DIEL PATTERNS OF AQUATIC INVERTEBRATE DRIFT IN STREAMS OF NORTHERN UTAH[1]

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INTRODUCTION

The downstream drifting of invertebrate animals, even at low discharge, is well recognized as a constant feature of streams. However, the discovery of a diel periodicity in drift, often with large quantities involved, has added new emphasis to the possible significance of this phenomenon to population dynamics and life histories of stream invertebrates, energy flow in stream ecosystems, and the trophic ecology of stream fishes. Earliest reported periodicities in drift took the form of low drift during daylight, high nocturnal drift, often including an explosive increase at about full darkness in the evening, and a sharp drop to daytime low levels at dawn; these early observations concerned primarily the mayfly genus *Baetis* and amphipods of the genus *Gammarus* (Tanaka 1960; Waters 1962; Miller 1963a,b). More recently, diel drift patterns other than the one described have been reported. Müller (1966) has emphasized two common patterns, each characteristically with two peaks: (1) the *bigeminus*-type, with the major peak occurring first, or following sunset, and a secondary peak occurring later just prior to dawn; and (2) the *alternans*-type, with the minor peak occurring first and a major peak later in the night. While the night-active forms appear to be more common, several investigators have reported day-active periodicities with highest drift during the daytime (Müller 1966; White 1966; Anderson 1967; Besch 1967). It appears likely that considerable variation occurs in shape of pattern, degree and type of behavior among different taxa, and effect of environmental factors.

Toward the objective of gaining basic data on such possible variation. I determined the diel drift patterns in a number of mountain streams in the region of northeast Utah in the summer of 1966. Spe-

[1]Paper No. 6846, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul.

cific purposes were to measure drift characteristics according to different species and environmental conditions, and if possible, to relate drift rate to bottom fauna abundance as a measure of relative propensity to drift among various taxa. Some new drift patterns were observed, drift propensities for heretofore unreported taxa were measured, and some new problems were defined. These were, however, short range observations only; long-term studies, ranging over at least a complete generation time, will be required before the full signficance of the drift phenomenon can be ascertained for the species involved.

Descriptions of Streams

Greatest emphasis was placed on streams in the Logan River drainage in northeast Utah. These included an upper reach of the Logan River (T14N, R3E, Sec. 14, Cache Co.), Beaver Creek (T16S, R3E, Sec. 14, Franklin Co., Idaho), Temple Fork T12N, R3E, Sec. 1, Cache Co.,) Spawn Creek, tributary to Temple Fork (T13N, R3E, Sec. 35, Cache Co.), and Right Fork (T12N, R3E, Sec. 21, Cache Co.). Two streams were included in the Uinta Mountains, one each on the north and south slopes: Henry's Fork (of the Green River) on the north (T2N, R14E, Sec. 11, Summit Co.) and Paradise Creek on the south (T2S, R21W, Sec. 36, Uintah Co.) In addition, one stream in the Pacific drainage, Deadman Creek (T34N, R116W, Sec. 6, Lincoln Co., Wyoming) and one small stream in Cache Valley, Mendon Creek (T11N, R1W, Sec. 8, Cache Co.), were included.

Despite some similarities, particularly among the Logan River tributaries, there were significant differences in their faunas such that no two streams of the nine sampled could be considered exactly comparable. The Logan River streams with Deadman Creek in Wyoming were all relatively hardwater streams with total alkalinity (as $CaCO_3$) from about 150 to 200 ppm; Mendon Creek was 310; and the two streams in the Uinta Mountains were very soft, 12 ppm. All mountain streams were of moderately high gradient at the sampling sites, with current velocities about 0.5 to 1 m/sec and bottom types ranging from coarse gravel to large rubble. Mendon Creek was a small, low-gradient valley stream with current velocity about 0.3 m/sec at the sample site and the bottom composed mainly of silt, sand and gravel. The invertebrate faunas of the mountain streams were dominated by the insect orders Ephemeroptera, Trichoptera, and Plecoptera, with other groups in a minor status quantitatively; drift and

bottom samples were analyzed only for taxa within these three orders. In Mendon Creek, the dominant invertebrate was the amphipod, *Gammarus lacustris,* while insects were relatively uncommon; while abundant, *G. lacustris* did not drift in large quantities nor did it exhibit any suggestion of a diel periodicity in drift, and consequently no further data from Mendon Creek is included in this report. No crustaceans were observed in any of the mountain streams.

Acknowledgments

I am indebted to the administration and staffs of Utah State University and the U.S. Fish and Wildlife Service, especially Drs. Robert H. Kramer, John M. Neuhold, and William F. Sigler, for their assistance and use of facilities in the Utah Cooperative Fishery Unit at Logan. I am particularly appreciative of the assistance and company of William D. Pearson, who aided me in all aspects of the sampling and in many practical ways in the field. Assistance in identification of the stream invertebrates was received from Drs. E. L. Bousfield (National Museum of Canada), Edwin F. Cook (University of Minnesota), George F. Edmunds(University of Utah), and Arden R. Gaufin (University of Utah). The research was financed by the National Science Foundation.

METHODS

Drift was sampled with stationary rectangular nets, 15 cm (6 in) wide by 30 cm (12 in) high, positioned approximately midstream of a riffle and extending from the stream bottom to above the water surface (Fig. 1). Net mesh was of Nitex of 471 μ opening. Two nets were used to provide two samples each hour for 24 hours, the sampling interval varying from 15 min. to 1 hour, depending on the degree of debris accumulation. The contents of the nets, including organisms and debris, were preserved in formalin and later sorted, counted and weighed (wet) in the laboratory; all data were expressed as drift rates in number or weight per hour per net.

Rough-quantitative bottom samples were taken to provide an approximate measure of bottom densities and relative abundance among taxa.

Current velocity and alkalinity were measured at the beginning of each 24-hour sampling series; air and water temperature and light intesity were measured through the sampling period at hourly intervals.

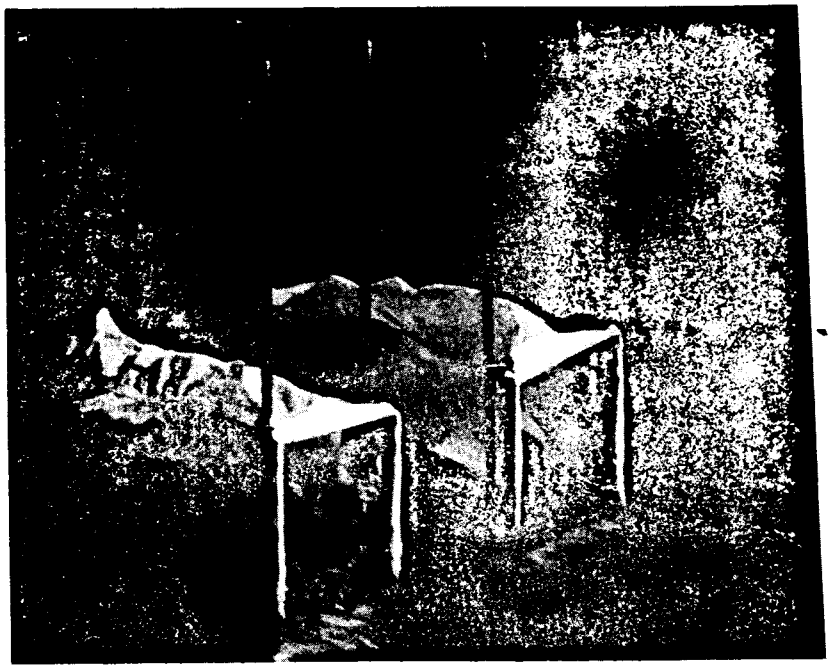


Figure 1

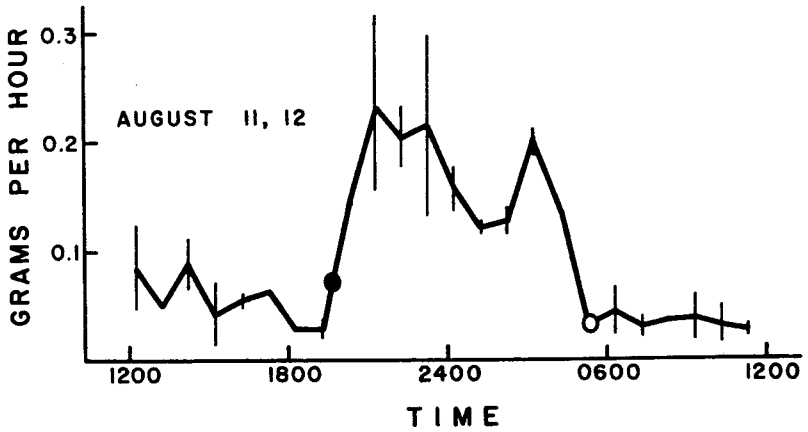


Figure 2

RESULTS

Logan River

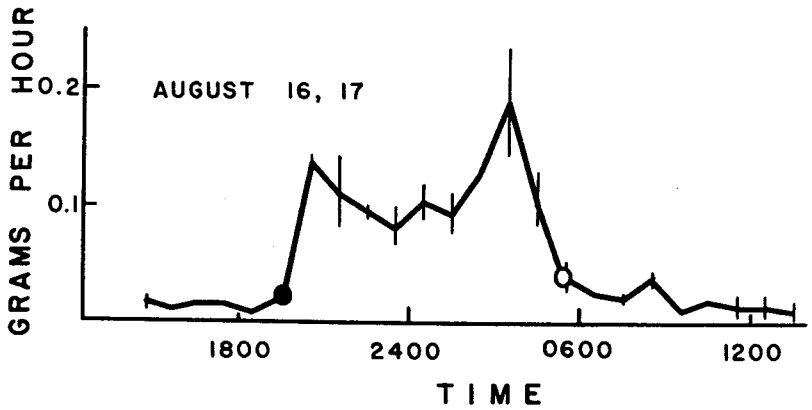
Drift in this upper reach of the Logan River (August 11-12) was relatively low. *Baetis bicaudatus* exhibited high drift rates in a marked diel periodicity; this pattern appeared to be the *bigeminus*-type, with a major peak after sunset and a secondary peak prior to sunrise (Fig. 2). No other species was common in the drift.

Baetis bicaudatus, Cinygmula sp., and *Ephemerella coloradensis* were abundant on the stream bottom, but the last two showed little tendency to drift. Also present in the bottom fauna at low densities were several trichopterans, including a hydropsychid and *Rhyacophila, Epeorus* (*Iron*) *longimanus,* and several plecopterans. Several of these latter appeared irregularly in the drift but never in significant numbers.

Beaver Creek

The fauna was somewhat similar in Beaver Creek (August 16-17) to that in the Logan River. *Baetis bicaudatus* again was the only group that drifted in large numbers (Fig. 3). The pattern included two

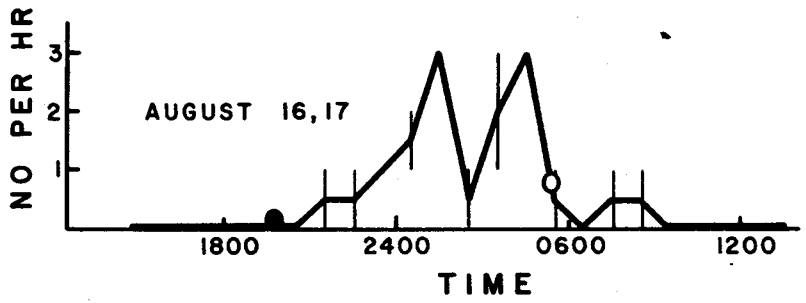
Figure 3



peaks, with the second prior to dawn being slightly larger. As in the Logan River, *Cinygmula* sp. and *Ephemerella coloradensis* were abundant on the stream bottom but drifted very little. A large mayfly nymph, *Ameletus* (probably *velox*), appeared in the drift in low num-

bers but with a definite night-active periodicity (Fig. 4). This species, more representative of a slow-water fauna, was not present in the riffle bottom samples; presumably it inhabited the many small beaver dam reservoirs in the area and drifted during the night due to increased activity.

Figure 4



Several trichopterans, including *Rhyacophila,* and several plecopterans were present in the bottom fauna at low densities and very infrequently in the drift.

Temple Fork

Drift rates in Temple Fork, considering all species, were among the highest of all streams sampled. This stream was visited twice, June 23-24 and July 16-17; for all species, drift rates were lower on the latter date, apparently because considerable emergence had taken place in the interim. Outstanding in the drift in Temple Fork was the marked day-active pattern exhibited by the larvae of the caddisfly, *Oligophlebodes sigma,* previously reported (Waters 1968). This small larva drifted with its case, constructed of small stones, with maximum drift at about noon; drift rates appeared strongly correlated with water temperature. Drift rates were extremely high; the daily total for the entire stream (discharge about 0.34 m^3/sec or 12 ft^3/sec) in June was about 400 g or 160,000 individuals.

Several mayfly nymphs exhibited marked night-active drift periodicities. *Baetis bicaudatus,* as expected, exhibited highest drift rates during the night on both dates (Fig. 5); the species was the same on both dates, although the nymphs in July were considerably smaller and probably constituted a succeeding generation. In June, in addition to the high nocturnal drift, there also appeared fairly high drift during the daytime.

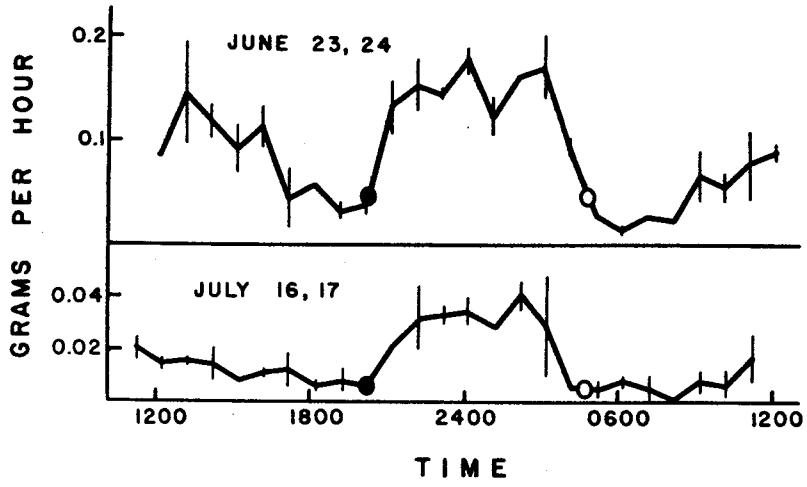


Figure 5

Ephemerella coloradensis exhibited a marked night-active periodicity on both dates (Fig. 6), although in June, as with *Baetis bicaudatus,* there appeared relatively high drift during the daytime. It appeared likely that the exceptionally high day-active drift of the caddisfly *O. sigma* induced a high drift of *B. bicaudatus* and *E. coloradensis* during the daytime. In July, the *O. sigma* drift was much reduced, and a high daytime drift of *B. bicaudatus* and *E. coloradensis* did not occur. Temple Fork was the only stream in which *E. coloradensis* was observed to drift appreciably.

Another mayfly, *Ephemerella doddsi,* also exhibited a marked night-active drift pattern (Fig. 7). This large nymph — a slow and apparently clumsy swimmer, with a friction hold-fast organ on its ventral abdomen — was present in other streams but was found in abundance only in Temple Fork. It apparently was strong enough to withstand the daytime disturbances of the *O. sigma* drift and itself drifted only during the night.

Common on the stream bottom in addition to all of those species above that drifted, were the mayflies *Rhithrogena* sp. and *Cinygmula* sp., which only occasionally were found in the drift samples. At lower densities were hydropsychids, *Rhyacophila,* and stoneflies of the genera *Alloperla* and *Nemoura;* these groups were also found in low numbers in the drift samples, although there was the suggestion of higher drift at night.

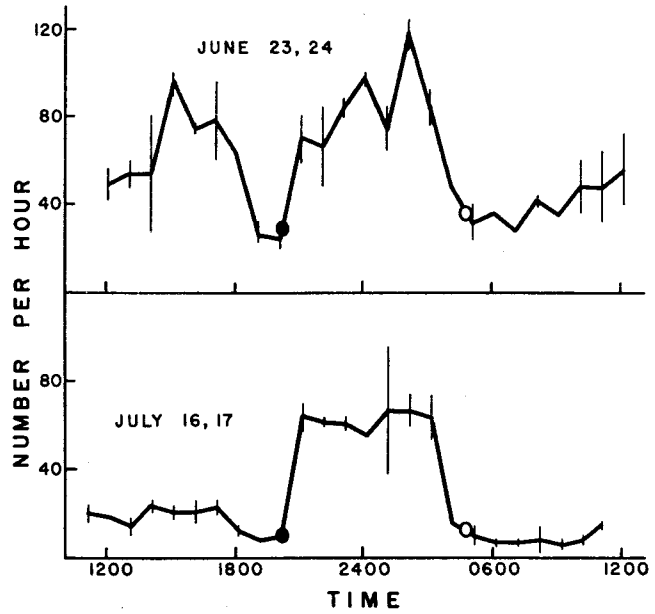


Figure 6

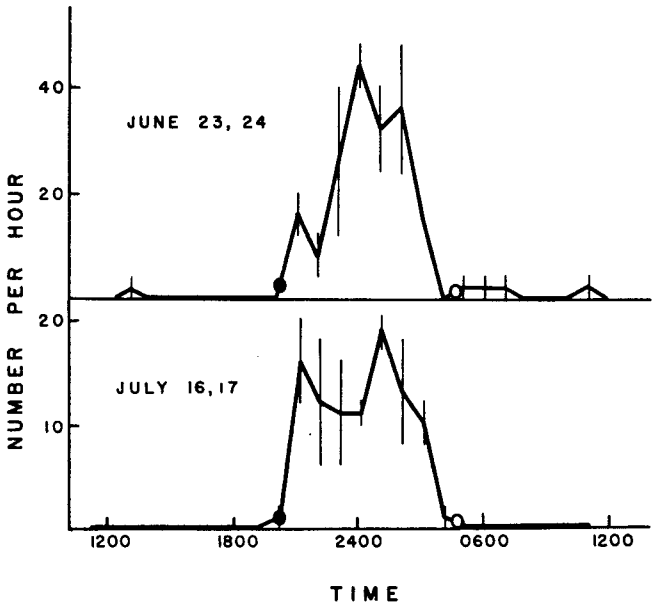


Figure 7

Spawn Creek

Prominent in Spawn Creek (June 27- 28) was the drift of *Baetis bicaudatus* in a marked night-active periodicity with two definite peaks and high drift rates (Fig. 8). Drift of *B. bicaudatus* in this stream was the highest observed among all streams sampled, the daily total being about 120 g or 100,000 individuals for the entire stream (discharge about 0.14 m^3/sec or 5 ft^3/sec). Even daytime drift rates were high, relative to other streams.

A small stonefly nymph, *Nemoura* (*Malenka*) sp., exhibited high drift rates in a marked periodicity that appeared to be a *bigeminus*-type (Fig. 9). These nymphs were virtually absent from the stream bottom at the sampling site and were therefore presumed to originate in a reach farther upstream. Because of their small size, they were not noticed at the time of sampling, and therefore no search was conducted for their source upstream. This was the only instance among the streams sampled wherein a riffle-inhabiting organism occurred in large quantities in the drift but not on the stream bottom at the sample site.

In the bottom samples, *B. bicaudatus* was common, *Nemoura* sp. was not. Also common on the bottom, but showing low propensity to drift, were the mayflies *Cinygmula* sp., *Rhithrogena* sp., and *Ephemerella coloradensis*. Relatively rare in both drift and bottom samples were the mayflies *Epeorus* (*Iron*) *longimanus* and *Ephemerella doddsi,* and the stonefly *Isogenus modestus;* also rare was the caddisfly *Oligophlebodes sigma,* the same species that drifted with a day-active periodicity in Temple Fork, to which Spawn Creek was tributary.

Right Fork

The Right Fork was sampled twice, June 20-21 and August 22-23. *Baetis tricaudatus* exhibited a clear example of an *alternans*-type diel pattern, with only a suggestion of a secondary peak in the early part of the night and a relatively high peak prior to dawn (Fig. 10). This was the only stream among those sampled in which this species of *Baetis* dominated, and in which the *alternans-type* pattern was so clearly exhibited. Drift rates were high, variation was small, and the same basic pattern was observed on both sample dates; there appeared little question, therefore, that the pattern type was significant. The nymphs on the August date were the same species as in June, although a succeeding generation.

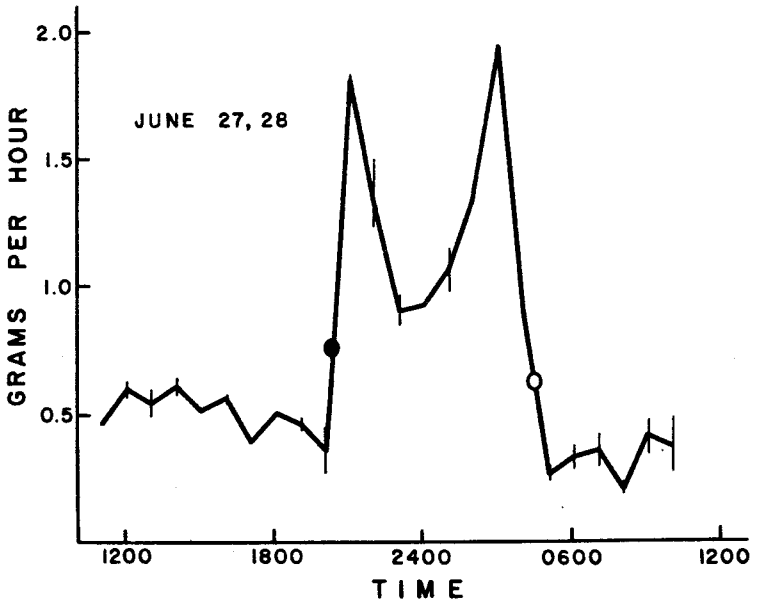


Figure 8

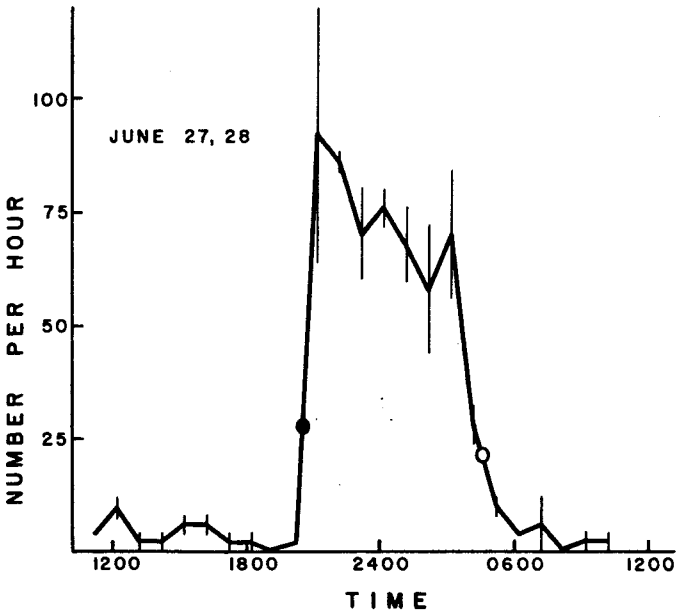


Figure 9

Nymphs of the small stonefly, *Nemoura* (*Malenka*) sp., exhibited marked periodicities in drift on both dates, the pattern appearing to be the *bigeminus*-type (Fig. 11). This stonefly appeared to be the same species as in Spawn Creek, where the daily pattern was similar. The drift in numbers was much lower in August, although drift in biomass was about the same, because growth had occurred; however, density on the stream bottom, while only measured roughly, did not appear to be reduced as much in numbers between June and August as in the drift. That is, there appeared here the suggestion that this species has its highest propensity to drift in early life history stages. The nymphs in August were approaching maturity.

The larvae of the caddisfly *Neothremma* sp. (Limnephilidae) showed a definite night-active periodicity; the degree of organization in the diel pattern was not as great as for other species, there appearing only a single, rounded peak during the night (Fig. 12). This caddisfly drifted with its case; the night-active character was not apparent from the samples, however, until the larvae were extracted from the cases and counted, because many empty cases were in the drift during the daytime. This species was present only in June, it apparently having emerged completely prior to the August sampling date.

The above three species were abundant on the stream bottom. The average size of the *B. tricaudatus* nymphs in June appeared to be significantly smaller in the bottom samples than in the drift, suggesting that propensity to drift was greater in later life history stages for this species; in August the mean size in the new generation was small in both bottom and drift. Also common on the bottom but rare in the drift samples were the mayflies *Epeorus* (*Iron*) *longimanus* and *Cinygmula* sp. on both dates. Uncommon on the bottom and in the drift were *Ephemerella coloradensis, Rhyacophila,* hydropsychids, leptophlebiids, and other stoneflies, including *Acroneuria.*

Henry's Fork

In Henry's Fork (July 7- 8), on the north slope of the Uinta Mountains, two major groups exhibited marked periodicities in drift. *Baetis bicaudatus* showed a typical *bigeminus*-type pattern, with relatively high drift rates, low variation, and prominent second peak (Fig. 13). Several stonefly nymphs showed night-active periodicities, including *Alloperla* sp. with an early peak but no secondary peak and *Nemoura* (*Zapada*) sp. with a more typical *bigeminus*-type pattern (Fig. 14).

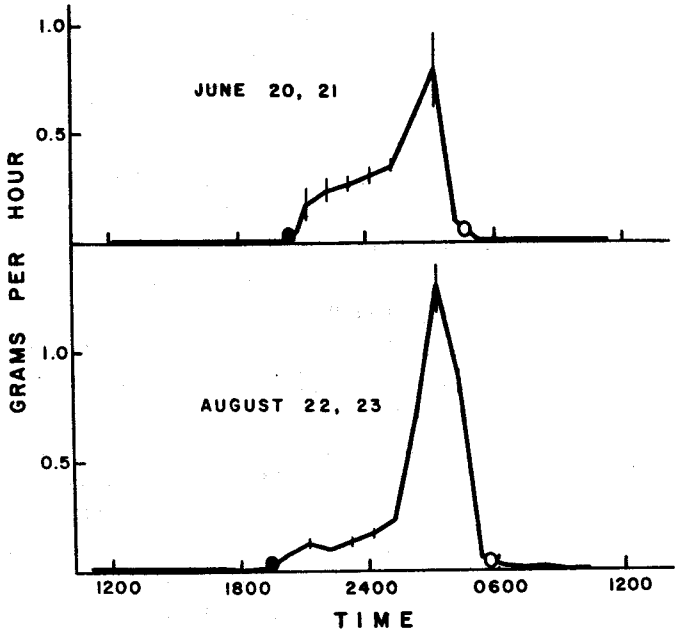


Figure 10

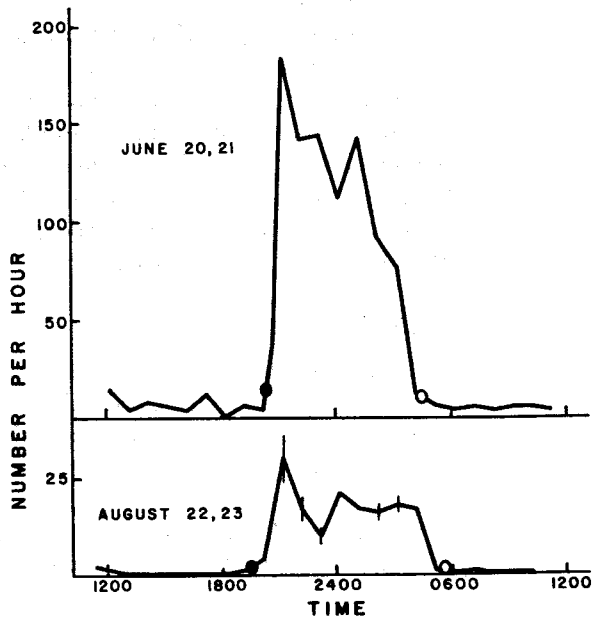


Figure 11

In the bottom samples, the above groups were common as well as *Cinygmula* sp. which showed little tendency to drift. Present on the bottom, and drifting with only a suggestion of night activity were the mayflies *Epeorus* (*Iron*) *deceptivus* and *Ephemerella doddsi,* the stonefly *Isogenus modestus,* and the caddisfly *Rhyacophila.* The stonefly *Leuctra* sp. was present in fair numbers on the bottom but was completely absent in the drift samples. Present in low numbers in both bottom and drift samples were the mayflies *Rhithrogena* sp., a leptophlebiid, *Ephemerella coloradensis* and *E. infrequens,* and several trichopterans.

Paradise Creek

In Paradise Creek (July 11-12), on the south slope of the Uintas, *Baetis bicaudatus* exhibited a marked night-active periodicity with two definite peaks approximately equal in height (Fig. 15). At least five species of stoneflies, *Alloperla* sp., *Nemoura* spp., *Isogenus modestus* and *Arcynopteryx parallela,* although in low numbers, exhibited at least the suggestion of higher nocturnal drift rates (Fig. 16). *Epeorus* (*Iron*) *longimanus* showed a marked night-active periodicity, apparently in a *bigeminus*-type pattern (Fig. 17); this was the only instance among all streams sampled in which this genus clearly showed such a periodicity with substantially high drift rates.

Baetis bicaudatus was abundant in the bottom samples, as were also *Cinygmula* sp., *Ephemerella coloradensis* and *E. tibialis,* although the last three appeared only irregularly in low numbers in the drift. All the stonefly nymphs in the drift also were present, though not abundant, on the bottom. *Epeorus* (*Iron*) *longimanus* was common on the bottom, though not abundant. Other mayflies, *Ephemerella doddsi* and a leptophlebiid, were present but rare in both drift and bottom samples.

Deadman Creek

Insect groups in Deadman Creek (August 7-8), while in the Pacific drainage in western Wyoming and separated from the streams in northern Utah, were about the same as those found in the Utah streams. Two unknown species of *Baetis*, together exhibited a marked night-active periodicity in a clearly defined *bigeminus*-type pattern (Fig. 18). Several stonefly nymphs, *Isogenus aestivalis* and *Nemoura* spp., showed clear night-active periodicities, although in low numbers (Fig. 19).

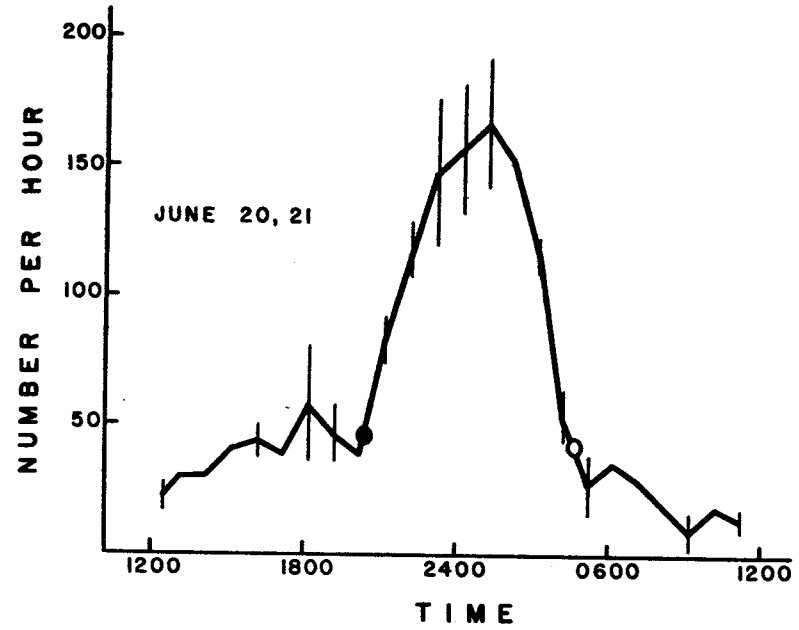
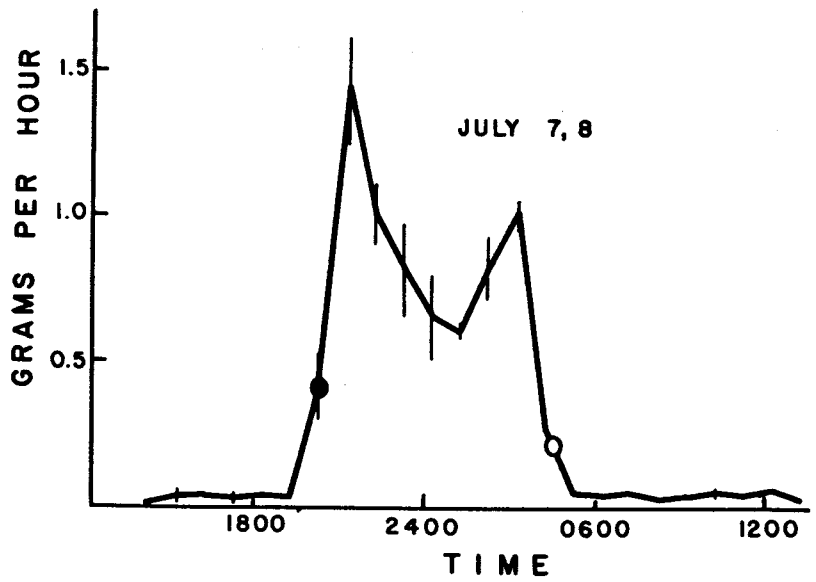


Figure 12



Fgiure 13

On the stream bottom, *Baetis, Cinygmula* sp., *Ephemerella coloradensis, E. tibialis*, and *Rhyacophila* were abundant, although with the exception of *Baetis,* none of these showed much propensity to drift; in some, there was a slight increase in drift at night. Also present on the bottom but rare or none in the drift, were a brachycentrid and the stonefly, *Acroneuria.*

DISCUSSION

The major component of the drift in almost all streams was constituted or mayfly nymphs. Of these, *Baetis* was by far the most common genus. In almost all streams, *B. bicaudatus* was the dominant species; this species apparently exhibited the *bigeminus*-type pattern, although with the second peak sometimes as high or slightly higher than the first. In one of the other streams (Right Fork), *B. tricaudatus* clearly exhibited the *alternans*-type pattern. In my first report on drift periodicities (Waters 1962), secondary peaks in *Baetis* drift were observed which I suggested were due to the occlusion of moonlight. In the present study, while secondary peaks were observed frequently for *Baetis,* in no instance was one observed to be related to moonlight occlusion or moonset. Therefore, while the precise effect of moonlight remains unknown, the secondary peak so frequently observed appears conclusively to be of endogenous origin.

The present results for *Baetis,* in concert with other published reports on stream invertebrate drift, suggest that this genus is universal in exhibiting diel periodicities in drift; indeed, the first reports of a diel periodicity in drift, from widely separated regions of the world, all included the genus *Baetis* (Tanaka 1960; Waters 1962; Müller 1963a). Other mayflies also clearly exhibited night-active periodicities, although not in all streams: *Ephemerella doddsi* and *E. coloradensis* (Temple Fork), and *Ameletus velox* (Beaver Creek). Still others, though abundant on the stream bottom, showed little or no propensity to drift; this group included *Ephemerella coloradensis* (most streams other than Temple Fork), *E. tibialis, Rhithrogena* sp., and *Cinygmula* sp. Consistently abundant in almost all streams was the last of these, *Cinygmula* sp., but it just as consistently showed virtually no tendency to drift. The mayflies *Epeorus* (*Iron*) spp. were present in most streams, but showed little tendency to drift with one exception (Paradise Creek), wherein *E.* (*I.*) *longimanus* exhibited a marked night-active periodicity, probably of the *bigeminus*-type; this species was also common in the Right Fork but did not drift.

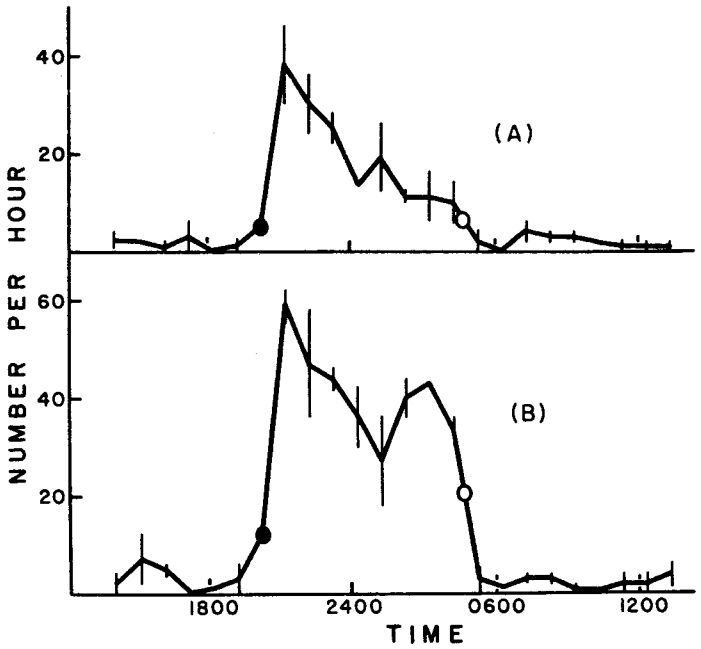


Figure 14

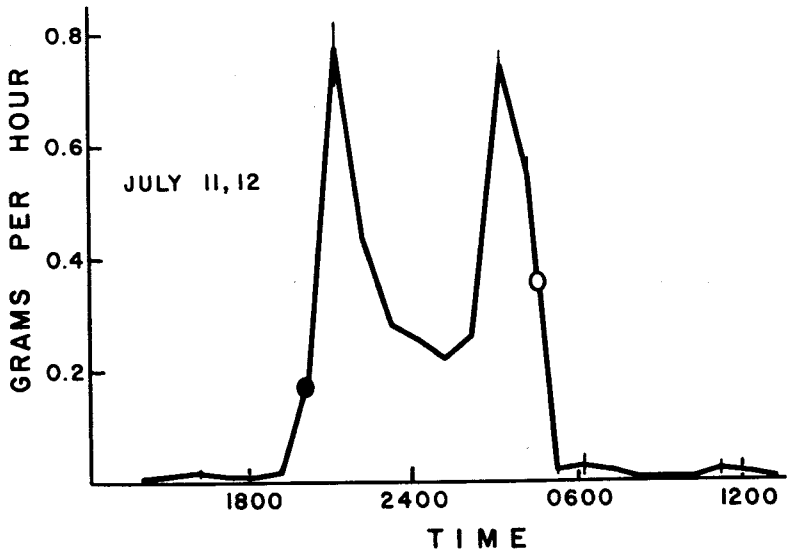


Figure 15

Other mayfly species were observed in low densities and for which, therefore, no conclusion as to propensity to drift could be firmly determined.

Stoneflies of the general *Alloperla, Nemoura, Isogenus,* and *Arcynopteryx,* while not abundant in all streams, exhibited night-active periodicities, apparently of the *bigeminus*-type, in all streams in which they were at least moderately abundant. In one instance (Henry's Fork), *Leuctra* sp. was present in fair numbers on the bottom but did not appear at all in the drift. Those stoneflies that exhibited a periodicity in drift were all night-active, but the propensity to drift, as with the mayflies, varied widely among species. The predaceous *Acroneuria,* while present in some streams, never occurred in the drift samples; it was not, however, found in abundance in any stream. Anderson (1967) reported a night-active periodicity for *Acroneuria* in an Oregon stream, where it was abundant as early instars.

The occurrence of caddisfly larvae in the drift was much less common than was the case for the two previous orders, although two species exhibited high drift rates, one day-active (*Oligophlebodes sigma* in Temple Fork; Waters 1968) and one night-active (*Neothremma* sp. in Right Fork). Both of these drifted with their cases. Other instances of caddisfly drift in a diel periodicity have been reported, some night-active and some day-active (Waters 1962; Müller 1966; Anderson 1967; White 1966). It appears that this order, while less commonly involved in diel periodicities, exhibits both night-active and day-active patterns. The rhythm of the day-active *Oligophlebodes sigma* in Temple Fork appeared strongly entrained by water temperature, while night-active patterns, as with those for mayflies and stoneflies as well, were entrained in an "on-off" fashion by light.

Müller (1966) has suggested that propensity to drift increases in later life history stages. This thesis could not be thoroughly tested in the present study because of the short period of the investigation. However, a larger mean size of *Baetis* nymphs in the drift in some streams relative to that in the bottom samples indicated the same relation. Elliott (1967) has also reported greater relative drift at later stages for some mayflies and stoneflies, and Anderson (1967) for caddisflies. On the other hand, the stoneflies of the genus *Nemoura* appeared in one stream (Right Fork) to exhibit higher relative drift at an earlier stage. Similar observations were made for *Brachycentrus americanus* by Anderson (1967) and for limnephilid larvae by Elliott (1967). Apparently there is variation in this respect also, with greater propensity to drift in the later stages being the more common.

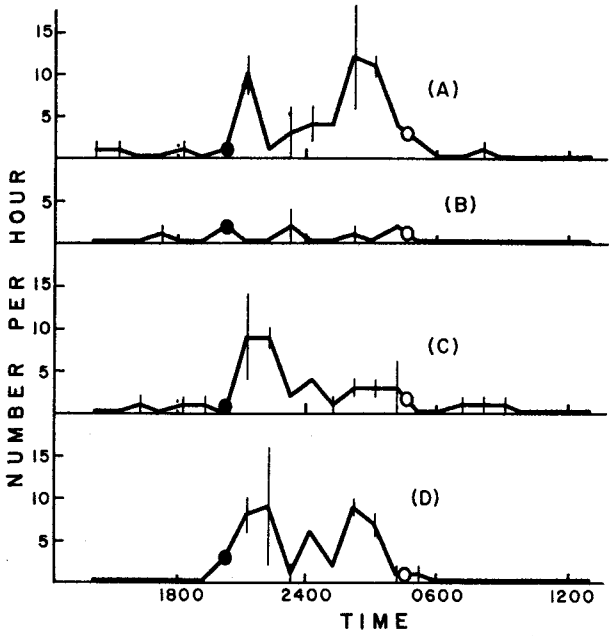


Figure 16

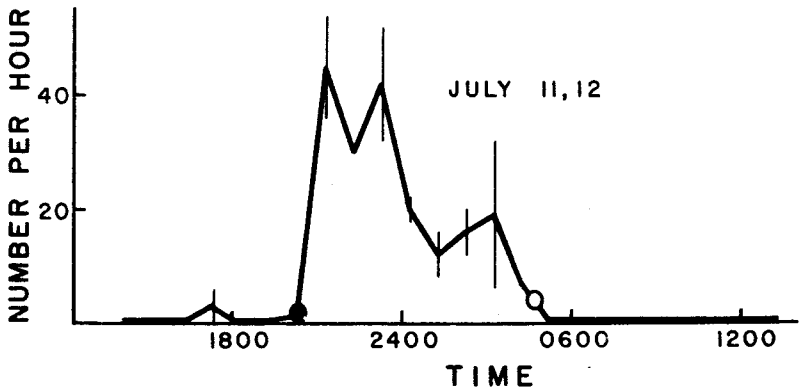


Figure 17

Rhyacophila and *Acroneuria* constituted the main invertebrate predators, but neither of these two groups exhibited a significant propensity to drift. Anderson (1967) has reported drift periodicities for both, but with very low drift rates relative to bottom densities. It may be suggested that invertebrate predators, most of which are large and strong swimmers, show little propensity to drift, except perhaps in early life history stages.

There appeared no consistent differences in drift or bottom fauna, either quantitatively or qualitatively, between the hard-water streams (150-200 ppm alkalinity) in the Logan River drainage and the very soft-water streams (12 ppm) in the Uinta Mountains. However, an investigation of longer duration would be much preferable for precise comparative studies on such relationships.

The absence of a periodicity in the drift of *Gammarus lacustris* in Mendon Creek was unexpected, in view of the marked periodicity that some other species of *Gammarus* exhibit. However, it would be premature to conclude that this species never exhibits a drift periodicity since the effect of other factors such as season, proximity to headwaters, etc., on the species is unknown. No other data on the drift of *G. lacustris* are presently available.

SUMMARY

1. Several 24-hr. series of drift sampling were carried out in eight small mountain streams and one low-gradient valley stream in the area of northeast Utah.

2. Daily patterns with two peaks appeared to be the typical form of night-active periodicities; no relationship between the secondary peak and moonlight could be detected.

3. Ephemeroptera nymphs constituted the major component of the drift in almost all streams.

4. The ephemeropteran genus *Baetis,* varying in species, exhibited marked night-active drift periodicities in all streams.

5. Other species of mayflies exhibited night-active periodicities; still other species, though abundant on the stream bottom, characteristically did not drift appreciably.

6. Several species of Plecoptera exhibited night-active periodicities, although some species exhibited no tendency to drift.

7. Among the Trichoptera, one species exhibited a day-active periodicity apparently entrained by water temperature, while another species showed a night-active periodicity entrained, as with Ephemeroptrea and Plecoptera, by light.

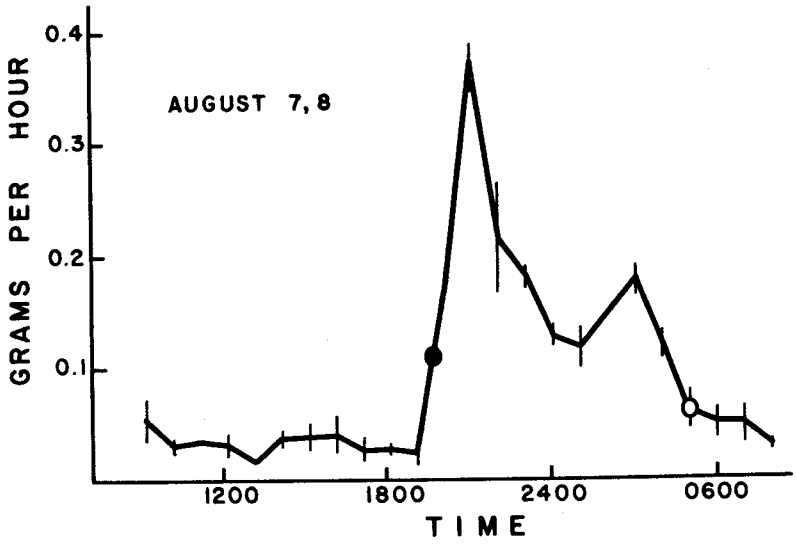


Figure 18

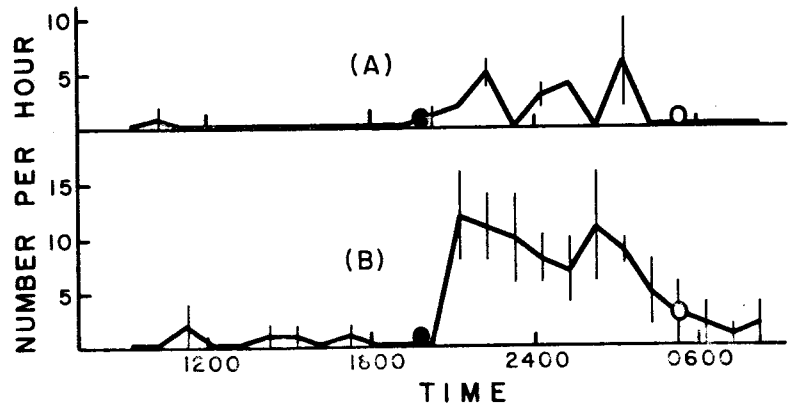


Figure 19

8. The predators, *Rhyacophila* and *Acroneuria,* did not exhibit appreciable drift.

9. In the valley stream, *Gammarus lacustris* did not exhibit a drift periodicity.

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Fig. 1—Drift nets set into sampling position on stream bottom.

Fig. 2—Drift of *Baetis bicaudatus* in Logan River, in quantity per hour per net (15 cm wide), mean of two samples. Vertical lines represent range. Closed circle represents time of sunset; open circle, time of sunrise.

Fig. 3—Drift of *Baetis bicaudatus in* Beaver Creek (legend as in Fig. 2).

Fig. 4—Drift of *Ameletus* (probably *velox*) in Beaver Creek (legend as in Fig. 2).

Fig. 5—Drift of *Baetis bicaudatus in* Temple Fork (legend as in Fig. 2).

Fig. 6—Drift of *Ephemerella coloradensis* in Temple Fork (legend as in Fig. 2).

Fig. 7—Drift of *Ephemerella doddsi* in Temple Fork (legend as in Fig. 2).

Fig. 8—Drift of *Baetis bicaudatus* in Spawn Creek (legend as in Fig. 2).

Fig. 9—Drift of *Nemoura* (*Malenka*) sp. in Spawn Creek (legend as in Fig. 2).

Fig. 10—Drift of *Baetis tricaudatus* in Right Fork (legend as in Fig. 2).

Fig. 11—Drift of *Nemoura* (*Malenka*) sp. in Right Fork (legend as in Fig. 2, except only one sample per hour in the June 20, 21 series).

Fig. 12—Drift of *Neothremma* sp. in Right Fork (legend as in Fig. 2).

Fig. 13—Drift of *Baetis bicaudatus* in Henry's Fork (legend as in Fig. 2).

Fig. 14—Drift of stonefly nymphs in Henry's Fork; (A) *Alloperla* sp., and (B) *Nemoura* (*zapada*) sp. (legend as in Fig. 2).

Fig. 15—Drift of *Baetis bicaudatus* in Paradise Creek (legend as in Fig. 2).

Fig. 16—Drift of stonefly nymphs in Paradise Creek: (A) *Alloperla* sp., (B) *Nemoura* spp., (C) *Issogenus modestus*, and (D) *Arcynopteryx parallela* (legend as in Fig. 2).

Fig. 17—Drift of *Epeorus* (*Iron*) *longimanus* in Paradise Creek (legend as as in Fig. 2).

Fig. 18—Drift of *Baetis* spp., in Deadman Creek (legend as in Fig. 2).

Fig. 19—Drift of stonefly nymphs in Deadman Creek; (A) *Isogenus aestivalis*, and (B) *Nemoura* spp. (legend as in Fig. 2).