

claval and costal areas white, veins broadly black or dark brown, with black spots along inner margin next to scutellum; disc of wing white to pale yellow, subhyaline with dark brown veins.

Female seventh sternum with lateral angles rounded to posterior margin which is shallowly concavely rounded each side of a broad median slightly produced lobe; lobe slightly notched at middle.

Holotype female Cuernavaca, Morelos, Mexico IX-8-39 (DeLong). Paratypes: 1 ♀ same as holotype except IX-25-45 (Plummer, DeLong, Hershberger, Elliott); 1 ♀ Tepotzlan, Mor. Mexico IX-11-41 (DeLong, Good, Caldwell, Plummer).

Remarks: All specimens were collected at elevations of 8000 to 9000 feet in shrub habitats. The striking coloration will distinguish *P. ornatata* from all other known species.

THE DRIFT OF MAYFLIES (Ephemeroptera) IN THE BRAZOS RIVER, TEXAS¹

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ABSTRACT

An investigation into the drift-ecology of the mayfly populations of the Brazos River, a Southwestern United States river, was conducted from April, 1972 to February, 1973. Bi-monthly drift samples were used to delineate the nocturnal periodicities and seasonal fluctuations of six species, three of which are new and as yet undescribed. Highest levels of behavioral drift, expressed in drift density units, occurred during the night of the summer sample dates. The drift of exuviae seems to be an accurate indicator of mayfly emergence in the Brazos River.

Extensive reviews by Elliott (1967a), Bishop and Hynes (1969), Waters (1969a, 1972), and Hynes (1970) indicate the importance of the Ephemeroptera as a functional component of downstream drift. To date, no investigations have been reported in the Southwest concerning the drift of mayfly populations. It was the objective of this study to elucidate the nature and extent of drift by the mayfly populations of the Brazos River, Texas. More specific objectives were the

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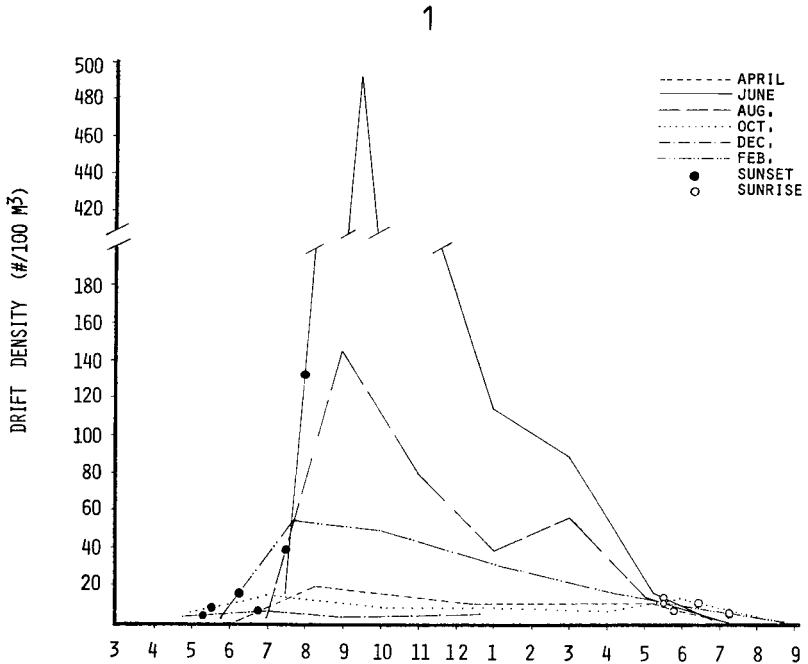


FIG. 1. Drift of *Nechoroterpes mexicanus* nymphs, Brazos River, 1972-1973.

establishment of drift densities, diel periodicities, periods of emergence, and seasonal fluctuations in drift composition.

STUDY AREA

All samples were taken at the downstream end of a large riffle, just below the confluence of the Brazos River and Dark Valley Creek, near the Texas State Highway 4 Bridge. The river at and above the study riffle is modified by the continuous leakage of 10-15 cfs of cold hypolimnion water around the hydroelectric generators of Possum Kingdom Dam, approximately 20 miles upstream. This results in minimal flows, low turbidities, and a rather stable temperature in this section of the river, which is atypical of the Brazos and other regional river systems throughout most of the year.

The dimensions of the study riffle vary considerably. However, at low to moderate levels during which times samples were taken, the riffle measured approximately 20 m in length and 11-20 m in width. Depths during sampling periods ranged from 5-35 cm, with a natural shallow-water to deep-water gradient extending toward the south

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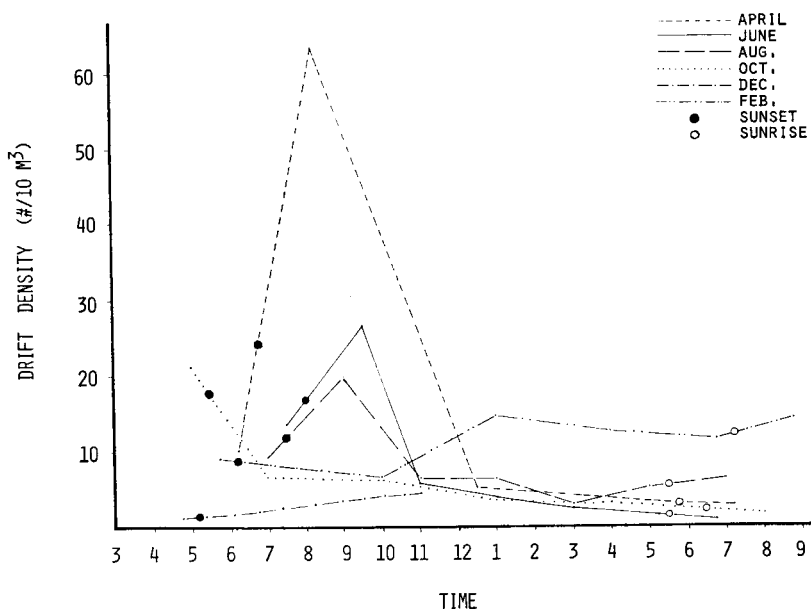


FIG. 2. Drift of *Neochoroterpes mexicanus* exuviae, Brazos River, 1972-1973.

bank of the eastwardly flowing river. The south bank and adjacent portions of the riffle were moderately shaded by willows and large elms.

The riffle substrate consisted of gravel and rubble-sized particles intermingled with sand beginning at about 5-10 cm, overlying at several points large limestone rubble beginning at about 40 cm.

Thirty to 40 species of riffle insects were found in the study riffle community. The stabilized minimal flow-temperature-turbidity conditions and nature of the substrate promote a relatively high species diversity and large standing crops. Unpublished data from this riffle over the past three years have shown mean standing crops of up to 38,516 insects/m² in late summer.

Recent studies by fisheries biologists of the Texas Parks and Wildlife Department have shown that physical and biological conditions of the river immediately below Possum Kingdom Dam are suitable for seasonal stocking of catchable-sized rainbow trout, *Salmo gairdneri* (Forshage 1972). Stocking began in February, 1973 and trout have been taken as far downstream as the study riffle during early April.

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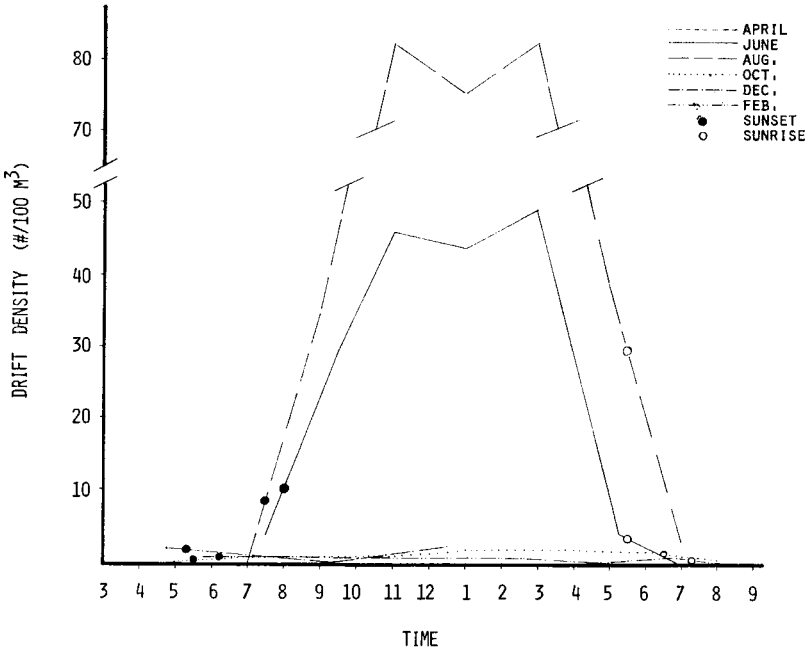


FIG. 3. Drift of *Tricorythodes*, sp. nymphs, Brazos River, 1972-1973.

MATERIALS AND METHODS

Drift samples were taken with a modified device similar to that of Müller (1958). The samplers consisted of a cylinder 10.5 cm in diameter and 17.5 cm in length; a tapering Nitex bag 45 cm in length with a mesh opening of 471 μ was attached. Standard Wildco plankton buckets (mesh opening = 363 μ) were fitted to the end of each net to allow quick removal of samples. To insure that only drifting invertebrates entered the net, a wooden board was set flush to the stream bottom prior to sampling. The samplers, fitted with ring adapters, were held in place by iron rods driven through the boards into the substrate (Waters 1962). The bottom of the cylinders rested approximately 4 cm above the substrate during sampling.

Samples were taken bi-monthly from April, 1972 to February, 1973. On each sampling date, except April and December, six 1-hr samples were taken concurrently at each of seven time periods during the day (42 total samples/date). These time periods were spaced as follows: (1) immediately prior to sunset; (2) beginning 0.5 hr after

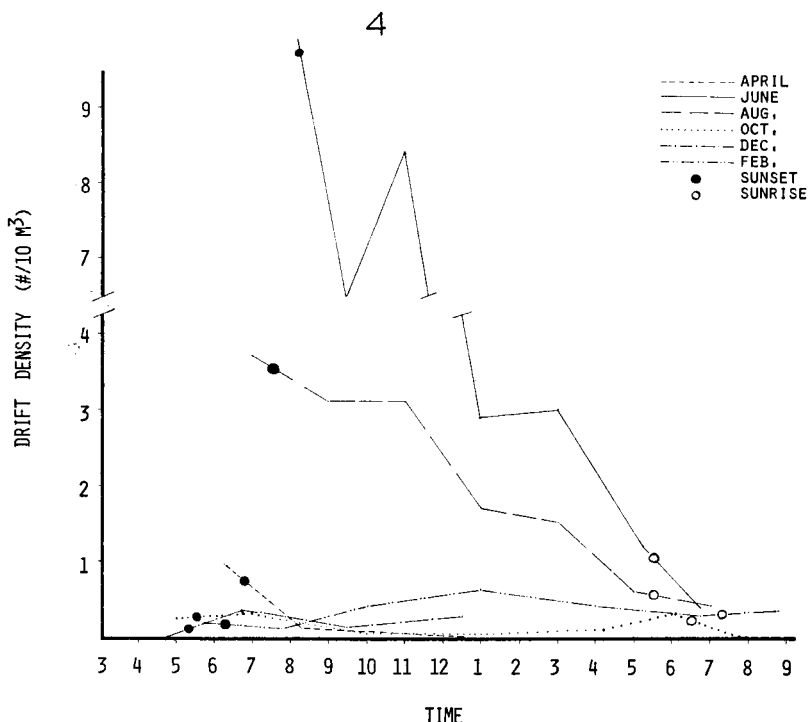


FIG. 4. Drift of *Tricorythodes* sp. exuviae, Brazos River, 1972-1973.

sunset; (3) three evenly spaced intervals throughout the night; (4) ending 0.5 hr before sunrise; and (5) immediately following sunrise. Because of this spacing, sample periods expressed in terms of Central Standard Time, varied seasonally. Such a sampling regime admittedly is less desirable than continuous hourly sampling; however, economy of sampling necessitated some reduction in the number of samples taken. Preliminary drift samples taken on this riffle in August, 1971 every hour over a 24-hr period, indicated very low daytime drift of mayflies.

Only five time periods were initially sampled during April, 1972 giving a total of 30 samples for that month. Flooding of the study riffle by water releases from Possum Kingdom Dam in December, 1972, during the night, necessitated termination of sampling after 24 samples had been taken. A total of 222 hourly samples were taken during the study.

Placement of the six samplers for each time period was such that duplicate samples were obtained at each of three stations located approximately 25, 50, and 75% of the distance across a transect at

TABLE 1. Cubic meters of water sampled/station Brazos River, 1972-1973.

Daily Sample Periods	STATIONS											
	April				June				August			
	1	2	3	PT ^c	1	2	3	PT	1	2	3	PT
1 ^a	38.6	61.2	190.2	190.0	90.2	93.0	147.0	330.2	20.6	28.4	107.8	156.8
2	37.2	33.6	81.8	152.6	83.2	100.4	154.2	337.8	17.2	25.4	107.8	150.4
3	—	—	—	—	73.4	80.8	151.8	306.0	13.6	20.6	100.4	134.6
4	34.0	32.0	78.8	144.8	63.6	66.2	150.8	280.6	17.2	22.0	106.8	146.0
5	—	—	—	—	75.8	61.2	127.4	264.4	18.0	22.0	105.2	145.2
6	34.0	18.6	73.8	126.4	73.4	93.0	129.8	296.2	19.6	22.0	98.0	139.6
7	34.2	18.4	65.2	117.8	71.0	74.4	126.4	271.8	13.6	23.4	101.8	138.8
Monthly Totals	731.6				2087.0				1011.4			

Daily Sample Periods	STATIONS											
	October				December				February			
	1	2	3	PT	1	2	3	PT	1	2	3	PT
1 ^a	41.6	102.8	138.0	282.4	85.8	68.6	107.8	262.2	44.0	85.8	171.4	301.2
2	39.2	100.4	137.2	276.8	88.0	49.0	93.0	230.0	41.6	78.4	166.6	286.6
3	34.2	95.6	146.0	275.8	36.8	44.0	78.4	159.2	44.0	78.4	161.6	284.0
4	39.2	92.0	132.2	263.4	27.0	29.4	56.4	112.8	39.2	73.4	156.8	269.4
5	39.2	95.6	134.8	269.6	—	—	—	—	39.2	83.2	161.6	284.0
6	34.2	34.2	91.6	257.0	—	—	—	—	39.2	78.4	144.4	262.0
7	36.8	89.6	137.2	263.6	—	—	—	—	34.2	73.4	156.8	264.4
Monthly Totals	1888.6				764.2				1951.6			

^a 1-hr preceding sunset^b 1-hr following sunrise^c PT indicates period totals

TABLE 2. Total drift estimates for Brazos River mayflies during the period 1-hr before sunset to 1-hr after sunrise, 1972-1973.

Month	Neo-choroterpes	Tri-corythodes	Baetis	Caenis	Heptagenia	Isonychia
April	1.65×10^4	5.68×10^2	3.97×10^3	5.68×10^2	2.84×10^2	2.84×10^2
June	5.31×10^5	8.98×10^4	5.63×10^4	3.47×10^4	3.64×10^3	2.25×10^3
August	1.04×10^5	9.66×10^4	1.97×10^4	1.41×10^4	8.57×10^2	8.57×10^2
October	1.72×10^4	1.85×10^3	1.78×10^4	1.16×10^2	4.64×10^2	—
December	1.70×10^4	4.49×10^3	—	—	—	—
February	8.77×10^4	9.61×10^2	—	4.61×10^3	5.76×10^2	—

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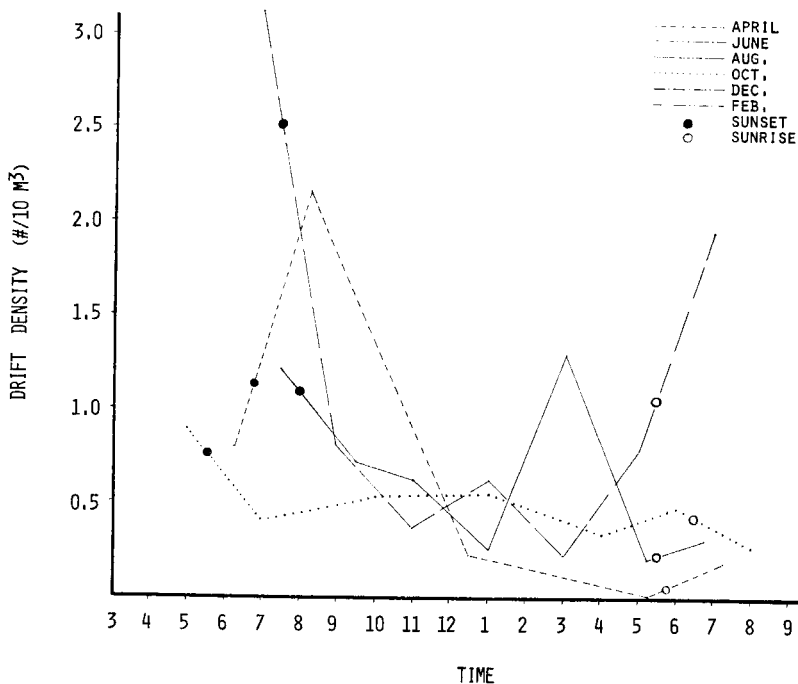


FIG. 6. Drift of *Baetis* sp. exuviae, Brazos River, 1972-1973.

munity, second in abundance only to the caddisfly genus *Cheumatopsyche*.

Drift density of the nymphs was minimal in October and December, never surpassing 15/100 m³ at any time period sampled (Fig. 1). April density never exceeded 20/100 m³, and moderate numbers of 20-54/100 m³ were drifting during the February sampling period. The greatest drift density observed for this species occurred during the June and August samples (Fig. 1), when maximums of 494/100 m³ and 144/100 m³, respectively, were reached.

In all months sampled, some degree of nocturnal periodicity was exhibited (Fig. 1). A single peak in drift density occurred just after sunset, except in August and October, when minor secondary peaks occurred at 3 a.m. and just before sunrise, respectively.

Neochoroterpes exuviae (Fig. 2) drifted in peak numbers in April (63/10 m³). Although the life cycle for this species is unknown, the seasonal pattern of drift in Figure 1 and observations of large numbers of exuviae in April suggests that the species probably has a

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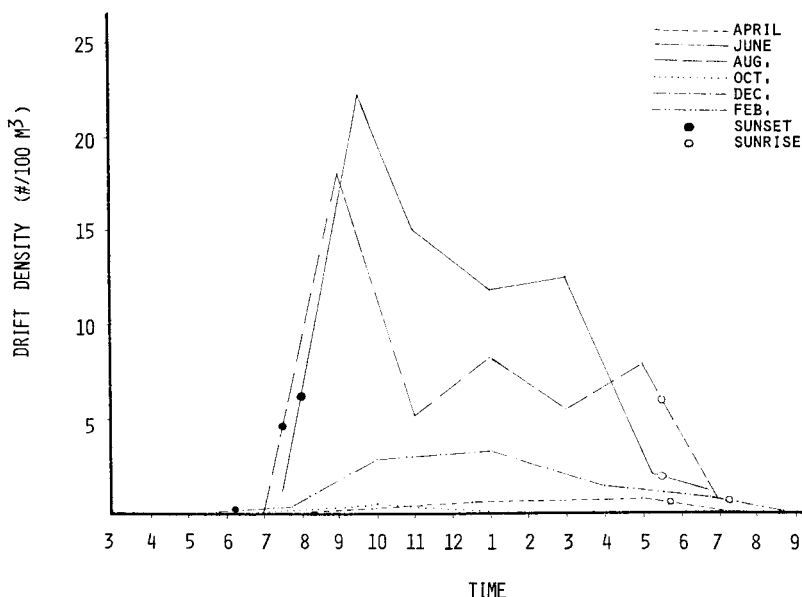


FIG. 7. Drift of *Caenis* sp. nymphs, Brazos River, 1972-1973.

multivoltine life cycle with peak emergences of three generations occurring in March-April, July, and September, and that the peaks in drift density occur in the month(s) just prior to emergence (February, June, August). The high April exuviae drift, at a time when drift of nymphs was low, could possibly be explained if the sampling date corresponded with the tail end of an emergence, combined with an accumulation of drifting exuviae over long distances upstream. Fewer nymphs would be available to drift short distances (behavioral) but the very buoyant, "passive" exuviae would represent an accumulation. The majority of the exuviae were of pre-emergent size. This is also suggested by the much higher density of exuviae over nymphs during this month.

An estimate of total numbers of drifting *Neochoroterpes* for the whole cross-sectional area of the Brazos sampled was calculated from observed net catches, sample volumes, and stream discharge employing the methods of Elliott (1970). The total volumes of water sampled (m^3) during the bi-monthly sample dates are presented in Table 1. These were calculated from linear current velocities and are given for each station (2 samples) at each daily sample period. Total cross-sectional stream discharge for the monthly sample periods was

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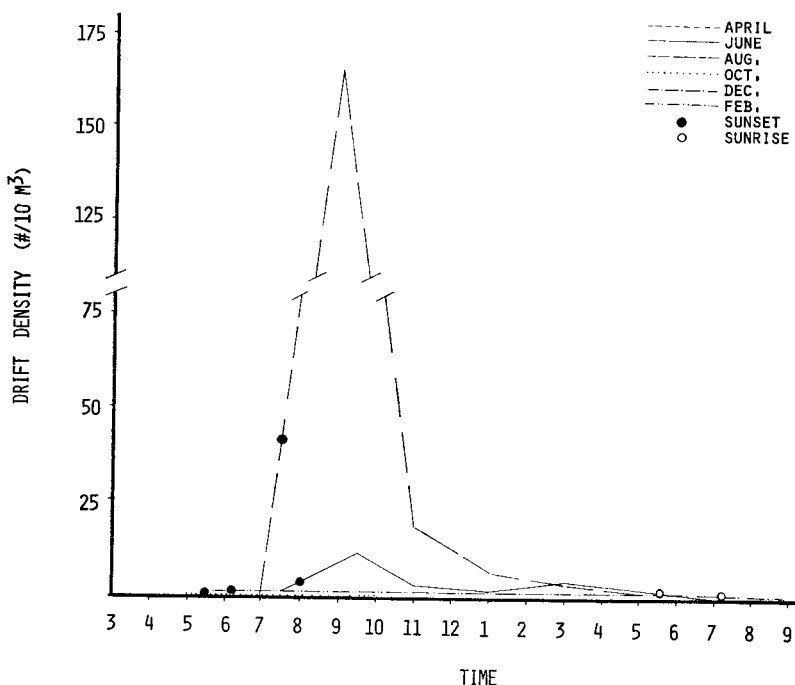


FIG. 8. Drift of *Caenis* sp. exuviae, Brazos River, 1972-1973.

calculated from depth and velocity readings taken periodically throughout the night. These calculated discharges correspond favorably with values recorded by a U.S.G.S. gauging station adjacent to the riffle. The maximum and minimum number of *Neochoroterpes* drifting 1-hr before sunset to 1-hr after sunrise was 5.31×10^5 and 1.65×10^4 , respectively (Table 2); these values are relatively high when compared with even the total invertebrate drift of several studies (Elliott and Corlett 1972). It should be kept in mind that the estimates for *Neochoroterpes* are minimal, since they cover drift only for the nighttime and adjacent two hours.

Tricorythodes sp. (Caenidae)

Members of this species drifted predominantly in the summer sample months of August and June with peak densities of over 80 nymphs/100 m³ being observed in August (Fig. 3). Samples in the

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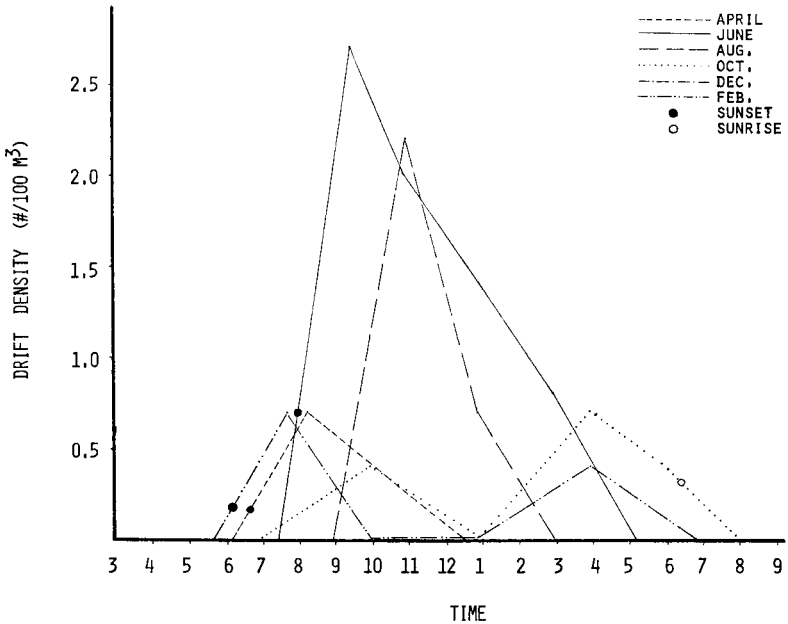


FIG. 9. Drift of *Heptagenia* sp. nymphs, Brazos River, 1972-1973.

other months showed very low drift densities, never surpassing 3/100 m³.

Tricorythodes exuviae (Fig. 4) showed a definite tendency to decrease in drift density throughout the night in the late spring and summer samples. Spring and summer emergence of *Tricorythodes* occurs chiefly in the afternoon on the Brazos, possibly explaining the high exuvial drift encountered 1-hr before sunset. Peaks in exuvial drift density coincided with those of maximal nymphal density in June and August (Figs. 3, 4).

Baetis sp. (Baetidae)

Maximum drift density for *Baetis* sp. of 48/100 m³ occurred in June at 1.5 hrs after sunset in a typical unimodal curve (Fig. 5). A "bigeminus-pattern" was exhibited in August and October. No drift of *Baetis* was detected in December and February, possibly due to nymphal diapause during winter.

The seasonal and diel pattern of drift of *Baetis vagans* (Waters 1962) is almost identical with this species. Pearson and Kramer

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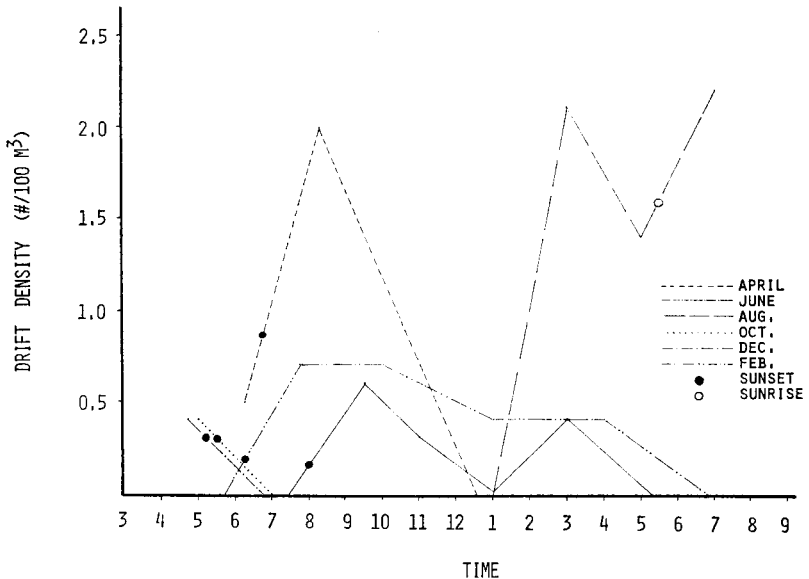


FIG. 10. Drift of *Heptagenia* sp. exuviae, Brazos River, 1972-1973.

(1972) noted a similar seasonal pattern in *Baetis bicaudatus* with very low winter rates.

Tanada (1960) also noted marked increases in drifting of *Baetis* sp. just after sunset, as have several other investigators (Waters 1962, 1965, 1969 b, Müller 1963, Södergren 1963, Elliott 1965 a, b, 1967 a, Holt and Waters 1967, Pearson and Franklin 1968, Bishop and Hynes 1969, Peterka 1969, Brusven 1970, and Wojtalik and Waters 1970).

Baetis exuviae (Fig. 6) were encountered in greatest numbers in the late afternoon and/or early morning hours of June, August, and October suggesting that emergence of this species on the Brazos takes place primarily during daytime. Pearson and Kramer (1972) noted large swarms of *Baetis bicaudatus* in the early morning hours over Temple Fork, Utah. Minor nocturnal peaks were encountered in each of these months. These may have represented molted exuviae from lateinstar nymphs. The high exuvial peak encountered just after sunset in April (Fig. 6) may have been the result of a late evening emergence.

A maximum of 5.63×10^4 *Baetis* (Table 2) were estimated to have drifted past the sample transect during the 12:5-hr sample time in June. This compares with Elliott and Corlett (1972) who found

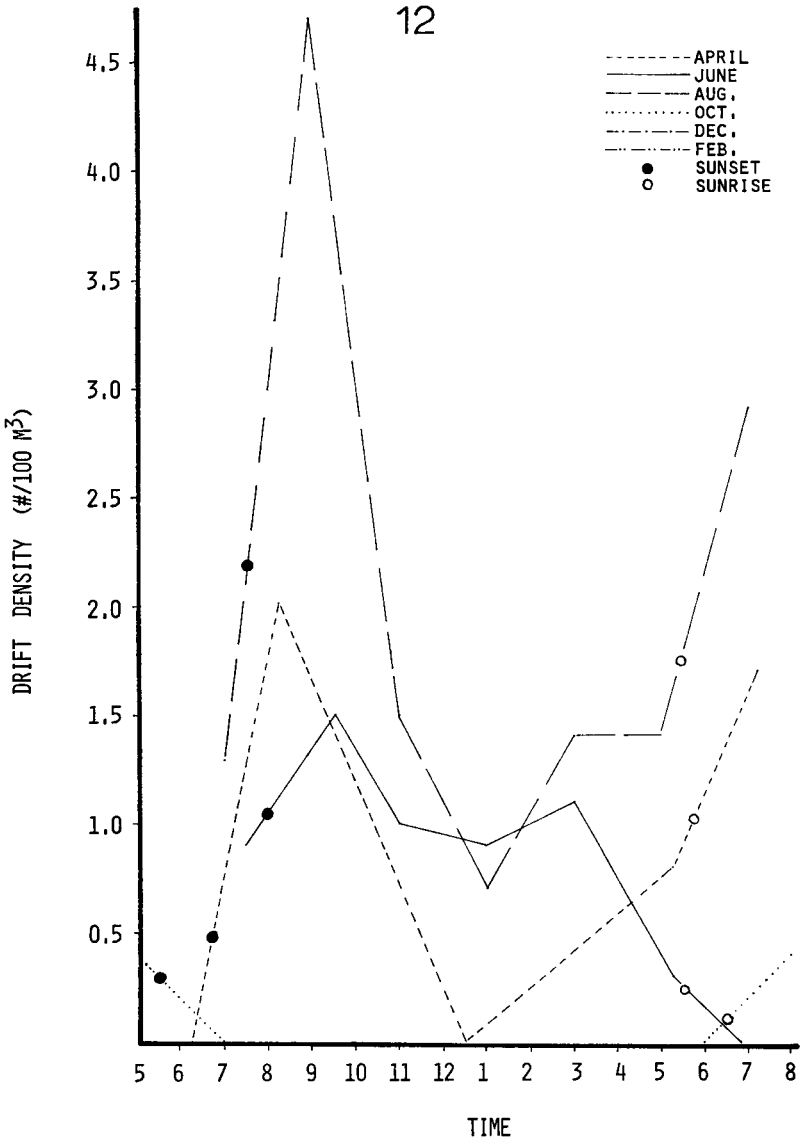


FIG. 12. Drift of *Isonychia sicca manca* exuviae, Brazos River, 1972-1973.

August after sunset may represent emergence. Morgan and Waddell (1961) have shown *Caenis horaria* to be an evening emerging form with most emergence taking place between 8 p.m. and 10 p.m. Kimmins (1954) observed emergence in *C. horaria* between 7 p.m. and 9:30 p.m.

Heptagenia sp. (Heptageniidae)

This is another new, undescribed mayfly species (R. K. Allen, personal correspondence). A maximum drift density of 2.7 *Heptagenia*/100 m³ was recorded in June. As in the previous mayfly taxa, the peak seasonal drift densities (Fig. 9) were encountered during the summer sample dates of June and August.

Heptagenia exhibited definite nocturnal periodicities; however, there was a great variation in monthly patterns. The reason for this discrepancy in drift pattern is not known. Elliott and Corlett (1972) have also reported a basic nocturnal pattern in the drift activity of *Heptagenia sulphurea*.

Monthly patterns in the drift density of *Heptagenia* exuviae (Fig. 10) were also highly variable. Peak drift densities of 2.0/100 m³ and 2.1/100 m³ were encountered in April and August, respectively.

Isonychia sicca manca (Baetidae)

Greatest drift densities observed for this species (2/100 m³) occurred during June and August (Fig. 11); a small catch of 0.7/100 m³ was also taken in April.

The drift activity was basically "bigeminus" with the exception of the single peak in April at which time drift densities were low.

Isonychia exuviae (Fig. 12) drifted in peak numbers in August (4.7/100 m³). Samples in April, August, and October suggest that periods of emergence may occur in the daylight before sunset and/or after sunrise.

DISCUSSION

All mayfly populations studied exhibited their greatest drift densities during the summer sample months of June and August. This is not unlike the findings of previous authors who have found basically the same pattern of seasonal invertebrate drift in other regional, stream ecosystems (Waters 1966, Anderson 1967, Elliott 1967 a, b, McLay 1968, Brusven 1970, Elliott and Corlett 1972). Although no attempt was made to statistically interpret the underlying factors related to drift, it appears that light intensity, season and/or life history events, and behavioral and morphological adaptations are of paramount importance.

Without exception, all of the Brazos River mayflies displayed nocturnal periodicities (Figs. 1, 3, 5, 7, 9, 11). In each species, highest drift densities were generally recorded immediately following sunset.

Since samples were taken at times of low to moderate current velocities and expressed in terms of standardized density units, it seems reasonable to assume that the differences in the magnitude of each individual species diel cycle is a result of behavioral activity. Whether this activity is of an "active" or "passive" nature, remains to be determined.

Although Table 1 indicates a rather substantial reduction in velocity throughout the night of the December sample date, there was no apparent effect upon observed drift densities. Elliott (1967 a, b) has shown that drift densities remain relatively constant during periods of abnormally high discharge.

Little variation in drift was noted between replicate samples. A significant variation in drift numbers did occur across the sample transect due to the variation in current velocities encountered. However, a goodness of fit comparison between expected catches and observed net catches indicated that the observed catch was directly proportional to water volume sampled.

The drift densities of *Heptagenia* and *Isonychia* nymphs were generally much less than those of other mayfly taxa. This was probably due in part to the low densities of these species in the standing crops of the benthos.

Some authors have associated the "drift potential" of an individual organism with its life history stage (Anderson 1967, Elliott 1967a), however, this paper represents one of the first accounts of drifting exuviae being used as indicators of mayfly emergence. Since pre-emergent activity is known to increase the organism's availability to the drift (Anderson 1967, Elliott 1967b, Reisen and Prins 1972), there should be an increased number of exuviae captured in the drift nets during periods of emergence, even though some exuviae are suspended in the stream's water column throughout the 24-hr period. In the Brazos River species, peaks in exuvial drift density were closely associated with observed emergences or reported times of emergence of closely related species by other authors. Therefore, the use of exuvial drift catches may be a beneficial supplement to bilateral insect trap and light-trap data in future studies.

ACKNOWLEDGMENTS

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PHEROMONE INDUCED BROODING BEHAVIOR IN *BOMBUS VOSNESENSKII* AND *B. EDWARDSII* (Hymenoptera: Bombidae)¹

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ABSTRACT

Queens of *Bombus vosnesenskii* and *B. edwardsii* incubate pollen clumps after ovipositing in them, and incubation continues until the adults emerge. The larvae and eggs are not incubated when removed and placed into or onto another pollen clump. However, the original (empty) pollen clump is incubated for at least ten days after the immatures have been removed from it. The bees locate and incubate their pollen clumps in the absence of visual cues but not when deprived of both antennae. When in the dark, the queens hold no preference for their own pollen clump over another having been utilized by others of their species, but they do not incubate brood clumps of the other species. The observations suggest that the queen deposits scent onto her brood clump. The scent, acting only at very close range or during contact, guides the queen (and subsequently workers) to the site at which her eggs or immatures are buried. The incubation behavior is released at this site in response to the scent.

Many social Hymenoptera are well-known to maintain a high nest temperature in the vicinity of their immatures (Himmer, 1932). However, for the most part, the regulatory mechanisms of this behavior are unknown.

The lone bumblebee queen, which initiates the colony (Alford, 1970), incubates her brood clump containing eggs, larvae and/or pupae for long durations each day. The behavior is distinct from the

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