The Replacement of *Stenonema* spp. by *Caenis diminuta* Walker as the Numerical Dominant in the Mayfly Assemblage of a Thermally-Stressed Stream

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ABSTRACT

Mayfly community structures in a thermally-stressed, previously thermally-stressed and an undisturbed stream were compared based on nymphal colonization of leaf packs incubated over a 48 d period from December 1982 to February 1983. Temperatures ranged from 7-31C in the thermally-stressed stream and from 4-12C in the other two streams. Accumulated degree days (>0C) were 734, 340 and 322 for the thermally-stressed, post-stressed and undisturbed streams, respectively. Stenonema spp. numerically dominated the mayfly fauna over the sampling period in the undisturbed (70%) and post-stressed (98%) streams, but was replaced by Caenis diminuta Walker (88%) in the stream receiving thermal effluent from a nuclear production reactor. Caenis diminuta is tolerant of rapidly fluctuating ($\Delta T > 11C/hr$) and high temperatures (possibly up to 40C).

INTRODUCTION

Changes in benthic macroinvertebrate community structure have been used frequently to investigate effects of thermal enhancement in lotic systems. However, these findings often appear contradictory, probably due to the differing intensity, duration and seasonal timing of the thermal perturbations under examination. For example, number of invertebrate taxa can increase as density values decrease (Benda and Proffitt 1974); both taxa and density can decrease (Dahlberg and Conyers 1974); and, community biomass can increase or decrease, depending on season (Rodgers 1980, 1982). Mayflies (Ephemeroptera) are considered a pollution-sensitive group (Hynes 1960; Sloan 1956), and several investigators have documented mayfly assemblage responses to thermal enhancement (Langford 1971; Benda and Proffitt 1974; Howell and Gentry 1974; Obrdlík et al. 1979).

The objective of this research was to compare the composition of mayfly assemblages on leaf packs in three tributary streams to the Savannah River, each with a unique thermal regime history. This study comprised a segment of the authors' investigation of invertebrate communities colonizing leaf packs in these three streams and in the Savannah River, the results of which will be published elsewhere. Although mayflies constituted only 5-14% of the total number of invertebrates collected, their distributional patterns were considered interesting enough to merit separate attention.

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METHODS AND MATERIALS

This project was conducted on the Savannah River Plant (SRP), a 778 km^2 area adjacent to the Savannah River on the upper Coastal Plain of South Carolina, U.S.A. (Fig. 1). Three streams with distinctly different thermal regime histories were selected for this study. Upper Three Runs Creek (U3RC) is a 4th order, blackwater stream that has never received thermal effluent. Steel Creek (SC), a 3rd order stream, received thermal effluent from a nuclear production reactor between 1954 and 1968. It is presently slightly thermally perturbed, as temperatures are 1-2C above ambient due to some heated effluent contribution from an upstream tributary. Four Mile Creek (4MC), also a 3rd order stream, has received thermal effluent (>70C) about 15 km above its mouth from 1954 to the present. Reactor operations affect both flow and temperature in this stream. All three streams were sampled within 0.1 km of their mouths, where they are well-canopied by riparian vegetation. Each of the sampling stations was subject to backflooding from the Savannah River during high flow. In the remainder of this paper, these three streams will be referred to as undisturbed, post-thermal and thermal.

Leaves of sycamore (*Platanus occidentalis*) and sweetgum (*Liquidambar styraciflua*), common riparian species on the SRP, were collected just prior to abscission (Short et al. 1980) and air dried to constant weight. Ten grams of

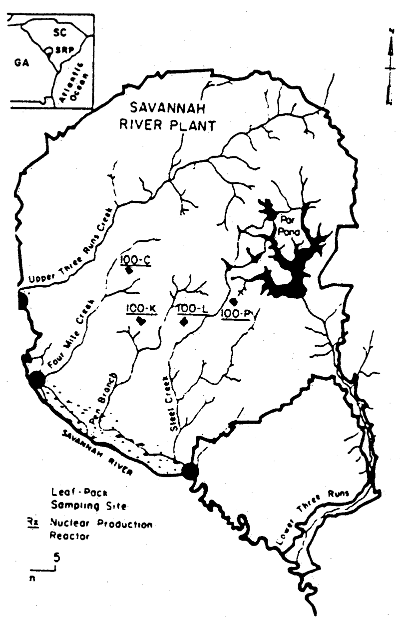

Figure 1. Map showing locations of Savannah River Plant, sampling sites and nuclear production reactors.

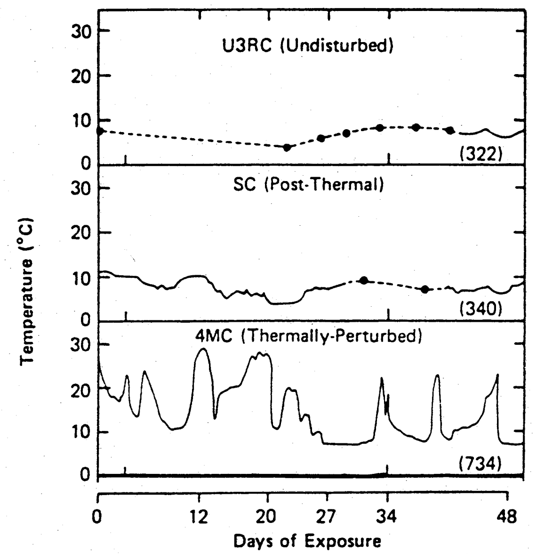

Figure 2. Temperature profiles and degree-days (>0C) accumulated for undisturbed, post-thermal and thermal stream sites from 29 Dec. 1982 to 15 Feb. 1983. Closed circles represent temperature measurements during periods of thermograph inoperation.

sycamore or 15 g of sweetgum were placed in plastic mesh bags (max. aperature = 5 x 25 mm). Three leaf packs of each species were secured in a chicken-wire basket, which was tied to a concrete block. Five such baskets, along with a continuously-recording thermograph (Peabody Ryan model J), were anchored on the bottom at each site. Baskets were placed in the streams on 29 December 1982, and one was retrieved randomly from each site following 12, 20, 27, 34 and 48 d (15 February 1983) of exposure. The three packs of each leaf type were removed, separately bagged, returned to the lab on ice, and separately rinsed over a 425 μm sieve. Invertebrates were sorted in a white enamel tray and stored in 75% EtOH. No significant differences ($p > .05$) in numbers or in composition of mayfly taxa occurred between the two leaf species; therefore, nymphs collected on both leaf types at each site were pooled on each sampling date. Data which met the assumptions of parametric ANOVA following an $(X + .05)^{.5}$ transformation were tested using Student-Newman-Keuls method (Steel and Torrie 1960) on SPSS. Other data were analyzed using the Kruskal-Wallis test (Conover 1971).

RESULTS AND DISCUSSION

The thermograph data (Fig. 2) show that seasonally-elevated and fluctuating temperatures characterized the thermal regime of the thermal stream. Low temperatures occurred when high flow in the Savannah River inundated the stream mouth, thus blocking the normal flow of warm water discharged from the continuously-operating reactor. The thermal regimes of the undisturbed and post-thermal streams, in contrast, were characterized by normal seasonal variations in temperature with only slight, river-induced thermal fluctuations. Approximate cumulative degree-days during the 48 d study period were 734 for the thermal, 340 for the post-thermal and 322 for the undisturbed streams. Other physical-chemical parameters (Table 1) fluctuated under the influence of river water intrusion. Generally, the thermal and post-thermal streams were similar with respect to water chemistry, but river backflooding of the undisturbed stream resulted in occasional overlaps in water quality at all three sites.

Table 1. Physical-chemical data for thermal, post-thermal and undisturbed streams.

	Thermal	Post-Thermal	Undisturbed	n*
D.O. (mg/l)	6-12	9-15	8-11	6
Flow (cm/s)**	0-10	0-36	0-67	8
Conductivity (µmhos/cm)	40-72	30-66	18-38	7
Total Alkalinity (mg $CaCO_3$/l)	13-31	25-37	3-18	3
pH	6.4-6.9	6.6-6.8	5.6-6.5	3

* Number of observations over the study period.
**Values of 0 represent periods of site inundation by the river.

Major between-site differences were apparent in the mayfly assemblages of the three streams (Fig. 3). Nymphs were most abundant in the post-thermal stream, where Stenonema spp. comprised 98% of all mayflies collected and were significantly more abundant than in either the undisturbed ($p < .01$) or the thermal ($p < .01$) streams. The mayfly assemblage in the undisturbed stream was also numerically dominated by Stenonema spp. (70%), which were significantly more abundant ($p < .01$) in this stream than in the thermal stream. Three other taxa (Ephemerella spp., Isonychia spp., and Neophemera youngi) were significantly more abundant ($p < .05$) in the undisturbed stream than in both the other streams. In the thermal stream, Caenis diminuta Walker comprised 88% of the mayflies collected, whereas Stenonema spp. contributed only 4%. Caenis diminuta was significantly more abundant ($p < .01$) in the thermal stream than in both the other streams, where none of this taxon were collected (except one specimen on a leaf pack from the post-thermal stream in March).

Our data suggest that the replacement of Stenonema spp. by C. diminuta as the numerical dominant of the mayfly assemblage in the thermal stream is largely attributable to the seasonally-elevated and temporally unpredictable thermal regime. Other research has also shown Caenis sp. (prob. diminuta) to be more abundant in the mouth of this thermal stream relative to the mouths of the other two streams in this study (e.g., drift studies: Specht and Painter 1983; Hester-Dendy studies: W. Specht, unpub. data). General water quality in the three streams showed considerable overlap (Table 1) and was, therefore, unlikely to account for the shift in community dominants.

Mayflies are microhabitat specialists (Edmunds et al. 1976). Although differences in such factors as current velocity and sediment particle size were noted between these streams, it is doubtful that these factors were as important as temperature in structuring the observed mayfly assemblages. Caenis species often occur in depositional reaches of streams (Berner 1950;

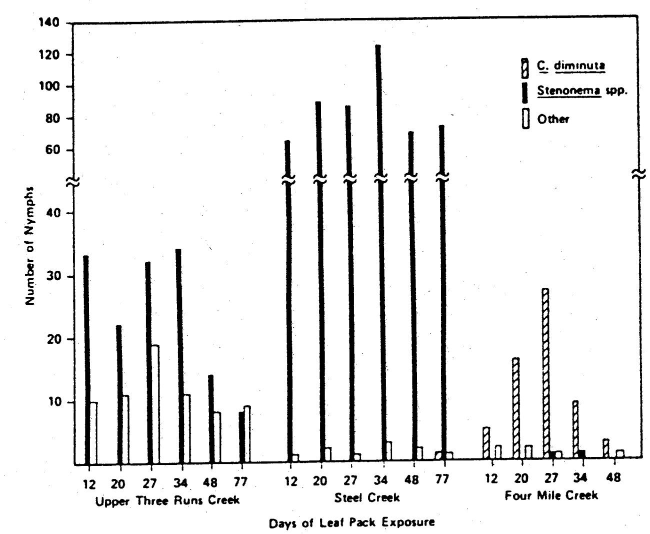

Figure 3. Number of Caenis diminuta, Stenonema spp. and other mayfly nymphs occurring on six leaf packs per collection date in, undisturbed (Upper Three Runs Creek), post-thermal (Steel Creek) and thermal (Four Mile Creek) streams.

Hubbard and Peters 1978), and current velocity was generally slower in the thermal stream (Table 1). However, Stenonema spp. also occur in streams in low velocity microhabitats, such as in leaf debris, underneath stones or in pools (Unzicker and Carlson 1983). One species of Stenonema (S. smithae) previously reported from the undisturbed stream (Morse et al. 1980) occurs in permanently flowing waters, "regardless of current velocity or depth" (Berner 1950). Moreover, C. diminuta is not restricted solely to depositional habitats, as this species has been collected, along with Stenonema spp., from leaf packs in erosional areas (shifting sand bottoms) on the SRP (Sadowski and Matthews 1984; B. Kondratieff, pers. comm.). Bottom sediments were finer (siltier) in the thermal stream (N.L. Poff, pers. obs.); however, sediments are not a probable colonization source for mayflies in soft-bottomed Coastal Plain streams (see Bencke et al. 1984), and leaf packs did not appear covered by sediments during their incubation.

The importance of thermal regime in the evolution and ecology of aquatic insects has received recent attention (Vannote and Sweeney 1980; Ward and Stanford 1982). Members of the Caenidae are frequently collected in warm waters in the Temperate Zone (Berner 1977). Rodgers (1980, 1982) reported Caenis sp. (= C. simulans, E. Rodgers, pers. comm.) at temperatures elevated to 35C, and this species has been observed on the SRP at winter temperatures approaching 40C (B. Kondratieff, pers. comm.). Caenis macrura was observed in Europe by Obrdlik et al. (1979) at temperatures elevated to 35.4C. Caenis diminuta has been variously reported to occur at temperatures up to 30C over an annual temperature range of up to 15C (Hubbard and Peters 1978, and refs. therein). In this study, C. diminuta tolerated a temperature variation of almost 25C for the winter season alone. Including Specht and Painter's (1983) summer drift data, this species (or at least the local population) apparently tolerates an annual temperature range of about 5-40C.

One regulator of the distribution of insects in lotic habitats may be the "temporal predictability" of a stream's thermal regime (Vannote and Sweeney 1980). The habitats from which C. diminuta has been previously reported are generally subject to great natural thermal variation. Such variation is diel and seasonal; it is also temporally predictable. The temperature regime in the thermal stream, however, is not predictable, due to the non-synchronous interaction between intrusion of cool hypolimnetic-release water from the Savannah River and variable reactor operation schedules. A non-seasonal and thermally-unstable environment prevails near the mouth of this stream. Caenis diminuta, possibly along with a few other taxa present (Poff and Matthews, unpub. data), appears capable of acclimating to this variable thermal regime, as it has been consistently collected throughout the year.

One possible mechanism facilitating the success of C. diminuta under this dramatically fluctuating and unpredictable thermal regime may be its asynchronous multi-voltinism (Berner 1950). If, as Brittain (1982) suggests, mayfly life cycle flexibility is in part a function of cumulative temperature conditions, C. diminuta may be able to maintain a viable population in this unpredictable environment through rapid and asynchronous completion of its life cycle.

The occurrence of C. diminuta in the thermal stream is interesting in terms of this organism's temperature tolerance alone; however, the mayfly's presence in this stream also has broader ecological significance. The biota in stream ecosystems with fluctuating environments may help stabilize the stressed system by counteracting the forces contributing to system instability, e.g., temperature fluctuations (Vannote et al. 1980). One way in which stream ecosystem instability occurs is through downstream loss of nutrients and carbon (Elwood et al. 1983). There is some evidence that the thermally-stressed stream ecosystem is a relatively inefficient processor of detrital energy inputs and that nutrients are lost from this stream to the Savannah River (Poff and Matthews, unpub. data). If this is the case, then the occurrence of tolerant species such as C. diminuta can contribute to the stability, productivity and nutrient retention within thermally-stressed ecosystems.

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LITERATURE CITED

Benda, R.S. and M.A. Proffitt. 1974. Effects of thermal effluents on fish and invetebrates, p. 438 In Thermal ecology. J.W. Gibbons and R.R. Sharitz (eds.). AEC Symposium Series (CONF-730505), NTIS, Springfield, VA.

Bencke, A.C., T.C. Van Arsdall, Jr., D.M. Gillespie and F.K. Parrish. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. Ecol. Monogr. 54:25.

Berner, L. 1950. The mayflies of Florida. University of Florida Press, Gainesville.

-----. 1977. Distributional patterns of southeastern mayflies (Ephemeroptera). Bull. Fla. State Mus. Biol. Sci. 22:1.

Brittain, J.E. 1982. Biology of mayflies. Ann. Rev. Entomol. 27:119.

Conover, W. J. 1971. Practical nonparametric statistics. John Wiley & Sons, Inc., New York, NY.

Dahlberg, M.D. and J.C. Conyers. 1974. Winter fauna in a thermal discharge with observations on a macrobenthos sampler, p. 414 In Thermal ecology. J.W. Gibbons and R.R. Sharitz (eds.). AEC Symposium Series (CONF-730505), NTIS, Springfield, VA.

Edmunds, G.F., Jr., S.L. Jensen and L. Berner. 1976. The mayflies of North and Central America. University of Minnesota Press, Minneapolis.

Elwood, J.W., J.D. Newbold, R.V. O'Neill and W. Van Winkle. 1983. Resource spiralling: an operational paradigm for analyzing lotic ecosystems, p. 3 In Dynamics of lotic ecosystems. T.D. Fontaine, III and S.M. Bartell (eds.). Ann Arbor Science Publications, Ann Arbor, MI.

Howell, F.G. and J.B. Gentry. 1974. Effect of thermal effluents from nuclear reactors on species diversity of aquatic insects, p. 562 In Thermal ecology. J.W. Gibbons and R.R. Sharitz (eds.). AEC Symposium Series (CONF-730505), NTIS, Springfield, VA.

Hubbard, M.D. and W.L. Peters. 1978. Environmental requirements and pollution tolerance of Ephermeroptera. USEPA (EPA-600/4-78-061), Cincinnati, OH.

Hynes, H.B.N. 1960. The biology of polluted waters. University of Toronto Press.

Langford, T.E. 1971. The distribution, abundance and life histories of stoneflies (Plecoptera) and mayflies (Ephemeroptera) in a British river, warmed by cooling water from a power station. Hydrobiol. 38:339.

Morse, J.C., J.W. Chapin, D.D. Herlong and R.S. Harvey. 1980. Aquatic insects of the Upper Three Runs Creek, Savannah River Plant, South Carolina. Part I: Orders other than Diptera. J. Georgia Entomol. Soc. 15:73.

Obrdlík, P., Z. Adámek and J. Zadrádka. 1979. Mayfly fauna (Ephemeroptera) and the biology of the species Potamanthus luteus (L.) in a warmed stretch of the Oslava River. Hydrobiol. 67:129.

Rodgers, E.B. 1980. Effects of elevated temperatures on macro-invertebrate populations in the Browns Ferry experimental ecosystems, p. 682 In Microcosms in ecological research. J.P. Giesy (ed.). DOE Symposium Series (CONF-781101), NTIS, Springfield, VA.

-----. 1982. Production of Caenis (Ephemeroptera:Caenidae) in elevated water temperatures. Freshwat. Invertebr. Biol. 1(2):2.

Sadowski, P.W. and R.A. Matthews. 1984. Effect of thermal effluents from the Savannah River Plant on leaf decomposition rates in onsite creeks and the Savannah River. USDOE Report DPST-84-399, E.I. du Pont de Nemours & Co., Savannah River Laboratory, Aiken, SC.

Short, R.A., S.P. Canton and J.V. Ward. 1980. Detrital processing and associated macroinvertebrates in a Colorado Rocky Mountain stream. Ecology 61:727.

Sloan, W.C. 1956. The distribution of aquatic insects in two Florida streams. Ecology 37:81.

Specht, W.L. and W.B. Painter. 1983. Final report on the preliminary biological measurement program in the Savannah River 1 March through 31 August 1982, Vol. II. Prepared for E.I. du Pont de Nemours & Co., Document no. ECS-SR-3, Savannah River Laboratory, Aiken, SC.

Steel, R.G.D. and J.H. Torrie. 1960. Principles and procedures of statistics, a biometrical approach. McGraw-Hill, NY.

Unzicker, J.D. and P.H. Carlson. 1983. Ephemeroptera, p. 3.1 In Aquatic insects and oligochaetes of North and South Carolina. A.R. Brigham, W.U. Brigham and A. Gnilka (eds.). Midwest Aquatic Enterprises, Mahomet, IL.

Vannote, R.L. and B.W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. Amer. Nat. 115:667.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell and C.E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130.

Ward, J.V. and J.A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. Ann. Rev. Entomol. 27:97.

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