DRIFT OF AQUATIC INSECTS IN THE

BRAZOS RIVER, TEXAS

APPROVED:

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KWS

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The objective of this study was to elucidate the nature and extent of drift by the aquatic insect populations of the Brazos River, Texas; such information has been heretofore unavailable for a major Southwestern United States river. The establishment of drift densities, nocturnal periodicities, and seasonal variations of drifting populations was determined from April, 1972 to February, 1973. The findings of this investigation were

(1) Drift was expressed as drift density; highest peak densities were 494, 397, and 144/100 m^3, respectively, for the three dominant insects in the river, *Choroterpes* sp., *Chaoborus* sp., and *Simulium* sp. Peak drift densities of other populations varied from 2 to 92.5/100 m^3.

(2) Total drift estimates were calculated for six dominant riverine insects, *Choroterpes* sp., *Cheumatopsyche* spp., *Chaoborus* sp., *Simulium* sp., Chironomidae, and *Baetis* sp. Total numbers drifting 1-hr before sunset to 1-hr after sunrise in June were 5.31×10^5 (maximum estimate during study), 8.53×10^4, 5.39×10^5, 7.13×10^4, 8.44×10^4, and 5.63×10^4, respectively. High estimates were also noted for these species in August, with lower totals drifting during sample dates in other months.

(3) Eighteen species previously unreported in drift studies included Ephemeroptera, *Choroterpes* sp., *Tricorythodes* sp., *Isonychia sicca manca*; Trichoptera, *Hydropsyche simulans*, *Ithytrichia clavata*, *Hydroptila icona*, *Chimarra obscura*, *Pycnopsyche* sp.; Diptera, *Palpomyia* sp.; Coleoptera, *Stenelmis bicarinata*, *Stenelmis mexicana*, *Dubiraphia vittata*, *Gyretes* sp.; Odonata, *Enallagma* sp., *Argia* sp., *Ophiogomphus* sp.; Lepidoptera, *Elophila* sp.; and Plecoptera, *Neoperla clymene*. This probably was due to the lack of previous drift studies in the Southwestern United States.

(4) All six mayflies encountered in the drift exhibited peak densities during June and August; this was also true of all Coleoptera and four of the caddisflies. *Hydroptila icona* and *Pycnopsyche* sp. larvae exhibited peaks in October and February, respectively. Two species of the three families of Diptera also exhibited fall and spring peaks in drift density, except *Chaoborus* sp. which were most abundant in June and August. Other members of the community exhibited variable seasonal drift patterns, with higher summer values roughly corresponding with activity of immatures and emergence.

(5) A high nocturnal drift pattern was observed in most species. Unimodal and bimodal patterns predominated throughout the yearly sample period; however, seasonal variations were noted between and among taxa.

(6) Examination of mayfly exuviae indicated that peaks in drift density and emergence are species-specific; Trichoptera

pupae exuviae, however, showed a clear nocturnal emergence periodicity, corresponding with observed emergence.

(7) The abundance of Dipteran pupae in the drift appears to be directly related to the emergence patterns of the various species.

DRIFT OF AQUATIC INSECTS IN THE BRAZOS RIVER, TEXAS

THESIS

Presented to the Graduate Council of the
North Texas State University in Partial
Fulfillment of the Requirements

For the Degree of

MASTER OF SCIENCE

By

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CHAPTER I

INTRODUCTION

The drift of aquatic invertebrates has recently received much attention among stream ecologists. This interest and research have resulted primarily from the realization that downstream drift is an integral component of a stream ecosystem. First reports on invertebrate drift (Needham 1928, Denham 1930, Lennon 1941, Ide 1942, Dendy 1944) established this downstream transport as a naturally occurring phenomenon, and subsequent investigations by numerous authors have dealt with the various aspects of stream drift. Waters (1972) discussed four aspects of drift which are important in stream ecology: (1) diel periodicities; (2) life histories; (3) population dynamics and production; and (4) fish feeding.

Diel periodicity, a recurrent temporal pattern over a period of twenty-four hours, was first documented by Tanaka (1960), Waters (1962), and Müller (1963a,b) all of whom reported a much greater rate of invertebrate drift at night than during the daylight hours. This characteristic, nocuturnal drift activity, has been shown to have three common patterns: (1) a single peak, usually occurring just after sunset (Tanaka 1960, Waters 1962, Müller 1963a,b); (2) the "bigeminus-pattern" in which two peaks of drift activity occur, one major peak shortly after sunset and one minor peak later in the night just before sunrise (Müller 1965, 1966, Waters 1969a); and (3) the "alternans-pattern" with the minor peak occurring shortly after sunset followed by the major peak later in the night (Müller 1965, 1966). Daytime drift rates are generally low for most species; however, the variations in some aquatic groups are great. Some Trichoptera have been shown to have day-active periodicities (Anderson 1967, Waters 1968, Bishop and Hynes 1969, Elliott 1970c, 1971) while some Diptera, especially Chironomidae, have been observed to display "continuous drift" (Brusven 1970a) as well as the typical nocturnal pattern (Mundie 1971). Observations on the activity of stream macrobenthos under varying conditions of light and illumination (Harker 1953, Müller 1965, Holt and Waters 1967, Chaston 1968, 1969, Bishop 1969) indicate that drift periodicities are probably due to circadian rhythms triggered by the reduction of light below a specific threshold value, resulting in the macrobenthos' subsequent displacement by stream currents. Other major factors which may contribute significantly to the variations in pattern and magnitude of this diel cycle include (1) current velocity or discharge of the stream (Minshall and Winger 1968, Anderson and Lehmkuhl 1968, Hughes 1970); (2) water temperature (Müller 1963c, Pearson and Franklin 1968, Wojtalik and Waters 1970); (3) population density and/or biomass (Müller 1954, Waters 1961, 1966, Pearson and Franklin 1968, Pearson and Kramer 1972); and (4) the stage of the life history of the invertebrate (Anderson 1967, Elliott 1967).

Pearson and Franklin (1968) found that at least three factors, illumination, population density, and water temperature, all had significant effects on drift rates of *Baetis* and Simuliidae.

The drift of aquatic macrobenthos has proven to be a very useful and supplemental tool in life history studies. According to Waters (1969a), there seems to be little question that in many species "behavioral drift", an active process, is related to the stage of life cycle. Undoubtedly, life cycles and production dynamics are closely linked, and downstream drift is a result of a complexity of factors one of which may be the removal of excess production above the stream bottom's carrying capacity (Waters 1961, 1966). This removal of only excess production would not require a "colonization cycle" (Müller 1954) for the recolonization of upstream areas once thought to be depleted to some extent by drift. However, the great variability between streams and insect species should be taken into consideration before the acceptance or rejection of either hypothesis.

The abundance of invertebrate drift in streams constitutes a major factor in the trophic relationships of those systems. Numerous studies have related the ability of fish to prey upon drifting invertebrates in addition to their natural bottom foraging activities (Baily 1964, Waters 1969a, Jenkins et al. 1970, Elliott 1970b, Mundie 1971). Therefore, downstream drift contributes to the availability of cryptic insect prey to predacious fishes.

More complete reviews and summaries on the phenomenon of drift have been recently published by Elliott (1967), Bishop and Hynes (1969), Waters (1969a, 1972), and Hynes (1970).

The objective of this study was to elucidate the nature and extent of drift by the insect populations of the Brazos River, Texas. More specific objectives were the establishment of drift densities, diel periodicities, and seasonal variations in drift composition; such information has been heretofore unavailable for a major Southwestern United States river.

Description of Study Area

The Brazos River, with its headwaters in north central and west central Texas, flows approximately 840 miles southeastwardly to the Gulf of Mexico. The river system serves as a watershed for some 41,700 square miles. Prior to the construction of Possum Kingdom Dam in 1941, the river at the study area was very similar to adjacent unmodified river systems and was characterized by turbid, intermittent flows (USGS data).

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.

Operations at Possum Kingdom Dam often result in highly erratic and unpredictable flow characteristics downstream. The hydroelectric function of Possum Kingdom Dam are dictated by power consumption, which is in turn affected by local weather conditions. A United States Geological Survey gauging station is located adjacent to the study riffle, and the average discharge rate recorded at the station over the past 46 years was 1,103 cfs.

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 to 35 cm, with a natural shallow-water to deep-water gradient extending toward the south bank of the eastwardly flowing river. The south bank and adjacent portions of the riffle are shaded by willows and large elms.

The riffle substrate consists 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 are 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/m^2 in late summer.

Carnivorous fish species in the river include the spotted and largemouth basses, Micropterus puncutlatus and M. salmoides, channel and flathead catfishes, Ictalurus punctatus and Pylodictis olivaris, and several species of Lepomis, Percina, and Etheostoma as well as other species (Forshage 1972).

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.

CHAPTER II

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 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 4 cm above the substrate during sampling.

Samples were taken semi-monthly in April, June, August, October, December, and February, 1972 to 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 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, samples varied in clock-time seasonally. Such a sampling regime admittedly is less desirable than continuous hourly sampling; however, economy of sampling and the goal of examining the whole insect community drift 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 macrobenthos.

Only five time periods were 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 and resulted in the loss of some equipment. A total of 222 hourly samples was taken during the study.

Placement of six samplers for each time period was such that duplicate samples were obtained at each of these stations located approximately 25, 50, and 75% of the distance across a transect at the base of the riffle. Samplers were lifted at the end of the 1-hr periods, and any organisms adhering to the inside of the netting were washed into the removable plankton buckets. Samples were preserved in 70% isopropanol.

Depth, flow, and water temperature were recorded at the beginning of each hourly sample time at each of the three stations. Flow was determined with a Kahl Pygmy Flow Meter, calibrated at 0.4714 m/rev. Volume of water sampled at each station (2 samplers) was calculated for later use in determining drift density and total drift estimates (Elliott 1970a).

Water temperature was measured with an immersible °C thermometer.

Dissolved oxygen and pH were measured twice daily on each sample date, once immediately after sunrise and again immediately prior to sunset. The Winkler Method was used for dissolved oxygen determinations, and pH was determined photometrically with a portable Hach Kit.

Total hardness, Ca hardness, alkalinity, chlorides, total dissolved solids, and conductivity were determined from water samples taken during the Fall of 1972, employing procedures suggested by Standard Methods (1965).

Organisms were separated from debris and sorted into different taxa with an Ednalite 2x macroscope (Ednalite Research Corp., Peekskill, N.Y.). Determinations of some genera, and in many instances species, were aided by the following persons: Ephemeroptera, Dr. R.K. Allen, California State University; Trichoptera, Drs. H.H. Ross, University of Georgia and G.B. Wiggins, Royal Ontario Museum; Coleoptera, Dr. H.P. Brown, University of Oklahoma.

After counting, each taxa of each sample was dried for 24 hrs in tared weighing vials at 80°C. Dried samples were weighed to the nearest 0.1 mg, using a Mettler analytical balance. From this, the mean dry weight/individual per month was determined.

Drift densities (numbers drifting per unit volume of water) were determined (Elliott 1970a) to be used in graphical presentation of data. For these presentations, all sampling times, sunrise, and sunset were expressed in terms of Central Standard Time.

A Chi-Square analysis was run on the April and June catch of the dominant species in the drift, Choroterpes sp. This was suggested by Elliott (1970a) to determine if observed catch was directly proportional to volume of water sampled by different nets. If such net catches are proportional to water volume sampled, it can be assumed that drift density is fairly constant at all points in the stream at a particular instant, and therefore is a desirable expression of drift. Variations in drift density can then be assumed to be due to other causes (behavioral, physical disturbances, etc.).

Total drift estimates, necessary for the comparison of drift between different streams (Elliott 1970a), were calculated for six dominant members of the Brazos River drift: Choroterpes sp., Cheumatopsyche spp., Chaoborus sp., Simulium sp., Baetis sp., and chironomidae larvae. Due to the daily sampling regime, these estimates were based upon total drift for the period of 1 hr before dusk to 1 hr after dawn, rather than total daily drift.

The drift density of exuviae, recognized for their importance in fish feeding (Mundie 1969, 1971) and production estimates (Tsuda 1960), were analyzed in an effort to relate their abundance to seasonal and diel emergence patterns.

CHAPTER III

RESULTS AND DISCUSSION

A list of taxa taken in the 222 drift samples is presented in Table 1. Mean individual weights (10^{-4} g) per semi-monthly period are given for all except those found in very small numbers.

The Ephemeroptera, Trichoptera, and Diptera were the most prevalent orders represented; this generally correlates with relative abundance of these groups in the insect standing crops of the river (unpublished data). Most species found in the river were present in the drift at some time during their life history, as suggested by previous investigators (Baily 1964, Elliott 1967, Bishop and Hynes 1969). All three of the nocturnal drift patterns previously discussed were exhibited by some members of the insect community. The predominant pattern was a "unimodal" one, with a peak exhibited soon after sunset. The variations will be discussed according to individual taxa.

The total volumes of water sampled (m^3) during the semi-monthly sample dates are presented in Table 2. These were calculated from linear flows and are given for each station (2 samples) at each daily sample period. Mean flows throughout the year were relatively high, with a maximum of 1.64 m/sec encountered in June; a minimum flow of 1.02 m/sec was noted in December just prior to a water release at Possum Kingdom Dam.

Table 1--Brazos River drift and mean individual weights (10^{-4} g) of abundant organisms, 1972-1973.

TAXA	SAMPLE MONTHS APR	JUNE	AUG	OCT	DEC	FEB
Ephemeroptera						
Choroterpes sp.	3.83	0.49	0.63	1.25	0.91	0.94
Baetis sp.	2.29	0.41	0.54	0.66	--	--
Caenis sp.	1.50	0.29	0.23	1.00*	--	0.83
Tricorythodes sp.	1.00*	0.48	0.25	0.37	0.11	1.20
Isonychia sicca manca	53.00*	2.54	44.70	--	--	--
Heptagenia sp.	2.00*	0.81	0.25*	0.75*	--	1.33*
Hexagenia limbata	--	--	--	--	--	--
Trichoptera						
Cheumatopsyche spp.	1.03	2.43	1.83	0.67	13.00*	10.80
Hydropsyche simulans	2.77	6.59	5.00	1.30	1.83	4.39
Hydroptila icona	0.12	0.12	16.00*	0.31	0.14	1.70
Chimarra obscura	--	0.29	0.06	--	--	--

Table 1--Continued

TAXA	SAMPLE MONTHS APR	JUNE	AUG	OCT	DEC	FEB
Trichoptera						
Ithytrichia clavata	0.25*	0.36	0.56	0.50*	--	0.71
Pycnopsyche sp.	--	7.86	--	--	--	1.00
Leptocella candida	--	--	--	--	--	--
Polycentropus sp.	--	--	--	--	--	--
Ochrotrichia sp.	--	--	--	--	--	--
Trichoptera pupae	--	--	--	--	--	--
Diptera						
Simulium sp. larvae	0.37	0.64	3.11	0.57	2.44	6.16
Simulium sp. pupae	1.00*	--	--	1.20	4.00*	5.75
Chironomidae larvae	0.42	0.52	1.32	0.22	0.76	0.63
Chironomidae pupae	0.46	0.58	0.58	0.34	0.62	0.79
Chaoborus sp. larvae	0.50*	0.52	0.22	0.38	2.00*	0.44
Chaoborus sp. pupae	4.00*	0.95	1.44	0.75*	--	--

Table 1--Continued

TAXA	SAMPLE MONTHS APR	JUNE	AUG	OCT	DEC	FEB
Diptera						
Pericoma sp.	--	--	--	--	--	--
Palpomyia sp. larvae	--	1.27	--	--	--	--
Culicinae larvae	--	--	--	--	--	--
Coleoptera						
Stenelmis spp. larvae	2.60	2.26	2.27	0.43	0.67	3.77
Stenelmis spp. adults	6.50	4.73	5.85	2.00*	--	7.23
Dubiraphia _vittata_ adults	--	1.57	0.69	--	--	--
Dubiraphia _vittata_ larvae	--	--	--	--	--	--
Berosus sp. larvae	--	8.64	--	--	--	2.80
Gyretes sp. larvae	--	23.00	13.10	--	--	--
Heterelmis _vulnerata_ adult	--	--	--	--	--	--
Peltodytes sp. adult	--	--	--	--	--	--
Helichus _suturalis_ adult	--	--	--	--	--	--
Dytiscidae adults	--	--	--	--	--	--

Table 1--Continued

	SAMPLE MONTHS					
TAXA	APR	JUNE	AUG	OCT	DEC	FEB
Odonata						
Enallagma sp.	--	2.08	--	0.50*	--	1.00*
Argia sp.	--	2.50	36.70*	--	--	--
Ophiogomphus sp.	2.67*	--	0.60	--	--	--
Erythemis sp.	--	--	--	--	--	--
Erpetogomphus sp.	--	--	--	--	--	--
Gomphus sp.	--	--	--	--	--	--
Hetaerina sp.	--	--	--	--	--	--
Lepidoptera						
Elophila sp. larvae	--	1.25	1.67*	1.18	2.00*	9.50
Plecoptera						
Neoperla clymene	11.00*	1.54	--	--	--	--
Zealeuctra sp. adult	--	--	--	--	--	--

Table 1--Continued

TAXA	SAMPLE MONTHS APR	JUNE	AUG	OCT	DEC	FEB
Megaloptera						
Corydalus cornutus larvae	--	--	--	--	--	--
Other Groups						
Corixidae	--	--	--	--	--	--
Branchiura	--	--	--	--	--	--
Oligochaeta	--	--	--	--	--	--

* Weights represent less than 5 individuals.

Table 2--Cubic meters of water sampled/station, Brazos River, 1972-1973

Daily Sample Periods	APRIL				JUNE				AUGUST			
	Stations				Stations				Stations			
	1	2	3	Period Total	1	2	3	Period Total	1	2	3	Period Total
1*	38.6	61.2	90.2	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 Total	731.6				2087.0				1011.4			

* 1-hr preceeding sunset
** 1-hr after sunrise

Table 2--Continued

Daily Sample Periods	OCTOBER Stations 1	2	3	Period Total	DECEMBER Stations 1	2	3	Period Total	FEBRUARY Stations 1	2	3	Period Total
1*	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	91.6	131.2	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 Total		1888.6				764.2					1951.6	
										G.T.	8434.4	

* 1-hr preceeding sunset
** 1-hr after sunrise

Water temperature at the study riffle ranged from 9 C on the December sample date to 28.5 C in August. Little or no variation occurred across the transect at given times, and expected reductions of 2-3 C occurred from sunset to sunrise when flow rates were relatively constant. Since the sampling regime was not designed to detect cause-and-effect relationships between temperatures and drift rates, and in view of the erratic flow-temperature characteristics of the river, no attempt is made here to assess the significance of temperature as a parameter affecting drift rates. The same can be said for dissolved oxygen, which was near saturation on sampling dates during Fall to Spring months (max. 11.1 ppm at 9 C in December), and as low as 6.4 ppm at 26 C in August. pH averaged 8.5 throughout the study period.

Mean physical-chemical conditions existing during October, December samples were (1) total hardness, 474 ppm; (2) Ca hardness, 360 ppm; (3) alkalinity, 90 ppm; (4) chlorides, 517 ppm; (5) total dissolved solids, 2420 mg/1; and (6) conductivity, 3300 micromhos/cm. These conform very closely with conditions prevailing in July (Vaught 1972).

The Chi-Square analysis of Choroterpes sp. drift indicated a significant difference in drift numbers across the sample transect for the months of April and June. A goodness of fit comparison between expected catches and observed catches to determine if net catch was directly proportional to water volume sampled proved acceptable for the April sample date, but not for the June date. This rejection is probably due to the greater volume of water sampled in June (Table 2). Since only a finite amount of macrobenthos are susceptible to the drift, it seems reasonable to assume that any increase in discharge above a certain value will not add to the total number of individuals in the drift. Therefore, this would tend to distort the proportionality of the catch and water volume. Regardless of this disparity, it was assumed that standardization of all drift samples to a known volume of water was the most desirable expression of drift due to the variations in flows encountered.

Choroterpes sp.

This new species, tentatively named *Neochoroterpes mexicanus* by R. K. Allen (unpublished), remains undescribed. Because of the present uncertainty of its taxonomic position, Dr. Allen (personal correspondence) suggested that it be listed as *Choroterpes* sp. This mayfly is a dominant member of the Brazos River insect community, second in abundance only to the caddisfly genus *Cheumatopsyche*.

Drift density was minimal in October and December, never surpassing 15/100 m^3 at any time period sampled (Fig. 1). April density never exceeded 20/100 m^3, and moderate numbers of 20-54/100 m^3 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 m^3 and 144/100 m^3 respectively, were reached. The June peak represented the greatest drift density for any organism observed during the study.

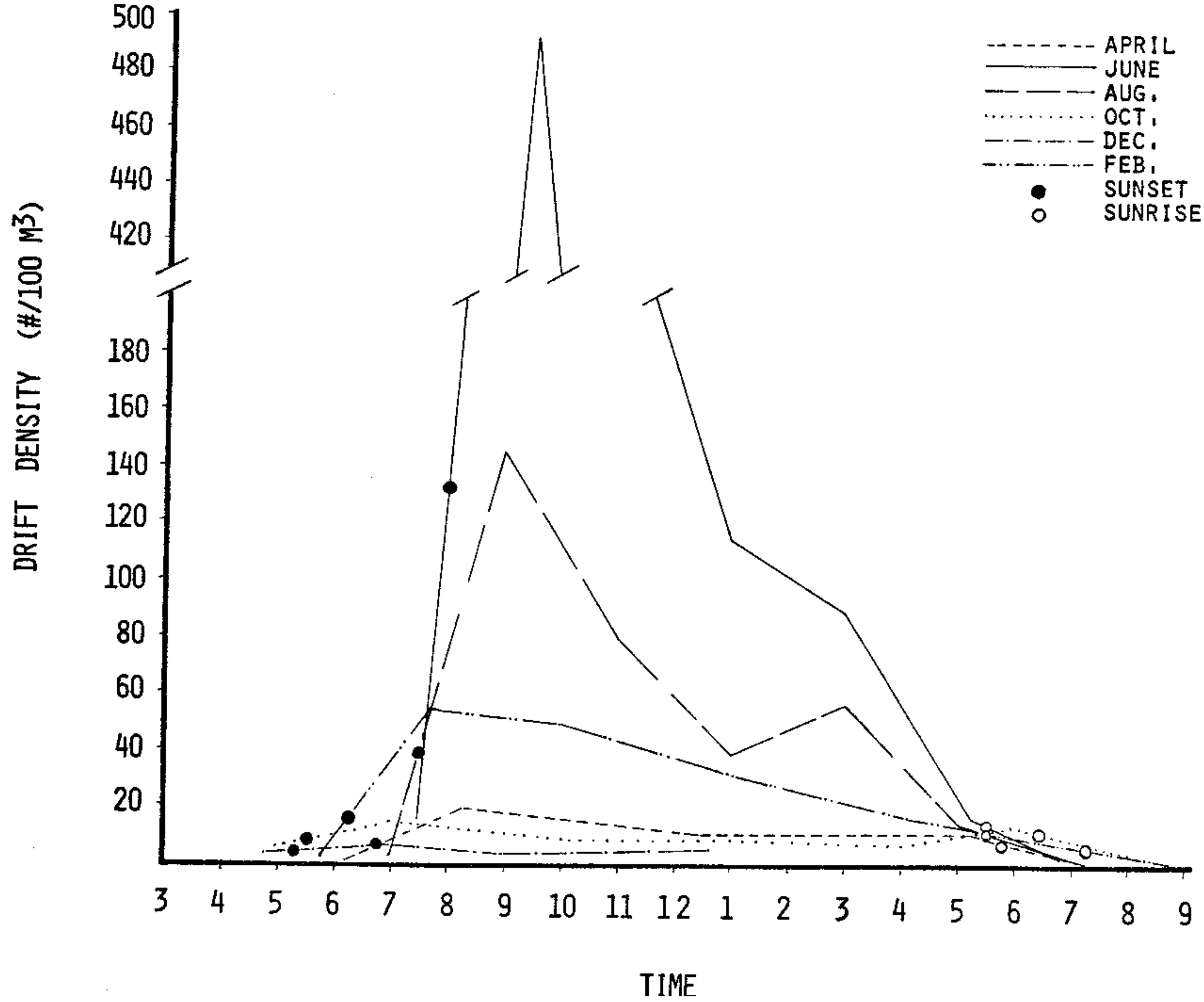
In all months sampled, some degree of nocturnal periodicity was exhibited (Fig. 1). A single peak in drift density occurred just after sunset, except in August and October, when minor secondary peaks occurred at 3 AM and just before sunrise, respectively.

Choroterpes exuviae (Fig. 2) drifted in peak numbers in April (63/10 m^3). 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 suggest that the species probably has a 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 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 great majority of exuviae were of pre-emergent size. This is also suggested by the much higher density of exuviae over nymphs during this month.

Another Leptophlebiid, Leptophlebia cupida, exhibited a similar nocturnal drift periodicity and much lower average nighttime drift densities of 1.5/100 m^3 (Clifford 1972a, b).

An estimate of total numbers of drifting Choroterpes for the whole cross-sectional area of the Brazos sampled was

Figure 1--Drift of *Choroterpes* sp. nymphs, Brazos River, 1972-1973.



APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
500
480
460
440
420
180
160
140
120
100
80
60
40
20
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

Figure 2--Drift of Choroterpes sp. exuviae, Brazos River, 1972-1973.

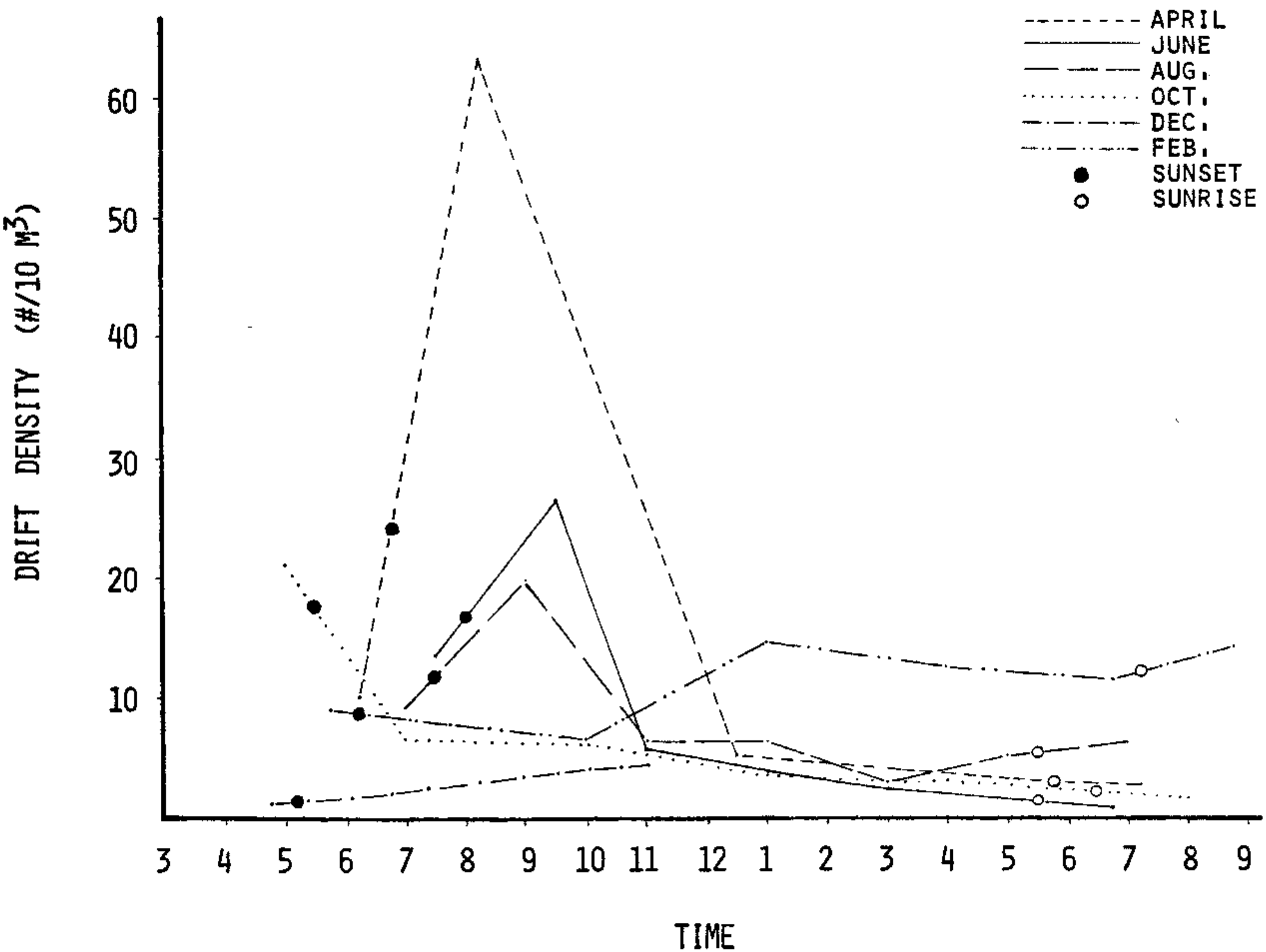

APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/10 M³)
60
50
40
30
20
10
3
4
5
6
7
8
9
10
11
12
1
2
3
4
5
6
7
8
9
TIME

Table 3--Total drift estimates of dominant organisms of the Brazos River Drift, during the period 1-hr before sunset to 1-hr after sunrise, 1972-1973.

	Choroterpes sp. nymphs	*Cheumatopsyche* sp. larvae
April	1.65×10^4	1.82×10^4
June	5.31×10^5	8.53×10^4
August	1.04×10^5	8.93×10^4
October	1.72×10^4	3.72×10^4
December	1.70×10^4	4.98×10^2
February	8.77×10^4	5.02×10^3

Table 3--Continued

Chaoborus sp. larvae	*Simulium* sp. larvae	*Baetis* sp. nymphs	Chironomid larvae
5.67×10^2	1.68×10^5	3.97×10^3	5.87×10^4
5.39×10^5	7.13×10^4	5.63×10^4	8.44×10^4
7.93×10^4	1.93×10^3	1.97×10^4	4.73×10^4
1.24×10^4	8.82×10^4	1.78×10^4	1.10×10^5
4.98×10^2	3.54×10^4	----	1.90×10^4
3.09×10^3	2.24×10^4	----	2.16×10^5

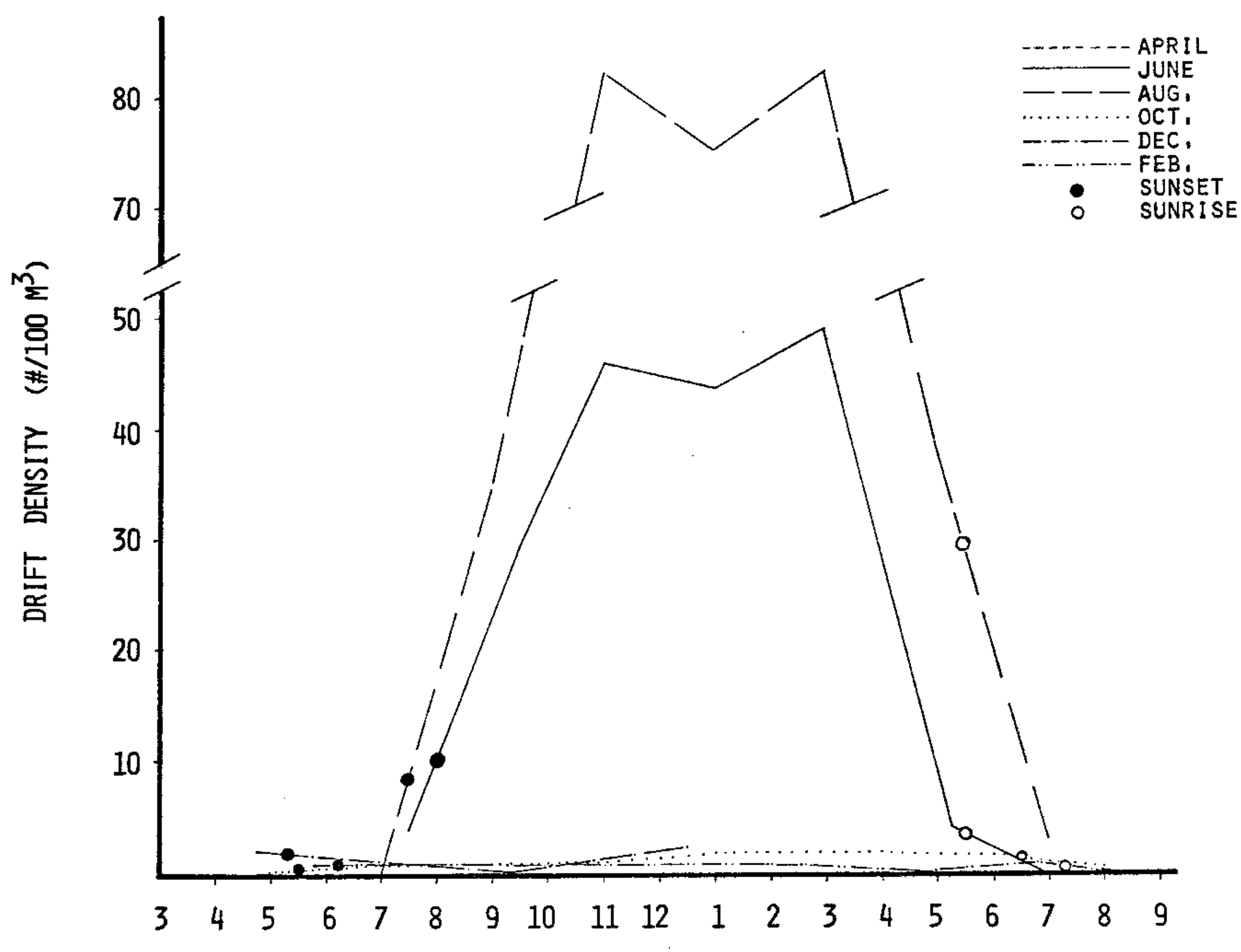
calculated according to the method of Elliott (1970a) and is given in Table 3. The maximum and minimum number of Choroterpes drifting 1-hr before sunset to 1-hr after sunrise of 5.31×10^5 and 1.65×10^4, respectively, are relatively high in comparison with even total invertebrate drift of several studies (Elliott and Corlett 1972). However, the estimates are much lower than those for Baetis (170×10^6) reported by Pearson and Franklin (1968) in the Green River, Utah. It should be kept in mind that the estimates for Choroterpes are minimal, since they cover drift only for the nighttime and adjacent 2 hrs.

Tricorythodes sp.

Peak seasonal drift density of Tricorythodes, as in Choroterpes, occurred in August and June with the highest in August (Fig. 3). Samples in other months showed very low drift densities, never exceeding 3/100 m^3.

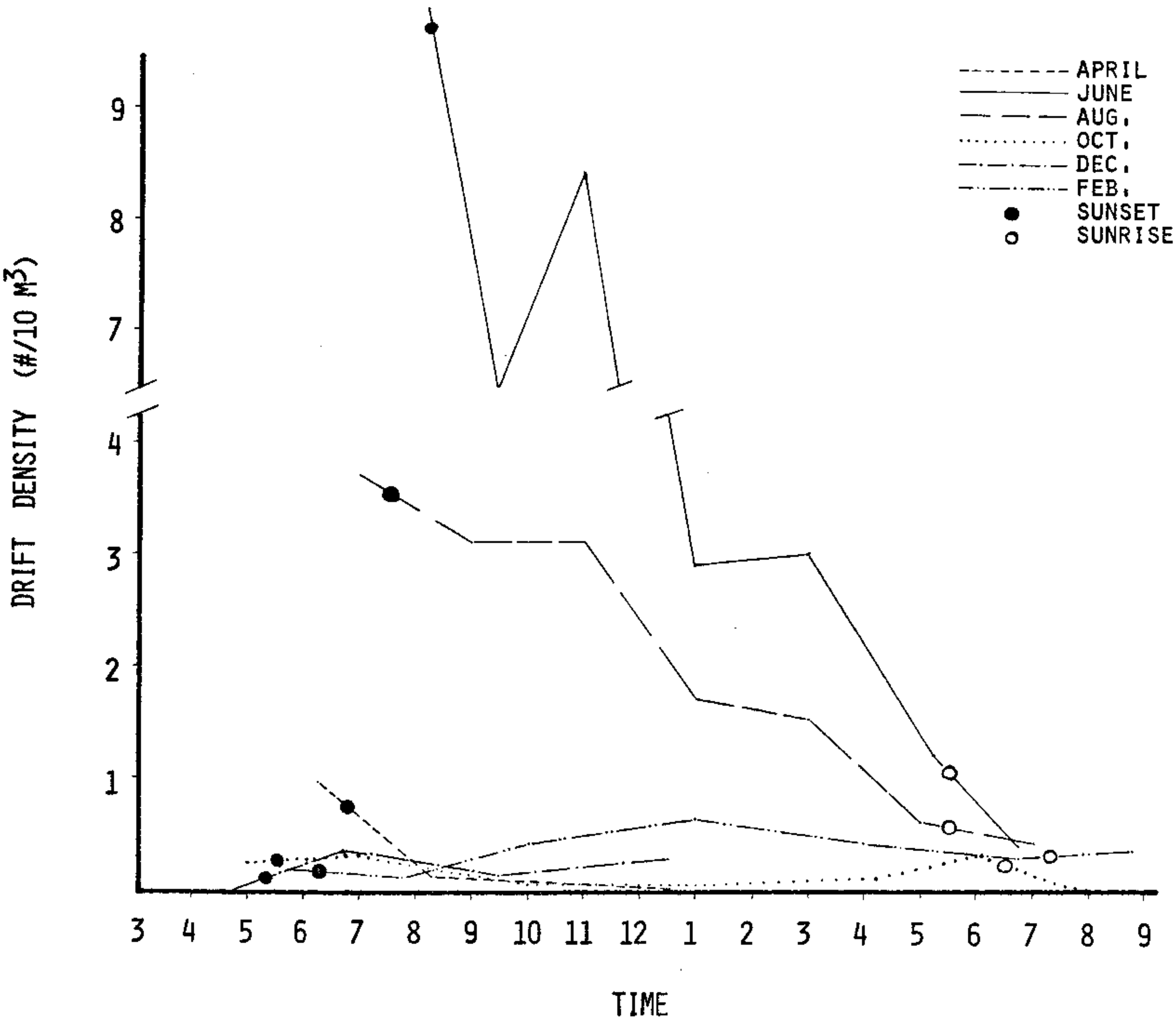
The nocturnal periodicity was bimodal with peaks of approximately equal magnitude occurring in both active months at 11 PM and 3 AM CST (Fig. 3). Clifford (1972a) found a total drift density of 227 Caenis simulans for 24-hr periods on 10 sample dates from May, 1970 to May, 1971 in Alberta, Canada; total Tricorythodes drifting only during nighttime and the adjacent 2 hrs over six sampling dates in this study were 506.9 (Table 4). The drift of Tricorythodes has been previously unreported.

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



APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
80
70
50
40
30
20
10
3
4
5
6
7
8
9
10
11
12
1
2
3
4
5
6
7
8
9
TIME

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


APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/10 M3)
9
8
7
4
3
2
1
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

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 exuviae drift density coincide with those of maximal nymphal density in June and August (Fig. 3,4).

Baetis sp.

Maximum drift density for *Baetis* sp. of 48/100 m^3 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 (1972) noted a similar seasonal pattern in *Baetis bicaudatus*, with very low winter rates.

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

Baetis exuviae (Fig. 6) were encountered in greatest numbers in the late afternoon and/or early morning hours of

Figure 5--Drift of *Baetis* sp. nymphs, Brazos River, 1972-1973.

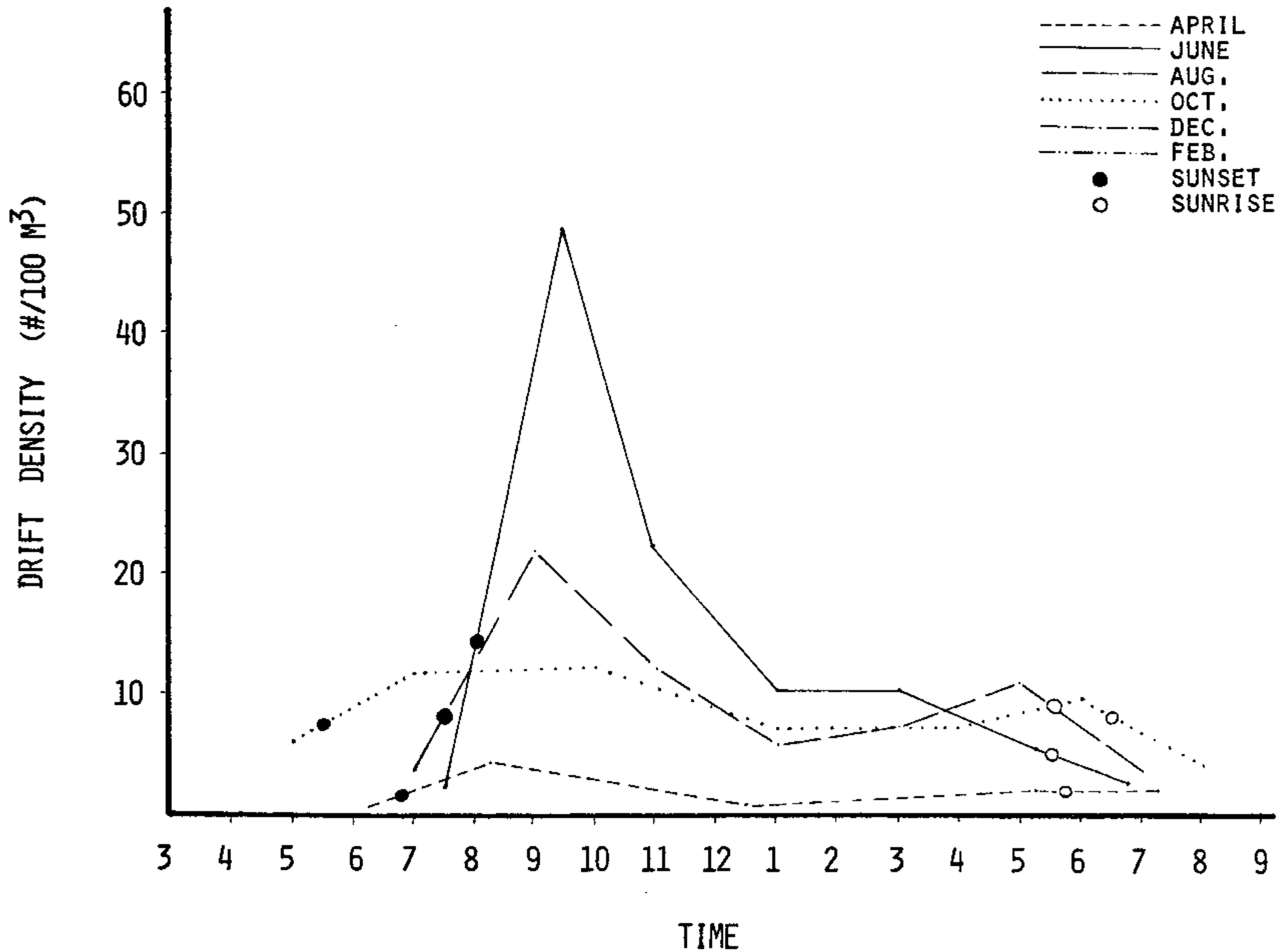
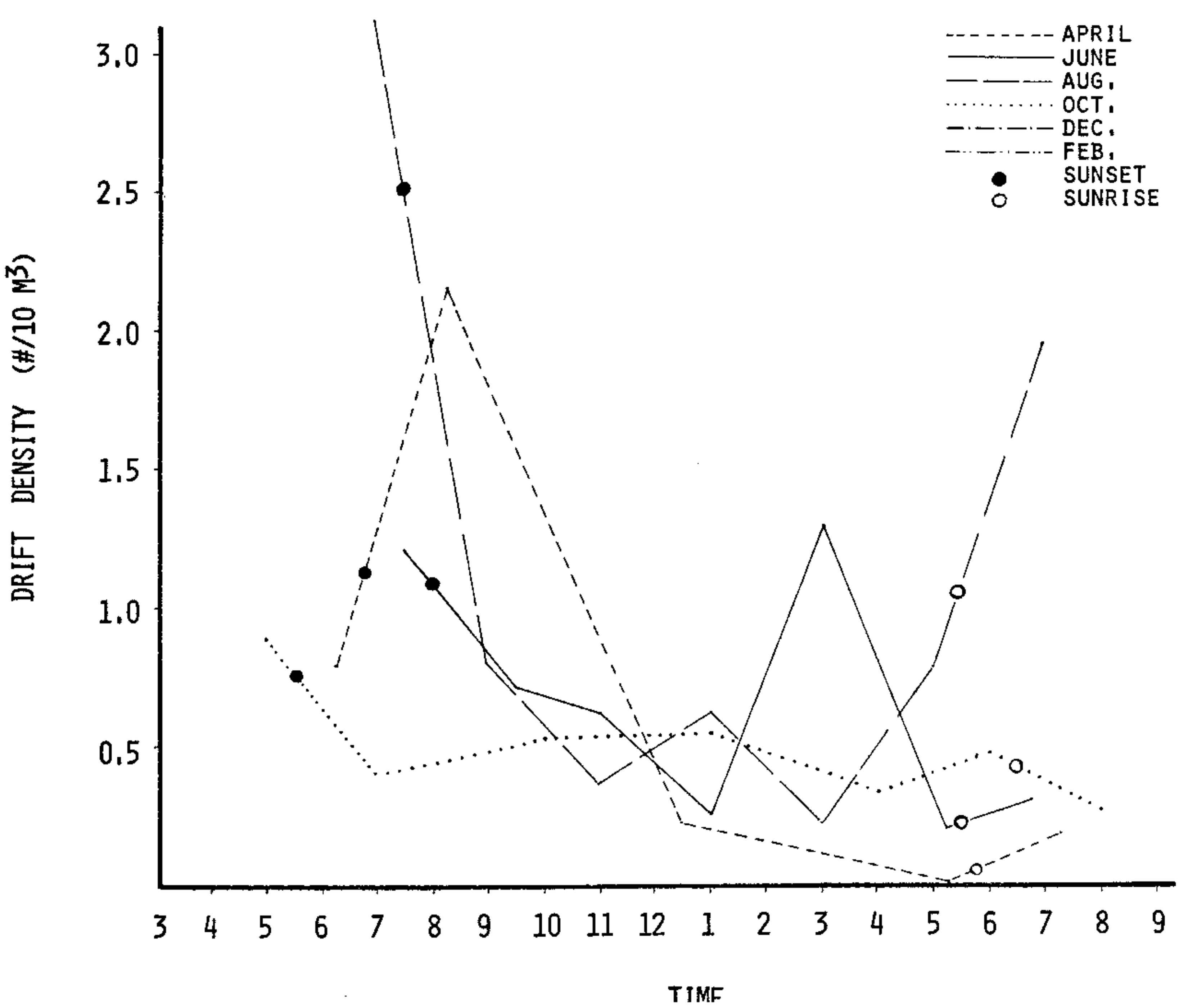

DRIFT DENSITY (#/100 M3)
60
50
40
30
20
10
TIME
3
4
5
6
7
8
9
10
11
12
1
2
3
4
5
6
7
8
9
APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE

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



APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/10 M3)
3.0
2.5
2.0
1.5
1.0
0.5
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

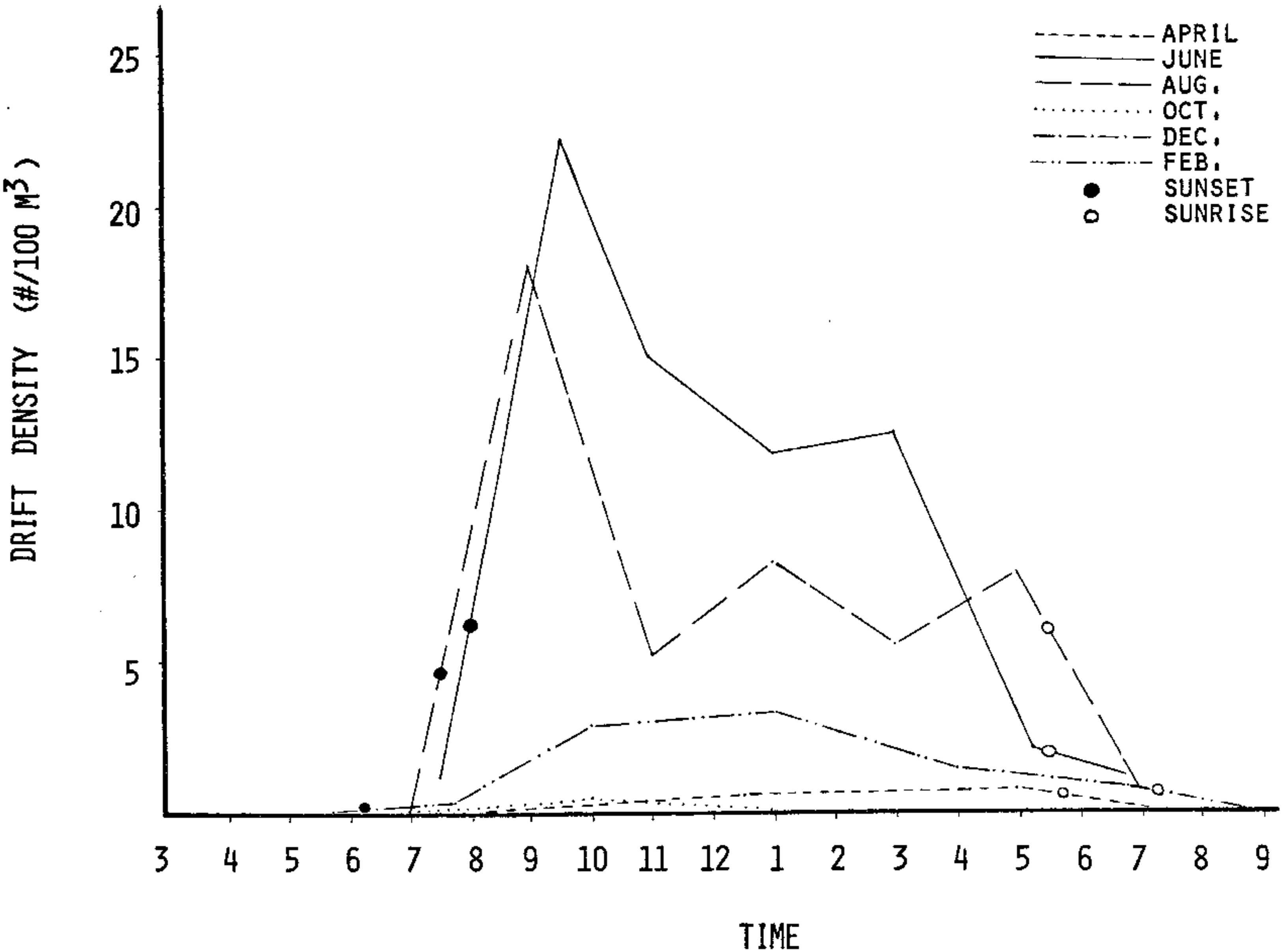
June, August, and October, suggesting that emergence of this species on the Brazos takes place primarily during daytime. Pearson and Kramer (1972) noted large swarms of *Baetis bicaudatus* in the early morning hours over Temple Fork, Utah. Minor nocturnal peaks were encountered in each of these months.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

A maximum of 5.63×10^4 *Baetis* (Table 3) 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 similar figures for their total drift of *Baetis rhodani*. The greatest estimate of total drift for *Baetis*, or any other species, was reported by Pearson and Franklin (1968), who indicated a total of 170×10^6 *Baetis* nymphs drifted past their sampling station on the Green River during one 24-hr period.

Caenis sp.

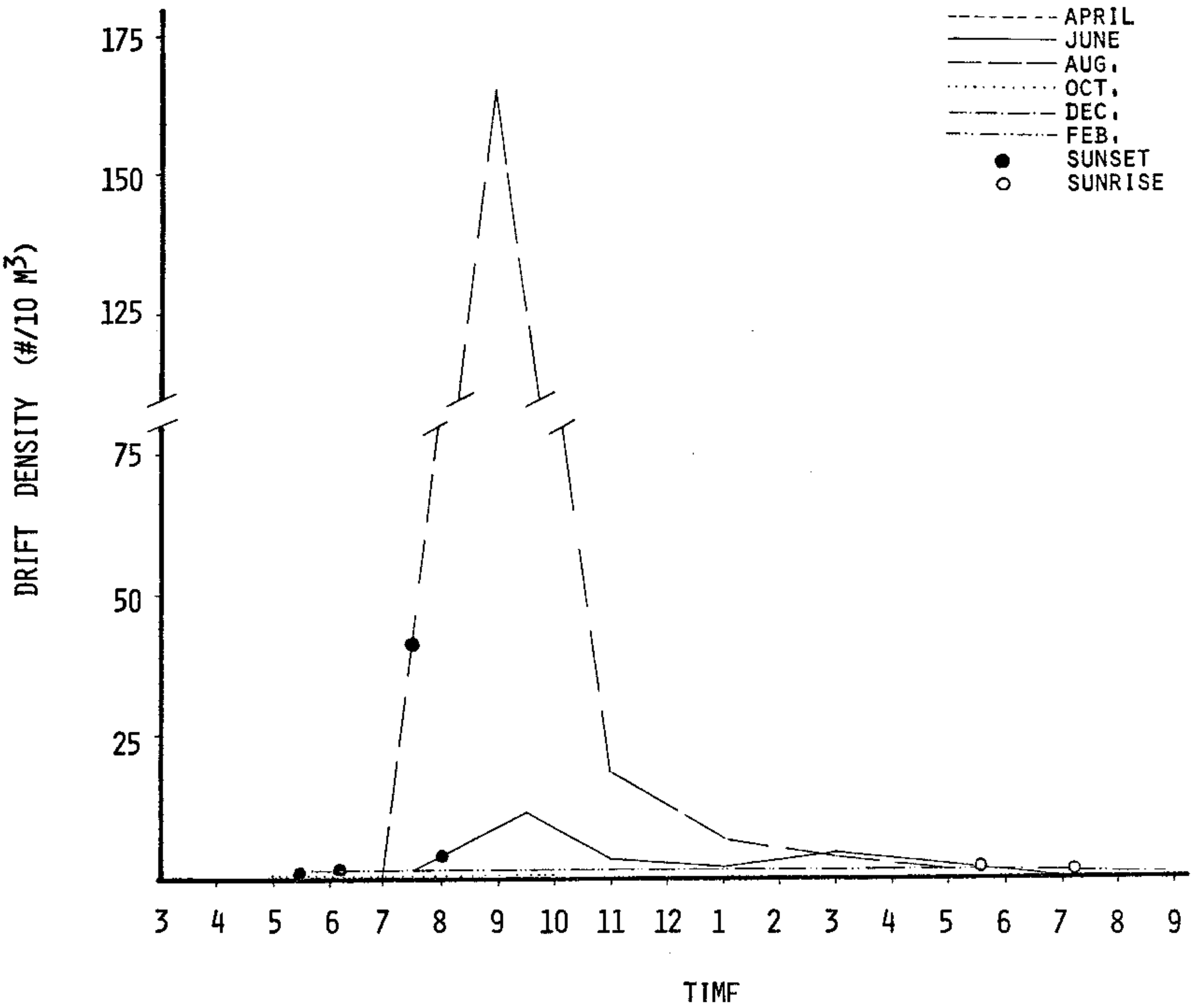
As in the other mayfly taxa, maximum seasonal drift densities of *Caenis* occurred in June and August, with slightly over 22/100 m^3 drifting in June (Fig. 7). Samples for the other semi-monthly sample dates showed much lower densities, which never exceeded 4/100 m^3.

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



APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M^3)
25
20
15
10
5
3
4
5
6
7
8
9
10
11
12
1
2
3
4
5
6
7
8
9
TIME

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



APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/10 M3)
175
150
125
75
50
25
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIMF

Periodicity of *Caenis* (Fig. 7) was of a "bigeminus-pattern" during the peak months of June and August; two secondary peaks did occur in August at 1 AM and 5 AM, respectively. This typical nocturnal periodicity has also been observed for *Caenis rivulorum* (Elliott and Corlett, 1972), *Caenis simulans* (Clifford 1972a), and *Caenis* spp. (Bishop and Hynes, 1969). As mentioned previously, Clifford (1972a) found a total drift density of 227 *Caenis simulans* for ten, 24-hr periods in a brown water stream of Alberta, Canada. The total drift density observed for *Caenis* sp. in the Brazos River, Texas over the yearly sample period was 121.9 (Table 4).

Maximum exuvial catches of 166/10 m^3 observed in August correspond with a time of greatest nymphal density in the drift (Fig. 8). The preponderance of *Caenis* exuviae in the drift in June and August after sunset probably represents emergence. Morgan and Waddell (1961) have shown *Caenis horaria* to be an evening emerging form with most emergence taking place between 8 PM and 10 PM. Kimmins (1954) observed emergence in *C. horaria* between 7 PM and 9:30 PM.

Heptagenia sp.

A maximum drift density of 2.7 *Heptagenia* sp./100 m^3 was recorded. As in the previous mayfly taxa, the peak seasonal drift densities (Fig. 9) were encountered on the same June, August sample dates.

Heptagenia exhibited definite nocturnal periodicities; however, there was a great variation in monthly patterns. In

Figure 9--Drift of <u>Heptagenia</u> sp. nymphs, Brazos River, 1972-1973.

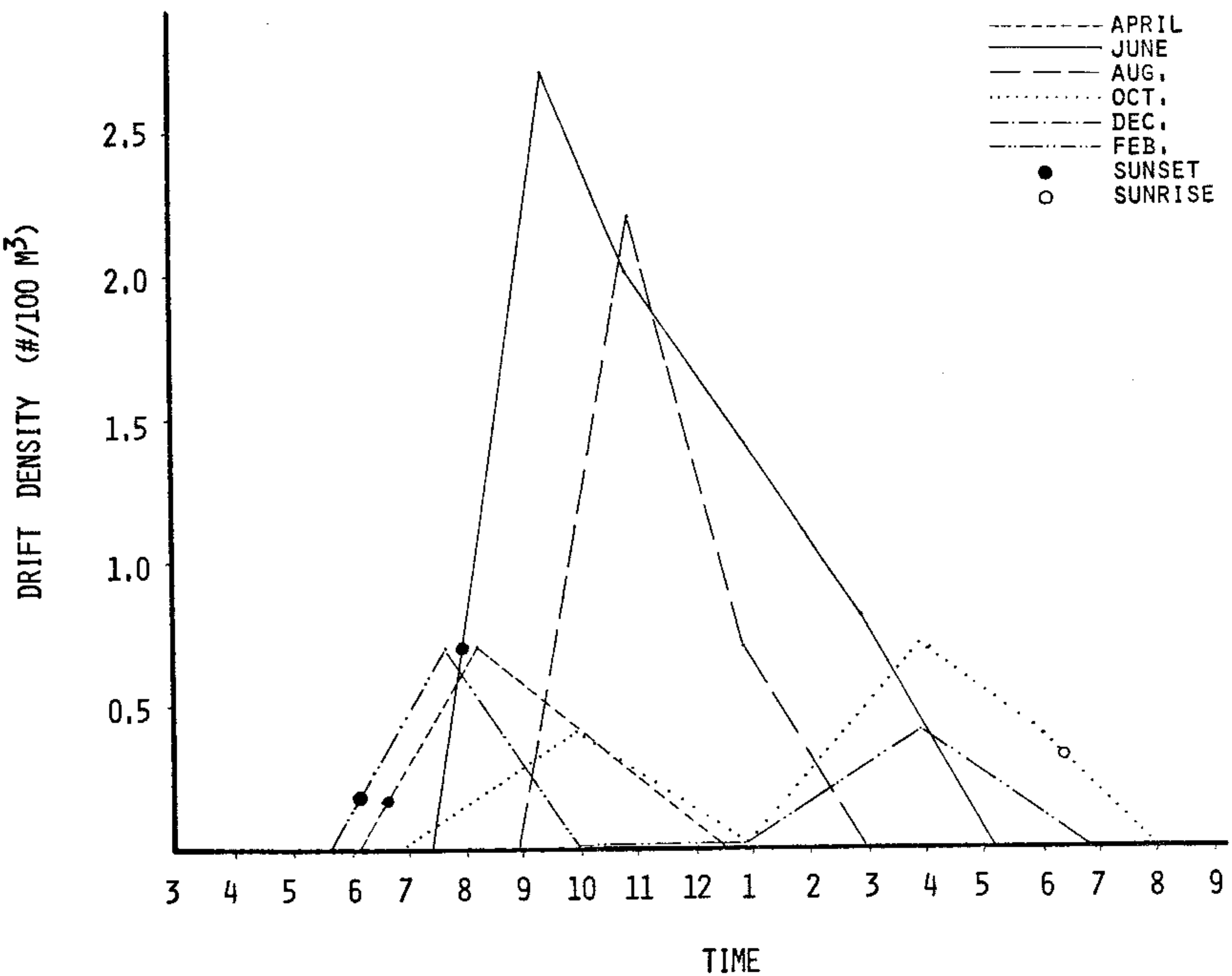
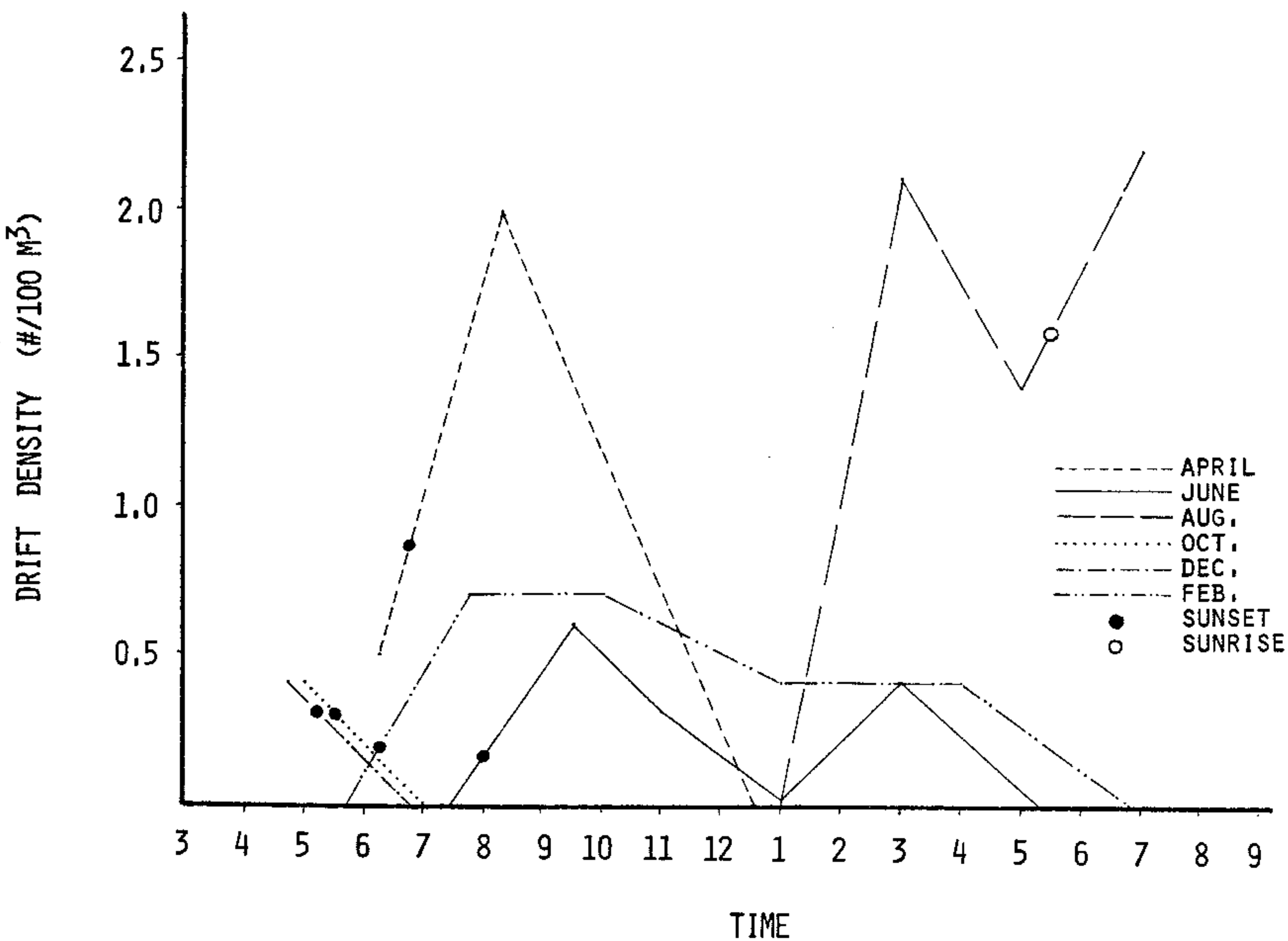

APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
2.5
2.0
1.5
1.0
0.5
DRIFT DENSITY (#/100 M3)
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

Figure 10--Drift of <u>Heptagenia</u> sp. exuviae, Brazos River, 1972-1973.



DRIFT DENSITY (#/100 M3)
2.5
2.0
1.5
1.0
0.5
3
4
5
6
7
8
9
10
11
12
1
2
3
4
5
6
7
8
9
TIME
APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE

April, June, and August one primary peak occurred in the early hours of the night followed by a precipitous return to zero drift density levels before dawn. Bimodal periodicities were observed in October and February. Heptagenia sulphurea also displayed a basic nocturnal pattern in its drift activity (Elliott and Corlett 1972).

Monthly patterns in the drift density of Heptagenia exuviae (Fig. 10) were also highly variable. Peak drift densities of 2.0/100 m^3 and 2.1/100 m^3 were encountered in April and August, respectively.

Isonychia sicca manca

Greatest drift densities observed for this species (2/100 m^3) occurred during June and August (Fig. 11); a small catch of 0.7/100 m^3 was also taken in April.

The drift activity of Isonychia sicca manca was clearly nocturnal; the predominant pattern was basically "bigeminus", with the exception of the single peak in April.

Isonychia exuviae (Fig. 12) drifted in peak numbers in August (4.7/100 m^3). Samples in April, August, and October suggest that periods of emergence possibly occurred in the daylight before sunset and/or after sunrise.

Cheumatopsyche spp.

Cheumatopsyche, the most abundant insect at the study riffle, consistently composed a large percentage of the total

Figure 11--Drift of *Isonychia sicca manca* nymphs, Brazos River, 1972-1973.

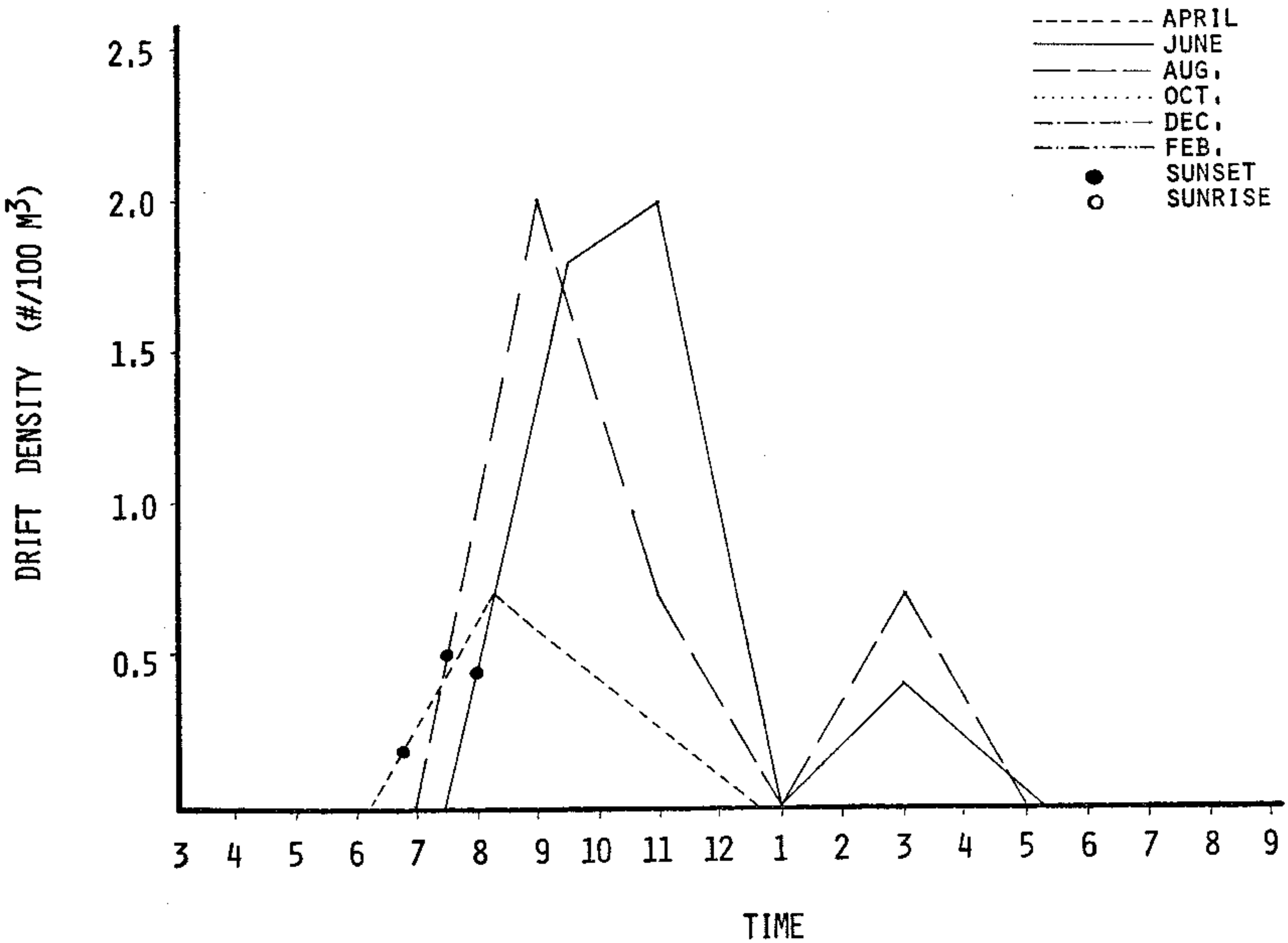
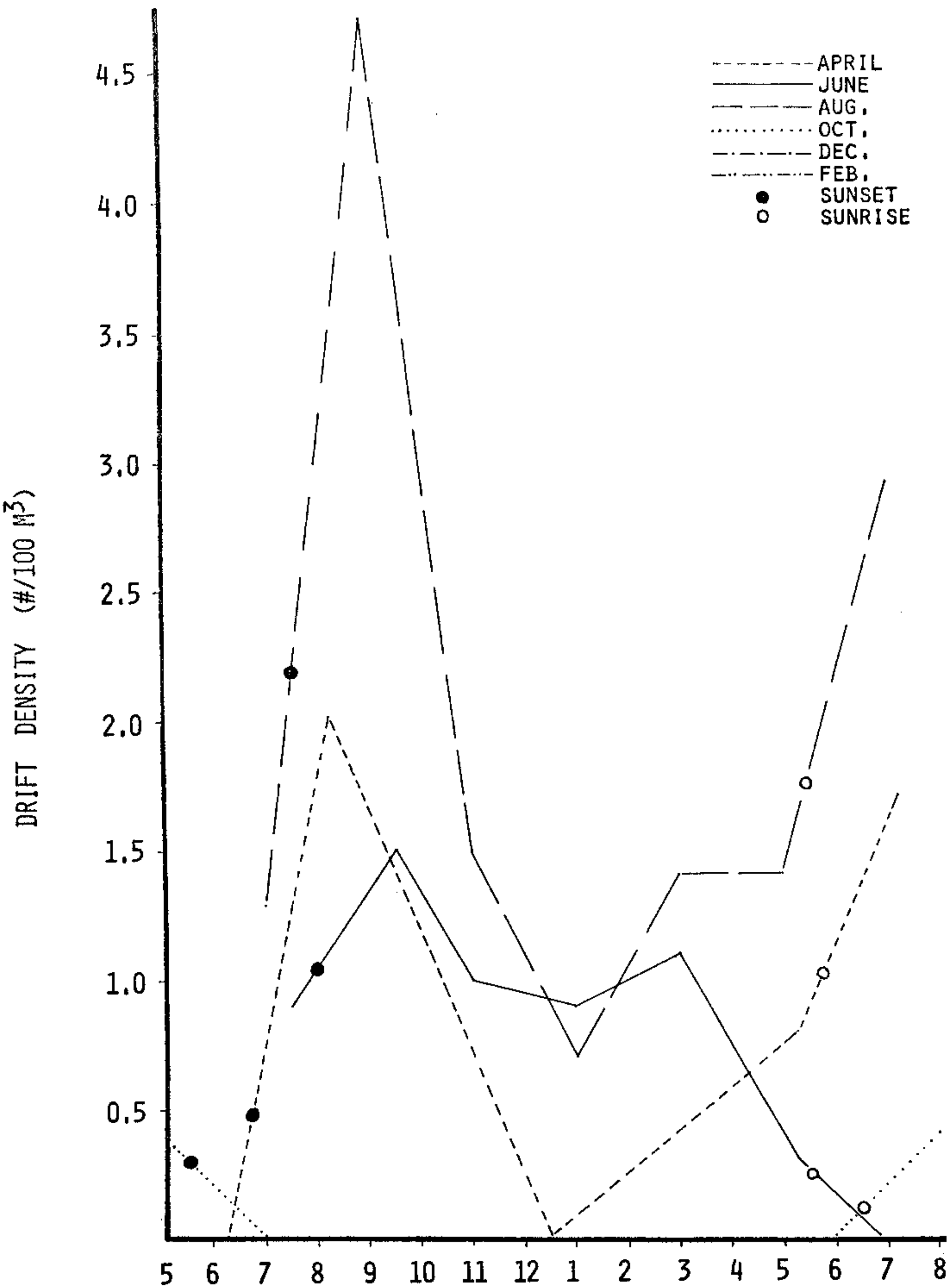

APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
2.5
2.0
1.5
1.0
0.5
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

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



DRIFT DENSITY (#/100 M3)
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8
APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE

drift density (Table 4). Only two adult species of this Trichopteran, C. lasia and C. campyla, have been taken in light trap collections. At present the larvae of these species are indistinguishable, necessitating consideration of drift at the genus level.

Numerous investigators have documented drift in the caddisflies (Tanaka 1960, Waters 1962, Baily 1964, Elliott 1965a,b, 1967, 1968, 1970c, 1971, Müller 1966, Besch 1967, Anderson 1967, McLay 1968, Waters 1968, 1969b, Bishop and Hynes 1969, Brusven 1970a, Pearson and Kramer 1972, Elliott and Corlett 1972, Clifford 1972a,b). Anderson (1967) was one of the first to report significant levels of Trichopteran drift during his studies on the Metolius River in Oregon. In this report Anderson noted the high diversity of the caddisfly fauna, but he specifically pointed out the absence of net-spinning forms such as the Hydropsychidae, Psychomyiidae, and Philopotamidae in the drift. In the present study the Hydropsychidae, composed primarily of Cheumatopsyche, were the dominant Trichopterans in the drift.

Maximum drift of Cheumatopsyche larvae occurred in August (92.5/100 m^3), with minimal drift densities in December and February (Fig. 13).

The nocturnal activity was unimodal on all of the sample dates. Elliott (1970c) also found a tendency toward unimodal curves in five species of caddisflies. Major peaks during June and August occurred just after sunset, but in October a pre-dawn peak was exhibited (Fig. 13).

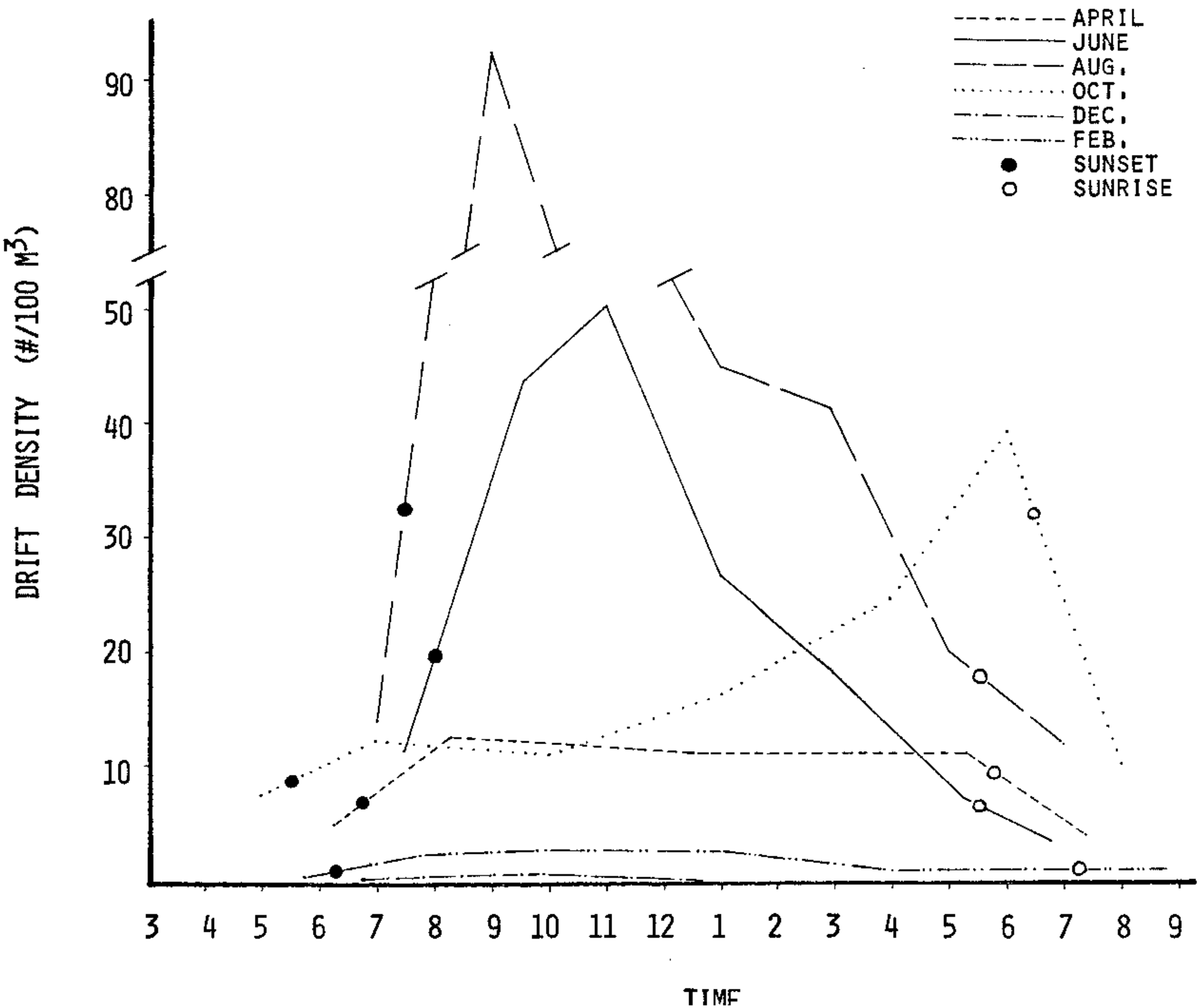
Table 4--Total drift densities (#/100 m^3) and % total drift densities of the Brazos River drift for the six semi-monthly sample dates, 1972-1973.

Taxa	Total Drift Density	% Total Drift
Ephemeroptera		
Choroterpes sp.	1562.4	19.49
Tricorythodes sp.	506.9	6.33
Baetis sp.	230.2	2.87
Caenis sp.	121.9	1.52
Heptagenia sp.	13.1	0.16
Isonychia sicca manca	7.6	0.09
Trichoptera		
Cheumatopsyche spp.	623.7	7.78
Hydropsyche simulans	110.2	1.38
Ithytrichia clavata	63.0	0.79
Hydroptila icona	58.1	0.72
Chimarra obscura	23.5	0.29
Pycnopsyche sp.	6.3	0.08
Diptera		
Chironomidae larvae	1237.0	15.44
Chironomidae pupae	452.9	5.65
Simulium sp. larvae	929.6	11.60
Simulium sp. pupae	19.3	0.24
Chaoborus sp. larvae	1317.5	16.44

Table 4--Continued

Taxa	Total Drift Density	% Total Drift
Diptera		
Chaoborus sp. pupae	187.4	2.34
Palpomyia sp. larvae	23.7	0.30
Coleoptera		
Stenelmis spp. adults	263.7	3.29
Stenelmis spp. larvae	107.5	1.34
Dubiraphia vittata adults	96.2	1.20
Gyretes sp. larvae	8.0	0.10
Odonata		
Enallagma sp.	10.3	0.13
Argia sp.	6.1	0.08
Ophiogomphus sp.	5.5	0.07
Lepidoptera		
Elophila sp.	18.4	0.23
Plecoptera		
Neoperla clymene	4.1	0.05

Figure 13--Drift of *Cheumatopsyche* spp. larvae, Brazos River, 1972-1973.


APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
90
80
50
40
30
20
10
DRIFT DENSITY (#/100 M3)
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

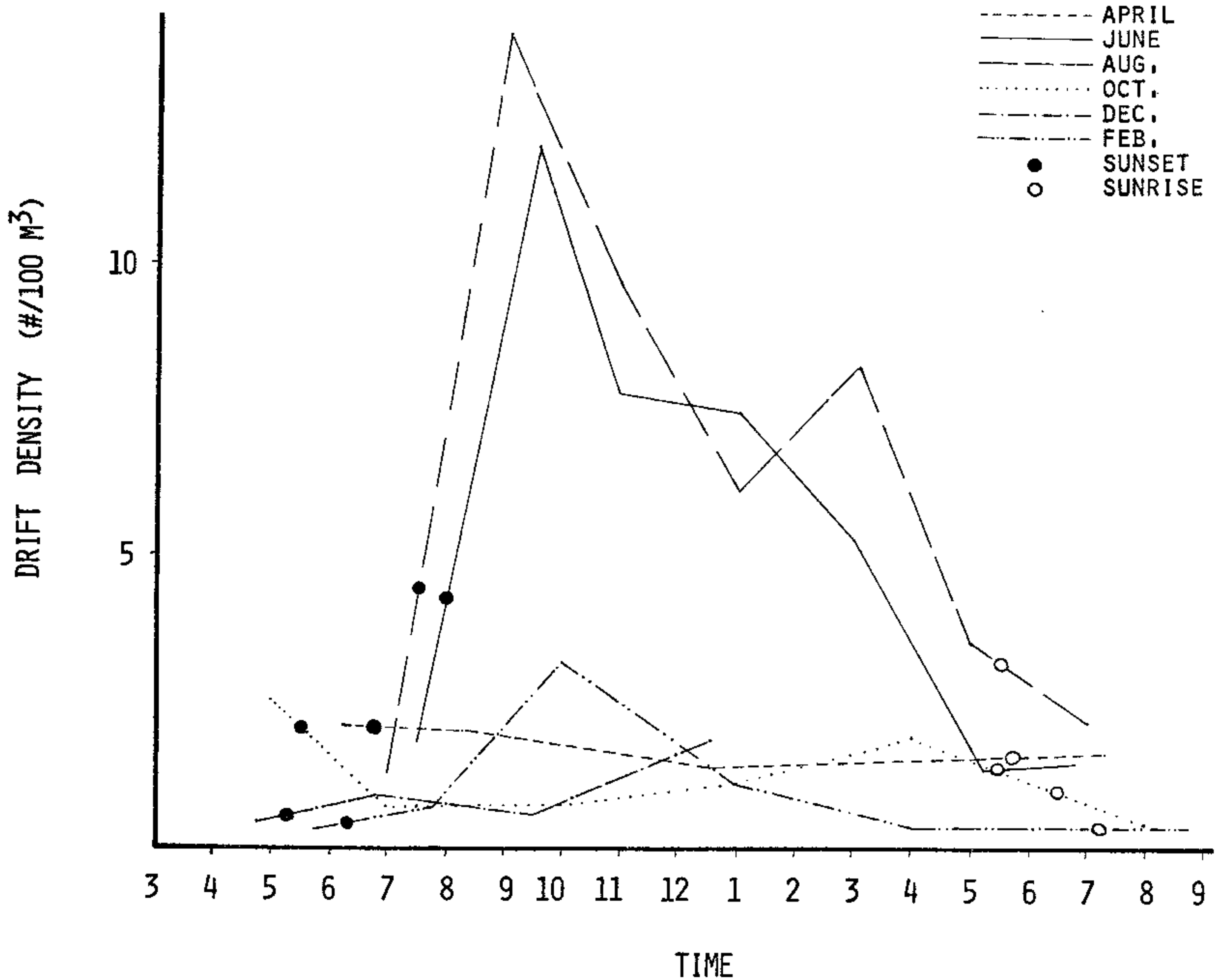
Estimates of the total number of *Cheumatopsyche* larvae drifting past the sample nets ranged from a minimum of 4.98×10^2 individuals per night in December to a maximum of 8.93×10^4 individuals per night in August, nearly a 200-fold increase (Table 3).

Hydropsyche simulans

Hydropsyche simulans exhibits a bivoltine life cycle in the Brazos River (unpublished data). The first generation emerges chiefly in February-April, with a second generation making its appearance in June-August. Maximum drift densities in June-August of 12/100 m^3 and 14/100 m^3, respectively, (Fig. 14) correspond very closely with seasonal standing crops on the riffle. It has been suggested by Elliott (1968) that the high level of larval drift for *Hydropsyche* may indicate large numbers leaving an overcrowded population. Thus, the drift of this species in the Brazos may result not only from seasonal variations but also from excess production inducing density-dependent responses (Waters 1966, Diamond 1967).

The periodicity of *Hydropsyche simulans* was highly variable between sample dates. Although Brusven (1970a) found little tendency for *Hydropsyche* sp. larvae to drift, this study as well as several others (Baily 1964, Elliott 1967, McLay 1968, Elliott and Corlett 1972) indicates that the drift of *Hydropsyche* is a natural occurrence. Elliott (1967) and Elliott and Corlett (1972) also noted higher nocturnal drift rates for *Hydropsyche instabilis*.

Figure 14--Drift of *Hydropsyche simulans* larvae, Brazos River, 1972-1973.


APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M³)
10
5
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

Ithytrichia clavata

Ithytrichia clavata is one of two common Hydroptilids occurring in the Brazos. Individuals were taken in all sample months except December. A maximum density of 12.1/100 m^3 occurred in the drift during June (Fig. 15). Lower drift densities were encountered in October and February, never exceeding 1.1/100 m^3 at any time period.

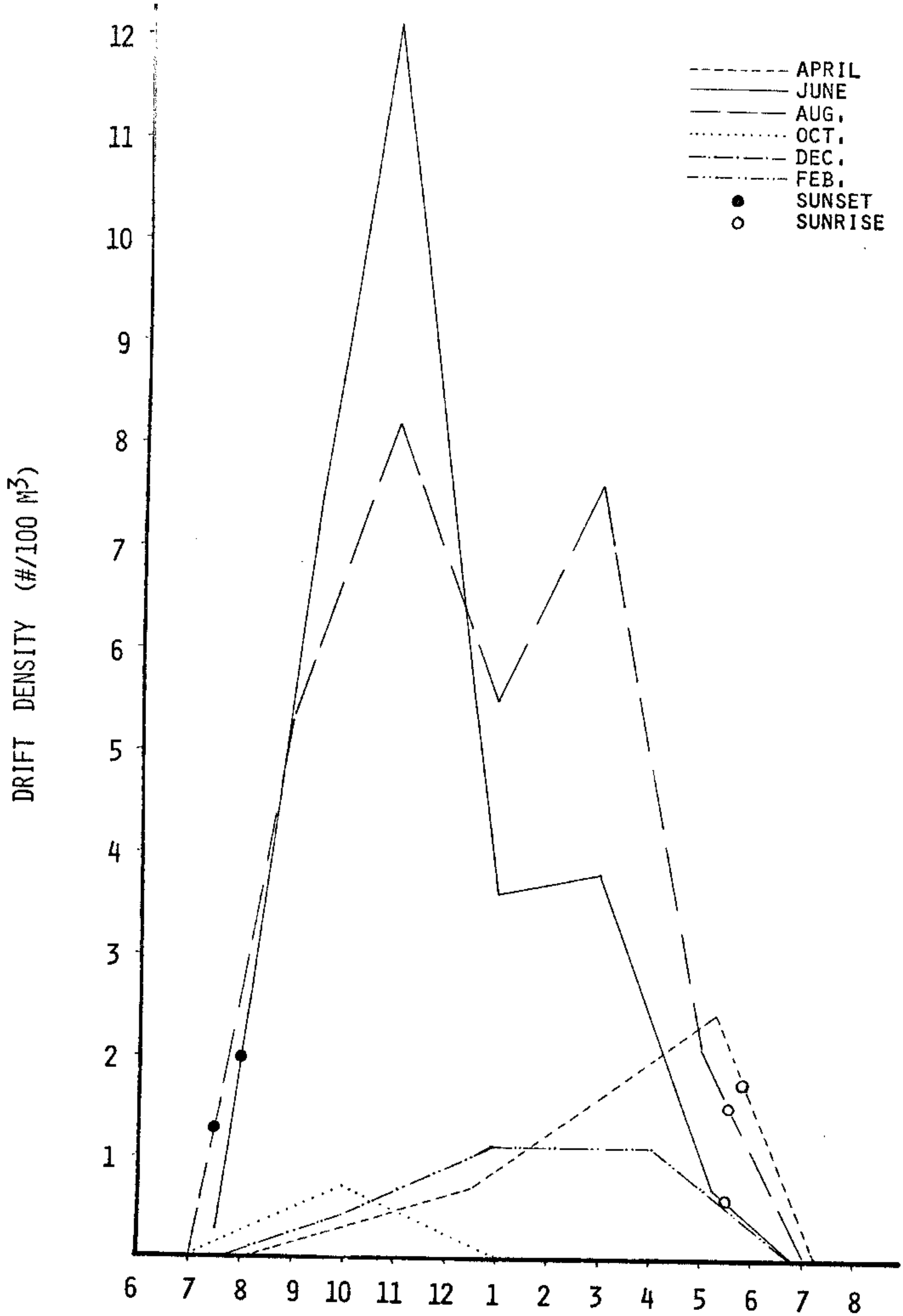
A definite nocturnal activity occurred; a basic "bigeminus-pattern" was exhibited in June and August, with single peaks occurring in October, February, and April. The February and April dates showed *Ithytrichia* having its greatest numbers in the drift during the late hours of the night just prior to dawn.

Hydroptila icona

Drift densities were highest on October and April when maximums of 7.6/100 m^3 and 4.1/100 m^3, respectively, were reached (Fig. 16). Anderson (1967), working with *Hydroptila rono* in Oregon, found a one year life cycle for this Hydroptilid with a drift pattern generally similar to this Brazos species.

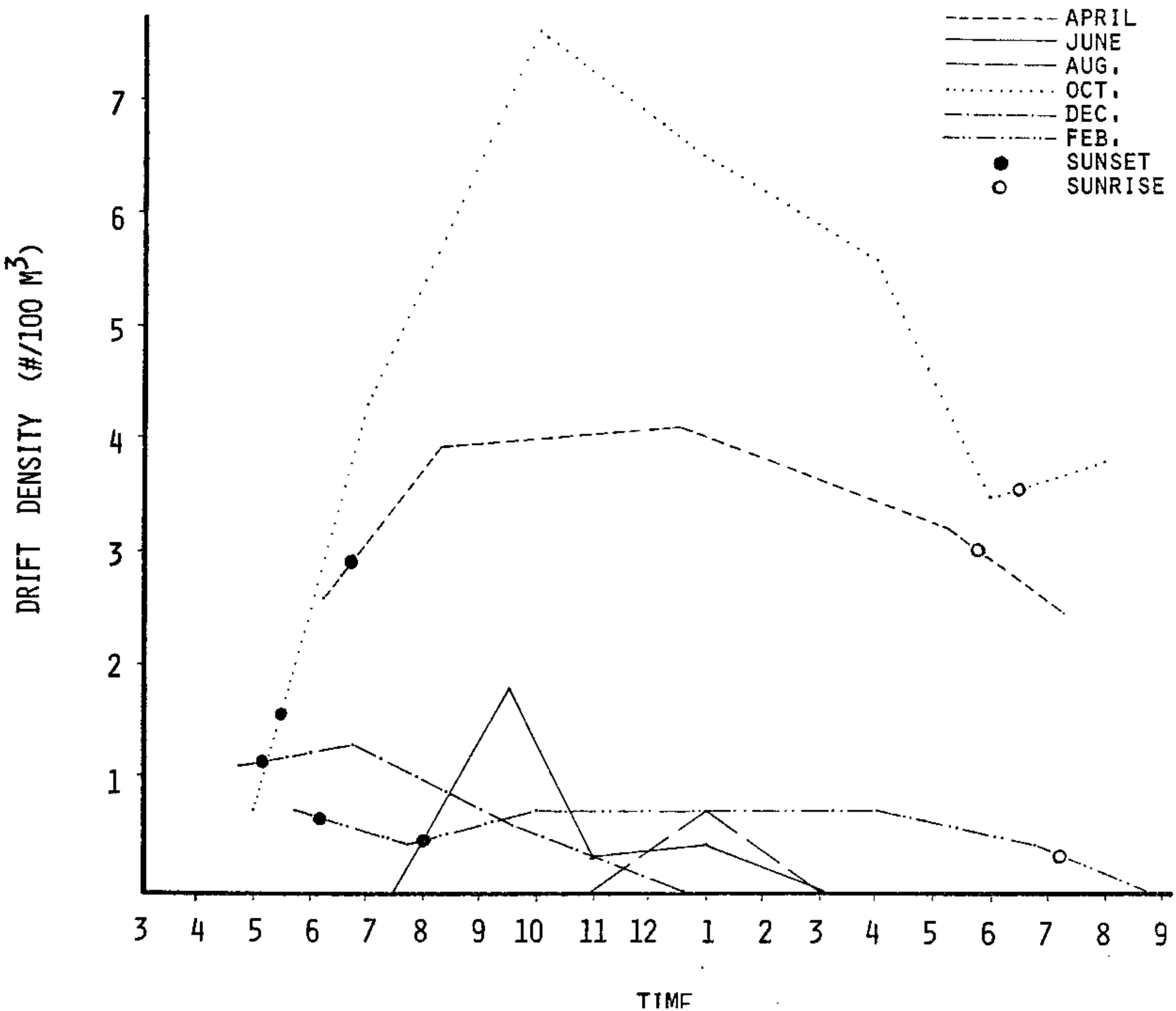
Diel periodicities not consistently noticed by Anderson (1967) for *H. rono* were apparent for *Hydroptila icona* in the Brazos. A nocturnal trend was noted, with drift density increasing in the early evening hours for the active months and returning to lower values in the early hours of morning. This greater propensity for Hydroptilids to drift nocturnally

Figure 15--Drift of *Ithytrichia clavata* larvae, Brazos River, 1972-1973.



APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
12
11
10
9
8
7
6
5
4
3
2
1
6
7
8
9
10
11
12
1
2
3
4
5
6
7
8

Figure 16--Drift of *Hydroptila icona* larvae, Brazos River, 1972-1973.



APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
7
6
5
4
3
2
1
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

was also observed by Bishop and Hynes (1969). Baily (1964) has shown Hydroptila to be a basic component of the invertebrate drift in a Devon river.

Chimarra obscura

Significant drift densities of Chimarra, a Philopotamid, were encountered only in the summer months of June and August (Fig. 17); a maximum of 6/100 m^3 drifted in August.

In both months drift density increased sharply approximately one hour after sunset and declined through the remainder of the night. A major secondary peak occurred on the August date at 1 AM and was only slightly less in magnitude than the primary peak at 9 PM.

Pycnopsyche sp.

Pycnopsyche (Fig. 18) was the only member of the family Limnephilidae found in the drift. Small numbers were noticed in February and June with individuals being taken only rarely on the other semi-monthly sample dates. Limnephilus sp., another member of this family, is found on the riffle.

Even though other investigators have shown diel periodicities in the Limnephilidae (Anderson 1967, Elliott 1971), the present study indicated no consistent pattern in Pycnopsyche drift (Fig. 18). Since larvae were caught both in and out of their cases, the stone cases may at times prevent drifting until particular current velocities are reached, resulting in

Figure 17--Drift of Chimarra obscura larvae, Brazos River, 1972-1973.

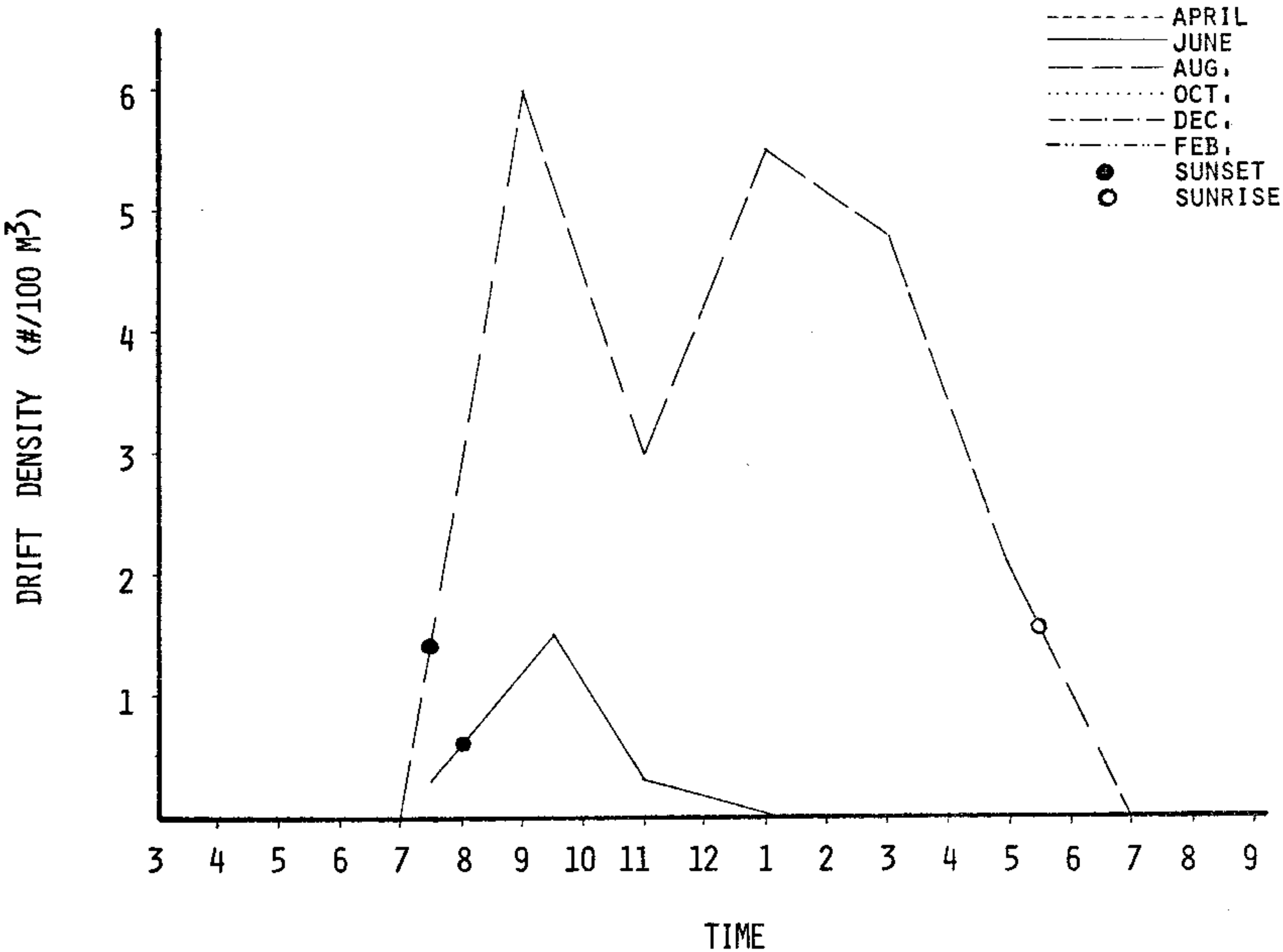
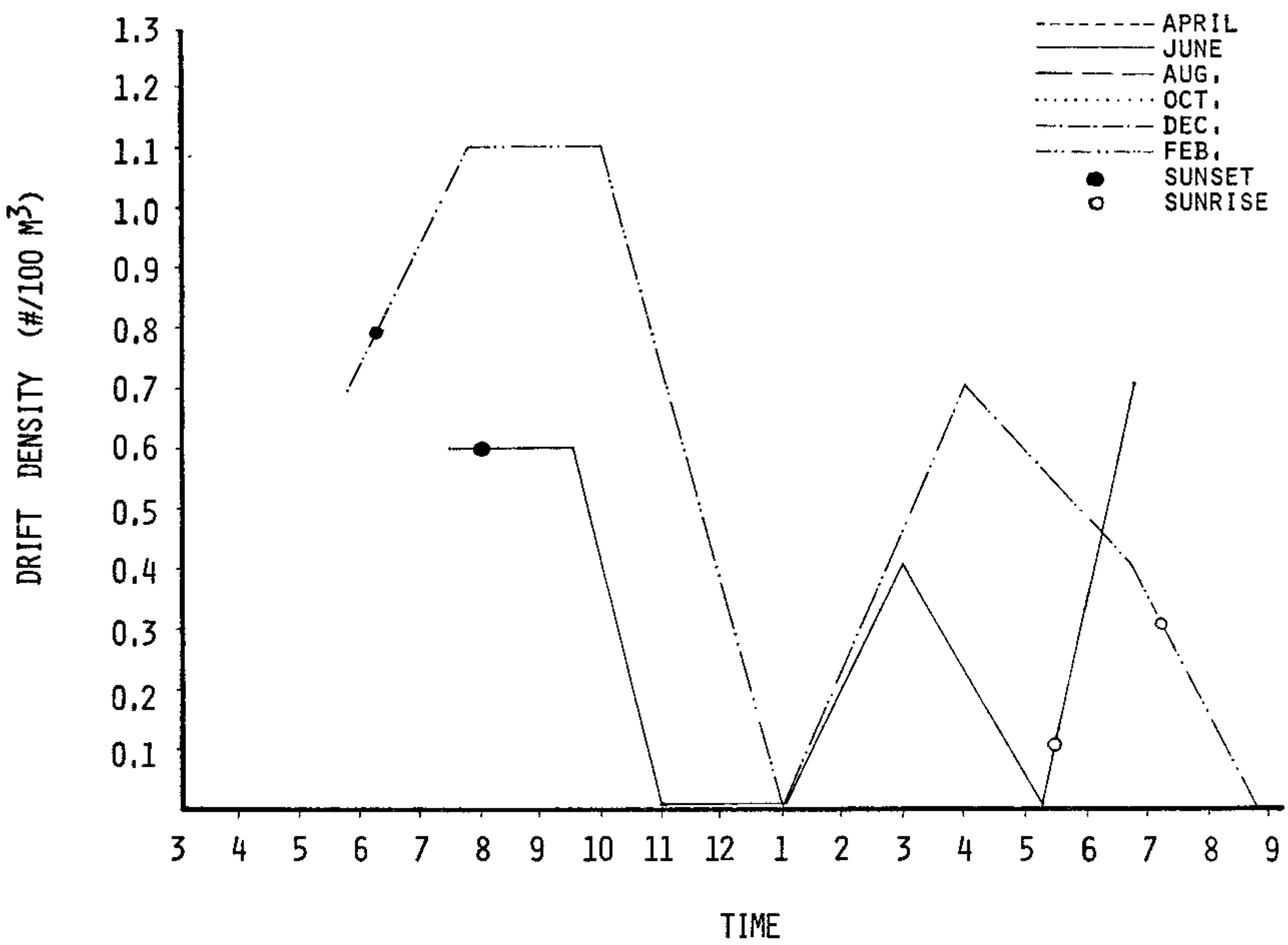

APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
6
5
4
3
2
1
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

Figure 18--Drift of *Pycnopsyche* sp. larvae, Brazos River, 1972-1973.



APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

drift of a more catastrophic than behavioral nature. Maximum discharges of 8.20 m^3/sec and 6.51 m^3/sec encountered during the study corresponded with the June and February Pycnopsyche drift peaks.

Trichoptera pupae exuviae

The exuviae of Trichopteran pupae (Fig. 19) displayed distinct seasonal trends, with the greatest drift densities occurring on the June and August sample dates. These correspond with known seasonal emergence of most caddisflies in the river. Maxima of 27.2/100 m^3 and 19.3/100 m^3, respectively, occurred during these months.

A basic nocturnal activity was evident for all six, semi-monthly sample dates. Peaks of drift density occurred in all months during the early nighttime hours (Fig. 19), which also corresponds with the late evening emergence of Brazos species. Morgan and Waddell (1961) have observed late evening periodicity in caddisfly emergence in England.

Chironomidae

Chironomid larvae composed the third largest group in regards to total drift densities encountered (Table 4). This high rate of chironomid drift has also been shown by several other investigators (Baily 1964, Brusven 1970a, Mundie 1971, Clifford 1972a). Maximum densities of 109/100 m^3 occurred in February, with moderate densities (38-72/100 m^3) on the fall, spring, and summer sample dates (Fig. 20).

Figure 19--Drift of Trichoptera pupae exuviae, Brazos River, 1972-1973.

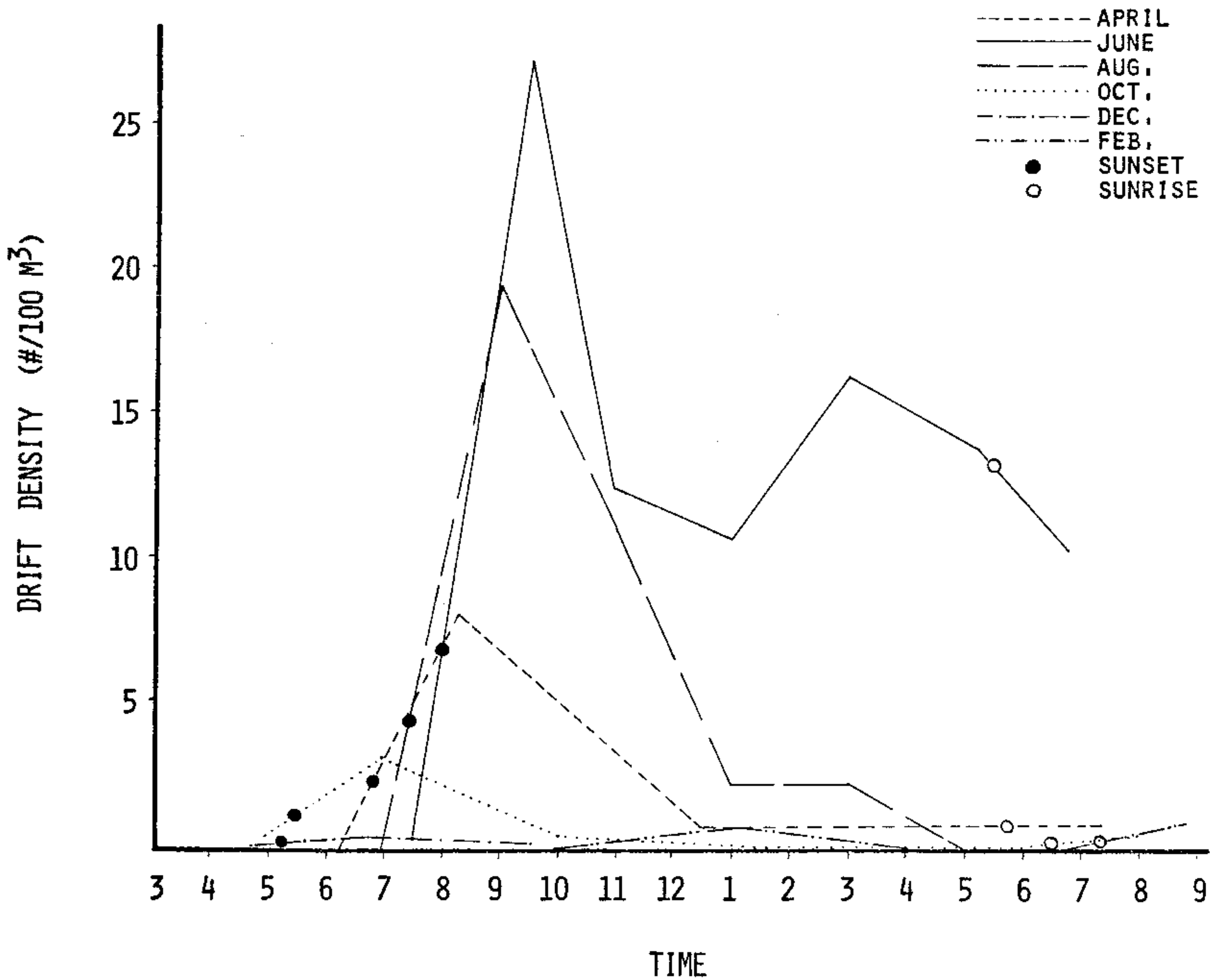

APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
25
20
15
10
5
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

Figure 20--Drift of Chironomidae larvae, Brazos River, 1972-1973.

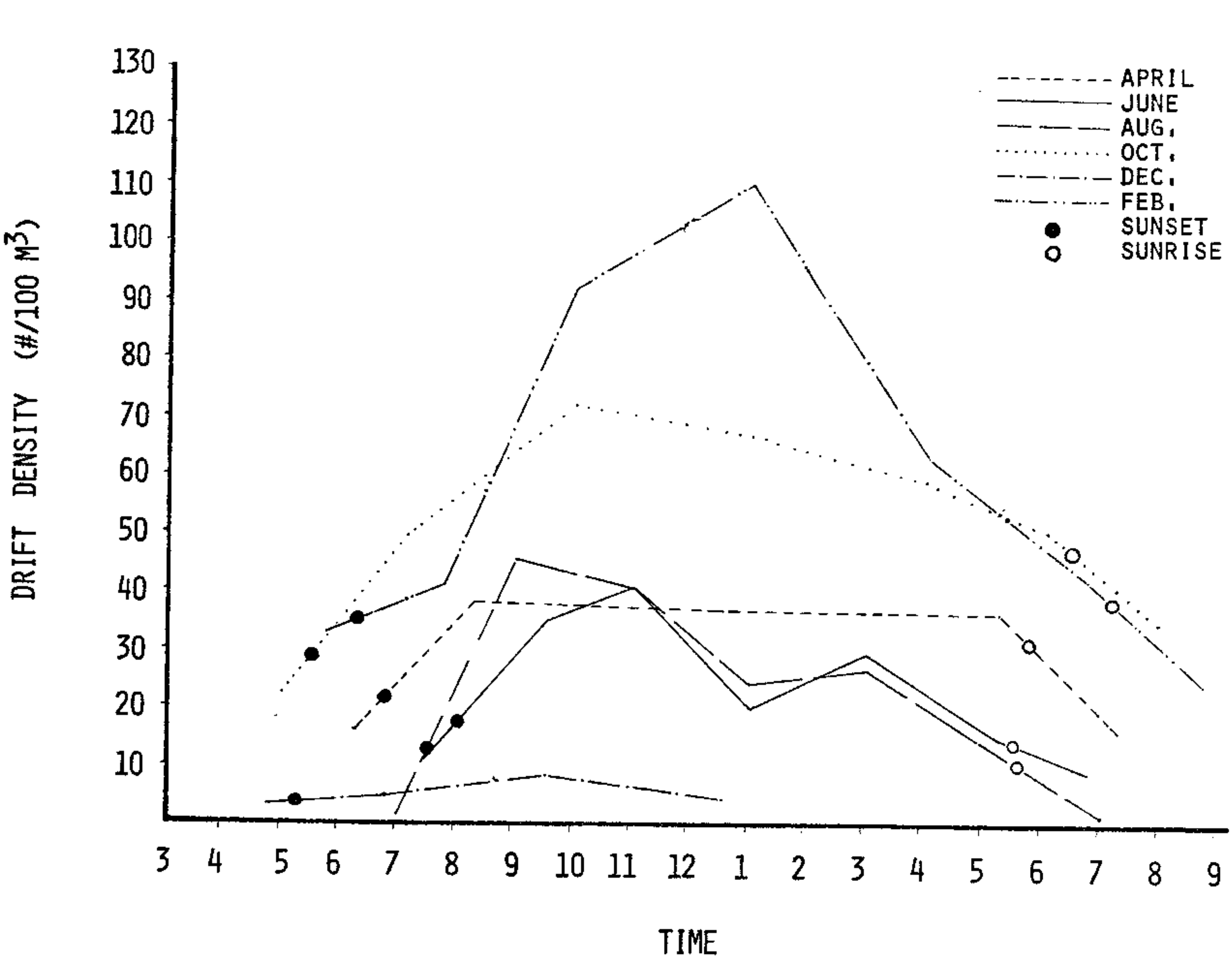
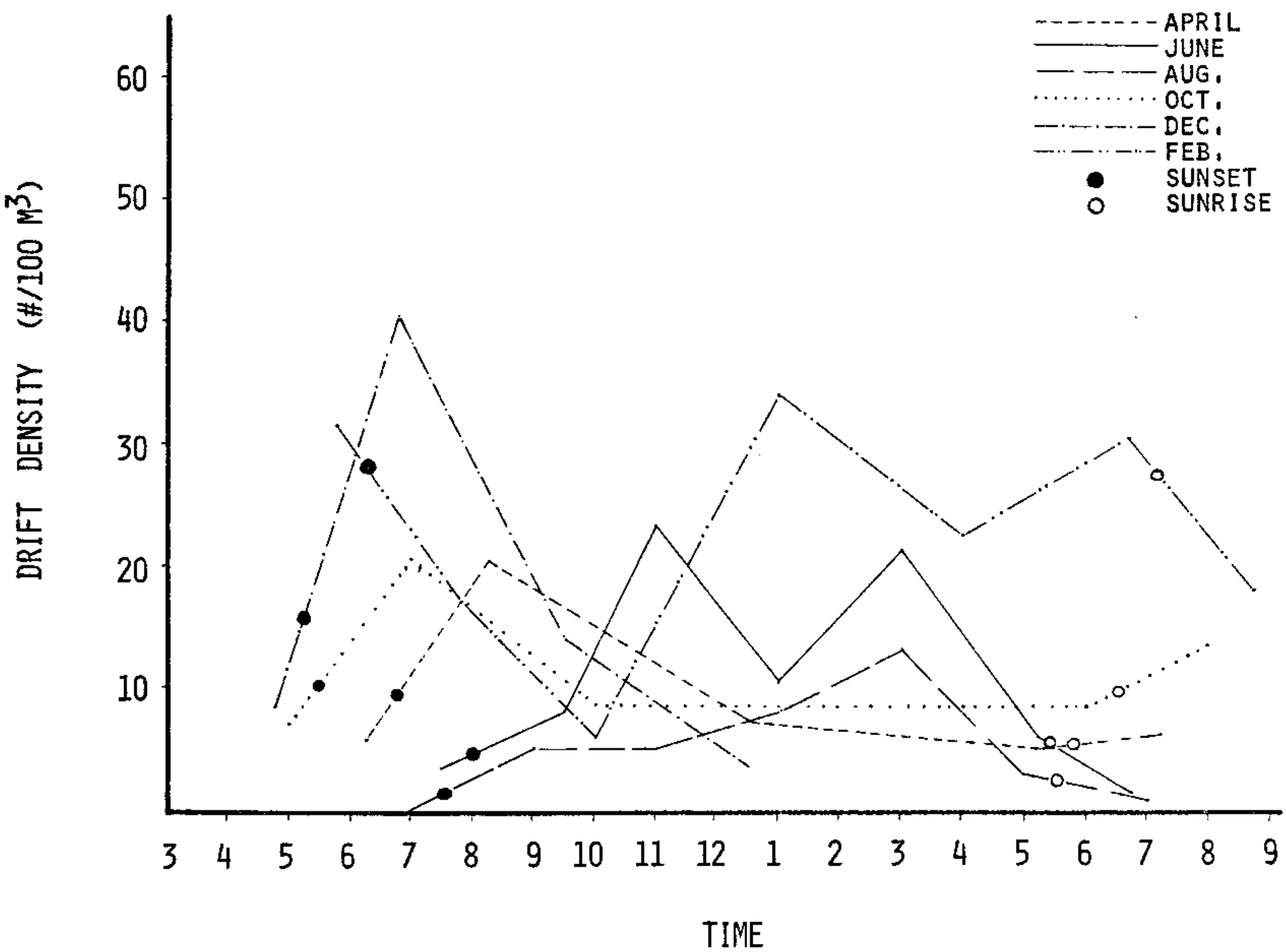

DRIFT DENSITY (#/100 M^3)
130
120
110
100
90
80
70
60
50
40
30
20
10
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME
APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE

Figure 21--Drift of Chironomidae pupae, Brazos River, 1972-1973.



APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
60
50
40
30
20
10
3
4
5
6
7
8
9
10
11
12
1
2
3
4
5
6
7
8
9
TIME

Increases in the drift density occurred on all sample dates during the postsunset hours (Fig. 20). The February peak corresponds to a period of high abundance of chironomid larvae in the standing crops of the study riffle (unpublished data). It was estimated that 2.16×10^5 individuals drifted past the sample transect during the nightly sample date in February; only 1.90×10^4 individuals drifted in December (Table 3).

Chironomid pupae (Fig. 21) displayed highly variable drift densities. Greatest densities of pupae, 40.5/100 m^3 and 34/100 m^3, occurred during December and February, respectively.

Periodicities of chironomid pupae (Fig. 21) suggest that emergence takes place more or less constantly throughout each 24-hr period, as noted by Elliott (1967) and Morgan and Waddell (1961) for several species. The February peak in drift activity probably represents an emergence, since large swarms of chironomids were observed in the vicinity of the study riffle before dusk and in the early evening hours. According to Anderson and Lehmkuhl (1968), these peaks in pupal drift may represent emergence rhythms in certain species.

Simulium sp.

Blackfly larvae appeared regularly in the drift throughout semi-monthly samples (Fig. 22). Maximum drift densities of 144/100 m^3 were noted in April, with moderate numbers

($60/100\ m^3$) occurring in October. The few individuals taken in August were of a larger size class and are probably the remaining members of a particular cohort before pupation. Grenier (1949) noted continual hatching for 50 days in one series of *Simulium nolleri* eggs. This was long enough for the first hatched specimens to have pupated before the remainder had hatched.

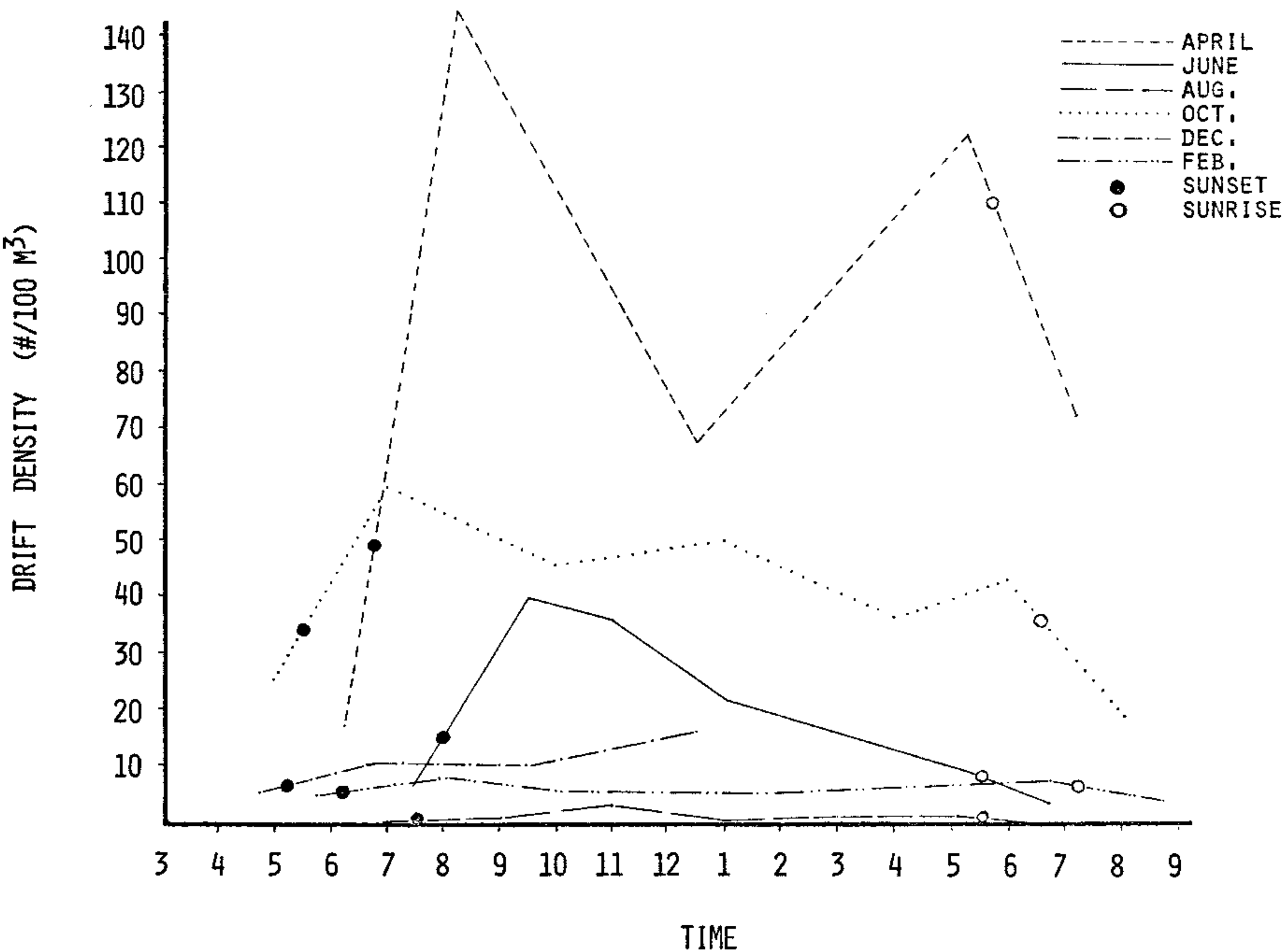
Simulium displayed a definite nocturnal activity in drift, with over an 8-fold increase occurring during the postsunset period of April. Although higher drift densities were encountered nocturnally, there seemed to be no definite pattern, and great variations in the type of curve appeared throughout the study. The presence of high nocturnal drift rates in *Simulium* has also been shown by several other investigators (Baily 1964, Elliott 1965b, Pearson and Franklin 1968, Bishop and Hynes 1969, Brusven 1970a, Elliott and Corlett 1972).

A maximum of 1.68×10^5 *Simulium* larvae were estimated to have drifted past the sample nets during the night of the April sample date (Table 3). Only 1.93×10^3 individuals passed the sample transect on August.

Maximum *Simulium* pupae drift densities occurred in February (Fig. 23). The high drift numbers in February correspond very closely to spring and early summer emergences on the Brazos, after which very few *Simulium* are found.

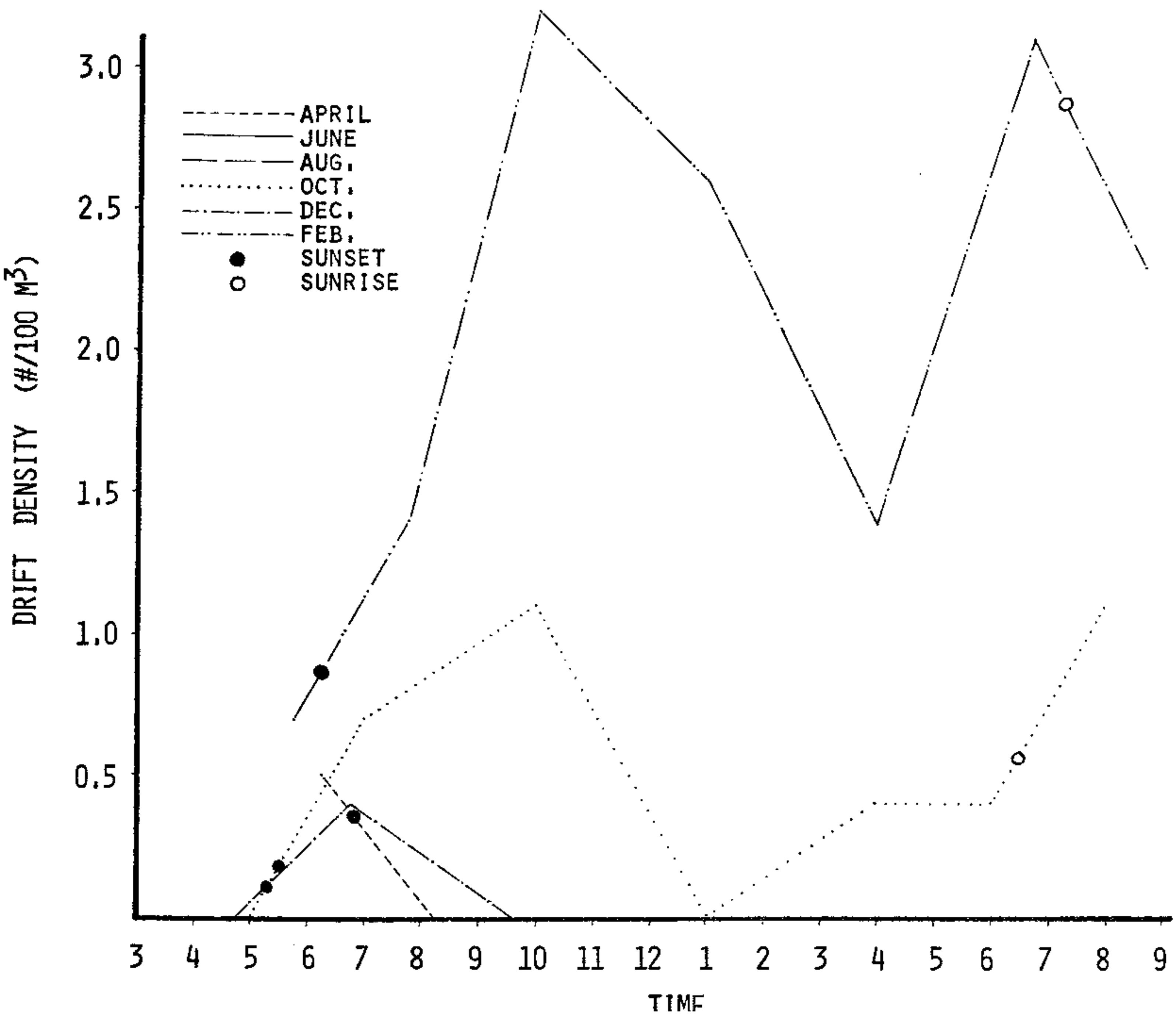
No discernible drift periodicity is apparent from the present samples; however, there is a suggestion that emergence

Figure 22--Drift of *Simulium* sp. larvae, Brazos River, 1972-1973.



DRIFT DENSITY (#/100 M3)
140
130
120
110
100
90
80
70
60
50
40
30
20
10
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME
APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE

Figure 23--Drift of *Simulium* sp. pupae, Brazos River, 1972-1973.



DRIFT DENSITY (#/100 M3)
3.0
2.5
2.0
1.5
1.0
0.5
APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

of this species occurs at both the day and night (Fig. 23).

Chaoborus sp.

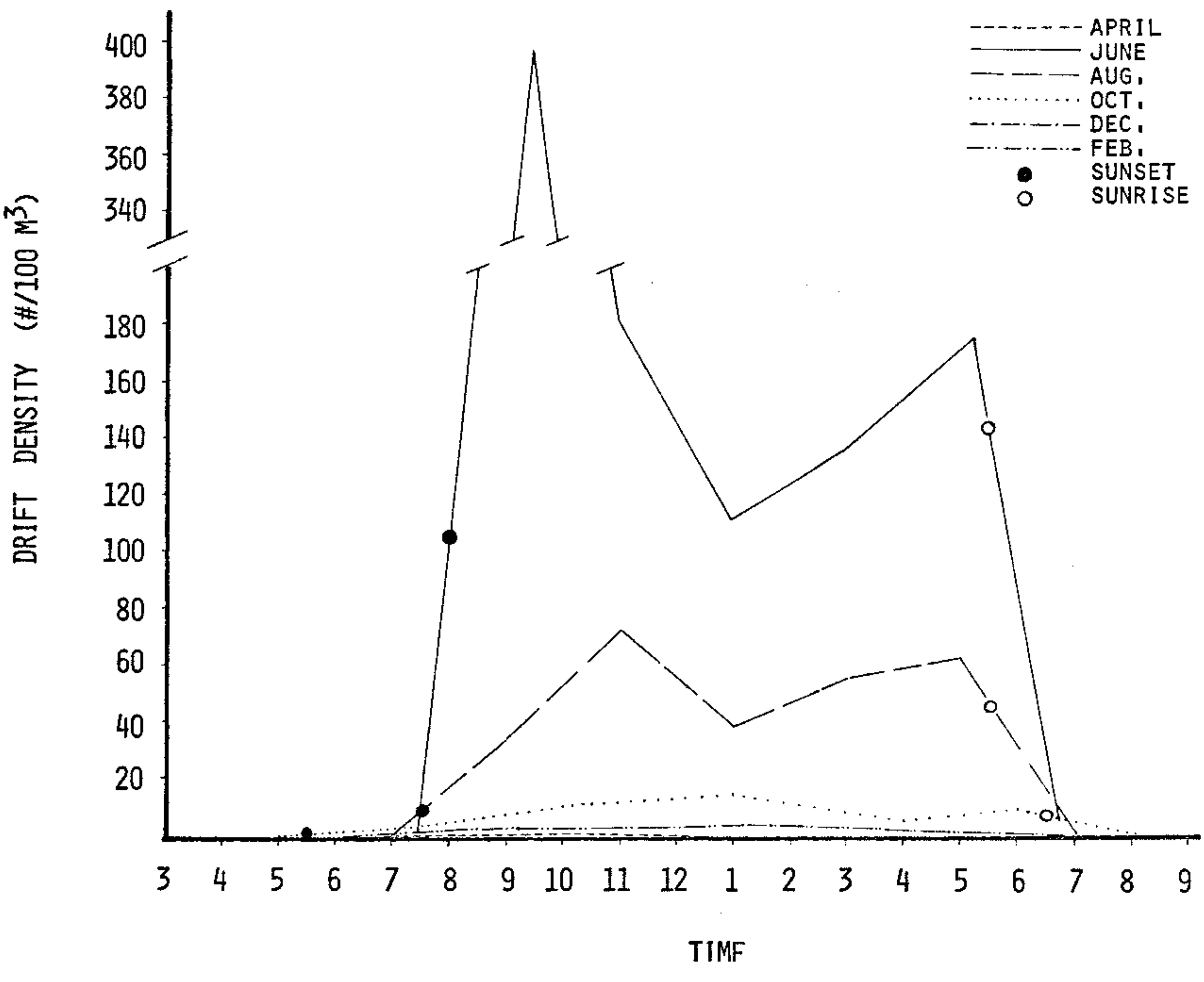
Although *Chaoborus* is not intimately associated with the riffle environment, extreme temporal variations in their numbers are of tremendous importance to the drift-ecology of the Brazos River. Their well known vertical migrations make them particularly susceptible to the pool currents in the Brazos, resulting in their subsequent appearance in the drift samples. Berner (1951), investigating the lower Missouri River, noticed *Chaoborus* composing 2.9% of the invertebrate drift fauna.

Very high drift densities occurred on the June sample date, with a maximum of 397/100 m^3 drifting approximately one to two hours after sunset (Fig. 24). In August 72/100 m^3 were sampled in the postsunset period.

Nocturnal periodicities were typically "bigeminus", with minor secondary peaks occurring shortly before sunrise (Fig. 24). Elliott and Corlett (1972) also noted higher nocturnal drift rates in the summer months for *Chaoborus* via the outflow of a lentic system.

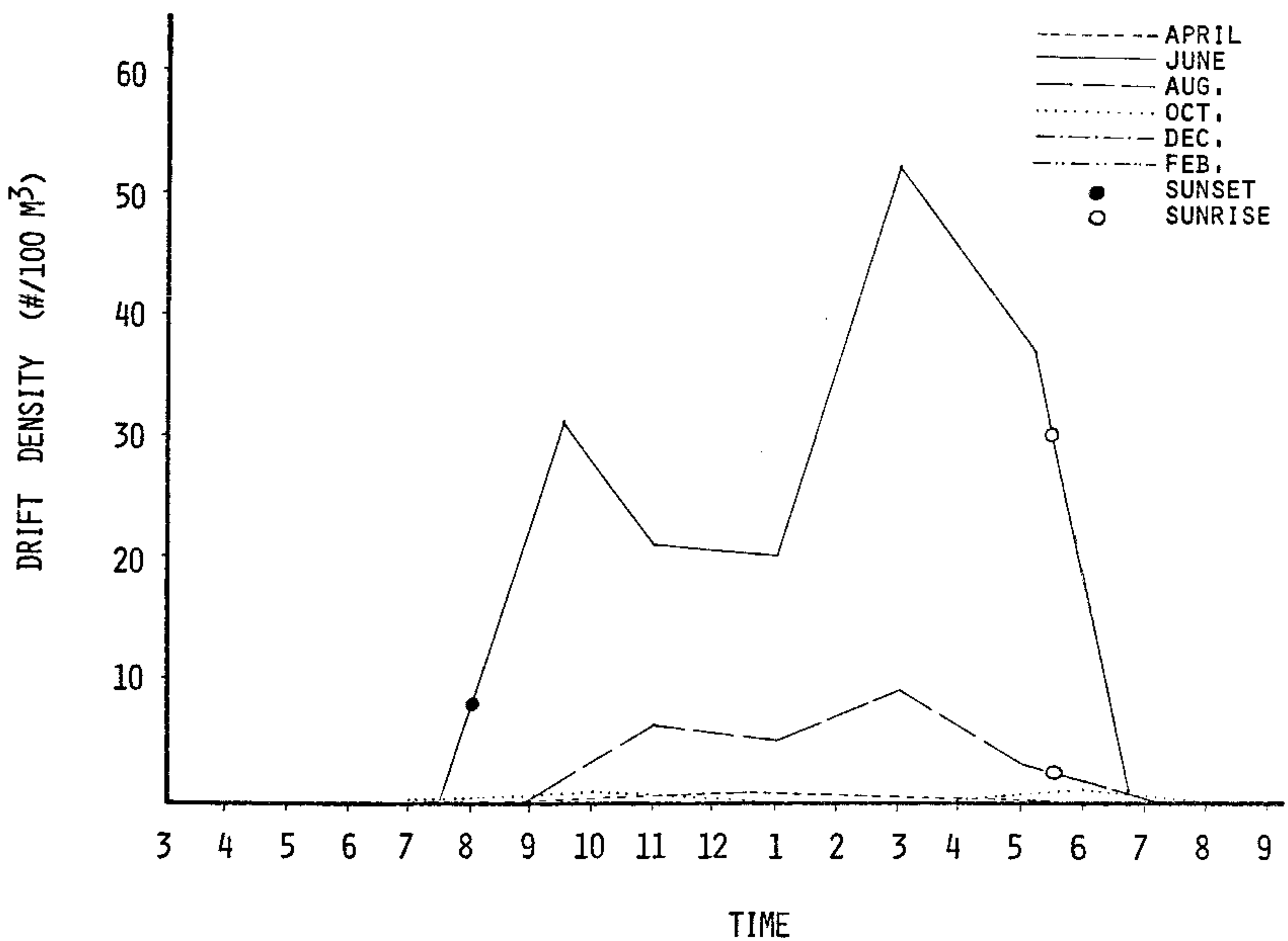
An estimated 5.39 x 10^5 *Chaoborus* larvae drifted past the sample site on the night of June 16-17th (Table 3). This was the highest drift estimate for any single species during the yearly sample period and represents approximately a 210-fold increase over those values reported by Elliott and Corlett (1972).

Figure 24--Drift of Chaoborus sp. larvae, Brazos River, 1972-1973.



APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
400
380
360
340
180
160
140
120
100
80
60
40
20
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIMF

Figure 25--Drift of *Chaoborus* sp. pupae, Brazos River, 1972-1973.


APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
60
50
40
30
20
10
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

Significant quantities of Chaoborus pupae, 5-52/100 m^3, were sampled only on the summer dates of June and August (Fig. 25). Chaoborus pupae, unlike the larvae, displayed a definite "alternans-pattern" of drift with a major secondary peak occurring in the early morning. This secondary peak may represent a high pre-emergence activity, since certain species of Chaoborus have been shown to emerge chiefly between midnight and dawn (Morgan and Waddell 1961).

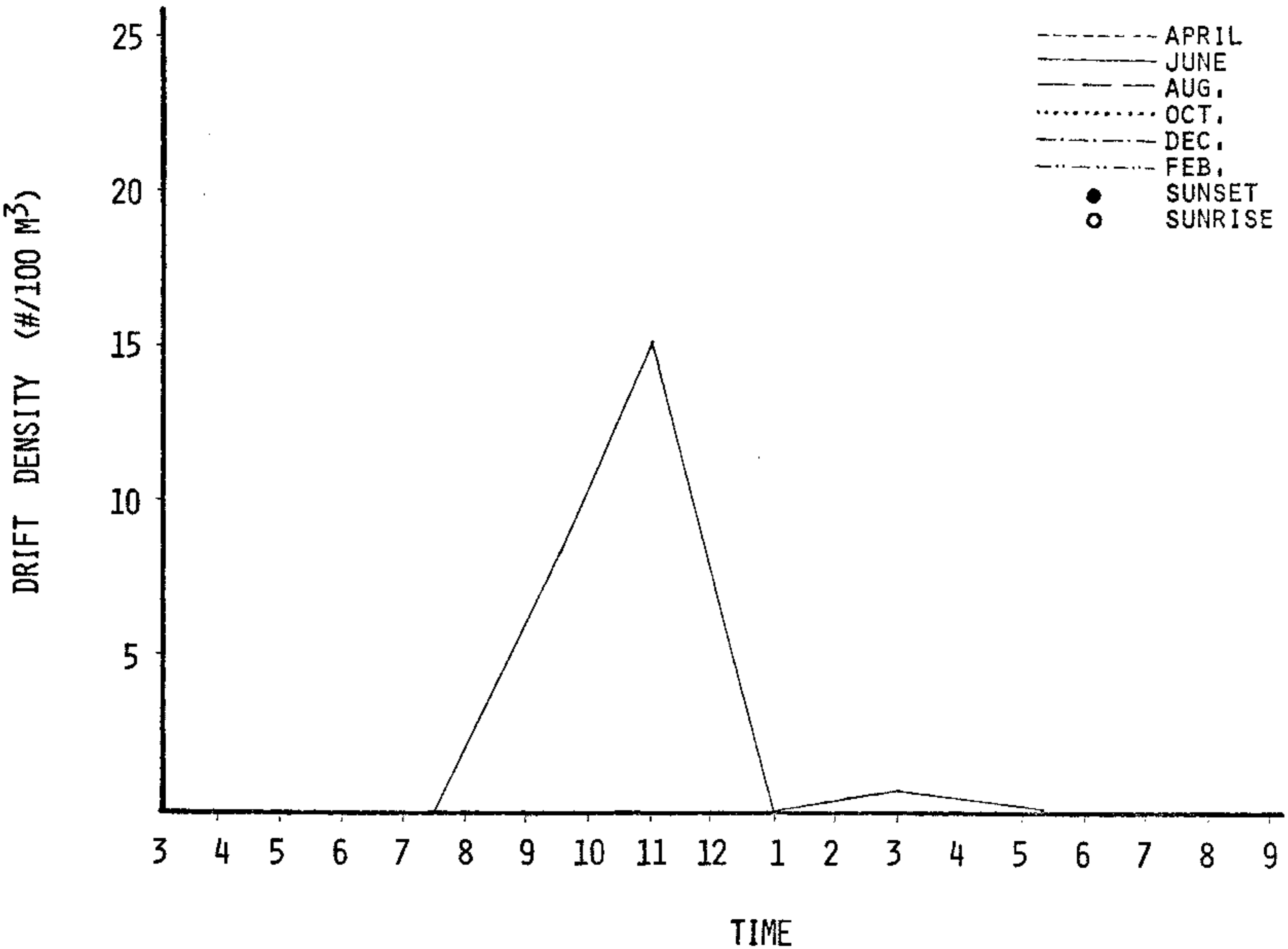
Palpomyia sp.

The Ceratopogonid, Palpomyia, occurred in the drift only during the June samples (Fig. 26). Maximum drift densities of these larvae (15/100 m^3) were noted in the evening prior to midnight; activity of this species appeared to be "bigeminus", similar to that pattern displayed by Chaoborus larvae (Fig. 24). Although the Ceratopogonidae have been reported previously in the drift (Waters 1961, Bishop and Hynes 1969, Clifford 1972a, b), no apparent conclusions can be drawn on the basis of the present samples concerning their regularity and periodicity in the drift of the Brazos River.

Stenelmis spp.

Moderate populations of the Elmid riffle beetle, Stenelmis, occur throughout the year on the study riffle. Two adult species, S. bicarinata and S. mexicana, composed approximately 3.3% of the total drift density (Table 4). Although both species were considered as a single group due to previous

Figure 26--Drift of Palpomyia sp. larvae, Brazos River, 1972-1973.


APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
25
20
15
10
5
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

analyses of drift samples, it is noteworthy that Stenelmis bicarinata outnumbered Stenelmis mexicana 10 to 1 at times of peak drift density.

Maximum drift (54/100 m^3) of Stenelmis adults occurred in June; the drift densities of August were very similar (Fig. 27). The pattern of drift was basically unimodal, with the maximum drift densities generally established four to five hours after sunset. This unimodal pattern has been reported for several other species of adult riffle beetles in Idaho (Brusven 1970b). Brusven's paper represents the only significant work reported to date on the drift of riffle beetles.

The peak seasonal drift density of Stenelmis larvae was observed in June (29.7/100 m^3) (Fig. 28). This month represents approximately a 10-fold increase in drift density over the other semi-monthly samples and corresponds to the period of greatest abundance of Elmid beetles at the study riffle. The lower levels of drift in the winter months may be the result of larval migrations within the substrate. Vertical migrations of up to 40 cm have been determined for Stenelmis larvae in current Brazos River community studies (unpublished data).

In all semi-monthly samples larval drift activity was nocturnal, with the highest drift densities generally occurring in the middle of the night (Fig. 28). Curves were unimodal similar to those for the adults (Fig. 27); however, the August samples did indicate a minor secondary peak shortly before dawn.

Figure 27--Drift of Stenelmis spp. adults, Brazos River, 1972-1973.

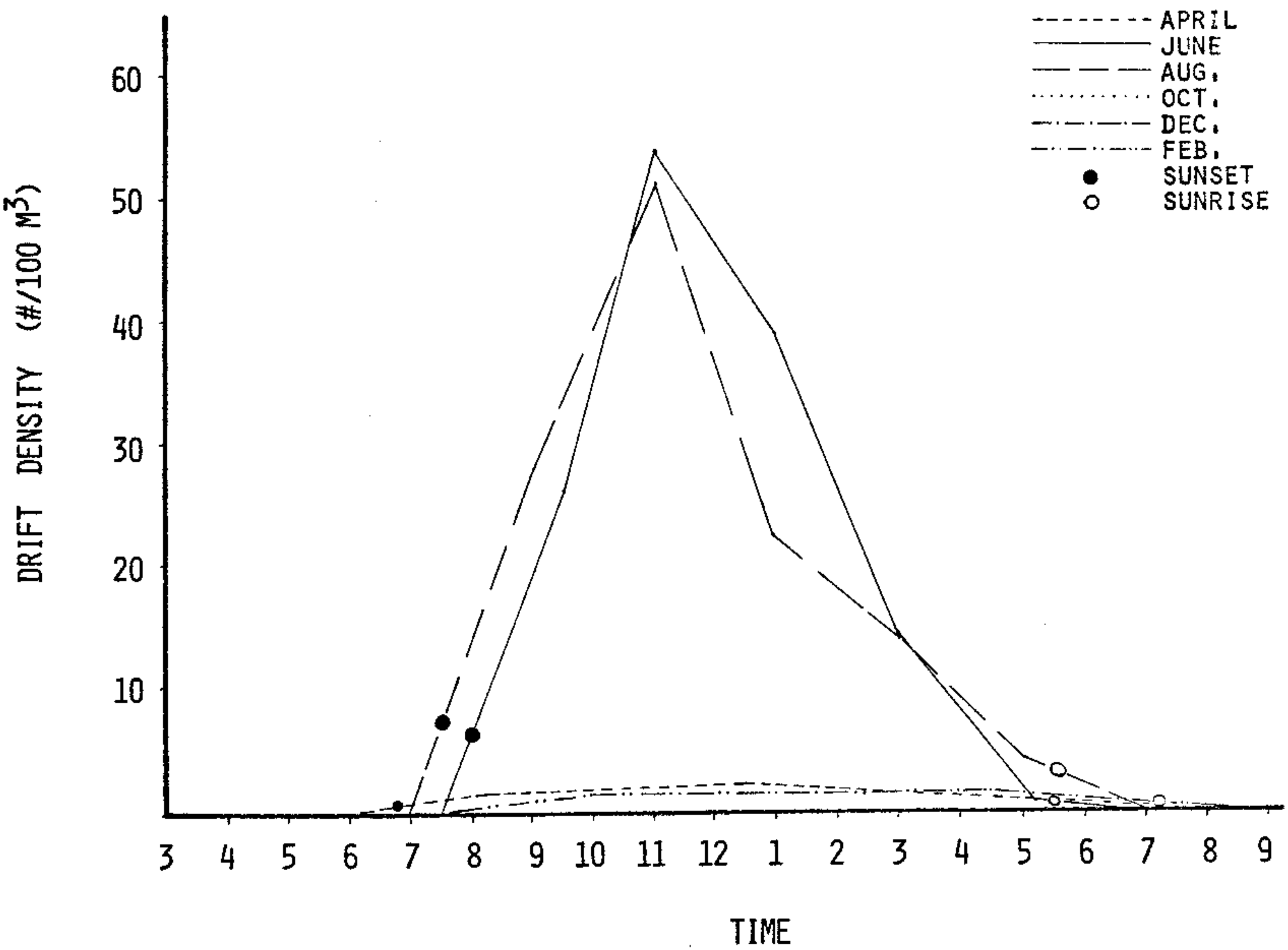
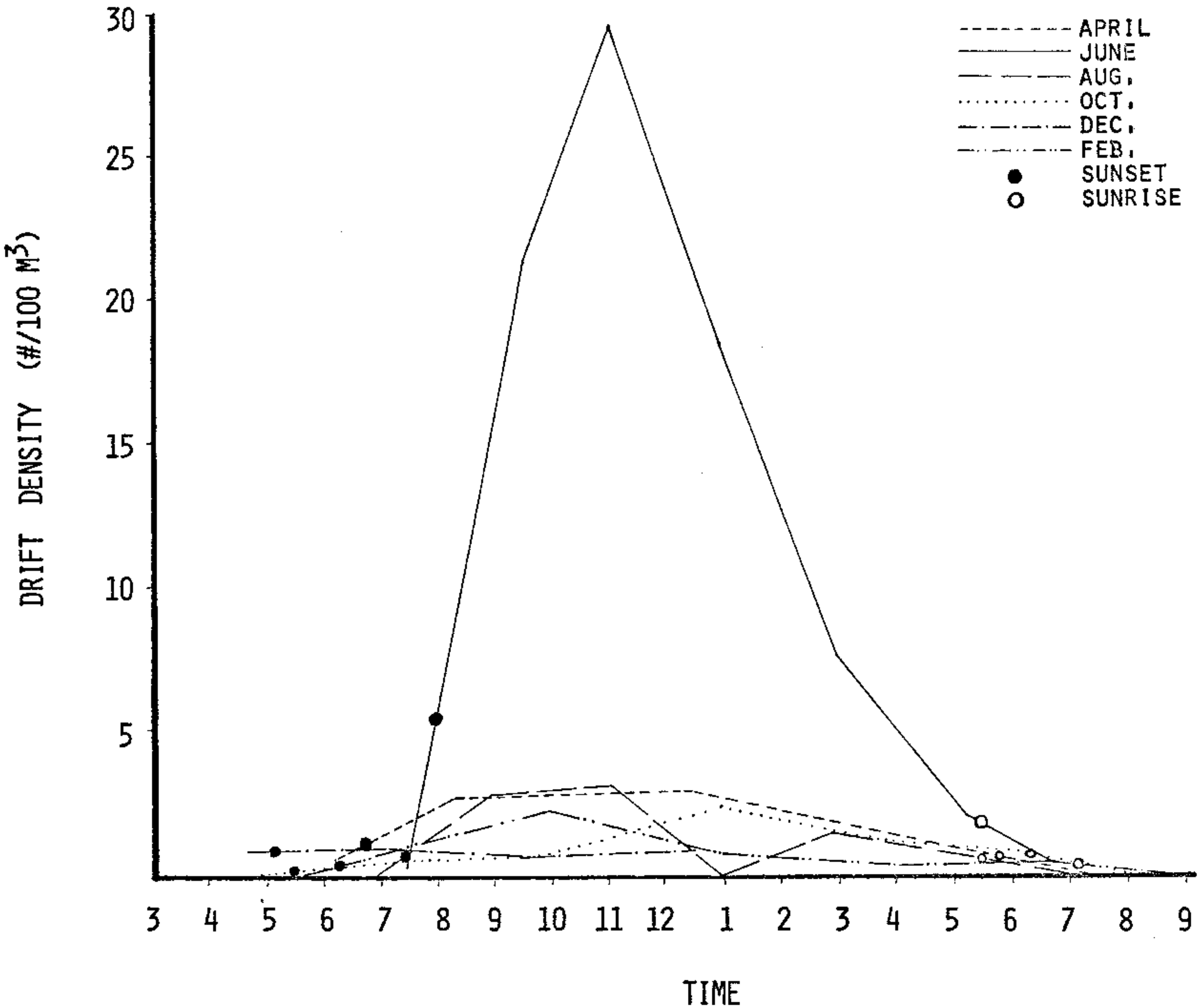

APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
60
50
40
30
20
10
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

Figure 28--Drift of Stenelmis spp. larvae, Brazos River, 1972-1973.


APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
30
25
20
15
10
5
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

Dubiraphia vittata

Dubiraphia vittata is a third member of the family Elmidae occurring at the Brazos River study riffle. Maximum numbers of 28/100 m^3 drifted in June (Fig. 29). Other significant quantities of *Dubiraphia* adults were noted in August and October.

The activity of this elmid was almost entirely nocturnal, (Fig. 29) with single peaks noted in each of the three semimonthly sample dates. In August the peak in drift activity occurred shortly before dawn.

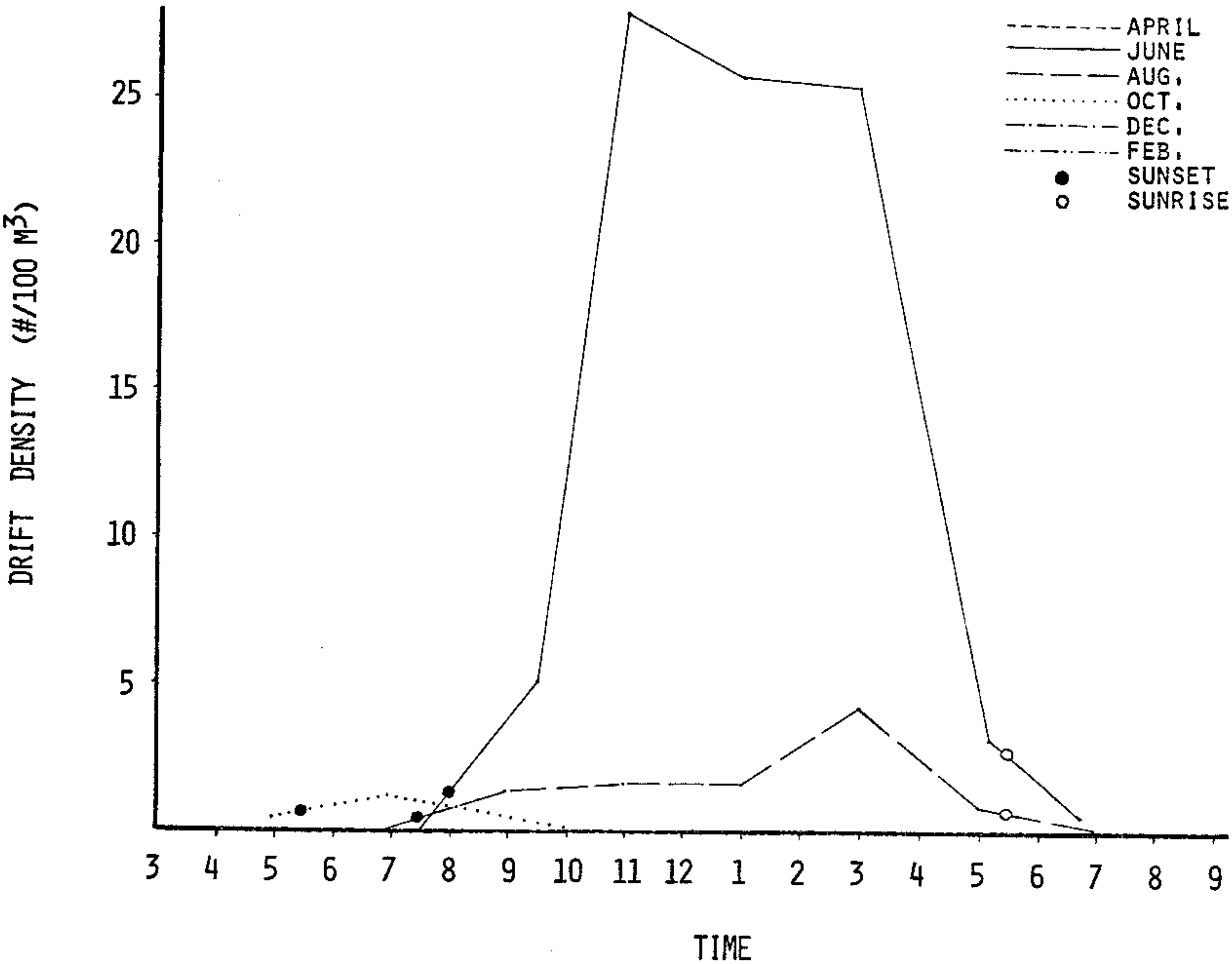
Gyretes sp.

The larvae of the whirligig beetle, *Gyretes*,were recorded in the drift during the summer sample dates of June and August (Fig. 30). A maximum of 2.7/100 m^3 were taken in the postsunset period of August followed by a rapid decline in numbers to zero density levels before dawn. In both months the drift pattern appeared "bigeminus" and probably resulted from periods of activity immediately following sunset.

Enallagma sp.

Enallagma was one of three Odonates consistently found in the Brazos River drift. Maximum drift density (2.1/100 m^3) occurred in June; February and October samples displayed somewhat lower drift numbers (Fig. 31).

Figure 29--Drift of *Dubiraphia vittata* adults, Brazos River, 1972-1973.



APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
25
20
15
10
5
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

Figure 30--Drift of _Gyretes_ sp. larvae, Brazos River, 1972-1973.

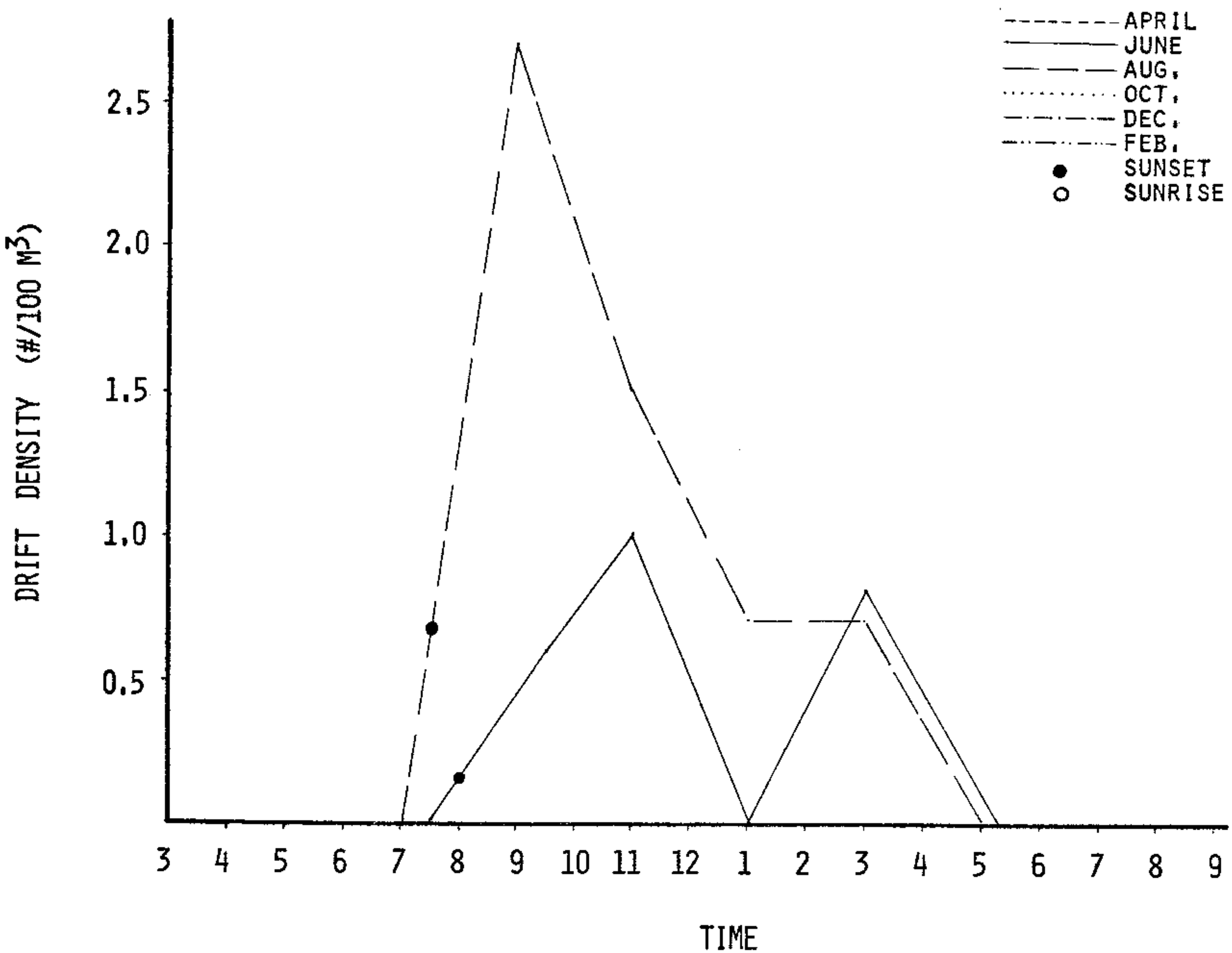
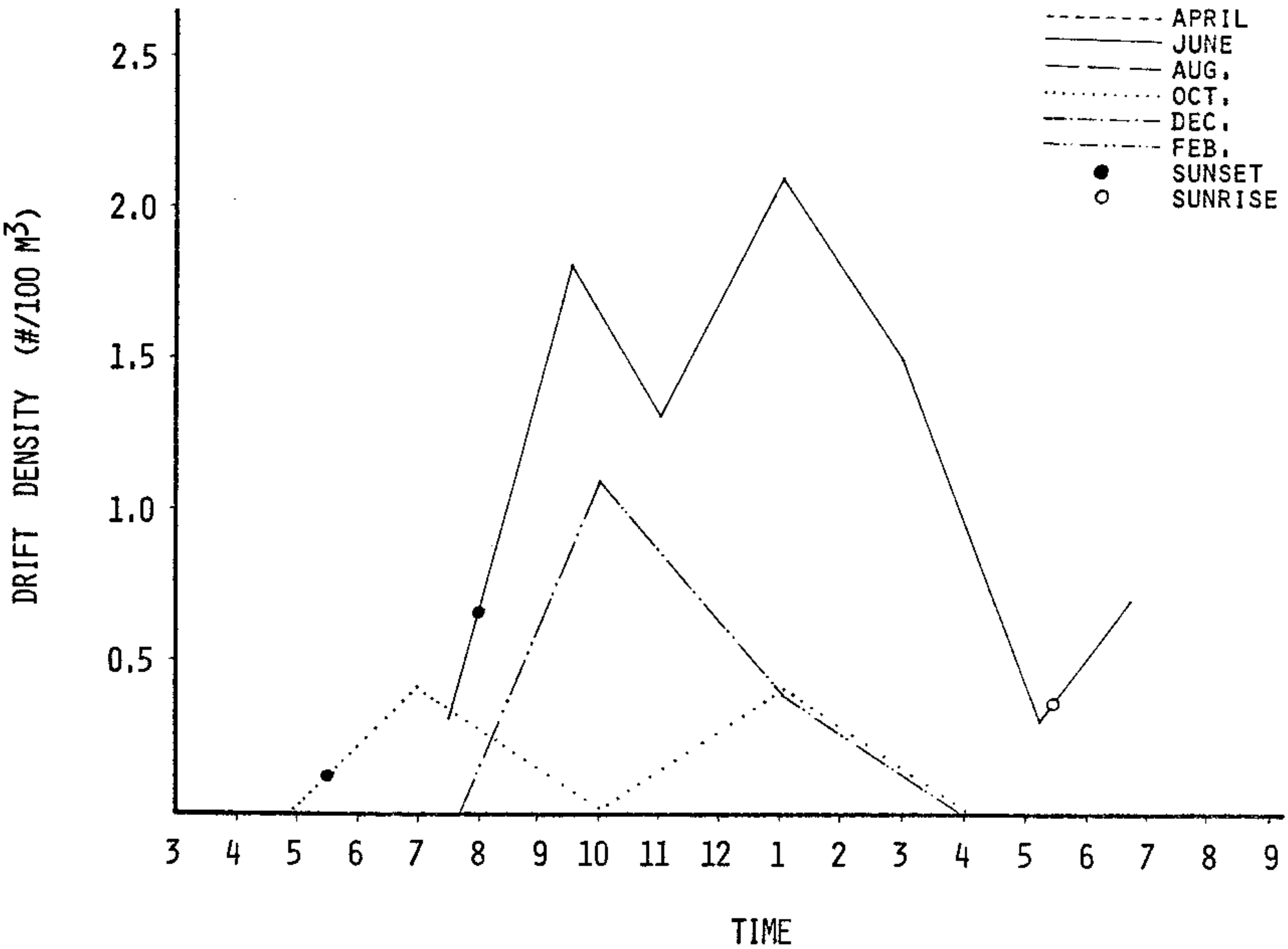

APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
2.5
2.0
1.5
1.0
0.5
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

Figure 31--Drift of *Enallagma* sp. nymphs, Brazos River, 1972-1973.


DRIFT DENSITY (#/100 M3)
2.5
2.0
1.5
1.0
0.5
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME
APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE

Two peaks of activity were recorded in June and October, with the former being suggestive of the "alternans-pattern". The higher drift densities suggested by Enallagma in the post-sunset period of June may be indicative of pre-emergence activity. Morgan and Waddell (1961) have recorded the emergence of Enallamga cyathigerum between the hours of 8 AM and 2 PM.

Argia sp.

The Zygopteran, Argia, was recorded in the drift only in June and August (Fig. 32). Peaks in drift density occurred immediately after sunset, with a return to zero density levels in the early morning hours. The unimodal and "alternans" curves encountered in June and August, respectively, are probably the result of increased nymphal activity, but no definite conclusions may be made on the basis of the present samples.

Ophiogomphus sp.

Ophiogomphus was the only dragonfly significantly represented in the drift. Maximum numbers were attained in August (2.2/100 m^3) with only 0.7/100 m^3 being recorded in April (Fig. 33). A series of two nocturnal peaks occurred in August; the major peak followed sunset, with the minor peak before dawn. One single peak was noted in April.

Figure 32--Drift of *Argia* sp. nymphs, Brazos River, 1972-1973.

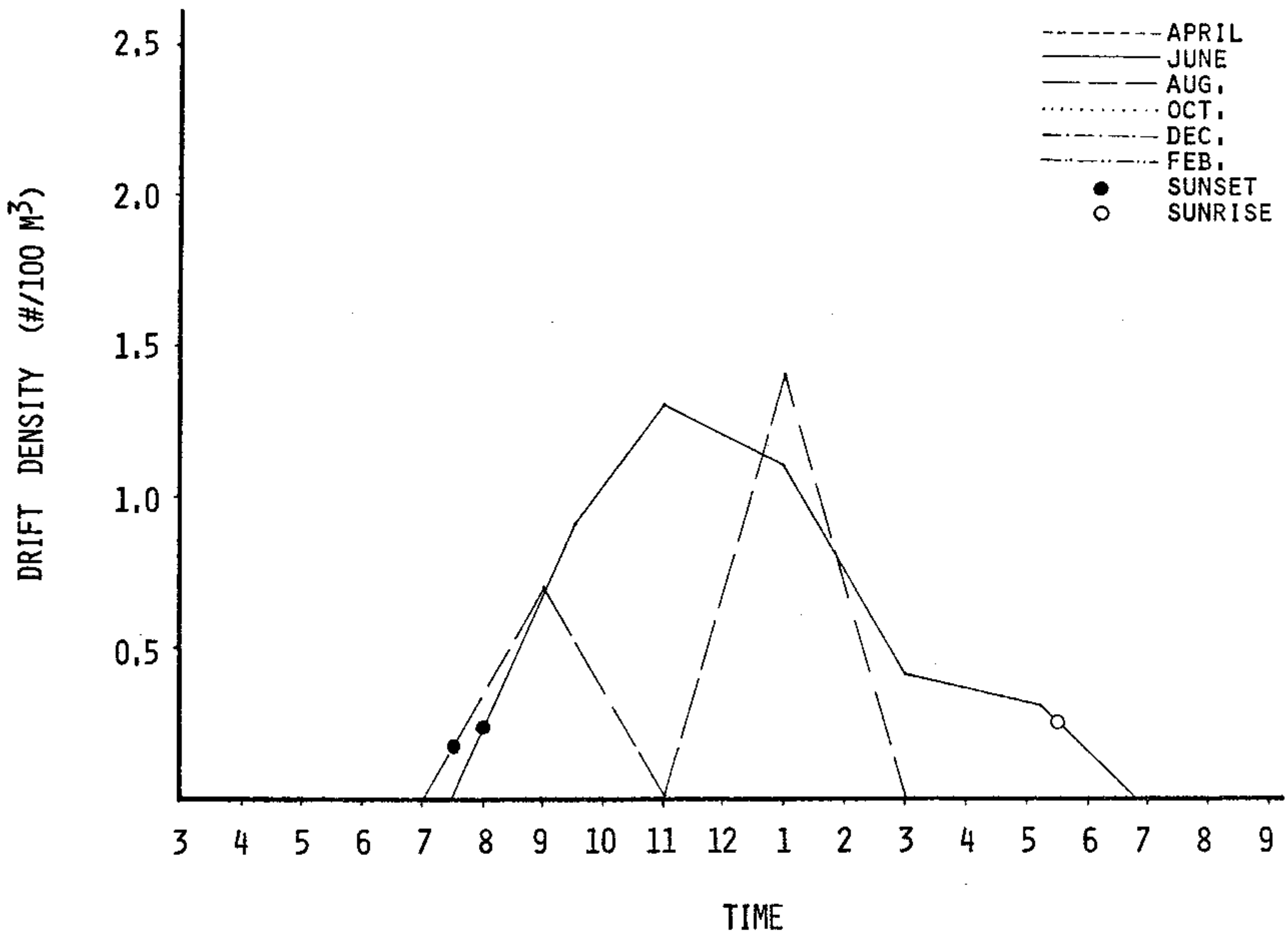
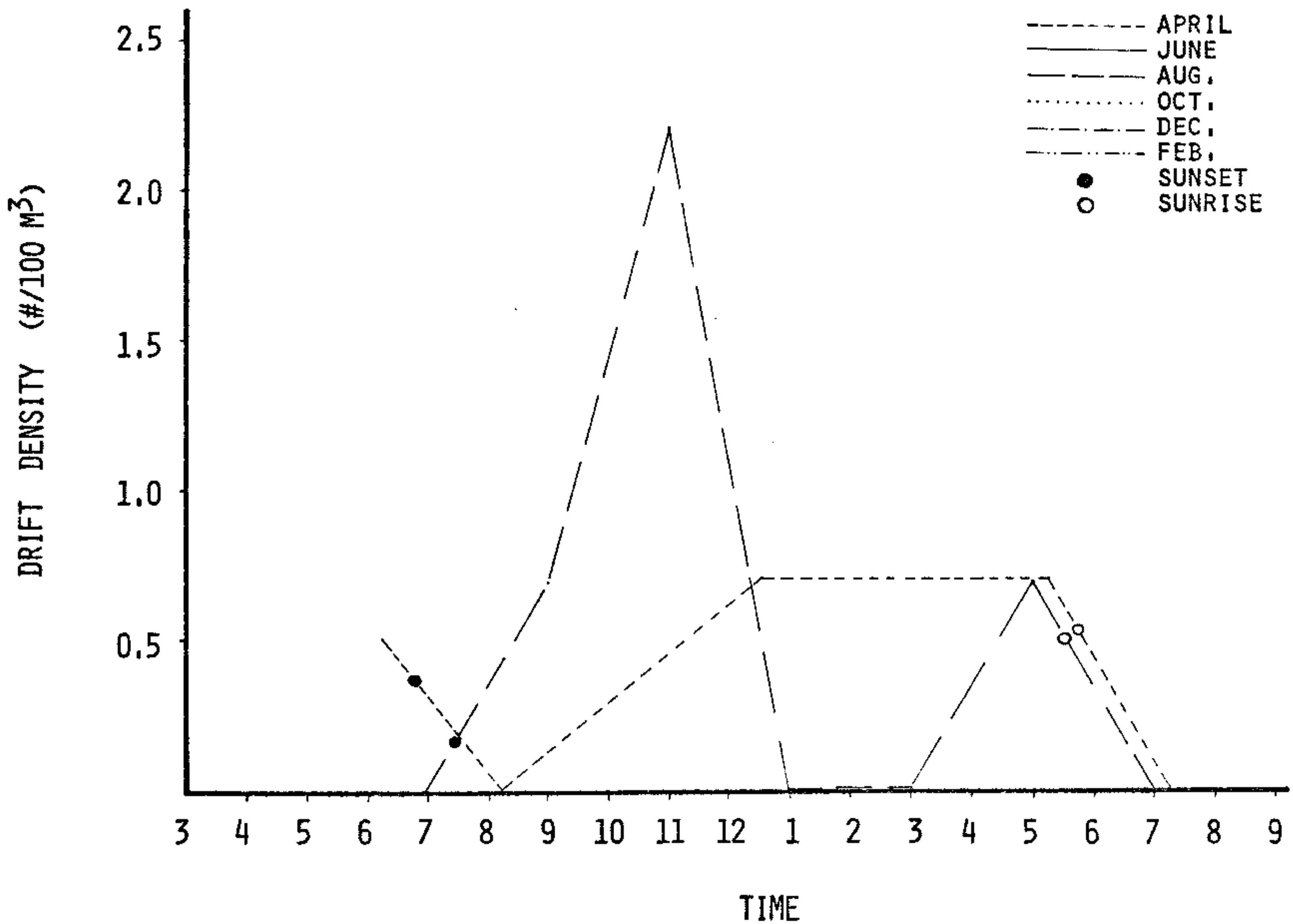

DRIFT DENSITY (#/100 M^3)
2.5
2.0
1.5
1.0
0.5
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME
APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE

Figure 33--Drift of *Ophiogomphus* sp. nymphs, Brazos River, 1972-1973.


APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M³)
2.5
2.0
1.5
1.0
0.5
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME

Elophila sp.

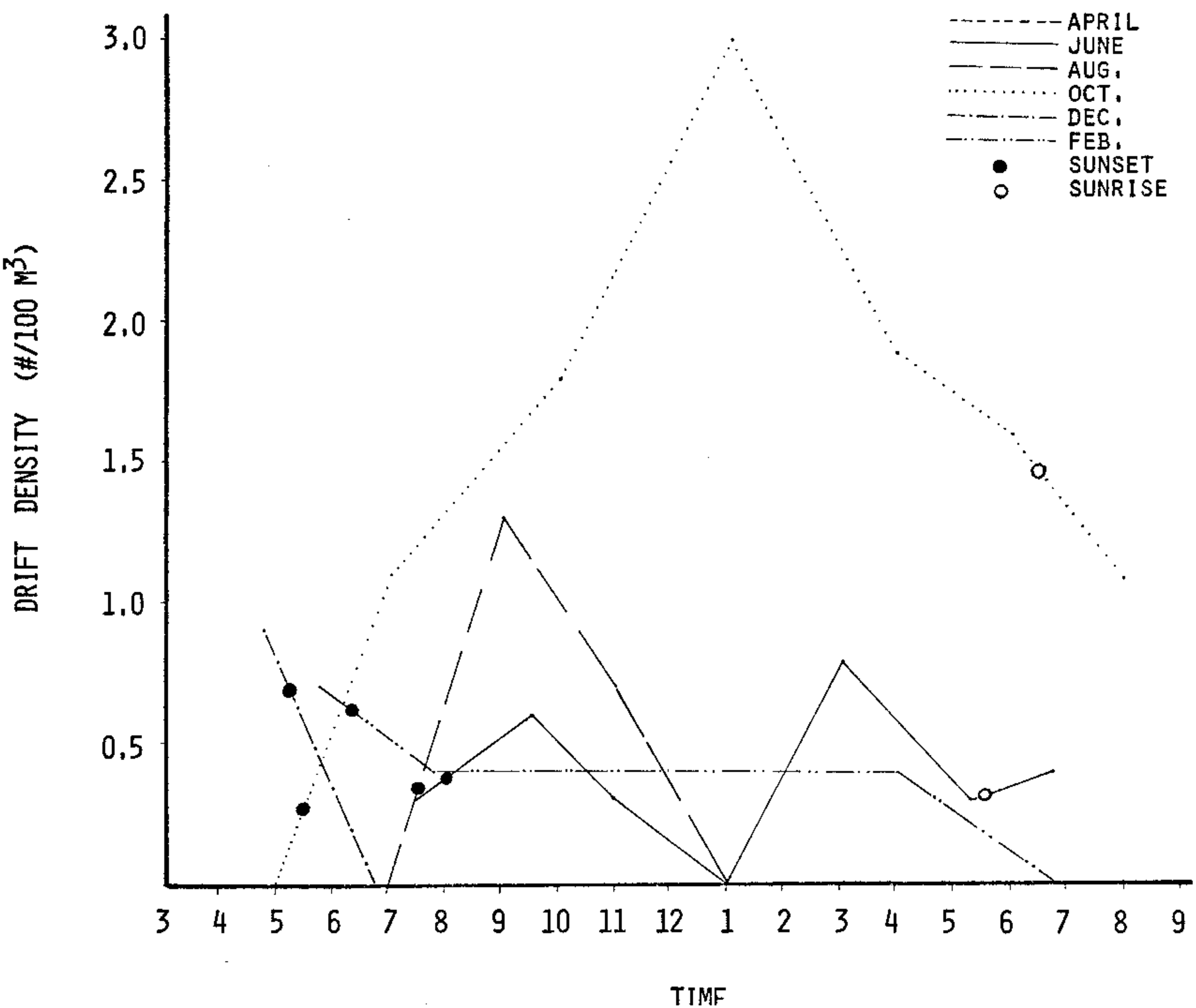
The Lepidoptera were represented in the drift quite regularly by one aquatic species, the Pyralid *Elophila*. Individuals were taken on every semi-monthly sample date except April (Fig. 34). Highest drift densities were recorded in October, with a maximum of 3/100 m^3 being taken in the middle of the night.

No consistent diel pattern was apparent for *Elophila*, although the June, August, and October samples tend to support a nocturnal pattern.

Neoperla clymene

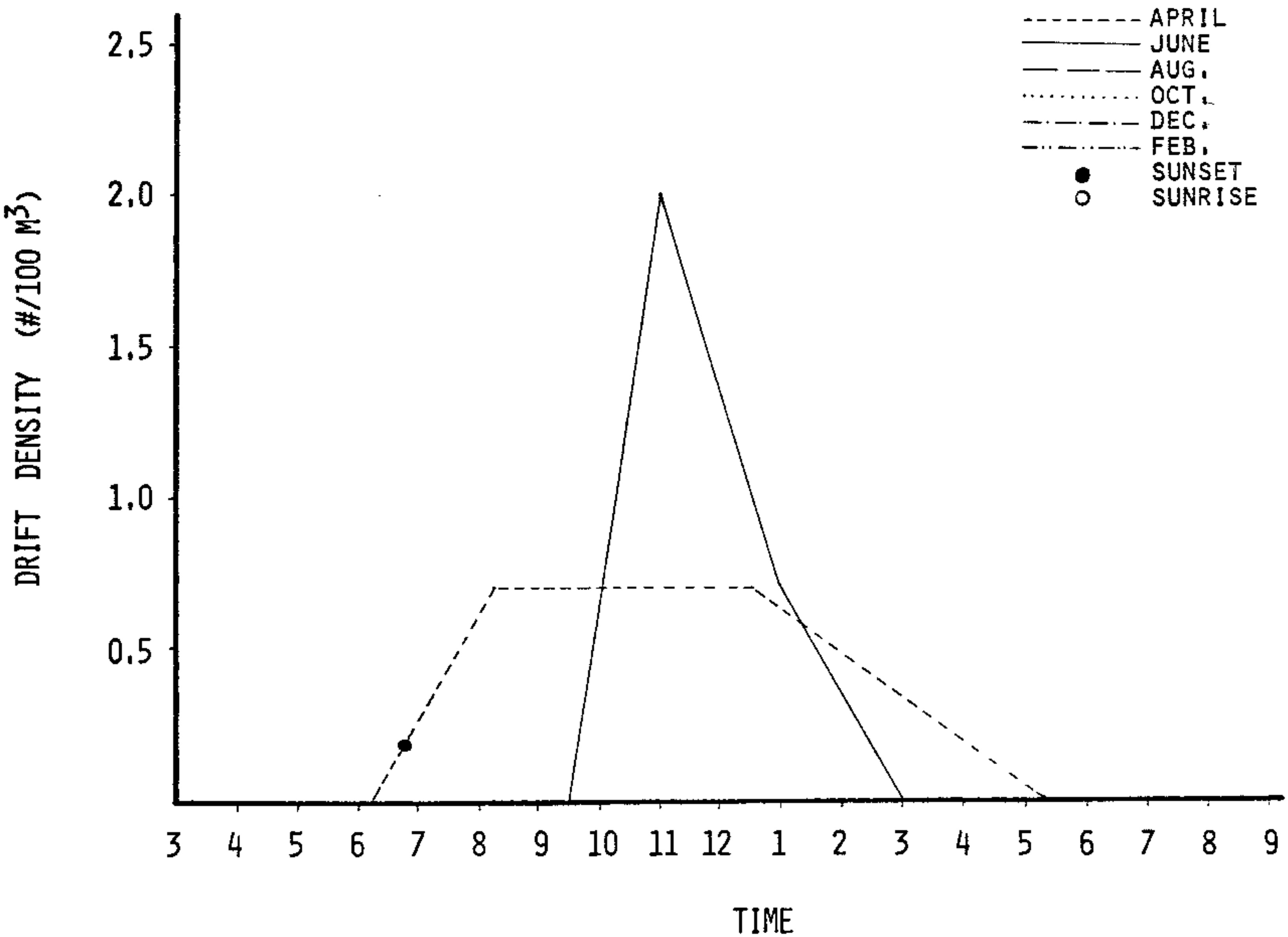
Neoperla clymene, the only stonefly represented in the bottom fauna of the study riffle, was poorly represented in the drift. Individuals were recorded only during the April and June sample dates, with a maximum of 2/100 m^3 being attained in June (Fig. 35). It is interesting to note, however, that maximum standing crops of *Neoperla clymene* on the study riffle are established in late spring, with maximum growth occurring in the late spring and early summer months (Vaught 1972). These events correspond very closely to the peaks of maximum drift density. Thomas (1970) showed that drift of several species of stoneflies obtained a maximum shortly before emergence or this period of maximal growth. On both semi-monthly sample dates, drift activity was distinctly nocturnal with unimodal curves exhibited after dusk. Other investigators

Figure 34--Drift of Elophila sp. larvae, Brazos River, 1972-1973.



APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE
DRIFT DENSITY (#/100 M3)
3.0
2.5
2.0
1.5
1.0
0.5
3
4
5
6
7
8
9
10
11
12
1
2
3
4
5
6
7
8
9
TIME

Figure 35--Drift of *Neoperla clymene* nymphs, Brazos River, 1972-1973.



DRIFT DENSITY (#/100 M3)
2.5
2.0
1.5
1.0
0.5
3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
TIME
APRIL
JUNE
AUG.
OCT.
DEC.
FEB.
SUNSET
SUNRISE

who have recorded the nocturnal periodicities of various Plecoptera include Elliott 1967, Bishop and Hynes 1969, Waters 1969b, Brusven 1970a, Radford and Hartland-Rowe 1971, Elliott and Corlett 1972).

CHAPTER IV

SUMMARY

1. Preliminary sampling in August, 1971, indicated a very low daytime drift off the study riffle, with highest numbers drifting during the scotophase and two adjacent daytime hours.

2. Semi-monthly drift samples, taken with a sampler modified after Müller (1958) and utilizing methods suggested by Elliott (1970a), established the seasonal and nocturnal drift periodicity of the Brazos River insect community during April, 1972, to February, 1973.

3. Drift was expressed as drift density; highest peak densities were 494, 397, and 144/100 m^3, respectively, for the three dominant insects in the river, Choroterpes sp., Chaoborus sp., and Simulium sp. Peak densities of other populations varied from 2 to 92.5/100 m^3.

4. Total drift estimates were calculated for the six dominant riverine insects, Choroterpes sp., Cheumatopsyche spp., Chaoborus sp., Simulium sp., Chironomidae, and Baetis sp. Total numbers drifting 1 hr before sunset to 1 hr after sunrise in June were 5.31×10^5 (maximum observed during study), 8.53×10^5, 5.39×10^5, 7.13×10^4, 8.44×10^4, and 5.63×10^4, respectively. High estimates were also noted for these species during August, with lower totals drifting during sample dates in other months.

5. Eighteen species, previously unreported in drift studies, included Ephemeroptera, *Choroterpes* sp., *Tricorythodes* sp., *Isonychia sicca manca*; Trichoptera, *Hydropsyche simulans*, *Ithytrichia clavata*, *Hydroptila icona*, *Chimarra obscura*, *Pycnopsyche* sp.; Diptera, *Palpomyia* sp.; Coleoptera, *Stenelmis bicarinata*, *Stenelmis mexicana*, *Dubiraphia vittata*, *Gyretes* sp.; Odonata, *Enallagma* sp., *Argia* sp., *Ophiogomphus* sp.; Lepidoptera, *Elophila* sp.; and Plecoptera, *Neoperla clymene*. Unreported drift in these species was probably due to the lack of previous drift studies in the Southwestern United States.

6. All six mayflies encountered in the drift exhibited peak densities during June and August; this was also true of all Coleoptera and four of the caddisflies. *Hydroptila icona* and *Pycnopsyche* sp. larvae exhibited peaks in October and February, respectively. Two species of the three families of Diptera also exhibited fall and spring peaks in drift density, except *Chaoborus* sp., which were most abundant in June and August. Other members of the community exhibited variable seasonal drift patterns with higher summer values roughly corresponding with activity of immatures and emergence.

7. A unimodal drift periodicity, with one major peak in density occurring immediately following sunset, was exhibited by *Choroterpes* sp., *Heptagenia* sp., *Cheumatopsyche* spp., *Hydropsyche simulans*, *Hydroptila icona*, chironomid larvae, *Stenelmis* spp. larvae and adults, and *Neoperla clymene*.

8. Bimodal drift periodicities were exhibited by the Ephemeroptera, *Choroterpes* sp., *Tricorythodes* sp., *Baetis* sp., *Caenis* sp., *Isonychia sicca manca*; Trichoptera, *Hydropsyche simulans*, *Ithytrichia clavata*, *Chimarra obscura*; Diptera, *Simulium* sp. larvae and pupae, *Chaoborus* sp. larvae and pupae, chironomid larvae, *Palpomyia* sp.; Coleoptera, *Dubiraphia vittata* adults, *Gyretes* sp.; and the Odonate *Enallagma* sp. "Bigeminus" and "alternans" drift patterns were both represented.

9. Due to the sampling regime and/or low numbers observed drifting, *Pycnopsyche* sp., chironomid pupae, *Argia* sp., *Ophiogomphus* sp., and *Elophila* sp. displayed little pattern in their drift periodicity.

10. Examination of mayfly exuviae indicated that peaks in drift density and emergence are species-specific; Trichoptera pupae exuviae, however, showed a clear nocturnal emergence periodicity, corresponding with observed emergence.

11. The abundance of Dipteran pupae in the drift appears to be directly related to the emergence patterns of the various species.

BIBLIOGRAPHY

American Public Health Association, Inc. 1965. Standard methods for the examination of water and wastewater. Amer. Public Health Assoc., Inc. New York, 626 pp.

Anderson, N.H. 1967. Biology and downstream drift of some Oregon Trichoptera. Can. Entomol. 99:507-521.

Anderson, N.H., and D.M. Lehmkuhl. 1968. Catastrophic drift of insects in a woodland stream. Ecology 49(2):198-206.

Baily, R.G. 1964. Observations on the nature and importance of organic drift in a Devon river. Hydrobiol. 27(3-4): 353-367.

Berner, L.M. 1951. Limnology of the lower Missouri River. Ecology 32:1-12.

Besch, W. 1967. Driftnetmethode und biologische Fliesswasseruntersuchung. Verh. Internat. Verein. Limnol. 16:669-678.

Bishop, J.E. 1969. Light control of aquatic insect activity and drift. Ecology 50(3):371-380.

Bishop, J.E., and H.B.N. Hynes. 1969. Downstream drift of the invertebrate fauna in a stream ecosystem. Arch. Hydrobiol. 66(1):56-90.

Brusven, M.A. 1970a. Drift periodicity and upstream dispersion of stream insects. Journ. Ent. Soc. of British Columbia 67:48-59.

________. 1970b. Drift periodicity of some riffle beetles (Coleoptera: Elmidae). Journ. Kan. Entomol. Soc. 43(4):364-371.

Chaston, I. 1968. Endogenous activity as a factor in invertebrate drift. Arch. Hydrobiol. 64(3):324-334.

________. 1969. The light threshold controlling the periodicity of invertebrate drift. Jour. Anim. Ecol. 38: 171-180.

Clifford, Hugh F. 1972a. A year's study of the drifting organisms in a brown water stream of Alberta, Canada. Can. Jour. Zoology 50(7):975-983.

________. 1972b. Drift of invertebrates in an intermittent stream draining marshy terrain of west central Alberta. Can. Jour. Zoology 50(7):985-991.

Dendy, J.S. 1944. The fate of animals in stream drift when carried into lakes. Ecol. Monog. 14:333-357.

Denham, S.C. 1939. A limnological investigation of the West Fork and Common Branch of White River. Invest. Indiana Lakes, Streams 1(5):17-71.

Diamond, J.B. 1967. Evidence that drift of stream benthos is density related. Ecology 48(5):855-857.

Elliott, J.M. 1965a. Daily fluctuations of drift invertebrates in a Dartmoor stream. Nature, London 205: 1127-1129.

________. 1965b. Invertebrate drift in a mountain stream in Norway. Norsk. ent. T. 13:97-99.

________. 1967. Invertebrate drift in a Dartmoor stream. Arch. Hydrobiol. 63:202-237.

________. 1968. The life histories and drifting of Trichoptera in a Dartmoor stream. Journ. Anim. Ecol. 37:615-625.

________. 1969. Diel periodicity in invertebrate drift and the effect of different sampling periods. Oikos 20: 524-528.

________. 1970a. Methods of sampling invertebrate drift in running water. Ann. de Limnol. 6(2):133-159.

________. 1970b. Diel changes in invertebrate drift and the food of trout Salmo trutta. L. Jour. Fish. Biol. 2: 161-165.

________. 1970c. The diel activity patterns of caddis larvae (Trichoptera). Jour. Zool., London 160:279-290.

________. 1971. Life histories and drifting of three species of Limnephilidae (Trichoptera). Oikos 22:56-61.

Elliott, J.M., and J. Corlett. 1972. The ecology of Morecambe Bay. IV. Invertebrate drift into and from the River Leven. Jour. Applied Ecology 9:195-205.

Forshage, Allen A. 1972. Investigation of a portion of the Brazos River. Job Prog. Rep. B-42, Fed. Aid in Fish. Rest. Act. pp 1-13.

Grenier, P. 1949. Contribution à l'étude biologique des Simuliides de France. Physiol. Comp. Oecol. I:165-330.

Harker, J.E. 1953. The diurnal rhythm of activity of mayfly nymphs. Jour. Exp. Biol. 30:525-533.

Holt, C.S., and T.F. Waters. 1967. Effect of light intensity on the drift of stream invertebrates. Ecology 48(2): 225-234.

Hughes, D.A. 1970. Some factors affecting drift and upstream movements of Gammarus pulex. Ecology 51(2): 301-305.

Hynes, H.B.N. 1970. The Ecology of Running Waters. Toronto: Univ. Toronto Press. 555 pp.

Ide, F.P. 1942. Availability of aquatic insects as food of the speckled trout, Salvelinus fontinalis. N. Am. Wildlife Conf. 7:442-450.

Jenkins, T.M., C.R. Feldmeth, and G.V. Elliott. 1970. Feeding of rainbow trout (Salmo gairdneri) in relation to abundance of drifting invertebrates in a mountain stream. Journ. Fish. Res. Bd. Canada 27(12):2356-2361.

Kimmins, D.E. 1954. A revised key to the adults of the British species of Ephemeroptera. Sci. Publ. Freshw. Biol. Ass. Brit. Empire 15:1-71.

Lennon, R.E. 1941. Drift-borne organisms in Pond Brook, Passaconaway, N. Hamp., Univ. N. H. Ext. Service, Contrib. No. 2, Biol. Instit.

McLay, C.L. 1968. A study of drift in the Kakanui River, New Zealand. Aust. Journ. Mar. and Freshw. Res. 19:139-149.

Minshall, G.W., and P.V. Winger. 1968. The effect of reduction in stream flow on invertebrate drift. Ecology 49(3):580-582.

Morgan, N.C., and A.B. Waddell. 1961. Diurnal variation in the emergence of some aquatic insects. Trans. Roy. Ent. Soc. London 113(6):123-137.

Müller, K. 1954. Investigations on the organic drift in North Swedish streams. Rep. Inst. Freshwater Res., Drottningholm 35:133-148.

________. 1958. Beitrag zur Methodik der Untersuchung fliessender Gewässer. Arch. Hydrobiol. 54:567-570.

________. 1963a. Tag-Nachtrhythmus von Baetidenlarven in der "Organischen Drift." Naturwiss. 50:161.

________. 1963b. Diurnal rhythm in "organic drift" of Gammarus pulex. Nature 198:806-807.

________. 1963c. Temperatur und Tagesperiodik der "Organischen Drift" von Gammarus pulex. Naturwiss. 50:410-411.

________. 1965. Field experiments on periodicity of freshwater invertebrates. Circadian Clock, ed. J. Aschoff, Amsterdam: North-Holland, 314-317.

________. 1966. Die Tagesperiodik von Fliesswasserorganismen. Z. Morph. Okol. Tiere 56:93-142.

Mundie, J.H. 1969. Ecological implications of the diet of juvenile coho in streams. Univ. of British Columbia Inst. Fisheries, H.R. MacMillan Lectures. Symposium on Salmon and Trout in Streams 1968, pp. 135-152.

________. 1971. The diel drift of Chironomidae in an artificial stream and its relation to the diet of Coho salmon fry, Oncorhynchus kisutch (Walbaum). Can. Entomol. 103(3):289-297.

Needham, P.R. 1928. A quantitative study of the fish food supply in selected areas. New York Cons. Dept. Suppl. Ann. Rep. 17:192-206.

Pearson, W.D., and D.R. Franklin. 1968. Some factors affecting drift rates of Baetis and Simuliidae in a large river. Ecology 49(1):75-81.

Pearson, W.D., and R.H. Kramer. 1972. Drift and production of two aquatic insects in a mountain stream. Ecolog. Monogr. 24:365-385.

Peterka, John J. 1969. Distribution, standing crops and drift of benthic invertebrates in a small Wisconsin stream. Wisconsin Acad. Sci., Arts and Letters 57: 155-161.

Radford, D.S., and R. Hartland-Rowe. 1971. A preliminary investigation of bottom fauna and invertebrate drift in an unregulated and regulated stream in Alberta. J. Appl. Ecology 8:883-903.

Södergren, S.E. 1963. Undersökningar av driftfaunen i Rickleån Laxforskningsinstitutet, Meddelande 5: 1-32.

Tanaka, H. 1960. On the daily change of the drifting of benthic animals in stream, especially on the types of daily change observed in taxonomic groups of insects. Bull. Freshwater Fish. Res. Lab. 9:13-24.

Thomas, E. 1970. Die drift von plecopterenlarven in beziehung zum larvalen wachstum und zur schlüpfzeit. Oikos Suppl. 13:65-69.

Tsuda, M. 1960. A study of exuvia of aquatic insects flowing in the stream. Jap. Journn. of Ecology 21:279-287.

Vaught, G. 1972. The life history and ecology of the stonefly Neoperla clymene (Newman) (Plecoptera: Perlidae). M.S. thesis, North Texas State University, Denton, Texas.

Waters, T.F. 1961. Standing crop and drift of stream bottom organisms. Ecology 42:532-537.

________. 1962. Diurnal periodicity in the drift of stream invertebrates. Ecology 43:316-320.

________. 1965. Interpretation of invertebrate drift in streams. Ecology 46(3):327-333.

________. 1966. Production rate, population density, and drift of a stream invertebrate. Ecology 47:595-604.

________. 1968. Diurnal periodicity in the drift of a day active stream invertebrate. Ecology 49:152-153.

________. 1969a. Invertebrate drift-ecology and significance to stream fishes. In Symposium on Salmon and Trout in Streams, ed. T.G. Northcote, 121-134. H.R. MacMillan Lectures in Fisheries, Vancouver: Univ. of British Columbia.

________. 1969b. Diel patterns of aquatic invertebrate drift in streams of northern Utah. Utah Acad. Proceed. 46(2):109-130.

Waters, T.F. 1972. The drift of stream insects. Annual Review of Entomology 17:253-272.

Wojtalik, T.A., and T.F. Waters. 1970. Some affects of heated water on the drift of two species of stream invertebrates. Trans. Amer. Fish. Soc. 99(4):782-788.