Life History of a Multivoltine Mayfly, *Tricorythodes minutus:*[1] an Example of the Effect of Temperature on the Life Cycle[2]

ROBERT L. NEWELL[3] AND G. WAYNE MINSHALL[4]

ABSTRACT

Ann. Entomol. Soc. Am. 71: 876–881 (1978)

The life history of the mayfly *Tricorythodes minutus* Traver (Ephemeroptera: Tricorythidae) was investigated at 2 locations in Deep Creek, Curlew Valley, Idaho-Utah. One has a spring source and relatively constant temperature of 18°C whereas the other has a normal seasonal fluctuation in water temperature. *T. minutus* is multivoltine at the 1st station and bivoltine at the other. Eggs are ovoid, 125×146 μm, covered by raised reticulations, and have an adhesive disc at one end. Adult females carry up to 1500 eggs and deposit them in small clusters with each visit to the stream surface. First instars are 0.45 mm long and lack gills and opercula. Males have about 19 instars and females 23. Mating occurs in flight and females deposit eggs in riffle areas. Standing crop was variable, with maxima of 11,250 m^{-2} at the 1st station and 1400 m^{-2} at the 2nd.

Tricorythodes minutus Traver is widespread and abundant in the northwestern United States (Argyle and Edmunds 1962, Pearson et al. 1968, Newell 1971). However, except for notes on late summer emergence in Utah (Needham and Christenson 1927), Idaho (Jensen 1966), and Alberta (Clifford 1969, Clifford et al. 1973), its biology, nymphal development, and behavior are poorly known. This study was undertaken to provide detailed description of the life history of *T. minutus* from two locations in Deep Creek, Idaho-Utah. The study revealed the unusual situation of a species bivoltine at one location and multivoltine at another. This discovery led to investigation of the effect of temperature on nymphal development.

Deep Creek lies in Curlew Valley, a 3460-km^2 drainage basin on the Idaho-Utah border (latitude 41°40′ to 42°30′ north, longitude 112°30′ to 113°20′ west). The climate is arid, with 15–39 cm precipitation/yr, and is classified as cool desert. We sampled at two of the four stations used by the IBP Desert Biome research team from Idaho State University. One (IBP Station 2) is approximately 5 km southwest of Holbrook, Idaho and 2 km below a large spring. From this spring about 1 $m^3\ sec^{-1}$ of water flows at a constant temperature of 18°C. The second station (IBP Station 4) is 4 km upstream from where the stream sinks into the desert near Snowville, Utah; water temperature showed a distinct seasonal pattern ranging from 0°C in winter to 29°C in midsummer. Koslucher and Minshall (1973) describe the stream more completely.

Methods and Materials

Four benthos samples of 625 cm^2 were taken monthly for 27 months from Station 2 with a modified Hess sampler (mesh size 390 μm). Two of the samples were taken in a riffle and two were collected in a non-turbulent reach. Two monthly samples also were collected from a reach at Station 4. Samples were preserved in 10% formalin in the field and returned to the laboratory, where all *Tricorythodes* were removed and counted. Head width, pronotum width, and total length were measured to the nearest 0.1 mm with an ocular micrometer on a dissecting microscope and length-frequency histograms were constructed. Sex was determined for mature nymphs (total length > 3.5 mm). Female nymphs were dissected and all eggs were removed, counted, measured (to the nearest 0.01 mm), and weighed. Approximately 300 nymphs were weighed individually in the wet and dry condition and following ignition at 550°C. Sixteen nymphal skins also were measured and dry weight was obtained on an electrobalance.

Janetschek's (1967) method of determining number of instars was utilized. A random sample of about 300 nymphs was selected and a size frequency histogram was constructed. A second histogram was then drawn giving the running means of measurements to show the trend of the samples; for example, a running average of five of the X^{th} size class ($\overline{Y_x}$) is equal to 1/5 ($Y_{x-2} + Y_{x-1} + Y_x + Y_{x+1} + Y_{x+2}$). When the second histogram is subtracted from the first, the resulting diagram indicates the periodic maxima and minima and thus is a rough method of determining the modes of a multimodal distribution. It can be expected that a determination of the number of modes in the size-frequency distribution of the nymphs will indicate the number of instars; and if Dyar's rule of a constant relative growth increment between successive instars is followed, the peaks should be at equal distances along a logarithmic scale.

Frequent visits to the study stations and 18 day-long observation periods provided emergence data such as timing, weather effects, sites of emergence, flight patterns, and oviposition behavior. Eggs were removed from ovipositing females and counted, and measurements were made on extruded egg clusters.

Eggs

Eggs of *T. minutus* are ovoid, measure $125 \pm 3 \times 146 \pm 4$ μm, have an adhesive disc on one end, and are covered with small, raised reticulations. Those *in utero* and extruded onto the subgenital plate are green. After a few minutes in water the eggs darken to brown or black. After several days in water unfertilized eggs become opaque white while fertile ones remain dark. Eggs of a closely related species, *T. atratus*, are similar in shape to those of *T. minutus* (Hall et al. 1975), but they are larger (200×250 μm), with scales around the outer edge, and with numerous filaments at one end.

Fecundity

As the nymphs near maturity, the eggs begin to develop and the females become more robust. Female nymphs as

---

[1] Ephemeroptera: Tricorythidae.

[2] This work is part of a dissertation for the partial fulfillment for a Ph.D. degree at Idaho State University. This research was funded in part by an IBP Desert Biome research assistantship. Received for publication Apr. 28, 1978.

[3] Environmental Sciences Div., Stearns-Roger Inc., P.O. Box 5888, Denver, CO 80217.

[4] Biology Dept., Idaho State Univ., Pocatello 83209.

0013-8746/78/0608-7606$00.75/0

small as 3.9 mm body-length contain as many as 325 eggs and the number increases until emergence (Fig. 1); the greatest number removed from an adult was 1500. There is a direct correlation between the total length of a female and the number of eggs present (Fig. 1). Mean dry weight for a single egg was 0.870 (±0.030 SE) μg, with a mean ash-free dry weight of 0.110 (±0.014 SE) μg, and a mean percent organic matter of 87.51 (N=8). The eggs of a 5.4 mm female weighing about 2.30 mg (Fig. 7) and carrying 1500 eggs weighing 1.305 mg would constitute over 56% of the total dry weight of the female. The eggs are extruded as a spherical mass and held on the subgenital plate until release. The mean diameter of 39 egg clusters removed from swarming females was 1.085 (±0.026 SE) mm. Egg cluster diameter is directly proportional to egg number (Fig. 2); the largest cluster (1.62 mm) contained 815 eggs and the smallest (0.93 mm) 280 eggs. Several clusters of eggs are produced. This is confirmed by the fact that females make several trips to the water's surface to deposit the eggs. Analysis of total egg numbers and number of eggs per cluster suggests that 2 to 4 clusters are extruded during oviposition.

Nymphs

Abundance

Early instars were always present in the collections at Station 2 but were never very abundant. Some of these may have passed through the collection net but it is doubtful that many escaped. From the regression relationships between total length (Y) and pronotum (X) or meso-metanotum width (Z) (where Y = −0.4132 + 3.9160X and 0.5009 + 2.4729Z, respectively), it can be determined that a nymph with a body narrow enough to pass through the net would be 1.1 to 1.4 mm long. This is not much longer than the nymph at hatching (0.45 mm). In addition, a nymph with a body narrow enough to pass through a 0.390-mm opening would have trouble getting through because of the additional width added by the legs. Finally, many of the nymphs when captured would be turned sideways making them too large to pass through the openings. A possible explanation for low numbers of very small nymphs in the collections is that they grow through the early instars very rapidly, so at any one moment large numbers are not present.

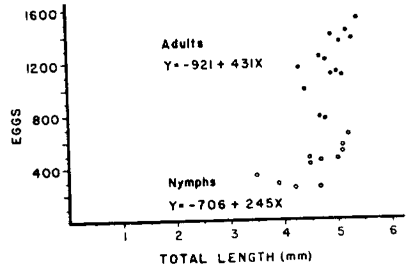


FIG. 1.—Relationship of total body length to number of eggs for nymphs (open circles) and adults (closed circles).

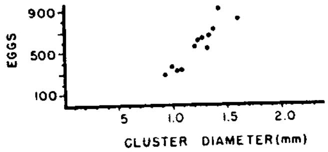


FIG. 2.—Relationship of egg cluster diameter to number of eggs.

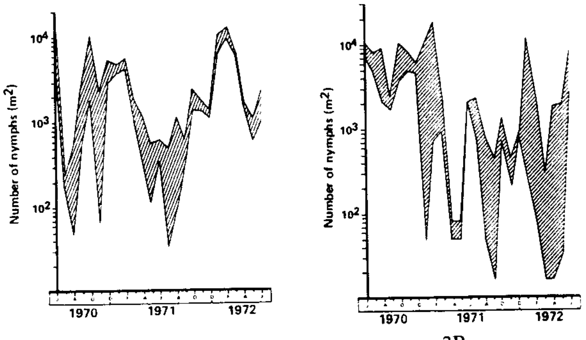
T. minutus was very abundant in Deep Creek Station 2, reaching densities as great as 11,250/m² (Fig. 3). During 1970–1971 benthic densities of *T. minutus* at Station 2 averaged 3610/m² and decreased to 2160/m² during the second year. A mean density of 2735/m² was observed over the 27 months of the study (Table 1). At Station 4 benthic densities of *T. minutus* were consistently lower than at Station 2, averaging 290/m² over the study period. Most (1400/m²) were collected during the winter. In many cases the numbers collected from monthly duplicate samples varied widely, suggesting the nymphs are clumped in distribution (Fig. 3, 4). Samples from riffle areas (Fig. 3A) varied less than those from pools (Fig. 3B). Densities of nymphs at both stations were low during summer months, and high during the winter. At Station 2 the seasonal trend was more evident in samples from riffle areas than from reach areas. Stream flow varied drastically, due to the periodic withdrawal of water for irrigation. The low summer densities may have resulted from the variations in flow which caused large numbers of organisms to leave the area via drifting (Minshall and Winger 1968). However, Hall (1975) also found a midsummer low in the density of *T. atratus* nymphs (like that shown for Station 4, Fig. 4) and attributed this to a break between spring and fall generations. In Utah, *T. minutus* nymphs reportedly are absent during the winter (Edmunds et al. 1976). Total dry weight biomass of *T. minutus* at Station 2 was very high (2350–2125 mg) during initial stages of the study but then showed a definite decline (Fig. 4). Dry weight biomass estimates at Station 4 showed recurrent trends of high values during June and August and low values during the remaining months. Yearly biomass totals and means were about five times less than at Station 2.

Length-Weight Relationships

The relationship of dry weight to wet weight was linear on a log-log plot (Fig. 6), as was total length vs dry weight

Table 1.—Benthos densities and dry weight biomass estimates of *Tricorythodes minutus* nymphs from Deep Creek, Stations 2 and 4.

Station	Time Period	Total Number (per m²)	$\bar{X}$	Total Weight (mg)	$\bar{X}$
Station 2	June 1970–June 71	43,318	3610	9.22	0.77
	June 1971–June 72	25,923	2160	4.02	0.34
	June 1972–Aug. 72	4,620	1540	0.99	0.33
Station 4	June 1970–June 71	3,604	300	1.30	0.11
	June 1971–June 72	2,808	234	0.92	0.08
	June 1972–Aug. 72	1,424	475	1.01	0.34



3A 3B

FIG. 3.—Population estimates for nymphs captured in riffle (A) and reach (B) areas at Station 2. The stippled area represents the variability between two samples taken each month.

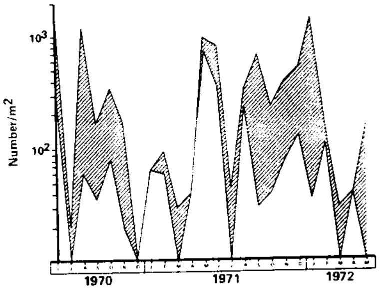


FIG. 4.—Population estimates for nymphs collected at Station 4 during the study period. The stippled area represents the variability between two monthly samples.

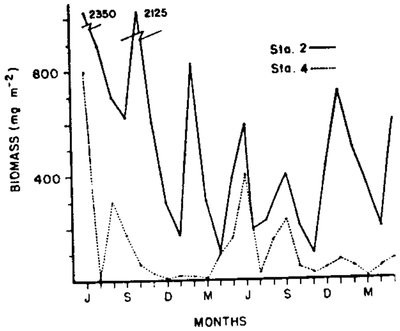


FIG. 5.—Biomass estimates (mg AFDW m^{-2}) for Station 2 (upper figure) and Station 4 (lower figure).

(Fig. 7). Organic matter content of the nymphs was: males, $\bar{x}$ = 82.7%; females, $\bar{x}$ = 85.6%; juveniles, $\bar{x}$ = 82.9%. These values were used to convert dry weight to ash free dry weight. Values for percent organic matter were converted to kcal/g by the formula Y = 0.0559 $\bar{x}$, where $\bar{x}$ = % organic matter (Winberg 1971). The values were similar to calorific values of *T. minutus* found by Brass (1971) (Y = 4.721 and 4.767 kcal/g, respectively). The weights of ecdysed skins followed a linear form, with the majority weighing between 0.155 and 0.280 mg ($\log_e$ Y (in mg) = −0.335 + 0.103 $\log_e$ X (in mm); r = 0.83; N = 16).

Development

T. minutus nymphs at Station 2 were multivoltine (Fig. 8). Very small instars and most other length classes were present during every month of the study period indicating continual recruitment. Fewer nymphs in the 1-mm class (0.6–1.5 mm) were captured than in some of the other classes, partly because of loss through the collecting net and partly because of faster growth by the earliest instars. Nymphs larger than 4.5 mm usually were present and their emergence resulted in adults being present throughout the year.

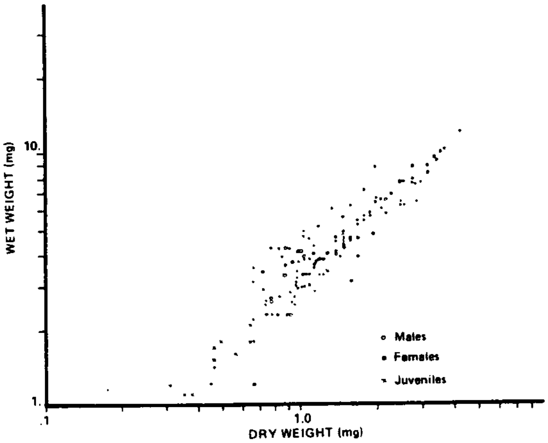


FIG. 6.—Relationship between dry weight and wet weight for male, female, and juvenile nymphs collected in Deep Creek.

The life cycle at Deep Creek Station 4 (Fig. 9) differed from that at Station 2. Only small size classes (< 4.0 mm) were present from November to April, after which time larger nymphs began appearing. Although the small number of nymphs collected makes interpretation difficult, it seems that *T. minutus* is bivoltine at this station. Apparently, emergence of mature nymphs present in June initiates the second generation (as evidenced by very small nymphs in June). These nymphs complete their development in the June–August period. An August–September emergence of this cohort starts the next generation. Growth of the latter is slowed by the cold fall water temperatures.

Number of instars was determined by means of head width, total length, and cast skin length according to the method of Janetschek (1962). Only six instars could be differentiated on the basis of head measurements alone, which appears to be too low for this species. The low instar number may be because head measurements were made only to the nearest 0.01 mm. McClure and Stewart (1976) applied the Janetschek method to the mayfly *Choroterpes mexicanus* and noted 16 instars in the overwintering and 19 instars in the combined summer generations.

Cast skins were obtained for almost every body length. They were difficult to measure precisely because of their limp nature. However, several modes appeared in the frequency histogram (Fig. 10A). If Dyar's rule of constant relative growth increment between successive instars is followed, the peaks should be equidistant along a logarithmic scale, but a line connecting the points is slightly curved (Fig. 11), which illustrates that Dyar's rule is not followed exactly. Dyar's rule has not been tested on Ephemeroptera. Laboratory and field growth tests (Newell 1976) show that growth rate is constant from the 1.5–2.0-mm class until maturity approaches (5.5–6.0 mm). Again some small nymphs may have passed through the net, but the proportion escaping probably is fairly constant from month to

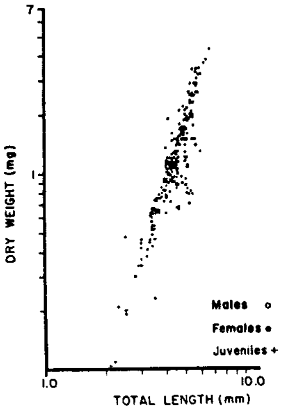


FIG. 7.—Relationship between total length and dry weight for male, female, and juvenile nymphs collected in Deep Creek.

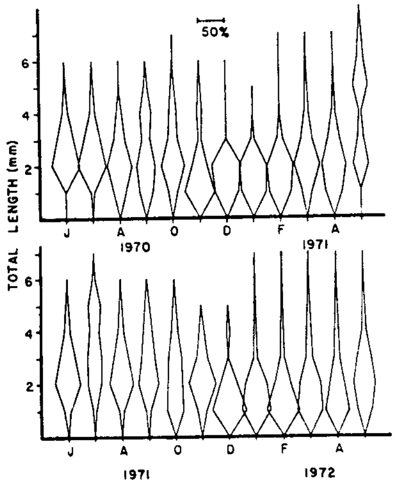


FIG. 8.—Percent of all size classes of *T. minutus* nymphs collected from bottom samples from 1970–72, at Deep Creek Station 2.

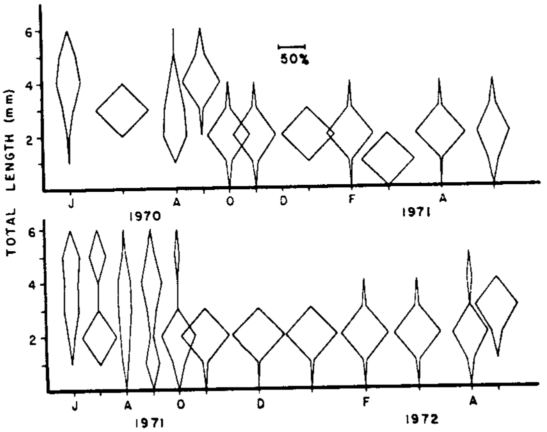


FIG. 9.—Percent of all size classes of *T. minutus* nymphs collected from bottom samples from 1970–72, at Deep Creek Station 4.

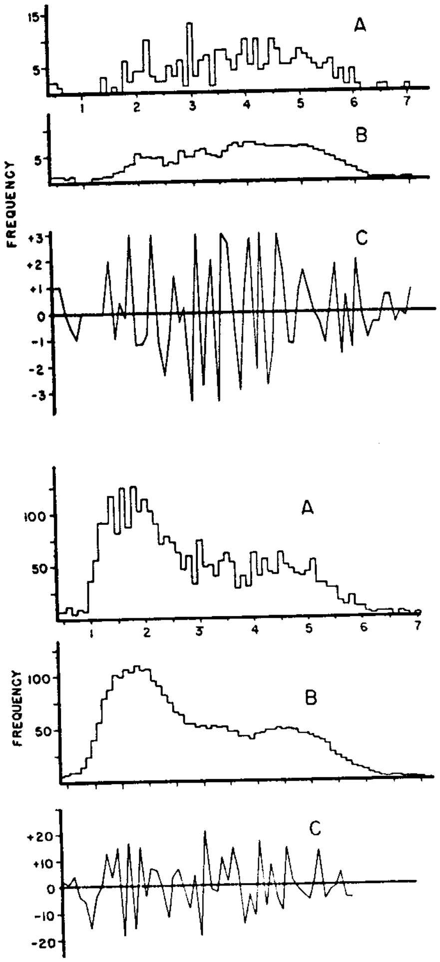


FIG. 10.—Instar analysis using total length of cast skins (top) and total length of nymphs (bottom). Top A is a frequency histogram of total length of cast skins from all sources, bottom A is a frequency histogram of total lengths of nymphs from Station 2 throughout the year, B is the algebraic sum of each measurement and the two values on either side, and C is a plot of the algebraic sum of histograms A and B. The positive peaks represent instars.

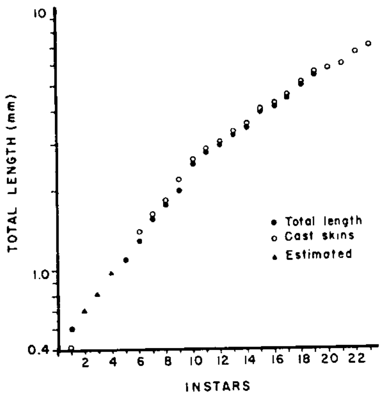


FIG. 11.—Relationship between number of instars and total length.

month. The number of instars for the smaller nymphs (Fig. 10) is only an estimate and may be incorrect. A gap between points one and two suggests the presence of at least one and probably three additional points, making a maximum of 23 instars. The same technique used with the nymphs (Fig. 10) resulted in the formation of 16 points. Again a gap is found; if three additional instars are added to fill it, a total of 19 instars results. The closeness of instar estimates for the two applications is noteworthy. In fact for 11 instars the two methods agree exactly (Fig. 11). The four extra points at the upper end of the curve probably are for females only, since males seldom grow larger than 5.5 mm in length. If so, males have a maximum of 19 instars, and females 23. The exact number realized for each sex probably varies somewhat with food, physical conditions, crowding, etc. Although there seems to be some variation in the total length at molting, enough molts occur at predetermined lengths that instar analysis is possible. The total number of molts possible during the insect's life cycle is not fixed as emergence can occur anytime the insect reaches about 4.5 mm in length. This variability complicates any attempts to estimate production or to predict emergence.

Subimagoes

Unlike subimagoes of *T. atratus* which can emerge at night underwater (Hall et al. 1975), successful emergence of *T. minutus* always occurred at the water's surface, usually in the afternoon. The subimago stage usually lasts less than 30 minutes. Often the subimago will emerge among the aquatic vegetation along the stream edge, crawl up the vegetation, inflate its wings, and undergo its final molt. The subimago differs from the adult in that it has opaque wings, cerci as long as the abdomen, and a longer body (by 0.1 to 0.2 mm). When the subimago molts, its entire body covering is shed exclusive of the wings, which presumably are shed later. The mean weight of 18 subimago skins was 470±2.40 μg (95% confidence limits).

Adults

Mating

Mating usually occurs in large airborne swarms from 1 to 8 m over the stream. Coupling and copulation are rapid. At Station 2, where *T. minutus* is multivoltine, mating probably occurs throughout the winter in the warm air immediately above the stream. The earliest mating flight observed was on February 25 but dead adults were observed on the snow along the stream throughout the winter. At Station 2, mating flights seem to occur during midday in the spring and fall and about two hours after sunrise and 2–3 hours before sunset during the summer. Hall et al. (1975) noted a similar temporal pattern in the swarming of *T. atratus* in the summer. At Station 4, mating flights were observed during the late afternoon from June to October. Adult *T. minutus* are weak fliers and a breeze of 6 km/h or greater forces them to cease flight.

Egg Deposition

Oviposition by *T. minutus* is similar to that described for *T. atratus* (Hall et al. 1975). In *T. minutus*, egg deposition typically takes place within two hours of mating. The adults die soon afterward, by being trapped in the surface film. A swarm collects about 1 m above a riffle area and as it moves downstream, females drop out, touch the water briefly, and return to the group. Now about 2 m above the water, this part of the swarm moves to the upstream portion of the riffle where it drops to the lower strata of adults and again moves downstream. Thus, the swarm adopts a parabolic pattern above a riffle, with the females making several trips to the water's surface. The spherical egg clusters sink as the female touches her abdomen to the water and the cluster breaks up in about 1 min, with the individual eggs becoming sticky. In *T. atratus*, on the other hand, the eggs remain in clusters of 25 to 100, held together by terminal filaments (Hall et al. 1975). *T. minutus* adults live less than 6 hours as shown by field and laboratory observations.

Discussion

Effects of Temperature on Life Cycle

The life cycle of *T. minutus* is unquestionably influenced by water temperature. This mayfly has a multivoltine cycle in one portion of Deep Creek, and yet is bivoltine in another section of the same stream. It also is bivoltine in Spring Creek, Bannock Co., Idaho (Newell 1976). In west central Alberta *T. minutus* is univoltine (Clifford 1969, Clifford et al. 1973). Hall (1975) also felt that water temperature was very important in determining the bivoltine life cycle of *T. atratus*.

Ephemeroptera life cycles are many and varied as illustrated by the classification system proposed by Landa (1968). Landa's system is based on the number of generations per year (A-one, B-two or more, C-less than one) with the first category further subdivided according to when growth and emergence occur. The life cycle of *T. minutus* in Deep Creek would fall into some category of group B. Clifford et al. (1973) found *T. minutus* in Alberta to belong in group A2 with adult emergence in August. There may be other exceptions to such classification schemes. The exception illustrates a point discussed by Macan (1970), that life cycles of any one species will vary depending upon geographical range and resultant change in environmental influence. Characteristics of local populations, including life cycle and morphology, reflect adaptions to different environmental conditions. Emergence dates of stream insects may be only partially determined by the rates of development of young stages and also may be controlled by the temperature at emergence (Macan and Maudsley 1966). However, in Deep Creek this does not seem to hold for *Tricorythodes*.

In the rainy tropical regions, where temperatures are constant and photoperiod uniform, multivoltine cycles with overlapping generations are common (Clifford et al. 1973). Berner (1950) found few seasonal species in Florida, and *Choroterpes mexicanus* is multivoltine in Texas (McClure and Stewart 1976). When emergence is cyclic, in tropical and subtropical areas, it is due to factors other than temperature and photoperiod, e.g., the lunar rhythms of *Povilla adusta* Navas (Hartland-Rowe 1958). Seasonally varying temperatures and photoperiods are present in the temperate regions (e.g., in North America to about latitude 42°). Mayflies in this region commonly have one to two generations per year, with some growth in winter. Summer species are found in fewer numbers than winter species. Above 42° latitude in North America there is a tendency for species lacking winter growth to predominate. There are few species with multivoltine life cycles, but univoltine species with summer cycles become increasingly more numerous.

T. minutus at Deep Creek Station 2 behaves like a tropical insect and, except for changing photoperiods, this site is somewhat similar to a tropical stream. In this regard it is noteworthy that the genus *Tricorythodes* is a northward extension of the Neotropical fauna (Edmunds et al. 1976). *T. minutus* seems to be little influenced by photoperiod. By contrast, the Odonata of Deep Creek Station 2 seem to be influenced more by photoperiod than by temperature. This is evidenced by their ability to maintain normal summer emergence whereas *T. minutus* and *Baetis intermedius*, and the caddisflies *Hydropsyche occidentalis* and *Tinodes provo* have all become multivoltine under these constant temperature conditions.

Some insect species illustrate flexible life cycles in response to different latitudes or altitudes by alterations in the number of generations per year (Zahar 1951). Flexibility in the life cycle of *T. minutus* may account for its wide distribution in the western United States.

In Deep Creek Station 2, *T. minutus* has apparently lost some of the accurate controls that a mayfly population normally requires to survive (i.e., timing of emergence). Because of the short life span of adult mayflies, timing of emergence is critical for successful mating. Premature or delayed emergence results in selection against those individuals and the result is a finely timed emergence of adults. This selection pressure has been removed at Station 2 since emergence during most days of the year results in a high probability of successful mating. The problem of synchronization of emergence is overcome by high densities of nymphs emerging simultaneously over much of the year. Synchrony of diurnal emergence and selection of definite swarm sites further increase the chance of male-female encounters.

Acknowledgment

We thank Dale A. McCullough for his help on various facets of the work, especially for weighing and ashing the nymphs.

REFERENCES CITED

Argyle, D. W., and G. F. Edmunds, Jr. 1962. Mayflies (Ephemeroptera) of the Curecanti Reservoir basin Gunnison River, Colorado. Univ. Utah Anthro Papers 59: 179–89.

Berner, L. 1950. The Mayflies of Florida. Univ. Florida Press, Gainesville. 267 pp.

Brass, D. W. 1971. Bioenergetics of selected stream-dwelling invertebrates. Unpubl. Master's Thesis, Idaho State Univ., Pocatello. 67 pp.

Clifford, H. F. 1969. Limnological features of a northern brownwater stream with special reference to the life histories of the aquatic insects. Amer. Midl. Nat. 82: 578–97.

Clifford, H. F., M. R. Robertson, and K. F. Zelt. 1973. Life cycle patterns of mayflies (Ephemeroptera) from some streams of Alberta, Canada. Proc. First Internat. Conf. Ephemer. 1: 122–31.

Edmunds, G. F., Jr., S. L. Jensen, and L. Berner. 1976. The Mayflies of North and Central America. Univ. Minnesota Press, Minneapolis. 330 pp.

Hall, R. J. 1975. Life history, drift, and production rate of the stream mayfly *Tricorythodes atratus* McDunnough in the headwaters of the Mississippi River. Unpubl. Ph.D. Dissert., Univ. of Minnesota, Minneapolis. 228 pp.

Hall, R. J., L. Berner, and E. F. Cook. 1975. Observations on the biology of *Tricorythodes atratus* McDunnough (Ephemeroptera: Tricorythidae). Proc. Entomol. Soc. Wash. 77: 34–49.

Hartland-Rowe, R. 1958. The biology of a tropical mayfly *Povilla adusta* Navas with special reference to the lunar rhythm of emergence. Rev. Zool. Bot. Afr. 58: 185–202.

Janetschek, H. 1967. Growth and maturity of the springtail, *Gomphiocephalus hodgsoni* Carpenter, from South Victoria Land and Ross Island. Antarctic Res. Ser. 10, Entomology of Antarctica, p. 295–305.

Jensen, S. L. 1966. The mayflies of Idaho (Ephemeroptera). Unpubl. Master's Thesis, Univ. Utah, Salt Lake City. 365 pp.

Koslucher, D. G., and G. W. Minshall. 1973. Food habits of some benthic invertebrates in a northern cool-desert stream (Deep Creek, Curlew Valley, Idaho-Utah). Trans. Am. Micros. Soc. 92: 441–52.

Landa, V. 1968. Developmental cycles of central European Ephemeroptera and their interrelations. Acta. Entomol. Bohemoslov. 65: 276–84.

Macan, T. T. 1970. A key to the nymphs of British species of Ephemeroptera with notes on their ecology. Freshwat. Biol. Assoc. Spec. Publ. 20, 68 pp.

Macan, T. T., and R. Maudsley. 1966. The temperature of a moorland fishpond. Hydrobiologia 27: 1–22.

McClure, R. G., and K. W. Stewart. 1976. Life cycle and production of the mayfly *Choroterpes (Neochoroterpes) mexicanus* Allen (Ephemeroptera: Leptophlebiidae). Ann. Entomol. Soc. Am. 69: 134–44.

Minshall, G. W., D. A. Andrews, F. L. Rose, D. W. Shaw, and R. L. Newell. 1973. 1972 progress report, validation studies at Deep Creek, Curlew Valley. Res. Memo. 73–48. U.S. IBP, Desert Biome. 99 pp.

Minshall, G. W., and P. A. Winger. 1968. The effect of reduction in stream flow on invertebrate drift. Ecology 49: 580–2.

Needham, J. G., and R. O. Christenson. 1927. Economic insects in some streams of northern Utah. Utah Agric. Exp. Stn. Bull. 201: 3–36.

Newell, R. L. 1971. Revisions to the checklist of Montana aquatic insects. Proc. Mont. Acad. Sci. 31: 69–72.

1976. The effect of temperature on growth and development of the mayfly *Tricorythodes minutus* Traver. Unpubl. Ph.D. Dissert., Idaho State Univ., Pocatello. 128 pp.

Pearson, W. D., R. H. Kramer, and D. R. Franklin. 1968. Macroinvertebrates in the Green River below Flaming Gorge Dam, 1964–65 and 67. Utah Acad. Sci. 33: 113–9.

Winberg, G. G. 1971. Methods for the Estimation of Production of Aquatic Animals. Academic Press, N.Y. 175 pp.

Zahar, A. R. 1951. The ecology and distribution of black-flies (Simuliidae) in southeast Scotland. J. Anim. Ecol. 20: 33–62.