns were evident.

Table 10. Pearson correlation coefficients (top number) and probabilities (bottom number) for leaf and shredder biomass in all samples (N=330)(significant relationships *p<0.10, **p<0.05, ***p<0.01).

leaf taxa	<i>Tallaperla maria</i>	<i>Tipula abdominalis</i>	<i>Pycnopsyche sp.</i>	Combined shredders
Total leaf biomass	0.17425 0.0015***	0.17683 0.0013***	0.12343 0.02490**	0.22099 0.0001***
Slow-processing species	0.14176 0.0099***	0.21459 0.0001***	-0.00090 0.9869	0.17500 0.0014***
Medium-processing species	0.17035 0.0019***	0.07207 0.1915	0.19434 0.0004***	0.18240 0.0009***
Fast-processing species	0.02808 0.6112	-0.02137 0.6989	0.25493 0.0001***	0.13263 0.0159**

Table 11. Pearson correlation coefficients (top number) and probabilities (bottom number) for leaf and shredder biomass in all samples (N=330)(significant relationships: *p<0.10, **p<0.05, ***p<0.01).

leaf taxa	<i>Tallaperla maria</i>	<i>Tipula abdominalis</i>	<i>Pycnopsyche sp.</i>	Combined shredders
Rhododendron	0.13125 0.0171**	0.18759 0.0006***	0.00230 0.9668	0.15548 0.0046***
Red oaks	0.07524 0.1727	0.02715 0.6231	0.00299 0.9569	0.02962 0.5919
White oaks	0.10038 0.0686*	0.16930 0.0020***	-0.00777 0.8882	0.13289 0.0157**
Red maple	0.23851 0.0001***	0.02279 0.6800	0.31245 0.0001***	0.21971 0.0001***
Black birch	0.09308 0.0914*	0.04096 0.4584	0.07321 0.1846	0.08198 0.1373
Dogwood	0.04595 0.4054	-0.00137 0.9802	0.20461 0.0002***	0.12065 0.0284**
American beech	-0.00113 0.9838	0.12667 0.0214**	0.01438 0.7947	0.10340 0.0606*
Yellow poplar	0.06506 0.2386	0.10038 0.0686*	0.07916 0.1513	0.12729 0.0207**
Other fast species*	-0.00111 0.9839	-0.04933 0.3717	0.21774 0.0001***	0.08741 0.1130

*includes: sassafras, basswood, greenbrier, blackberry, grape, shrubs.

Table 12. Pearson correlation coefficients and probability of significant relationships (* $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$) for leaf and *Pycnopsyche* biomass in samples from disturbed forest streams (monthly $N = 15$, annual $N = 165$).

leaf taxa	NOV	DEC	JAN	FEB	MAR	MAY	JUN	JUL	AUG	Annually
Rhododendron	-0.27	0.16	-0.37	0.05	-0.30	-0.15	0.05	0.72 ^{***}	-0.12	0.02
Red oaks	-0.24	-0.13	0.65 ^{***}	-0.09	-0.13	0.88 ^{***}	0.0	0.0	-0.07	0.17 ^{**}
White oaks	-0.33	-0.13	0.76 ^{***}	0.63 ^{**}	0.04	0.91 ^{***}	-0.09	0.39	0.12	0.41 ^{***}
Beech	0.56 ^{**}	0.18	0.0	-0.22	-0.11	0.94 ^{***}	0.0	0.0	0.0	0.19 ^{**}
Red maple	-0.08	0.48 [*]	0.49 ^{**}	0.23	0.78 ^{***}	0.87 ^{***}	-0.14	-0.07	0.92 ^{***}	0.46 ^{***}
Black birch	0.12	0.0	-0.19	-0.20	0.60	0.87 ^{***}	-0.14	-0.10	-0.09	0.11
Yellow poplar	0.08	0.17	0.0	0.06	0.0	0.83 ^{***}	0.0	0.10	-0.07	0.15 [*]
Dogwood	0.67 ^{***}	0.28	-0.08	0.14	0.0	0.0	-0.09	-0.11	-0.16	0.25 ^{***}
Other fast species	0.46 [*]	0.55 ^{**}	0.32	-0.18	0.48 [*]	-0.02	-0.12	0.0	-0.11	0.26 ^{***}

^{*}includes: sassafras, basswood, greenbrier, blackberry, grape, shrubs.

Shredder growth studies

Two-week growth studies of *T. maria* and *T. abdominalis* were conducted on treatments consisting of various combinations of 7 leaf species, 6 conditioning time intervals, and 4 stream sites (Table 2, page 18). Growth treatments were compared based on mean Relative Growth Rate (RGR) of each shredder species (Figures 15, 16, and 17).

Growth and survivorship of shredders

Data for each leaf treatment over various conditioning time intervals were pooled for analysis of percent survivorship (Table 13). Percent survivorship of *T. maria* and *T. abdominalis* in 2 week growth studies ranged from about 73 to 100%. Survivorship of both species was relatively low on yellow poplar conditioned in a disturbed stream and rhododendron conditioned in a pasture-to-forest successional stream. *T. abdominalis* survivorship was notably low on chestnut oak in a reference stream. Survivorship of *T. maria* was relatively low on blackberry conditioned in a disturbed stream, red maple in a grass-to-forest stream, and yellow poplar in a reference stream.

Only middle instar larvae were used in growth studies, and individual growth rates were not affected by stage of development. The possibility of insect size affecting RGR was tested for each species by fitting regressions of individual RGR versus Mean Individual Weight (MIW). Regressions of MIW on RGR were not significantly different from zero, indicating that individual growth rates were independent of individual mass of the organisms used in growth studies. RGR of *T. abdominalis* was nearly twice as high as RGR of *T. maria* as would be expected considering differences in the voltinism of the 2 species.

Growth of *T. maria* was affected mostly by leaf conditioning, and site of exposure had little effect on RGR. *T. maria* growth rates were not significantly different for different leaf species, and RGR did not follow a pattern of faster growth on early versus late successional leaf species (Figure 15). *T. maria* grew well on all leaf species tested.

Good *T. maria* growth rates were often accompanied by high mortality, but many of the leaf treatments provided good growth and good survivorship. Overall, growth was best on blackberry conditioned in the disturbed stream (Table 16), but survivorship on blackberry ranked twelfth of 14 treatments (Table 13). *T. maria* growth was consistently higher on rhododendron conditioned in a grass-to-forest versus a mature forest stream, but survivorship was 20% lower on rhododendron from the grass-to-forest stream. Growth rates were generally high on yellow poplar conditioned in a disturbed forest stream, but survivorship was only 73%. At the other end of the scale, negative growth of *T. maria* fed black locust conditioned for 144 days in a disturbed forest stream was accompanied by 100% survivorship. Fast growth of *T. maria* fed yellow poplar conditioned 117 days in a grass-to-forest stream and a coppice-forest stream was accompanied by good survivorship. Dogwood conditioned 54 days, and black locust conditioned 86 days in the disturbed stream provided good growth and high survivorship.

Mean RGR of *T. abdominalis* was good in all treatments, and there were few significant differences in mean RGR among sites, leaf species, or conditioning intervals. Growth rates were consistently high on chestnut oak and blackberry. Growth rates were fast on yellow poplar conditioned for 19 days (Figure 16). For other leaf species, growth rates generally improved with longer conditioning intervals. RGR of *T. abdominalis* on dogwood and black locust conditioned in a grass-to-forest stream increased significantly from December to March. Slow decomposing species provided consistently good growth rates of *T. abdominalis* after 54, 117, and 248 days of conditioning (Figure 17).

Over the course of the study Survivorship of *T. abdominalis* was only 81% on chestnut oak (Table 13), but growth was better on chestnut oak than any other species (Table 16). *T. abdominalis* survivorship was lowest on rhododendron conditioned in the grass-to-forest stream, a leaf treatment that also produced low survivorship of *T. maria*. Survivorship of *T. abdominalis* was > 88% on all other leaf treatments.

Table 13. Percent survivorship of shredders fed leaf treatments in 2 week laboratory studies (initial N = sample size; N surv. = number of survivors).

Leaf species	Forest type	<i>Tallaperla maria</i>			<i>Tipula abdominalis</i>		
		initial N	N surv.	Percent survivorship	initial N	N surv.	Percent survivorship
Yellow poplar	grass-to-forest	26	25	96.2	26	25	96.2
Yellow poplar	disturbed forest	26	19	73.1	26	23	88.5
Yellow poplar	coppice-forest	26	25	96.2	26	26	100.0
Yellow poplar	reference forest	19	16	84.2	19	19	100.0
Dogwood	grass-to-forest	19	18	94.7	19	17	89.5
Dogwood	reference forest	19	18	94.7	19	18	94.7
Red maple	grass-to-forest	19	16	84.2	19	18	94.7
Red maple	reference forest	12	12	100.0	12	11	91.7
Blackberry	disturbed forest	12	10	83.3	13	13	100.0
Black locust	grass-to-forest	19	18	94.7	19	18	94.7
Black locust	disturbed forest	26	24	92.3	26	23	88.5
Chestnut oak	reference forest	14	13	92.9	21	17	81.0
Rhododendron	grass-to-forest	14	11	78.6	14	10	71.4
Rhododendron	reference forest	14	14	100.0	14	14	100.0

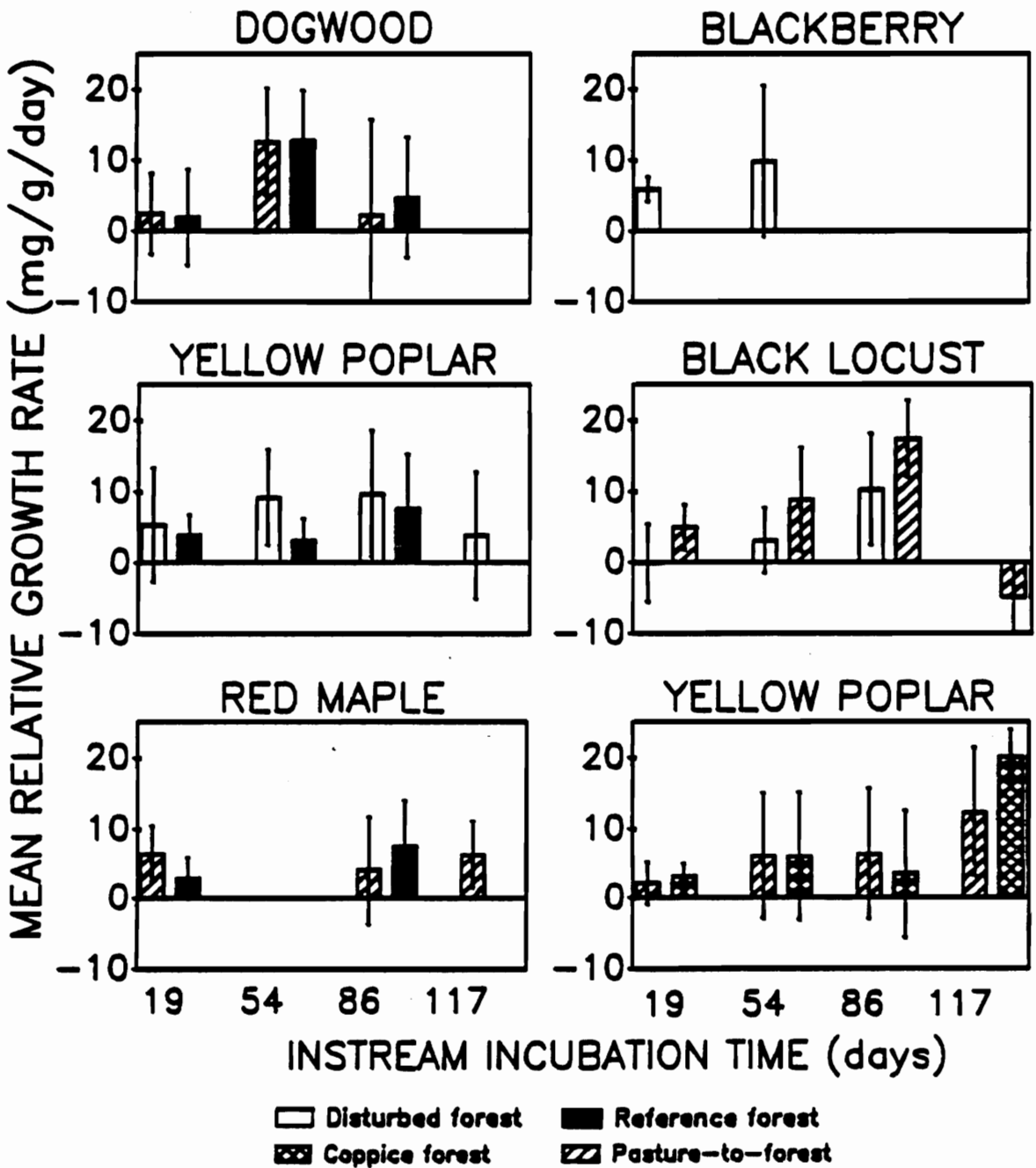


Figure 15. Mean relative growth rates (and 1 S.D.) of *Tallaperla maria*.

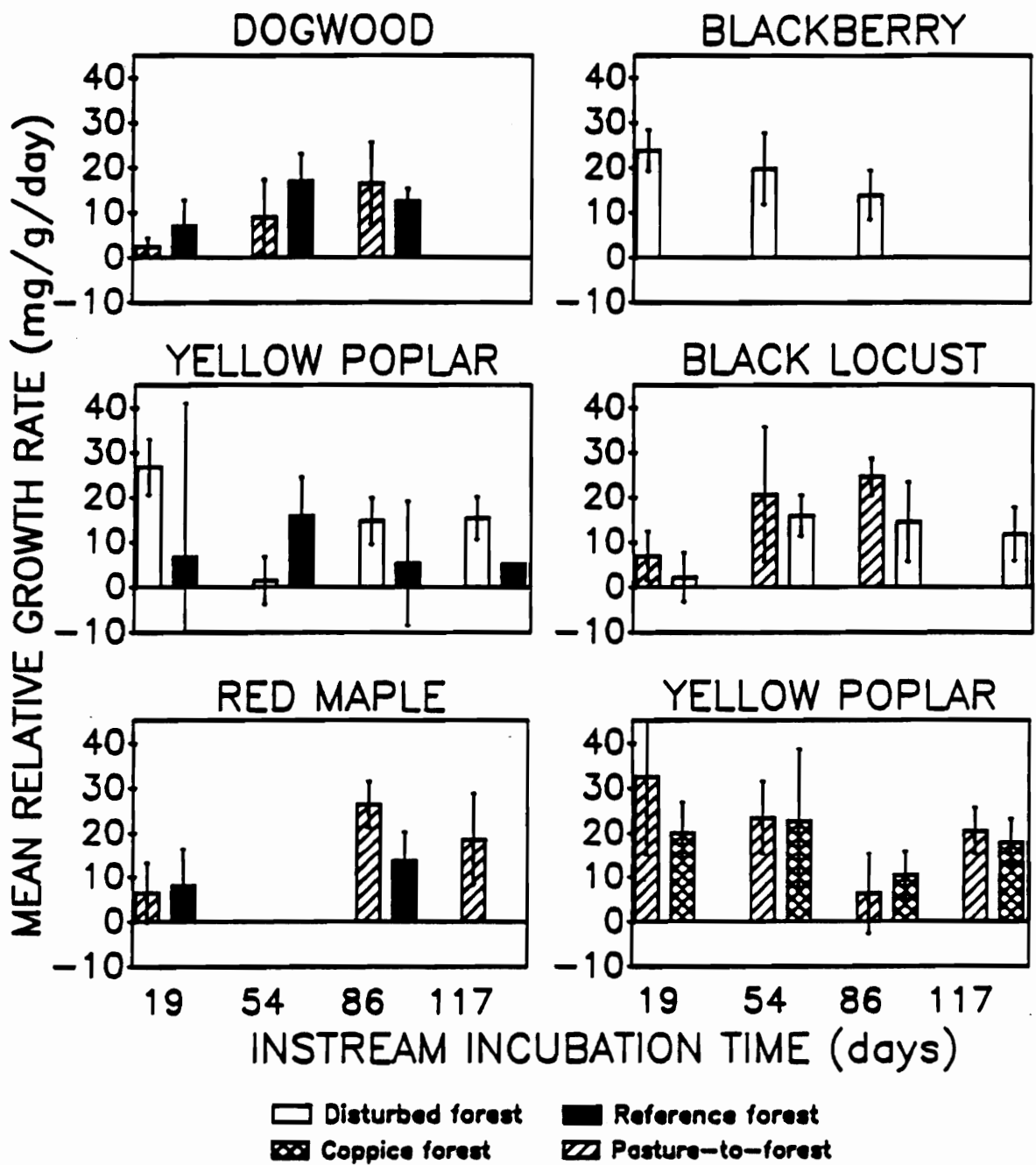


Figure 16. Mean relative growth rates (and 1 S.D.) of *Tipula abdominalis*.

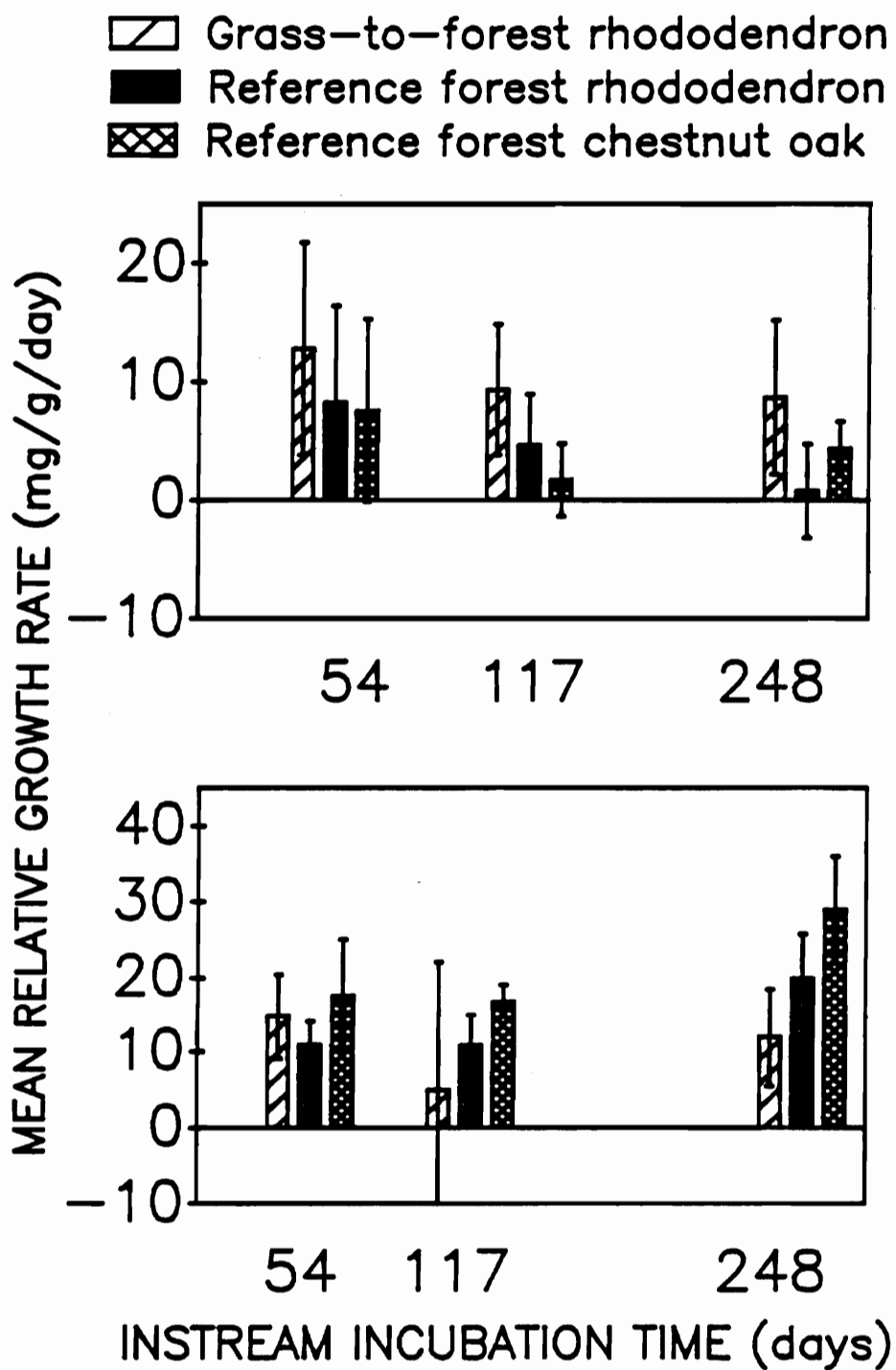


Figure 17. Mean relative growth rates (and 1 S.D.) of *Tallaperia maria* (top) and *Tipula abdominalis* (bottom) on slow-processing leaf species.

Growth analysis

Further growth analyses were conducted by pooling data to test for leaf treatment effects in an overall model. The experimental design for shredder growth on yellow poplar was balanced except 1 missing cell. Mean RGR of each shredder species on yellow poplar was compared at 4 sites over 4 conditioning time intervals using 2-way ANOVA. The variables conditioning time, site of exposure, and interaction of site*conditioning did not significantly effect RGR of either shredder species on yellow poplar.

For leaf species other than yellow poplar there were insufficient data to test for 2 and 3-way interactions between leaf species, site, and conditioning. One-way ANOVA and Least Squares Means procedures were used to test for the effect of site on relative growth rate of shredders (Table 14). The results of these tests for site of exposure should be interpreted cautiously because only a limited number of leaf species were used to represent each site. In coppice WS 13, for example, RGR was measured on the dominant species yellow poplar, whereas the grass-to-forest stream was represented by 5 leaf species. Rhododendron, an important species in all streams, was exposed at only 2 of 4 sites. RGR of both shredders was not significantly affected by site of exposure in the overall model.

Data from all leaf species on all watersheds were pooled to analyze for effects of conditioning time interval on RGR (Table 15). Data for conditioning were unbalanced in terms of leaf species and exposure site combinations. For example, leaf treatments at 19 and 54 days consisted of a variety of leaf species and sites, but leaf treatments conditioned for 248 days were rhododendron in a grass-to-forest stream and rhododendron and chestnut oak in a reference forest stream. Leaf material used in growth treatments at various conditioning intervals was representative of the leaf material available in streams, but slow-processing leaf species were represented in only 2 of 4 streams. The 2 shredder species responded differently to conditioning times. Relative growth rates of *T. maria* were significantly higher on leaf material conditioned 54, 86, and 117 days than leaf material conditioned 19 or 248 days, whereas RGR of *T. abdominalis* was significantly faster on leaf material conditioned 248 days.

Table 14. Mean Relative Growth Rate (RGR mg/g/day) of shredders fed leaves conditioned in 4 Coweeta watersheds (RGRs with same letter not significantly different, $p > 0.05$).

<i>Tallaperla maria</i>			<i>Tipula abdominalis</i>		
Forest type	RGR		Forest type	RGR	
coppice	8.08	A	coppice	17.6	A
disturbed	7.84	A	grass-to-forest	15.8	A
grass-to-forest	6.87	A	reference	15.6	A
reference	5.10	A	disturbed	13.9	A

The effect of leaf species on shredder RGR was tested by pooling data over site and conditioning intervals. Pooling of data was somewhat confounded because species such as dogwood and blackberry were available through only 2 to 3 months of conditioning because of their rapid decay rates. In contrast, growth studies on slow-processing species such as rhododendron and chestnut oak were conducted on leaves that had been conditioned for 54, 117, and 248 days. However, as noted above, leaf species were representative of the leaf material available to shredders in streams at various time intervals. Growth of *T. maria* in the overall data set was greatest for blackberry and lowest for chestnut oak, but differences in RGR were not significant among leaf species (Table 16). Growth of *T. abdominalis* was significantly greater when fed chestnut oak or blackberry versus rhododendron or dogwood. The expected trend of best growth on early successional leaf species and least growth on late successional leaf species was not obtained.

Although there were few significant differences in shredder growth rates on various leaf treatments, there did appear to be two patterns of growth for the two shredders. *T. maria* appeared to grow well on leaf material that had been conditioned in streams for 54 to 117 days. *T. abdominalis* grew best on slow-processing leaf material that was conditioned in streams for 248 days. Of the leaves conditioned in a grass-to-forest stream, *T. maria* grew best on rhododendron and dogwood conditioned 54 days, black locust conditioned 117 days, and yellow poplar conditioned 144 days. *T. abdominalis* grew best on yellow poplar and blackberry conditioned 54 days, dogwood, black locust, and red maple conditioned 86 and 117 days, and chestnut oak and rhododendron conditioned 254 days. Growth rates of *T. maria* on yellow poplar in a grass-to-forest stream increased somewhat with continued conditioning, while growth of *T. abdominalis* decreased over the exposure interval. *T. maria* growth on slow-processing leaf species was good initially, but decreased with continued conditioning. Growth of *T. abdominalis* on slow-processing leaf species increased with increased conditioning. Each leaf species appeared to have a different conditioning interval when it provided the best growth rate for each shredder species.

Table 15. Mean Relative Growth Rate (RGR mg/g/day) of shredders fed leaves placed in streams November 20, and conditioned for days shown (RGRs with same letter not significantly different, $p > 0.05$).

<i>Tallaperla maria</i>			<i>Tipula abdominalis</i>		
days	RGR		days	RGR	
19	3.41	B	19	15.4	A
54	8.47	A	54	15.2	A
86	7.47	A	86	15.1	A
117	6.92	A	117	14.5	A
248	3.28	B	248	21.9	B

Table 16. Mean Relative Growth Rate (RGR mg/g/day) of shredders fed 7 leaf species (RGRs with same letter not significantly different, $p > 0.05$).

<i>Tallaperla maria</i>			<i>Tipula abdominalis</i>		
Leaf species	RGR		Leaf species	RGR	
Blackberry	8.65	A	Chestnut oak	19.7	A
Yellow poplar	7.21	A	Blackberry	18.9	A
Rhododendron	6.67	A	Yellow poplar	17.1	AB
Black locust	6.51	A	Red maple	15.8	AB
Dogwood	6.46	A	Black locust	14.5	AB
Red maple	5.63	A	Rhododendron	12.3	B
Chestnut oak	4.47	A	Dogwood	11.4	B

Discussion

This is the first study of secondary production of stream insects that used a replicated experimental design, thus providing legitimate mean values for comparing the effect of a forest disturbance on shredder production in streams (Hurlburt, 1984; Resh, *et al.*, 1988). Significantly greater production in disturbed versus reference forest streams was unexpected and has important implications for the influence of forest secondary succession on trophic dynamics of stream ecosystems. The ensuing discussion provides an account of differences in leaf quality and shredder population dynamics between disturbed and reference forest streams.

Abiotic influences of stream basins

Basin morphology is a critical factor when selecting streams for comparative studies (Resh, *et al.*, 1988), because morphological aspects of stream basins and the resulting hydrologic regimes are primary determinants of community structure and function (Minshall,

et al., 1983; Statzner, *et al.*, 1988). Morphological attributes of stream basins were not significantly different between disturbed and reference forest streams.

Shredder production within streams has been shown to be dependent on substrate size (Huryñ & Wallace, 1987). Random sampling of streams in my study resulted in a variety of substrata being represented. Similarities in basin morphometry between forest types, and random sampling within each stream precluded identifying substratum related influences on shredder life history and production. Significant physical differences between forest types included thermal regime, basin orientation, and forest canopy composition.

Stream temperature

Studies have shown that seasonal temperature profiles are more extreme (colder in winter, warmer in summer) following forest disturbance (Webster, *et al.*, 1983; Holtby, 1988). However, the seasonal and day-to-day stream temperature fluctuations recorded in this study were more extreme in the reference than in the disturbed streams. Differences in seasonal temperature profiles in disturbed versus reference streams could not be explained by differences in forest canopy or basin orientation. Eleven years of forest regrowth apparently shaded disturbed forest streams adequately to prevent extreme temperature fluctuations. Less extreme temperature fluctuations in disturbed streams may have been the result of geomorphological processes such as groundwater retention time. Longer groundwater retention time in disturbed streams may have buffered stream temperature so that seasonal and day-to-day temperature profiles more closely approximated mean annual temperature in disturbed versus reference streams.

Factors affecting shredder life history

Temperature differences between disturbed and reference streams apparently affected the chronology of shredder life history events. Differences in the timing of peak larval density suggested differential egg hatching periods between stream types, but emergence did not appear to be affected by stream type. Peak density of *T. maria* appeared to occur 1 month earlier and peak density of *Pycnopsyche* appeared to occur 3 or 4 months earlier in disturbed versus reference streams. In contrast, peak density of *T. abdominalis* occurred 4 months later in disturbed versus reference streams, and pupation was also delayed 4 months in disturbed streams. In terms of the chronology of major life cycle events, each shredder species appeared to respond differently to differences in stream thermal regimes.

Temperature has been shown to affect egg development time, hatching synchrony, and hatching success of aquatic insects (Brittian, 1977; Brittian & Mutch, 1984; Brittian, *et al.*, 1984; Lillehammer, 1985; Brittian & Lillehammer, 1987; Elliott, 1988). An inverse relationship between egg incubation period and water temperature exists for many aquatic insects that are closely related to those studied here including stoneflies (Brittian, 1978; Elliott, 1984; Lillehammer, 1986; Brittian & Lillehammer, 1987; Elliott, 1987), limnephilid caddisflies (Berte' & Prichard, 1986), and crane flies (reviewed by Prichard, 1983). The relationship between stream temperature and egg incubation period may partially explain variations in shredder life history in disturbed versus reference streams.

Variations in *Tallaperla maria* life history

For *T. maria* differences between disturbed and reference streams included the timing of peak density, mean individual weight, and survivorship. Differences in the timing of peak density may have been temperature related, but differences in growth and survivorship did not appear to be temperature related. Although peak density of *T. maria* occurred only 1

month earlier in disturbed streams, there were significantly more early instar larvae in disturbed versus reference streams 2 months prior to the occurrence of peak density. The time frame during which peak density occurred was similar to that reported for *T. maria* in 2 other Coweeta watersheds (O'Hop, *et al.*, 1984) and Walker Branch, Tennessee (Elwood & Cushman, 1975). Recruitment of *T. maria* in disturbed streams appeared to precede recruitment in reference streams by 2-3 months.

Reference streams had 2-3°C warmer mean daily temperatures than disturbed streams during the period of *T. maria* egg diapause. The inverse relationship between stream temperature and egg hatching period typical of many stoneflies (Brittian, 1978; Elliott, 1984; Lillehammer, 1986; Brittian & Lillehammer, 1987; Elliott, 1987) was of little value in predicting *T. maria* peak density. The leaf-shredding stonefly *Nemoura cinerea* (Retzius) has an egg diapause similar to that of *T. maria*, and the relationship between 50% egg hatching of *N. cinerea* and degree-day accumulation is best described by a curvilinear model (Brittian & Lillehammer, 1987). In the laboratory, 50% egg hatching of *N. cinerea* required <300 degree-days at 12° C, 320 degree-days at 16°C, and 380 degree-days at 20°C. Assuming that the curvilinear model of degree-day accumulation with water temperature for egg hatching of *N. cinerea* may also apply for *T. maria*, greater degree-day accumulation accompanied by higher mean daily stream temperature may have resulted in delayed egg hatching in reference versus disturbed streams.

Although recruitment of *T. maria* in disturbed streams appeared to precede recruitment in reference streams by 2-3 months, peak density was not significantly different, thus egg hatching success was apparently similar in all streams. Similarly, no relationship was found between water temperature and egg hatching success of *N. cinerea* (Brittian & Lillehammer, 1987). Temperature differences did not appear to result in differences in emergence of adult *T. maria* between disturbed and reference streams. Temperature has been shown to affect emergence chronology of 2 stoneflies (Lillehammer, 1985), but temperature differences were more extreme than those observed in the present study. Differences in *T. maria* recruitment

between disturbed and reference streams may have been temperature related, but temperature did not appear to affect egg hatching success or the adult emergence period.

On an annual basis, *T. maria* Cohort I mean individual weight (MIW) was significantly greater in disturbed versus reference streams. Greatest monthly differences in *T. maria* MIW between stream types occurred during the summer. In the summer, Cohort I individuals were larger in disturbed streams, but mean daily temperature and degree-day accumulation were lower in disturbed versus reference streams. Temperature may have been a factor resulting in larger Cohort II individuals during the winter in disturbed streams, but Cohort II MIW and the pre-emergence weight of larvae were not significantly different between disturbed and reference streams. Temperature differences between disturbed and reference forest streams did not appear to affect growth of *T. maria*.

Survivorship of *T. maria* differed considerably between disturbed and reference streams. There was little evidence that survivorship was temperature related however, temperature effects were not closely examined in this study. Greatest mortality in disturbed forest streams appeared to occur in October through September, a period of moderately decreasing stream temperature. Greatest mortality in reference streams appeared to occur in March, shortly after peak abundance of early instar larvae. Greatest mortality of *T. maria* in disturbed streams occurred for Cohort II during leaf fall. Survivorship of early instars was substantially better in disturbed versus reference streams, and significantly greater density on an annual basis in disturbed streams was the result of better survivorship.

Variations in *Tipula abdominalis* life history.

Differences in the chronology of the *T. abdominalis* life cycle between disturbed and reference streams included earlier peak density and pre-pupal migration in the reference streams. In disturbed and reference streams at Coweeta, *T. abdominalis* was univoltine, as it is in other Coweeta streams (J. B. Wallace, personal communication), White Clay Creek, Pennsylvania (Vannote & Sweeney, 1985), and a coastal plain stream of Virginia (Roeding & Smock, 1989). Two peak recruitment periods occurred in disturbed and reference streams at

Coweeta. Early and late starting recruits were found in all streams, but reference streams had mostly early recruits that grew rapidly and pupated by May. Disturbed streams had mostly late recruits that grew slowly and pupated in late August.

Differences in the proportion of each population of *T. abdominalis* in each recruitment period may have been temperature related (J. B. Wallace, personal communication), and it is probable that temperature affected the onset of pupation more than duration of egg incubation. Egg incubation is generally temperature dependent, and tipulids have a relatively high Q_{10} (Prichard, 1983). Eggs collected from White Clay Creek, Pennsylvania, hatched within 10 days at 20°C (Vannote & Sweeney, 1985). Of the 5 well-studied terrestrial species of *Tipula*, 4 undergo winter egg diapause, and at least 1 species has a summer egg diapause. Eggs of *T. abdominalis* at Coweeta probably do not diapause.

Larvae of *T. abdominalis* migrated from Coweeta streams to pupate in moist areas under moss that covered stream-side rocks and logs. In White Clay Creek, Pennsylvania, *T. abdominalis* migrated to soil above the water line or under humus and moss to pupate (Vannote & Sweeney, 1985). Although *T. sacra* is uncommon in streams, life history of *T. sacra* more closely approximates that of *T. abdominalis* than any other well-studied tipulid (Prichard, 1976). *T. sacra* left beaver ponds to pupate, but most of the other aquatic tipulids remain submerged during pupation (Prichard, 1983). Prichard (1983) proposed that tipulids living in fast-flowing, well-oxygenated streams can respire cutaneously, allowing them to remain submerged during pupation. The fact that *T. abdominalis* lives in fast-flowing coldwater streams but leaves the stream to pupate downplays the importance of cutaneous respiration as a reason for movement to the terrestrial environment prior to pupation.

Presence of *T. abdominalis* larvae from March through July indicated that they did not leave disturbed streams to pupate until late summer, approximately 4 months after they had begun pupating in the reference stream. Pupal migration from coastal plain streams in Virginia begins as early as April (Roeding & Smock, 1989), but in other streams pupal migration occurs in August (Vannote & Sweeney, 1985) or September (Harris, 1950). Disturbed streams were 2-3°C cooler during the summer and required 40 days longer to accumulate the

same number of degree-days as reference forest streams. Differences in degree-day accumulation between disturbed and reference streams, however, were insufficient to account for 4 month differences in the onset of *T. abdominalis* pupation.

Differences in the onset of pupation may occur within a given tipulid population. Bimodal peak emergence of *T. sacra* followed bimodal pre-pupal migration from a pond (Prichard, 1976). Over a 3 year period, 80-85% of *T. sacra* emerged in early June while 15-20% of the population emerged in July. *T. sacra* also had day-to-day fluctuations in adult emergence. Daily fluctuations in the number of larvae leaving the pond to pupate seemed to be related to air temperature and rainfall.

Differences in chronology of the *T. abdominalis* life cycle between forest types may have been due to factors other than differences in temperature. Prichard (1976) felt that the most probable explanation for occurrence of 2 separate peak emergence periods of *T. sacra* was that they represented 2 cohorts that had different larval growth rates. A model of cohort-splitting was proposed to explain the bimodal distribution of slow and fast growing larvae on a given date (Prichard, 1978). Cohort splitting observed in other aquatic insects may also have been related to differential growth of larvae (Horst & Marzolph, 1975; Iversen, 1975; Resh, 1976; Rosenberg, *et al.*, 1977). In laboratory studies, 90% of *Tipula oleracea* L. pupated in 11-12 weeks, 10% pupated after 16-17 weeks, and differences in onset of pupation were attributed to differences in growth of fourth instar larvae (Laughlin, 1960). Prichard (1980) concluded that differential growth rates of larvae, periods of poor oviposition, and lack of recruitment due to disturbance were factors resulting in differential emergence patterns of *T. sacra*.

Despite the chronological differences in *T. abdominalis* life history in disturbed versus reference streams, density and mean individual weight were not significantly different on a monthly or annual basis. Peak density of early instar larvae was not significantly different between stream types, suggesting that egg hatching success was also similar. Survivorship patterns appeared similar after correcting for 4-month differences in the life cycle between

stream types. Mean individual weight of pre-emergent nymphs was not significantly different between stream types.

Variations in *Pycnopsyche* life history

Differences were found in the timing of peak density, annual mean density, and mean individual weight of *Pycnopsyche* between disturbed and reference streams. Delayed peak density suggests that egg hatching or oviposition was delayed in reference streams. Delayed peak density of *Pycnopsyche* in reference streams followed a pattern similar to that of *T. maria*, however these 2 species exhibit considerable differences in life history. Diapausing eggs of *T. maria* were exposed to higher summer temperatures, whereas *Pycnopsyche* eggs were exposed to cooler fall temperatures in reference versus disturbed streams.

The delayed appearance of *Pycnopsyche* in reference streams may have occurred partly as a result of lower water temperature. Reference streams were 2-3°C cooler than disturbed streams during the *Pycnopsyche* egg incubation period. A 2 or 3°C difference between streams ranging from 5-10°C mean daily temperature would result in an approximately 20 - 30-day difference in peak egg hatching based on models of the relationship of temperature and peak egg hatching for 2 other species of limnephilid caddisflies (Berte' & Prichard, 1986). A potential 30-day difference in egg incubation periods could not fully account for a 3-month difference in peak density in disturbed versus reference streams.

Differences in the timing of oviposition may have also contributed to delayed peak density in reference streams. Peak emergence may have occurred earlier in disturbed versus reference streams as a result of delayed maturation of larvae in reference streams during the winter. Mature larvae, however, were only slightly smaller in reference versus disturbed streams in late spring. In addition, pupae and fifth instar larvae were found in all streams through July, suggesting that emergence occurred during a similar time frame in disturbed and reference streams.

An extended flight period could result in differences in the relative proportion of early and late flying adults ovipositing in disturbed and reference streams. Emergence of

Pycnopsyche was asynchronous, with adults present over a 2-month period from mid-August through early November in southern Quebec (Mackay, 1972) and early August through early October at Coweeta (Huryn & Wallace, 1988). A 2-month flight period could partially explain the 3-month difference in peak egg hatching dates between disturbed and reference forest streams. Delayed oviposition in conjunction with lower egg incubation temperature may explain a 3-month delay in peak density of larvae in disturbed versus reference streams. In addition, the relatively large degree of error associated with sampling *Pycnopsyche* may have contributed to the apparent 3-month difference in peak density between forest types.

Significantly greater annual mean density of *Pycnopsyche* in disturbed versus reference forest streams was attributed mostly to better growth and survivorship of early instar larvae in disturbed streams. Earlier recruitment in disturbed streams resulted in more individuals obtaining maximum weight prior to overwintering as mature larvae. Significantly greater MIW in disturbed versus reference streams in December and January appeared to be the result of faster growth of early recruits in disturbed streams, and larvae appeared to have attained somewhat higher MIW in disturbed streams prior to emergence. Reference streams had mostly late recruits that grew slowly during winter and merged with early recruits by May as fifth instar larvae.

Recruitment of *Pycnopsyche* was less synchronous than recruitment by *P. gentilis* populations in Quebec (Mackay, 1972) and in a 3rd order stream at Coweeta (Huryn & Wallace, 1988). Early starting, rapidly growing recruits have not been reported for *P. gentilis*, but early and late recruitment periods followed by cohort merging have been observed in a number of caddisflies (Grafius & Anderson, 1980; Martinson & Ward, 1982; Resh, 1974; Richardson & Mackay, 1984; Roeding & Smock, 1989). Early and late recruits of *Pycnopsyche* in this study may have represented 2 different genotypes or closely related species, but larval morphology and case construction were similar to those reported for *P. gentilis* in other streams (Flint, 1960; Mackay, 1972; Huryn & Wallace, 1988). Significantly greater annual MIW and mean density of *Pycnopsyche* in disturbed versus reference streams resulted mostly from lower mortality of early recruitment individuals in disturbed streams.

Availability and utilization of leaf resources by shredders

Composition of leaf biomass in disturbed and reference streams reflected the composition of the early and late successional forest canopies (Boring, *et al.*, 1984). These findings agree with results of a study in the same watersheds 2 years previous, showing about 20% more total leaf biomass (TLB) in a reference than a disturbed forest stream after leaf-fall (Golladay, *et al.*, 1989). TLB was significantly greater in reference versus disturbed streams on an annual basis but was not significantly different during the first 4 months after leaf-fall.

Leaf quantity and quality

Even though TLB was initially only 20% greater in reference streams, faster disappearance of leaf material resulted in 40% lower TLB in disturbed streams on an annual basis. TLB disappeared faster in disturbed forest streams for 3 reasons. First, TLB in disturbed streams had a large proportion of fast-processing leaf species. The initial slow-processing leaf biomass in disturbed streams was approximately 40% that of reference streams; medium-processing leaf biomass in disturbed streams was 60% that of reference streams; and fast-processing biomass was 750% greater in disturbed versus reference streams. Secondly, leaf material may have disappeared faster from disturbed than from reference streams because winter water temperatures were a few degrees warmer in disturbed streams. Finally, annual shredder biomass was 23% greater in disturbed streams. Warmer winter stream temperature, a higher proportion of fast decaying leaf species, and greater shredder biomass contributed to faster disappearance of leaf material from disturbed versus reference streams.

Association of shredders with leaf resources

The significant positive relationship between total shredder biomass (TSB) and TLB was as expected, and there were no significant negative correlations between TSB and TLB on a monthly, annual, or forest basis. Significant positive correlations indicate that in general, the

larger the leaf accumulation the greater the biomass of shredders in a given sample. Correlation coefficients of shredder and leaf biomass were similar to those reported elsewhere (Huryn & Wallace, 1988). Generally low correlation coefficients indicate that shredder biomass cannot be accurately predicted from leaf biomass in a sample area on an annual basis. Lack of predictability occurs because large accumulations of leaf material often become tightly packed in depositional areas of streams, resulting in anaerobic conditions towards the center of the leaf accumulation (personal observation), whereas small accumulations in fast flowing water are often accompanied by high shredder biomass (Cummins, *et al.*, 1989). Microbial colonization and hydrodynamics may be more important determinants of shredder biomass than leaf quantity in a sample.

Because TLB and TSB correlated significantly on an annual basis, it was interesting that biomass of individual shredder species varied significantly in their relationships with biomass in slow, medium, and fast leaf processing categories. Correlations of each shredder species with various of the 3 processing categories suggests that shredders colonized certain types of leaf material more than others. *T. abdominalis* was most abundant in leaf accumulations consisting mostly of slow-processing leaf material, while *Pycnopsyche* biomass correlated significantly with medium and fast-processing leaf biomass.

Associations of shredders with different types of leaf material may have been due to physical limitations of shredders rather than preference or avoidance of specific leaf materials. *Pycnopsyche* may not be able to cut through vascular tissue of slow-processing leaves until the leaves have been in the stream for some time. Mandibles of *Pycnopsyche* are prognathous, extending from the distal end of the headcapsule, and *Pycnopsyche* feeds by cutting disks from leaves and chewing cut edges (Wiggins, 1977). Leaf toughness may limit leaf consumption by Lepidoptera, an insect order closely related to Trichoptera (Strong, *et al.*, 1984). Consumption of *Alnus* leaves by the trichopteran *Lepidostoma quercina* Ross was relatively low during the first 3 weeks of conditioning but increased significantly after 4 weeks of conditioning (Anderson & Grafius, 1975). In contrast, the mandibles of *T. abdominalis* are hypognathous; *T. abdominalis* feeds by boring through leaf packs, and leaf consumption rates

may not be significantly affected by instream conditioning time (Lawson, *et al.*, 1984). Peltoperlids feed by peeling cuticle, epidermis, and mesophyll tissue and avoiding veins (Wallace, *et al.*, 1970; Ward & Woods, 1986), thus the rigid structure of vascular tissue does not hamper feeding, and *T. maria* biomass was greatest in the most abundant leaf material available.

T. maria biomass correlated significantly with a variety of leaf taxa, whereas very little overlap was observed in the significant correlations of *T. abdominalis* and *Pycnopsyche* with various leaf taxa. *T. maria* was associated mostly with the dominant leaf taxa including slow, medium, and fast-processing species. *T. abdominalis* correlated significantly with rhododendron, white oak, beech, and yellow poplar. *Pycnopsyche* correlated significantly with medium-to-fast-processing leaves including red maple, dogwood, and early successional vegetation. Correlations of shredder biomass with biomass of various leaf taxa suggested that some partitioning of leaf resources may occur among the 3 dominant shredders.

Laboratory growth rates of shredders

Laboratory growth studies were conducted at 10°C to provide a background for comparing effects of leaf species, instream conditioning time, and site of leaf exposure on growth of 2 shredders. The range of growth rates exhibited by *T. maria* and *T. abdominalis* in the laboratory were similar to growth rates of field populations. Site of leaf exposure had no significant effect on shredder growth. Leaf species and leaf conditioning time had some significant effects on shredder growth, but each shredder species responded differently to leaf species and conditioning.

Differences in relative growth rates between shredders on each leaf treatment were not surprising, because coexisting shredder species often differ in their diet selection (Resh 1976; Prichard & Berte', 1987). Shredder feeding preferences and feeding rates depend on leaf

species (Wallace, *et al.*, 1970; Kaushik & Hynes, 1971; Iversen, 1974; Otto, 1974; Irons, *et al.*, 1988) and conditioning (Anderson & Grafius, 1975; Golladay, *et al.*, 1983; Bird & Kaushik, 1985). Opinions differ as to whether shredders such as *T. abdominalis* can (Anderson & Cummins, 1979) or cannot (Vannote & Sweeney, 1985) increase consumption to compensate for poor quality food.

T. maria growth was not significantly different ($p < 0.05$) among leaf species, but *T. maria* growth appeared to be twice as fast on blackberry, a fast-processing, early successional species, than on chestnut oak, a slow-processing, late successional species. *T. abdominalis* growth rates were fastest on chestnut oak, a late successional species, and slowest on dogwood. *T. abdominalis* grew well on blackberry but poorly on dogwood. There was no consistent trend of faster shredder growth on early versus late successional leaf species.

The length of conditioning of leaves had different effects on each shredder species. It has been hypothesized that greatest shredder utilization of a leaf resource will occur when leaf material has lost about 50% of its original mass (Cummins, *et al.*, 1989). Dogwood, black locust, and yellow poplar provided greatest *T. maria* growth rates when they were approximately 50% decomposed, but other leaf species did not fit this pattern. For instance, chestnut oak and rhododendron were slow-processing species but provided faster *T. maria* growth rates when they were conditioned for 54, versus 117 or 248 days.

Lawson *et al.* (1984) found very little growth of *T. abdominalis* on pignut hickory leaves that had been conditioned for only 1 week, but he found significantly greater growth after 3 weeks. Growth decreasing thereafter through 12 weeks of conditioning. Faster growth of *T. abdominalis* at intermediate conditioning intervals was not consistent in this study. However, growth was not measured until leaves had been conditioned for at least 19 days, an interval that produced rapid growth of *T. abdominalis* fed pignut hickory (Lawson, *et al.*, 1984). *T. abdominalis* grew best on slow-processing leaf species that were exposed for 254 days. Slow-processing leaf species from the previous autumn comprised the majority of leaf resources available to early instar *T. abdominalis* in late summer.

Shredder production in streams

Significantly greater production by *T. maria* in disturbed versus reference streams was the result of greater density and somewhat greater mean individual weight in disturbed streams. Survivorship appeared to be a more important factor than growth in causing differences in *T. maria* production between stream types.

T. abdominalis exhibited similar P/B in disturbed and reference forest streams despite temperature induced differences in life history. Differences in *T. abdominalis* life history did not significantly affect production: 54% greater *T. abdominalis* production in disturbed versus reference streams was due to somewhat greater density and pre-emergence larval weight.

Significantly greater production by *Pycnopsyche* in disturbed versus reference streams was the result of better growth and survivorship of early recruits. Differences in *Pycnopsyche* annual P/B reflected differences in early versus late recruitment in disturbed versus reference streams. Early recruitment may have been temperature induced, but better survivorship of early instar larvae may have been related to an abundance of fast decomposing leaf species in disturbed streams. Production by *Pycnopsyche* in reference streams was greatest in Stream 5, which had greater medium-processing leaf biomass, particularly black birch, than other reference streams. Overall, *Pycnopsyche* production was greatest in Stream 1, a disturbed stream that had greater biomass of medium and fast decaying leaf material than other streams.

Of the disturbed streams, total shredder production was greatest in Stream 1 even though total leaf biomass was greatest in Stream 2. Stream 1 had greater fast and medium-processing leaf biomass, but less slow-processing leaf biomass than other disturbed streams. In reference forest streams, total shredder production was greatest to least according to greatest to least total leaf biomass. Relatively low production of *Pycnopsyche* was accompanied by relatively high production of *T. abdominalis* in Stream 4. Total leaf biomass in Stream 4 was similar to other reference forest streams, but biomass of chestnut oak was 4 times

greater than in other reference streams. The relationship of *T. abdominalis* with chestnut oak in field and laboratory studies suggests that an abundance of chestnut oak may have resulted in higher production of *T. abdominalis* in Stream 4.

Effect of forest disturbance on shredder production

While stream temperature appeared to affect shredder life history, differences in production of shredders in disturbed versus reference streams could not be accounted for on the basis of temperature alone. Survivorship did not appear to be temperature related because peak mortality of each shredder species occurred during periods of moderate temperature. Sweeney & Vannote (1978) hypothesized that size of individuals would vary within drainage networks because of differences in sub-basin thermal regimes. Disturbed and reference streams varied by at most 350 degree-days, a difference that was apparently insufficient to cause significant differences in pre-emergent larval weight. Although temperature did not directly affect production in this study, it has been suggested that temperature and food quality gradients may interact to affect shredder production and growth (Sweeney & Vannote, 1986).

It was surprising that growth rates of 2 shredder species responded differently to different slow-processing leaf species, because biomass of both shredder species correlated significantly with slow-processing leaf biomass in streams. Growth of *T. maria* was slowest on chestnut oak, but relatively fast on rhododendron. Rhododendron dominated the leaf biomass in all streams and appeared to be an important resource for *T. maria*. *T. abdominalis* growth was greatest on chestnut oak but significantly lower on rhododendron. Chestnut oak was the second most abundant leaf resource in reference streams and appeared to be an important leaf resource for *T. abdominalis*.

Pycnopsyche sp. exhibited the greatest difference in production between disturbed and reference streams and contributed more than *T. maria* or *T. abdominalis* to greater total

shredder production in disturbed streams. Although growth studies were not conducted on *Pycnopsyche*, it was the only shredder whose biomass correlated significantly with fast-processing leaf biomass in streams, and early life history stages were present when fast-processing leaf material was present in streams. Caddisflies have been shown to exhibit considerable diet selectivity (Mackay & Kalff, 1973; Hurbst, 1982; Motyka, *et al.*, 1985; Prichard & Berte', 1987), and some species switch diets during the larval growth period (Winterbourne, 1971; Resh, 1976; Huryn & Wallace, 1985; Berte' & Prichard, 1986). Growth of detritivorous caddisflies may be limited by availability of fast-processing leaves such as alder (Anderson & Grafius, 1975; Grafius & Anderson, 1979; Irons, *et al.*, 1988). Nearly 3 times greater production of *Pycnopsyche* in disturbed versus reference streams appeared to be related to significantly greater biomass of fast-to-medium-processing species such as dogwood, basswood, sassafras, red maple, and herbaceous species in the disturbed streams.

In experimental streams, differences in production of *Soyedina carolinensis* were attributed more to differences in survivorship than growth (Sweeney, *et al.*, 1986). It was apparent that survivorship played a greater role than growth in causing significantly greater production of *T. maria* in disturbed versus reference streams. In the present study, survivorship of shredders in short-term laboratory growth studies provided little evidence for extrapolating to field conditions, except that it was apparent that there were some differences in survivorship among leaf treatments. Diet-induced mortality has been observed in growth studies of other aquatic insects (Bird & Kaushik, 1984; Sweeney & Vannote, 1986). It is possible that allelochemical interactions may occur between shredders and leaf species, as is the case for many terrestrial arthropods (Strong, *et al.*, 1984).

It is difficult to determine whether leaf quality caused substantial differences in survivorship of the 3 dominant shredders in the field study. Predominantly detritivorous peltoperlid stoneflies have been known to feed on alternative food resources (Chapman & Demory, 1963). *T. abdominalis* is probably an obligate leaf shredder due to mandibular arrangement and feeding method, but survivorship of *T. abdominalis* was apparently similar in disturbed and reference streams. *Pycnopsyche* growth and survivorship may have benefitted

from greater fast decaying leaf biomass in disturbed versus reference streams, but alternative food resources may have been important in producing greater total shredder production in disturbed streams.

Shredder production in forest streams appears to fit a pattern of community response to disturbance. Leaf resources and shredder production respond negatively to forest clearcutting, but early successional vegetation 10 to 20 years after disturbance provides adequate shading and detrital food base for recovery of shredders to pre-disturbance levels (Woodall & Wallace, 1972; Haefner & Wallace, 1981a). Shredder production in early successional forest streams exceeded production in late successional forests, even though total leaf biomass was 20% lower. Greater total shredder production was attributed to higher production by each of the 3 dominant shredders, and particularly to *Pycnopsyche* which appeared most capable of exploiting early successional leaf resources in disturbed forest streams. Should shredder production continue to follow the typical pattern of community response to disturbance, I estimate that total shredder production will decline gradually to 3-4 g/m²/yr in disturbed forest streams over the next few decades as mid-and-late successional vegetation begins to dominate the leaf biomass of the forest.

Conclusions

Shredder production was significantly greater in disturbed versus reference forest streams, even though reference streams had significantly greater leaf biomass. Production of the 3 dominant shredders in streams was: *T. abdominalis* > *Pycnopsyche* > *T. maria*. *Pycnopsyche* contributed more than the other shredders in causing greater total shredder production in disturbed versus reference streams.

Pycnopsyche biomass in 330 samples correlated significantly with biomass of fast and medium-processing leaf species but not with slow-processing leaf biomass. *Pycnopsyche* production was nearly 3X greater, and fast decaying leaf biomass was about 7.5X greater in disturbed versus reference streams. Greater production of *Pycnopsyche* was attributed to better growth and survivorship in disturbed streams.

T. maria comprised <10% of total shredder production in the study streams. *T. maria* biomass correlated significantly with medium and slow-processing leaf biomass in both stream types, but production was greater even though there was less medium and slow-processing leaf biomass in disturbed versus reference streams. Growth of *T. maria* in short-term laboratory studies was not significantly different on fast versus slow-processing leaf species. Significantly greater production of *T. maria* in disturbed versus reference forest streams was attributed mostly to better survival rate than better growth in disturbed streams.

T. abdominalis dominated the shredder biomass and production in most streams, but production of *T. abdominalis* was not significantly different in disturbed versus reference streams. *T. abdominalis* biomass correlated significantly with slow-processing leaf biomass in samples. Growth rates of *T. abdominalis* in the laboratory were significantly greater on chestnut oak and blackberry than on rhododendron and dogwood. There was no trend of faster growth of *T. maria* or *T. abdominalis* on early versus late successional leaf species in laboratory studies. Differences in temperature profiles between disturbed and reference streams may have contributed to differences in growth and survivorship of shredders.

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Tennessee Technological University
Thesis title: "Leaf-litter Processing by Aquatic Macroinvertebrates
in Lotic and Lentic Waters Near Soddy-Daisy, Tennessee."

Faculty advisor:

C. B. Coburn, Jr., Professor

Doctor of Philosophy in Biology

Virginia Polytechnic Institute and State University
Dissertation title: "Effect of a Forest Disturbance on Leaf Quality
and Shredder Production in Headwater Streams."

Faculty advisor:

E. F. Benfield, Professor

Employment

•**Research Assistant** 1980-1982
Tennessee Technological University

•**Instructor for the Biological Sciences** 1982-1985
Southern West Virginia Community College
Williamson, West Virginia

•**Teaching Assistant** 1985-1989
Virginia Polytechnic Institute and State University

•**Research Assistant** 1987-1988 and 3 summers.
Virginia Polytechnic Institute and State University

•**Academic Advisor** Spring, 1989
Virginia Polytechnic Institute and State University

•**Postdoctoral Associate** *current*
Division of Forestry, West Virginia University

Grants-in-aid

1984-1986. Trout Unlimited, Kanawha Valley Chapter,
Charleston, WV. Baseline surveys of macroinvertebrates
inhabiting a reproducing brown trout (*Salmo trutta*) stream.

1987-1988. Virginia Academy of Science.
Distribution of limnephilid and phryganid caddisflies:
northern species in the southeastern Appalachians.

1988. Jandel Scientific, Corte Madre, California.
Automated measuring of aquatic insects.

1989-current. West Virginia Department of Natural Resources.
Northern caddisfly distribution in wetlands of West Virginia.

Affiliations

Sigma Xi Scientific Research Society
North American Benthological Society
The American Entomological Society
Beta Beta Beta Biological Honorary Society

Personal data

Birth data: December 21, 1957
Birthplace: Morgantown, West Virginia
Family: Married

Publications

- Stout, Ben M. III, and C. B. Coburn, Jr. 1989.
Impact of highway construction on leaf processing in aquatic habitats of eastern Tennessee. *Hydrobiologia* 178:233-242.
- Stout, Ben M. III, and James S. Stout. 1989.
Northern caddisfly (Trichoptera) fauna in remnant boreal wetlands of West Virginia. *Entomological News* 100(1):37-40.
- Benfield, E.F., J.R. Webster, S.W. Golladay, G.T. Peters, and B.M. Stout. 1990. Effects of forest disturbance on leaf breakdown in southern Appalachian streams. *in press Verhandlugen*
- Stout, Ben M. III., Kathy K. Stout, and Craig Stihler. *in prep.*
Predation by *Banksiola dossuaria* (Trichoptera) on eggs of the spotted salamander *Ambystoma maculatum*.
- Stout, Ben M. III. *in prep.*
Ecology of *Platycentropus radiatus* in ponds of the Alleghany Highlands of West Virginia.

Presentations

- Stout, Ben M. III. 1984. Effect of highway construction on leaf decomposition in wetlands of eastern Tennessee. May 22. Association of Southeastern Biologists.
- Stout, Ben M. III. 1986. Leaf breakdown in a variety of lake and stream habitats below the Cumberland Plateau of eastern Tennessee. Lawrence, Kansas. May 23. Bull. North American Benthological Society (3)2:113 *abstract*.
- Stout, Ben M. III. 1987. Ecology of two case-building caddisflies: partitioning of resources. Orono, ME. June 4. Bull. North American Benthological Society 4(1):91 *abstract*.
- Stout, Ben M. III, and Carol J. Haley. 1988. Automated measuring of aquatic insects. Tuscaloosa, AL. June 4. Bull. North American Benthological Society 5(1):55 *abstract*.
- Stout, Ben M. III. 1988. Northern caddisflies in southern Appalachian wetlands. Charlottesville, VA. May 25. Virginia J. Science 39(2):122 *abstract*.
- Stout, Ben M. III, E. F. Benfield, and J. R. Webster. 1989. Effect of forest disturbance on leaf quality and production of a leaf shredding insect. Guelph, Ontario, Canada. May 17. Bull. North American Benthological Society 5(1):104 *abstract*.
- Stout, Ben M. III. 1989. Effect of forest disturbance on leaf shredding aquatic insects in headwater streams. University of Miami, Oxford, Ohio. October 26, 1989.