Production of *Caenis* (Ephemeroptera: Caenidae) in Elevated Water Temperatures[1]

ELIZABETH B. RODGERS

Tennessee Valley Authority, Biothermal Research Station, Decatur, AL 35602

Abstract. Annual production rates of a mayfly (tentatively *Caenis* sp. nr. *amica*: Ephemeroptera) inhabiting large outdoor channels at four diurnally and seasonally fluctuating temperature levels were calculated. Temperature levels were ambient Tennessee River temperature, and about 3°, 6°, and 9°C above ambient. *Caenis* were sampled from December 1977 through September 1978. Emergence was accelerated 4 to 31 days by elevated temperatures. Long emergence periods (80 to 100 days) and size-frequency data indicated bivoltinism. Production in ambient temperatures (676.04 ± 237.56 mg DW/m^2/yr) was significantly greater than in any other temperature level. Production rates in the three elevated temperatures were 205.66 ± 67.30 mg DW/m^2 in +3 channels, 272.86 ± 78.23 mg DW/m^2 in +6 channels, and 271.10 ± 93.47 mg DW/m^2 in +9 channels. These data imply that this population of *Caenis* is existing at or above its optimal temperatures.

The study presented here was part of an ongoing effort at the Tennessee Valley Authority's Biothermal Research Station to evaluate the effects of elevated water temperatures on aquatic organisms. The purpose of the effort is to provide information for establishing temperature criteria for protection of important sport and commercial fish species. The natural colonization of the channels by diverse communities of algae, zooplankton, and macroinvertebrates also allows studies of the entire aquatic ecosystem to provide a basis for the evaluation of temperature criteria.

During the first experiment with heated water in the channels (March - August 1977), responses of aquatic organisms varied with trophic level. Production of algae increased, biomass of the total macroinvertebrate community decreased, while final yield of adult bluegill (*Lepomis macrochirus* Rafinesque), a predator of macroinvertebrates in the channels, was not significantly affected by temperature treatment (Wrenn et al. 1979; Rodgers 1980). The effect of increased temperature on each member of the macroinvertebrate community was variable, but certain species were severely affected.

One of these was *Caenis* sp. (Ephemeroptera: Caenidae) whose dry weight decreased from a peak of 465 mg/m^2 (about 34% of the total macroinvertebrate dry weight) to 1 mg/m^2, less than 1% of the macroinvertebrate community, during four to five months in temperatures 6°C above ambient. Increased foraging activity by bluegills at elevated temperatures almost certainly played a part in the decline of *Caenis* and other invertebrates in those channels. Previous data have shown *Caenis* sp. to be important in the bluegill diet in the channels (Wrenn et al. 1979; Rodgers & Armitage, unpubl. ms.), as well as in other locations (Sadzikowski 1976; El Shamy 1978; Hall et al. 1970).

Despite the decrease in biomass of *Caenis* sp. and the total macroinvertebrate population, second-year bluegill grew at all temperature levels at a rate (about 1 mm/day, Wrenn et al. 1979) comparable to the greatest rates of growth reported in the Southeastern U.S. (Carlander 1977). Bluegill were evidently not food-limited during the six-month period of this study. In June and July, when the population densities of *Caenis* sp. and

---

[1] I thank J.C. Chowning and W.E. Barksdale for field and laboratory assistance, P.F. Pütman for typing, and T.F. Waters, O.J. Sexton, L.D. Wright, J.S. Mattice, B.J. Armitage, J.H. Heuer, and K.J. Tennessen for reviewing drafts of the manuscript.

certain other macroinvertebrate species declined abruptly in elevated temperatures, bluegill found alternate sources of food, including their own young-of-the-year (Rodgers unpubl. data).

Theoretically, production and/or the P/B ratio of *Caenis* could have been increased by elevated temperatures and bluegill predation despite reduced densities, by means of increased voltinism. Onset of emergence of *Caenis* from the channels had been accelerated by warmer temperatures, suggesting increased voltinism and thus greater productivity. Winberg (1971) cited studies which indicated that, "cropping by fish of a certain proportion of an invertebrate population stimulated its regenerative capacity." Benke (1978) summarizing a study of predation on benthos by dragonflies indicated that, "It is necessary for prey to be turning over at an unusally high rate and it is possible that odonates function in stimulating the rate of prey production." Presumably, this stimulation may occur as a result of reduced competition among prey organisms and could have occurred in the channels as a result of bluegill predation. Rapid regeneration of *Caenis* could ameliorate what appeared to be a declining food source in terms of biomass. Also, increased primary production at elevated temperatures provided an abundant algal food source for primary consumers, and water quality (pH, DO, PO_4, turbidity, NO_2, NO_3, alkalinity) was not significantly different from that in ambient channels (Armitage unpubl. data).

For these reasons, and because production rate could be a clear expression of temperature, annual production of the sole species of *Caenis* occurring in the channels was estimated. This species has tentatively been identified as *Caenis* sp. nov. nr. *amica* Hagen (Paul Carlson pers. com.).

Responses of macroinvertebrates to elevated temperatures include changes in density and biomass (Kajak 1976; Rodgers 1980), life cycles (Aston 1968; Lutz & McMahon 1973), behavior (Bovbjerg 1975), distribution (Brittain 1976), growth and development (Sweeney 1978; Friesen et al. 1979), and physiology (Buckingham 1976). Work by Vannote and Sweeney (1980) has clarified the ways in which temperature can influence factors such as individual size and fecundity which contribute significantly to production. Production rates of freshwater macroinvertebrates, however, have not been directly related to temperature.

MATERIALS AND METHODS

The study site was the Browns Ferry Biothermal Research Station located on the north bank of the Tennessee River (Wheeler Reservoir) near Athens, Alabama (34° 42′ N, 87° 07′ W). The experiment was conducted in 12 channels with controlled flow and temperature. The concrete channels are 112-m long, 4.3-m wide, and 1.2-m deep. Substrates consist of six alternate zones of clay-silt and limestone rock (5-15 cm diameter) which provide six pools and six rock areas in each channel. Water depth is 1.2 m over the clay-silt areas and 0.3 m over the rock areas.

Flow rate was 0.66 m^3/min; ambient Tennessee River temperature, which ranged between 1.3 and 29.6° C during the study, was maintained in three channels. Temperatures elevated approximately 3, 6, and 9° C above ambient were each maintained in the inlets of three channels. Occasional variations of 1 or 2° C in target levels occurred downstream due to insolation and changing weather conditions. Elevated temperatures ranged between daily means of 1.8 and 31.7° C, 5.1 and 33.8° C, and 7.3 and 35.2° C, respectively, for each increment. These temperatures were superimposed on the diurnal and annual temperature fluctuations of ambient temperature (Fig. 1). See Armitage (1980) for a complete description of the facility.

All organisms but fish colonized naturally in 1974 (Armitage et al. 1978), providing habitat similar to littoral areas of large reservoirs in the southeastern United States. In

October 1977, two months before this study was begun, all channels were drawn down, leaving about 0.3 m of water in pool areas. Rotenone (2 ppm) was applied to pools for recovery of fish. Although many *Caenis* found refuge in moist algae on sediments of the rock areas, some were probably killed by the rotenone (see Helfrich 1980). Therefore, partial recolonization of the channels occurred during the study. Channels were again drawn down and treated with rotenone in October 1978.

Caenis were collected monthly (December 1977 - September 1978) near both the inlet and outlet of the 12 channels. As channels were drawn down during October and November, sampling was not possible during those months. The three major habitats, pool sediments, limestone rock areas, and concrete wall surfaces, were sampled. Pool areas contributed 48%, wall surfaces 28%, and rock areas 24% to the total habitat area within the channels. Data from these three habitats were pooled proportionally to give estimates of total densities in the channels.

Each month, 12 pool sediment samples were taken in both the second and fifth pool from the inlet in all channels. A 1.8 m length of PVC pipe was twisted into the substrate to give a core (25.76 cm^2 diameter) about 12 cm deep. Rock area samples were collected following 30-day colonization in galvanized trays (0.09 m^2) filled with crushed limestone rock like that in the channels. One rock area in each upper and lower channel section (the second and fifth rock areas from the inlet) was sampled with three rock trays. Initial treatment of rock tray samples in the laboratory involved gently brushing each rock to remove attached organisms. Trays with cleaned rocks were replaced in the channels on the same day they were removed. Concrete wall surfaces adjacent to pool areas were sampled using a scraping device with an attached net. This sampler was a 0.25 m long beveled blade supported by a semi-circular ring of metal from which a nylon plankton net was hung. The metal ring was attached to a broom stick handle. The sampler removed algae and associated organisms in a 0.25 m^2 area. Four samples each were collected from walls of the second and fifth pools of each channel each month. The second and fifth pool or rock area were chosen as sampling areas representing inlet sections, where temperatures were generally isothermal, and outlet sections, where there was occasional degradation of temperature (1-2°C). Sample locations within these inlet and outlet areas were randomized. Each month, a total of 114 samples were taken per temperature level (24 cores, 6 rock trays, and 8 wall scrapings). All types of samples were sieved (212 μm mesh) and then subsampled in a partitioned plexiglass tray. The 212 μm mesh sieve did not retain many very small instars (0-1.5 mm total length) because of head widths of less than 212 μm. The partitioned plexiglass tray (63 x 20 x 10 cm) was divided into ten equal volumes by removable partitions. Samples were placed in the tray without partitions and were evenly distributed across the bottom by stirring. Two partitions delineating one-tenth of the total sample were slid into place and the subsample was removed through an opening at the base of the subsampler.

Statistically significant differences among densities of *Caenis* in the four temperature levels were calculated using the Mann-Whitney U test (Elliott 1971) in order to illustrate population fluctuations occuring during the study of production. Total length of each *Caenis* nymph was measured from the tip of the head to the base of the cerci using an ocular micrometer and binocular microscope. Nymphs were grouped by 0.50 mm size class, channel habitat, and date, and were freeze-dried and weighed on an electrobalance to the nearest 1×10^{-4} mg. Emergence was monitored by observation five days a week of final nymphal and subimago exuviae on water and dry channel surfaces, respectively. This provided information on the initiation of emergence and the times of greatest numerical emergence.

Production rates and their approximate confidence limits were estimated by the size-frequency method (Hynes & Coleman 1968; Hamilton 1969) as modified by Krueger

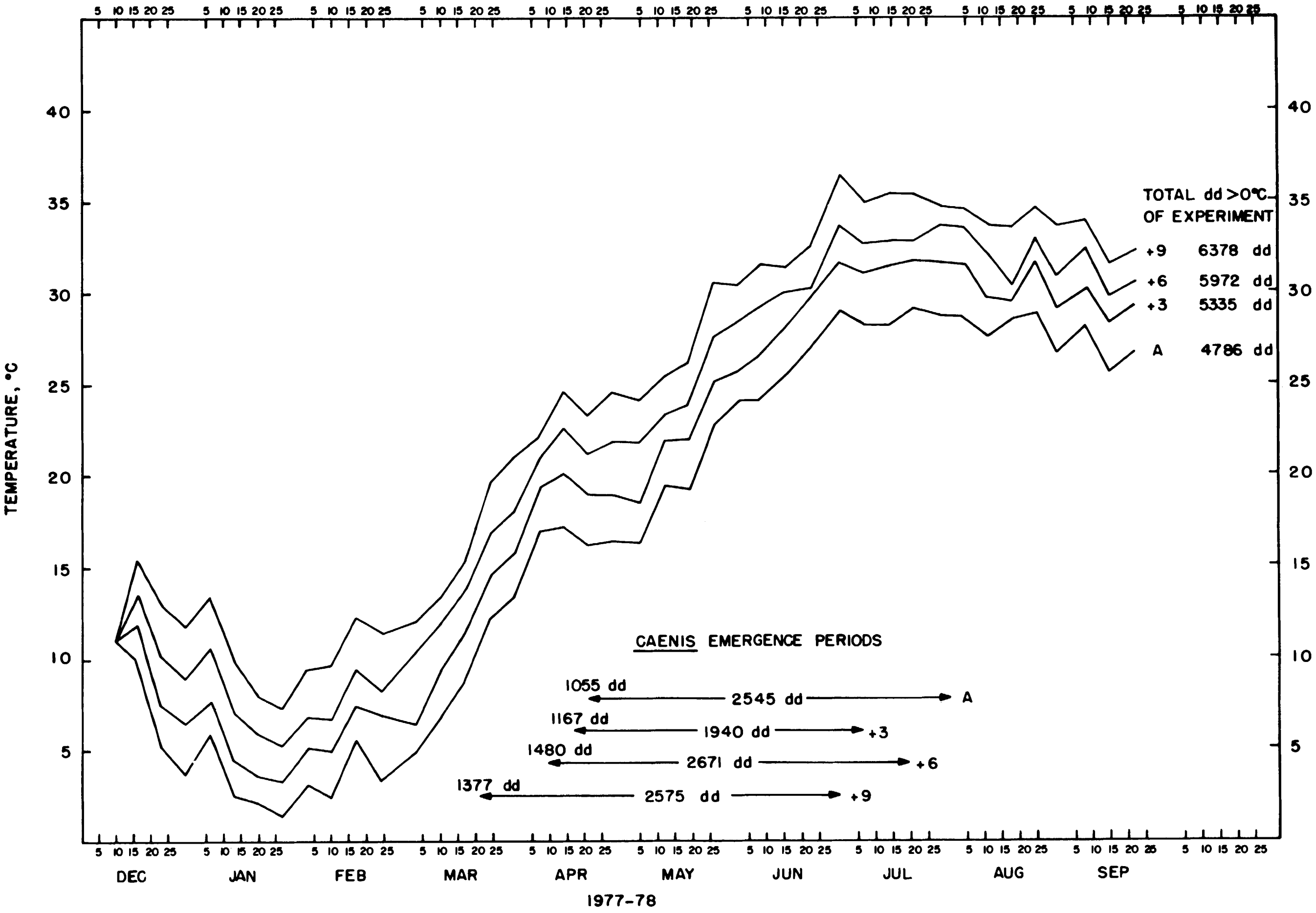

Fig. 1. Mean daily temperatures (°C) of four temperature levels in outdoor channels: A (ambient temperature of Wheeler Reservoir, Tennessee River) and 3°, 6°, and 9° C above ambient. Horizontal lines indicate duration of emergence periods. Number of degree-days (dd > 0° C) accumulated between December 10 and onset of emergence periods, and between December 10 and September 22 are presented.

and Martin (1980). Mean individual weights of small size classes were derived graphically by visual extrapolation of length by weight regressions as there were too few very small instars collected to give a dependable mean weight. Because samples were available for a period of only 10 months (December 1977 - September 1978), the remaining months of the year (October - December 1978) were included as one sampling period in which it was assumed, for the purposes of the calculations, that no *Caenis* were present. The resultant estimates were considered annual production, assuming that nymphs present in the winter of 1978 were overwintering with negligible growth.

RESULTS AND DISCUSSION

Nymphal Density

Estimates of *Caenis* densities indicated deleterious effects of elevated temperatures (Table 1). Warmer temperatures appeared conducive to population growth in May when the number of *Caenis* in +9 C channels ($605/m^2$) was greater than that in any other temperature level ($P \leq 0.05$). Daily mean temperatures in +9 C channels had risen from about 25° C during the preceding thirty days to 28° C. In June and July, population densities in +9 C channels were lower than those in any other temperature level. Between the May and June sampling dates, mean daily temperatures had risen to a maximum of 32.3° C in these channels. Temperatures were above 30° C for 18 days. Between June and July, temperatures were even higher, with a maximum of 36.2° C and 28 days above 31° C. One may infer that these temperatures were higher than optimum for growth of *Caenis* nymphs and that they caused declining densities. By August, *Caenis* in ambient channels were more abundant than in any other temperature ($P \leq 0.5$). This relationship persisted through September when there were $523/m^2$ in ambient channels but fewer than $50/m^2$ in other channels. Peaks seen in mean densities of *Caenis* in January in elevated temperatures were probably due to sampling error, as they did not reflect statistical changes in the populations. Differences between densities of *Caenis* within each temperature level from December to March were not significant ($P < 0.12$) and thus are not indicative of life-cycle events such as emergence or recruitment.

Emergence and Generation Time

Emergence of *Caenis* from +9 C channels began March 21, 31 days before that from ambient channels (Fig. 1). Emergence from +3 and +6 channels began four and eleven

TABLE 1

Mean densities (No./m^2 and 1 SE of the mean) of *Caenis* by temperature level, and their pair-wise significance of difference using the Mann-Whitney U test.

	Temperature				
Month	A	+3	+6	+9	U-Test, (P≤0.05)
12	998 ± 476.2	6 ± 2.5	29 ± 27.4	49 ± 40.7	
1	418 ± 194.9	11 ± 6.8	280 ± 212.2	175 ± 70.4	A > +3, +9
2	338 ± 259.2	31 ± 28.4	111 ± 110.7	34 ± 26.5	
3	384 ± 126.8	17 ± 11.6	7 ± 1.7	25 ± 13.0	+9 > +6
4	153 ± 59.1	52 ± 26.9	81 ± 57.7	54 ± 23.9	
5	197 ± 86.2	61 ± 41.2	259 ± 81.7	605 ± 111.4	+9 > A, +3, +6
6	527 ± 231.7	747 ± 305.9	290 ± 129.4	51 ± 37.8	A, +3, +6 > +9
7	716 ± 257.7	662 ± 240.3	568 ± 79.2	168 ± 62.6	A, +3, +6 > +9
8	639 ± 271.2	85 ± 24.3	190 ± 67.7	48 ± 30.8	A > +3, +6, +9 +6 > +9
9	523 ± 202.4	35 ± 14.2	12 ± 6.2	43 ± 31.9	A > +3, +6 +9

days, respectively, before that from ambient channels. Total lengths of nymphs at emergence ranged from about 6.0 to 7.5 mm. Mean daily temperatures at onset of emergence, were about, 16.2, 21.0, 22.3, and 13.6° C in ambient, +3, +6, +9 C channels, respectively. Evidently, initial emergence did not depend upon a thermal threshold (see Langford 1975; and Vannote & Sweeney 1980) but appeared to correlate quite closely with accumulation of degree-days. Between the beginning of the experiment in mid-December and initial emergence, there were 1,055 degree days (> 0° C) in ambient channels and 1,167, 1,480, and 1,377 in +3 C, +6 C, and +9 C channels, respectively (Fig. 1). Duration of emergence was very close to 100 days except in +3 channels where *Caenis* emerged for only about 80 days. The longest emergence period reported previously for *Caenis* spp. was that of *Caenis macrura* whose emergence lasted 84 days in the River Thames in Britain. Both *C. horaria* and *C. robusta* had considerably shorter emergence periods, about 49 days, in the same locale (Mackey 1978). The long emergence periods may be explained by the tendency for several mayflies, especially some Baetidae and Caenidae, to become non-seasonal in southern climates (Edmunds et al. 1976).

The type of voltinism of the Caenidae is undecided. While Moon (1939) found *Caenis horaria* and Sweeney (1976) found *Caenis simulans* to be univoltine, Edmunds et al. (1976) claim that Caenidae have two generations per year. Edmunds et al. (1976) suggested that there is almost certainly a tendency to overestimate the length of time needed for development of ephemeropteran nymphs. The length of the emergence periods of *Caenis* in the biothermal channels implies the possibility of more than one generation per year. An examination of size frequency diagrams (Fig. 2) supports this possibility.

The diagrams indicate that *Caenis* overwinter as nymphs whose range of total length is 1.0-5.75 mm, suggesting a lack of synchronism before emergence. This asynchronism was reflected in the lengthy periods of emergence during the summer. Although the frequency diagrams obscure all but peak abundances of size groups at monthly intervals, these peaks suggest at least two generations of *Caenis* per year at each temperature level. Large nymphs (7.0 to 7.5 mm total length), ready to emerge, were abundant enough to be collected only in April in +6 and +9 channels, and only in May in ambient channels. The largest nymphs collected in +3 channels were 6.5 mm long; these did not appear until June.

Although indicated only sporadically in Figure 2, recruitment of small instars appeared late in the summer, suggesting a second generation (e.g., in July and September in ambient channels, and in July in +3 C and +9 C channels). This recruitment was probably the result of a second generation developing during the warm summer months. The largest nymphs of this second generation were smaller than those of the earlier winter generation as would be expected (Sweeney 1978).

Although earlier onset of emergence in warmer channels could have indicated increased voltinism, the similarity of both duration of emergence and number of degree-days accumulated during emergence supported the assumption of the same voltinism in all channels. There were 2,545, 1,940, 2,671, and 2,575 degree-days accumulated in the four temperature levels during the emergence periods (Fig. 1). Only the +3 channels were different, as discussed later. Had there been a greater number of degree-days during the emergence period in elevated temperatures, one might have expected a greater number of generations. The total degree-days during the experiment in each elevated temperature (5,335, 5,972, and 6,378) was greater than in ambient (4,786), but did not effect increased voltinism.

Production

Calculations of annual production rates (mg DW/m^2), assuming two generations per year, appear in Tables 2 through 5. The cohort production interval (CPI factor) (Benke 1979) was not used, as eggs from natural swarms of females hatch within six days in the

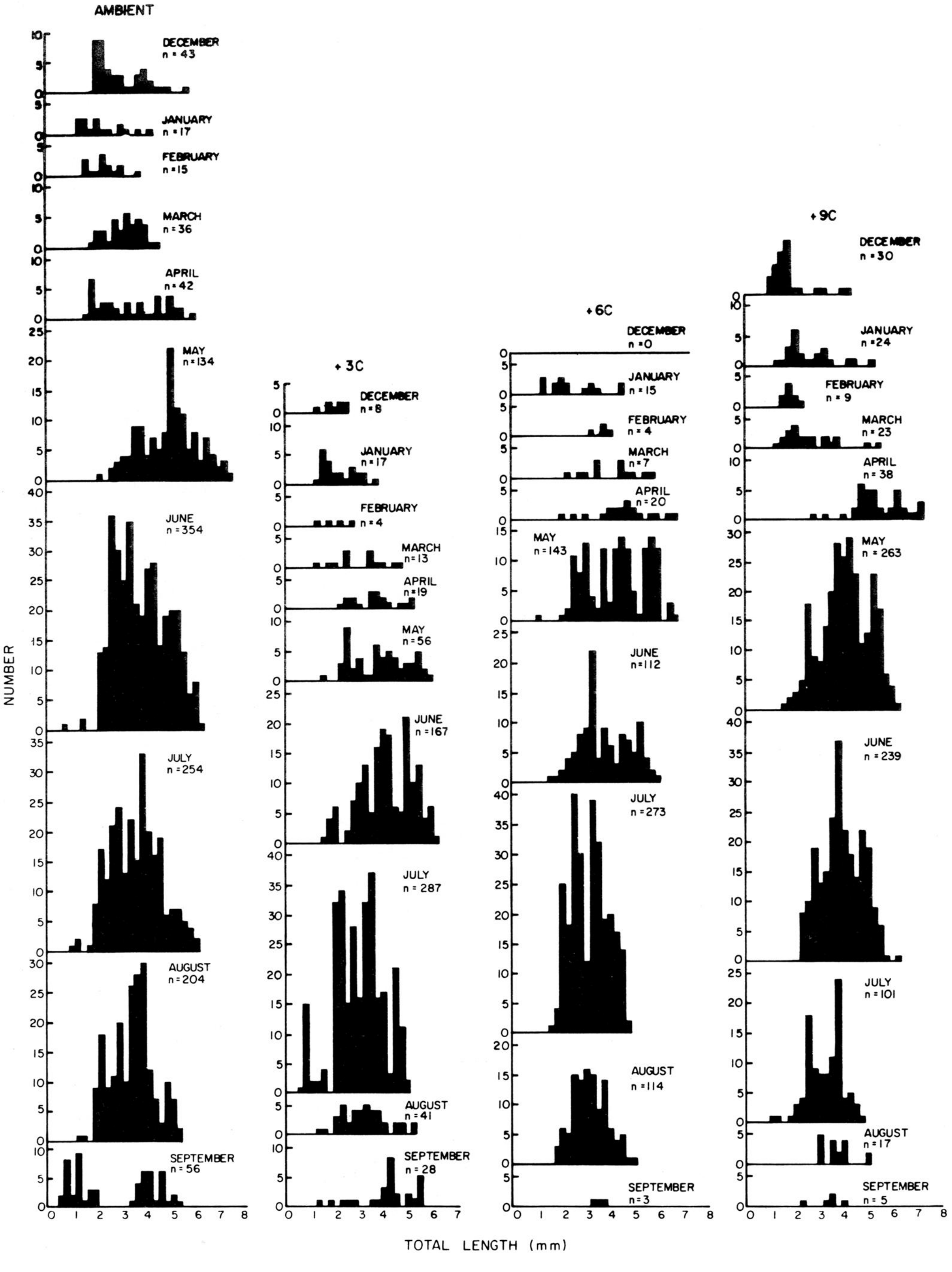

Fig. 2. Number of *Caenis* nymphs in mm size classes, by month, in four temperature levels.

TABLE II

Calculation of annual production of *Caenis* (mg DW/m^2) in ambient channels by size-frequency method. Zeros in the first three rows replace negative values resulting from inadquate sampling of small instars. Densities of these instars, their variances, and their individual weights are retained in the second, third, and fifth columns, respectively.

Size Class (mg)	$\bar{x}$ Annual No./m^2	Variance	No. Lost per m^2	$\bar{x}$ mg DW per Indiv.	Wt at Loss	Wt Loss (mg/m^2)	Production*
0-0.5	0	0		0.0125			
			0		0	0	0
0.5-1.0	0.8	0.2		0.0180			
			0		0	0	0
1.0-1.5	8.6	58.5		0.0255			
			0		0	0	0
1.5-2.0	116.4	1058.3		0.0341			
			48.3		0.042	2.029	30.429
2.0-2.5	68.1	445.1		0.0518			
			9.1		0.060	0.546	8.190
2.5-3.0	59.0	263.3		0.0703			
			13.3		0.099	1.317	19.751
3.0-3.5	45.7	87.7		0.1400			
			-6.8		0.106	-0.721	-10.812
3.5-4.0	52.5	153.7		0.1597			
			19.4		0.177	3.434	51.507
4.0-4.5	33.1	65.5		0.1968			
			15.8		0.241	3.808	57.177
4.5-5.0	17.3	13.4		0.2957			
			-3.4		0.350	-1.190	-17.850
5.0-5.5	20.7	48.9		0.4152			
			16.1		0.546	8.791	131.859
5.5-6.0	4.6	1.2		0.7176			
			3.6		0.854	3.074	46.116
6.0-6.5	1.0	0.1		1.0153			
			-0.1		1.023	-0.102	-1.535
6.5-7.0	1.1	0.2		1.0433			
			0.6		1.276	0.766	11.484
7.0-7.5	0.5	0.1		1.5606			
			0.5		1.561	0.561	11.707

*Values are 15 x values in preceding column.

Annual Production (P) = 338.02 x 2 = 676.04 mg DW/m^2
Variance = 881.82
95% Confidence Region = $438.48 \leq P \leq 913.60$
P/B = 12.72

TABLE III

Calculation of annual production of *Caenis* (mg DW/m^2) in +3 C channels by the size-frequency method. Zeros in the first two rows replace negative values resulting from inadequate sampling of small instars. Densities of these instars, their variances, and their individual weights are retained in the second, third, and fifth columns, respectively.

Size Class (mg)	$\bar{x}$ Annual No./m^2	Variance	No. Lost per m^2	$\bar{x}$ mg DW per Indiv.	Wt at Loss	Wt Loss (mg/m^2)	Production*
0-0.5	0.1	0		0.0161			
					0	0	0
0.5-1.0	1.6	0.9		0.0200			
			0		0	0	0
1.0-1.5	3.3	5.7		0.0243			
			0.7		0.027	0.019	0.246
1.5-2.0	2.6	0.7		0.0310			
			-13.9		0.040	-0.556	-7.228
2.0-2.5	16.5	41.4		0.0529			
			-1.9		0.064	-0.122	-1.581
2.5-3.0	18.4	20.9		0.0786			
			4.4		0.106	0.466	6.063
3.0-3.5	14.3	17.5		0.1441			
			-0.2		0.164	-0.033	-0.426
3.5-4.0	14.5	4.6		0.1874			
			4.3		0.228	0.980	12.745
4.0-4.5	10.2	1.8		0.2772			
			1.6		0.359	0.574	7.467
4.5-5.0	8.6	2.6		0.4646			
			2.5		0.547	1.368	17.778
5.0-5.5	6.6	2.2		0.6436			
			4.1		0.754	3.091	40.188
5.5-6.0	2.0	0.8		0.8832			
			1.5		1.021	1.532	19.910
6.0-6.5	0.5	0.1		1.1800			
			0.5		1.180	0.590	7.670

*Values are 13 x values in preceding column.

Annual Production (P) = 102.83 x 2 = 205.66 mg DW/m^2
Variance = 70.76
95% Confidence Region = $138.36 \leq P \leq 272.96$
P/B = 10.08

TABLE IV

Calculation of annual production of *Caenis* (mg DW/m^2) in +6 C channels by the size-frequency method. Zeros in first two rows replace negative values resulting from inadequate sampling of small instars. Densities of these instars, their variances, and their individual weights are retained in the second, third, and fifth columns, respectively.

Size Class (mg)	$\bar{x}$ Annual No./m^2	Variance	No. Lost per m^2	$\bar{x}$ mg DW per Indiv.	Wt at Loss	Wt Loss (mg/m^2)	Production*
0-0.5	0	0		0.0130			
			0		0	0	0
1.0-1.5	10.4	29.0		0.0265			
			0.7		0.030	0.021	0.294
1.5-2.0	9.7	32.1		0.0335			
			-10.8		0.040	-0.432	-6.048
2.0-2.5	20.5	71.8		0.0472			
			4.2		0.065	0.273	3.822
2.5-3.0	16.3	9.4		0.0890			
			-6.8		0.112	-0.762	-10.662
3.0-3.5	23.1	60.0		0.1406			
			-2.3		0.160	-0.368	-5.152
3.5-4.0	25.4	20.0		0.1814			
			16.0		0.213	3.408	47.712
4.0-4.5	9.4	7.1		0.2490			
			-2.9		0.291	-0.844	11.815
4.5-5.0	12.3	4.9		0.3399			
			9.4		0.424	3.986	55.798
5.0-5.5	2.9	0.2		0.5287			
			-0.2		0.575	-0.115	-1.610
5.5-6.0	3.1	1.2		0.6243			
			1.0		0.780	0.780	10.920
6.5-7.0	2.1	0.3		0.9750			
			1.5		0.998	1.497	20.958
7.5-8.0	0.6	0.1		1.0218			
			0.6		1.022	0.613	8.585

*Values are 13 x values in preceding column.

Annual Production (P) = 136.43 x 2 = 272.86 mg DW/m^2
Variance = 95.63
95% Confidence Region = $194.64 \leq P \leq 351.09$
P/B = 11.60

TABLE V

Calculation of annual production of *Caenis* (mg DW/m^2) in +9 C channels be size-frequency method. Zeros in first three rows replace negative values resulting from inadequate sampling of small instars. Densities of these instars, their variances, and their individual weights are retained in the second, third, and fifth columns, respectively.

Size Class (mg)	$\bar{x}$ Annual No./m^2	Variance	No. Lost per m^2	$\bar{x}$ mg DW per Indiv.	Wt at Loss	Wt Loss (mg/m^2)	Production*
0-0.5	0	0		0.0135			
			0		0	0	0
0.5-1.0	0.1	0		0.0195			
			0		0	0	0
1.0-1.5	0.7	0.1		0.0275			
			o		0	0	0
1.5-2.0	16.4	33.4		0.0342			
			9.8		0.044	0.431	6.468
2.0-2.5	6.6	7.5		0.0560			
			-8.1		0.067	-0.543	-8.141
2.5-3.0	14.4	12.7		0.0796			
			-0.6		0.102	-0.061	-0.918
3.0-3.5	15.3	13.9		0.1314			
			-17.4		0.156	-2.714	-40.716
3.5-4.0	32.7	9.4		0.0849			
			16.7		0.230	3.841	57.615
4.0-4.5	16.0	29.9		0.2871			
			7.0		0.316	2.212	33.180
4.5-5.0	9.0	3.5		0.3479			
			2.2		0.432	0.950	14.256
5.0-5.5	6.8	3.7		0.5354			
			3.9		0.615	2.399	35.978
5.5-6.0	2.9	0.5		0.7075			
			1.7		0.806	1.370	20.553
6.0-6.5	1.2	0.4		0.9185			
			0.1		1.033	0.103	1.550
6.5-7.0	1.1	0		1.1607			
			0.6		1.492	1.895	1.343
7.0-7.5	0.5	0		1.9175			
			0.5		1.918	0.959	14.381

*Values are 15 x values in preceding column.

Annual Production (P) = 135.55 x 2 = 271.10 mg DW/m^2
Variance = 136.51
95% Confidence Region = $177.63 \leq P \leq 252.39$
P/B = 11.47

laboratory (Rodgers, unpubl. data). Despite large variance within samples, production was significantly greater in ambient channels 676.04 ± 237.56 mg DW/m^2/yr than in any other temperature level. Production rates at the three elevated temperatures were 205.66 ± 67.30 mg DW/m^2, 272.86 ± 78.23 mg DW/m^2, and 271.10 ± 93.47 mg DW/m^2 (Fig. 3). Annual P/B ratios were similar in all channels; they were 12.72, 10.08, 11.60, and 11.47 in ambient, +3 C, +6 C, and +9 C channels, respectively.

Caenis in +3 channels exhibited an anomaly during this study. Their maximum length did not reach 7.0 mm, as it did in all other temperature levels, and their emergence period was only 80 days, about 20 days shorter than in other channels. A consequence of the shorter emergence period was a lesser accumulation of degree-days during the emergence period. Their production rates and P/B ratios were the lowest of the four temperature levels, although not significantly so. The +3 channels had received the warmest (+6° C) temperature level during an experiment the previous year, and this previous treatment had reduced the density of *Caenis* to 150/m^2 in August 1977. Further reduction caused by rotenone and natural mortality left a population of only about 6/m^2 in +3 channels at the beginning of the present experiment. Extreme variance in numbers of nymphs in samples taken from ambient channels at the beginning of the present experiment in December 1977 obscured the probable real differences in densities between ambient and +3

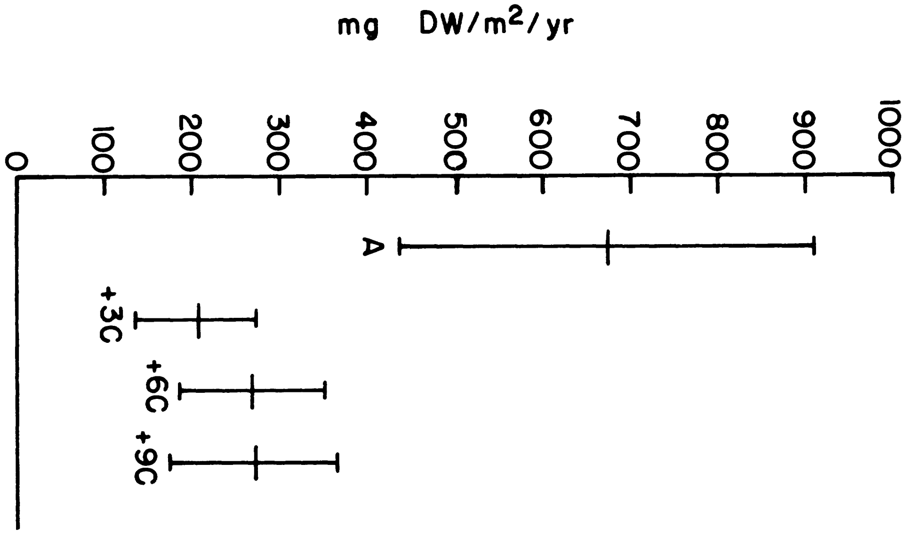

Fig. 3. Rates of production (mg DW/m^2/yr) of *Caenis* at four temperature levels estimated by the size-frequency method (Hynes & Coleman 1968; Hamilton 1969) as modified by Krueger and Martin (1980).

channels. Nymphal populations in +3 channels were probably smaller than those in ambient channels, although the statistical analysis failed to show this (December, Table 1). By February, densities of *Caenis* in +3 channels had reached a level similar to that in other channels. But the depressed population caused by the earlier experiment in +3 channels, may have effectively limited size and emergence period in 1978.

Estimates of *Caenis* production in the channels are low relative to most published estimates of ephemeropteran production. The range of production estimates for Ephemeroptera cited by Waters (1977) is 120 to 4450 mg/m^2. Of these estimates production of *Caenis* in ambient channels exceeded only that of *Hexagenia limbata* (Serville) (Ephemeroptera: Ephemeridae) in a Kansas reservoir (Horst & Marzolf 1975) and of *Choroterpes* sp. in Texas (McClure & Stewart 1976). Turnover ratios calculated for *Caenis* (10.08-12.72) were generally higher than those reported by Waters (1977), most of which were 8.4 or lower. Although small organisms, like *Caenis*, often demonstrate very high rates of production by virtue of short generation times and high P/B ratios, they must be abundant to contribute significantly to production in the community. In this case, *Caenis* had relatively high P/B ratios but low population densities (6-998/m^2), limiting potential for production per unit area. Predation by bluegill and other invertebrates such as odonates no doubt caused some reduction in densities of *Caenis*.

Several sources of error exist in the production estimates. The most important error may have arisen from the assumption of bivoltinism. The available evidence implies two asynchronous generations per year. Intra-sample variance, particularly in ambient channels, was great, but it was incorporated into the calculation of confidence limits. Many small instars were undoubtedly lost while sieving, some nymphal mortality was balanced by recruitment between samples (Winterbourn 1974), and nymphal growth through more than one size class undoubtedly occurred between samples (Waters & Crawford 1973). Another source of error is the assumption of negligible growth of nymphs during October and November when sampling was not possible. These sources of error would all lead to an underestimate of production. A source of error modifying this underestimate was the assumption that second generation nymphs reached the same maximum length as first generation nymphs.

Despite these possible errors, it is evident that *Caenis* did not produce as much biomass in elevated temperatures as in ambient temperatures. Instead, production rate was significantly reduced in elevated temperatures and the P/B ratio was unaffected due to decline in biomass. Two apparent possible causes for these effects are mortality caused directly by warmer temperatures, and increased bluegill predation. A more subtle cause could be change in the partitioning of assimilated energy by *Caenis*. Non-optimal temperatures, whether too high or too low, can lead to the channelling of a disproportinate amount of energy into maintenance metabolism rather than into growth and development of adult tissues. Generally, there is a positive correlation between adult female size and fecundity in aquatic insects (Clifford 1970). Temperatures higher than optimal can shorten life cycle duration, decreasing the time available for larval growth. Smaller, less fecund females are the result. Vannote and Sweeney (1980) present models describing these phenomena in relation to local and geographic water temperature regimes. They hypothesize that "subpopulations in non-optimum habitats are characterized by low population density and small individuals with reduced fecundity." Since this study, it has been shown that fecundity of *Caenis* in the channels is reduced in temperatures 9°C, but not 3° or 6°C above ambient (Rodgers, In Press). The reduced production of *Caenis* in this study was probably the result of a combination of direct temperature-caused mortality, bluegill predation, reduced fecundity, and other undetermined causes.

These production data suggest that this population of *Caenis* is at or near the southern limit of the species range. *Caenis* spp. in the southeastern United States are lower boreal in origin and range southward into Mexico and sometimes into South America (Berner 1977). However, *Caenis amica*, to which the species in the biothermal channels appear to be closely related, has been collected only in North Carolina, South Carolina, and Tennessee (Berner 1977). *Caenis* sp. nov. nr. *amica* thrived in ambient mean daily temperatures which ranged between 1.3° and 29.6° C during this study. Further research is needed to determine whether these temperatures are optimal for this species.

LITERATURE CITED

ARMITAGE, B.J., FORSYTHE, T.D., RODGERS, E.B., & WRENN, W.B. 1978. Browns Ferry Biothermal Research Series I. Colonization by periphyton, zooplankton, and macroinvertebrates. EPA Ecological Research Series, EPA-600/3-78-020, Duluth, MN.

ARMITAGE, B.J. 1980. Effects of temperature on periphyton biomass and community composition in the Browns Ferry experimental channels. *In* Giesy, J.P., ed., *Microcosms in Ecological Research,* DOE Symposium Series (CONF-781101), NTIS, Springfield, VA.

ASTON, R.J. 1968. The effect of temperature on the life cycle, growth, and fecundity of *Branchiura sowerbyi* (Oligochaeta: Tubificidae). *J. Zool. Lond.,* 154: 29-40.

BENKE, A.C. 1978. Interactions among coexisting predators - a field experiment with dragonfly larvae. *J. Anim. Ecol.,* 47: 335-350.

BENKE, A.C. 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. *Limnol. Oceanogr.,* 24: 168-171.

BERNER, L. 1977. Distributional patterns of southeastern mayflies (Ephemeroptera). *Bull. Fla. State Mus. Biol. Sci.,* 22: 1-56.

BOVBJERG, R.V. 1975. Dispersal and dispersion of pond snails in an experimental environment varying to three factors, singly and in combination. *Physiol. Zool.,* 48: 203-213.

BRITTAIN, J.E. 1976. Experimental studies on nymphal growth in *Leptophlebia vespertina* (L.) (Ephemeroptera). *Freshwat. Biol.,* 6: 445-449.

BUCKINGHAM, M.J. & FREED, D.E. 1976. Oxygen consumption in the prosobranch snail *Viviparus contectoides* (Mollusca: Gastropoda). II. Effects of temperature and pH. *Comp. Biochem. Physiol.,* 53A: 249-252.

CARLANDER, K.D. 1977. *Handbook of Freshwater Fishery Biology.* Vol. 2, Iowa State University Press, Ames.

CLIFFORD, H.H. 1979. Analysis of a northern mayfly (Ephemeroptera) population with special reference to allometry of size. *Can. J. Zool.,* 48: 305-316.

EDMUNDS, G.F., JR., JENSEN, S.L. & BERNER, L. 1976. *The Mayflies of North and Central America.* University of Minnesota Press, Minneapolis.

ELLIOTT, J.M. 1971. *Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates.* Scientific Publication No. 25, Freshwater Biological Association, The Ferry House, Ambleside, Westmoreland.

EL-SHAMY, F.M. 1978. Dynamics of feeding and growth of bluegill (*Lepomis macrochirus*) in Lake Wingra and Lake Mendota, Wisconsin. *Hydrobiol.,*60: 113-124.

FRIESEN, M.K., FLANNAGAN, J.F. & LAWRENCE, S.G. 1979. Effects of temperature and cold storage on development time and viability of eggs of the burrowing mayfly *Hexagenia rigida* (Ephemeroptera: Ephemeridae). *Can. Ent.,* 111: 665-673.

HALL, D.J., COOPER, W.E. & WERNER, E.E. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.,* 15: 839-928.

HAMILTON, A.L. 1969. On estimating annual production. *Limnol. Oceanogr.,* 14: 771-782.

HELFRICH, L.A. 1980. Effects of rotenone on macrobenthic invertebrates of a Pennsylvania stream. *Proc. Ann. Conf. S.E. Assoc. Fish and Wildl. Agencies,* 32: 401-408.

HORST, T.J. & MARZOLF, G.R. 1975. Production ecology of burrowing mayflies in a Kansas reservoir. *Verh. Internat. Verein. Limnol.,* 19: 3029-3038.

HYNES, H.B.N. & COLEMAN, M.J. 1968. A simple method of assessing the annual production of stream benthos. *Limnol. Oceanogr.,* 13: 569-573.

KAJAK, Z. 1976. Effect of heated waters on biocenosis of the moderately polluted Narew River. General Conclusions. *Pol. Arch. Hydrobiol.*, 23: 555-561.

KRUEGER, C.C. & MARTIN, F.B. 1980. Computation of confidence intervals for the size-frequency (Hynes) method of estimating secondary production. *Limnol. Oceanogr.*, 25: 773-777.

LANGFORD, T.E. 1975. The emergence of insects from a British river, warmed by power station cooling-water. Part II. The emergence patterns of some species of Ephemeroptera, Trichoptera, and Megaloptera in relation to water temperatures and river flow, upstream and downstream of the cooling-water outfalls. *Hydrobiol.*, 47: 91-133.

LUTZ, P.E. & McMAHON, E.A. 1973. Five year patterns of emergence in *Tetragoneuria exilis* (Odonata). *Ann. Ent. Soc. Am.*, 66: 1343-1348.

MACKEY, A.P. 1978. Emergence patterns of three species of *Caenis* Stephens (Ephemeroptera: Caenidae) *Hydrobiol.*, 58: 277-280.

McCLURE, R.G. & STEWART, K.W. 1976. Life cycle and production of the mayfly *Choroterpes* (*Neochoroterpes*) *mexicanus* Allen (Ephemeroptera: Leptophlebiidae). *Ann. Entomol. Soc. Amer.*, 69: 134-144.

MOON, H.P. 1939. The growth of *Caenis horaria, Leptophlebia vespertina,* and *L. marginata. Proc. Zool. Soc. Lond.*, (A) 108: 507-512.

RODGERS, E.B. 1980. Effects of elevated temperatures on macroinvertebrate populations in the Browns Ferry Experimental Ecosystems. *In* Giesy, J.P., ed., *Microcosms in Ecological Research,* DOE Symposium Series (CONF-781101), NTIS, Springfield, VA.

RODGERS, E.B. In Press. Fecundity of *caenis* sp. (Ephemeroptera: Caenidae) in elevated temperatures.

SADZIKOWSKI, M.R. 1976. A comparison of the food habits of size classes of three sunfishes (*Lepomis macrochirus* Rafinesque, *L. gibbosus* (Linnaeus), and *L. cyanellus* Rafinesque). *Am. Midl. Nat.*, 95: 220-225.

SWEENEY B.W. 1976. The response of aquatic insects to thermal variation. Ph.D. Thesis, Univ. Pennsylvania, Philadelphia. 203 p.

SWEENEY, B.W. 1978. Bioenergetic and developmental response of a mayfly to thermal variation. *Limnol. Oceanogr.*, 23: 461-477.

VANNOTE, R.L. & SWEENEY, B.W. 1980. Geographic analysis of thermal equilibria: A conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *Am. Nat.*, 115: 667-695.

WATERS, T.F. & CRAWFORD, G.W. 1973. Annual production of a stream mayfly population. A comparison of methods. *Limnol. Oceanogr.*, 18: 286-296.

WATERS, T.F. 1977. Secondary Production in Inland Waters. *In* MacFayden, A., ed., *Advances in Ecological Research,* Vol. 10, Academic Press.

WINBERG, G.G. 1971. *Methods for the Estimation of Production of Aquatic Animals.* Academic Press, N.Y.

WINTERBOURN, M.J. 1974. The life histories, trophic relations, and production of *Stenoperla prasina* (Plecoptera) and *Deleatidium* sp. (Ephemeroptera) in a New Zealand river. *Freshwat. Biol.*, 4: 507-524.

WRENN, W.B., ARMITAGE, B.J., RODGERS, E.B., & FORSYTHE, T.D. 1979. Browns Ferry Biothermal Research Series II. Effects of temperature on bluegill and walleye, and periphyton, macroinvertebrate, and zooplankton communities in experimental ecosystems. EPA Ecological Research Series. 600/3-79-092.