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Seasonal and diel periodicity in the drift of aquatic insects in a subtropical Florida stream

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Summary

A study of insect drift was conducted in a small, subtropical Florida stream from December 1971 *to December* 1972 *to describe the seasonal and diel periodicity and to determine factors influencing behavioural drift. Paired samples of* 2 *h duration beginning* 15 *min after sunset were taken biweekly, and hourly collections over a 24-h period were made quarterly. Benthic invertebrates were collected on each date from three habitats (riffle, pool and aquatic vegetation) and temperature, dissolved oxygen and current velocity were measured.*

Drift rates ranged from 100 *to* 2125 *organisms/m*^{2}.*h* (0·03 *to* 0·49 *organisms/m*^{3}) *and were greatest in winter and early spring; minimal rates occurred in the summer months. The following six taxa, in order of relative abundance, comprised* 87% *of the drift: Baetis intercalaris, Cheumatopsyche sp., Stenonema exiguum, Chironomidae, Stenelmis fuscata and Simulium sp. Total drift showed no significant correlation with temperature, dissolved oxygen or mean benthic abundance and only slight correlation with current velocity* (r=0·34). *Stepwise, multiple regression analyses indicated that riffle density and mean size of drifting organisms were important factors influencing the drift rates of B. intercalaris* (R=0·67) *and S. exiguum* (R=0·82)*; mean size, riffle density and water temperature influenced the drift of Cheumatopsyche sp.* (R=0·78). *The other taxa of drifting insects showed no significant correlation with the variables measured.*

Diel (24 *h*) *studies of the major taxa showed marked differences in the periodicity, both within and between taxa, indicating the need for long-term studies with frequent sample intervals in subtropical habitats. A new drift pattern for the family Chironomidae, alternans type, was observed for late instars of Polypedilum halterale.*

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Introduction

Invertebrate drift in moving waters has been recognized as a factor of considerable ecological importance for approximately 15 years. Early studies (see Müller, 1954; Waters, 1961, 1965; Elliott, 1965, 1967a, b) indicated that daily and seasonal fluctuations in the drift are determined by a complex of factors including benthic density, life history stage, activity and behaviour of the organism, and current velocity. Subsequent discovery of diel periodicity in the drift, first reported by Tanaka (1960) and independently observed by Waters (1962) and Müller (1963), stimulated further research on: (1) the nature of the rhythms involved; (2) the density dependence and production of drifting organisms; and (3) the significance of drift to the trophic ecology of fishes. Excellent reviews of the more recent literature are given by Bishop & Hynes (1969), Waters (1972), and Müller (1974).

However, almost all of these studies have been conducted in northern, cold-temperature streams (see Müller, 1974) during ice-free periods of the year. There have been only two studies in tropical latitudes (Bishop, 1973; Hynes, 1975) and no studies have been made in subtropical areas; the studies of Reisen & Prins (1972) in South Carolina (35°N latitude) and Cloud & Stewart (1974) in Texas (33°N) represent the southernmost areas investigated in North America. Only a few studies have measured drift over an entire year (e.g., Bishop & Hynes, 1969; Clifford, 1972a, b; and Reisen & Prins, 1972). Thus, the main objectives of this study were to determine the magnitude of the drift in a subtropical Florida stream and to describe seasonal and diel periodicity. Collection of preliminary data on factors influencing behavioural drift was a secondary objective.

Study area

Blackwater Creek (28° 10′N), a tributary of the Hillsborough River, drains approximately 285 km^2 of land in Hillsborough and Polk Counties, Florida, U.S.A. The creek has an average discharge of 2·86 m^3/s, but varies from 0·015 to 32·5 m^3/s (U.S.G.S. 1970). The mean annual rainfall at Tampa, 30 km SW of the study area, is 130·9 cm, but more than 60% falls during the June to September 'rainy season' (U.S. Dept. Comm. 1971). The stream is clear during the dry season (November to May) but is heavily coloured by tannins from adjacent swamps during the rainy season.

During the year of study, water temperature ranged from 16·5°C in January to 27·9°C in June. Dissolved oxygen concentration varied only slightly with values ranging from 5·9 to 7·2 mg/l.

At the sample site (Sec. 9, R. 21 E., T. 27 S., Hillborough County, Florida) Blackwater Creek is 8–10 m wide and is comprised of a series of shallow pools connected by riffles. The bottom is rocky with limestone boulders, cobbles, and gravel except in the deeper pools where it is covered by sand, silt and organic debris. Dense growths of *Vallisneria neotropicalis* Marie Victorin and *Potamogeton illinoensis* Morong occur in currents and *Egeria densa* Planch., is found in eddies. The riffle where drift nets were placed is approximately 20 m long and is partially covered by *V. neotropicalis*; average depth is 0·25 m. Directly upstream and downstream from this riffle are pools averaging 3·5 and 1·2 m deep, respectively.

Method

Drift samples were taken at 2–3-week intervals from December 1971 to December 1972 using Nitex nets with aperture size of 0·47 mm. The nets were 20 × 20 cm at the mouth and had a total length of 1 m. Nets were placed in water approximately 20 cm deep and were fastened to metal rods driven into the stream bed. The sampling interval normally was 2 h beginning 15 min after sunset, but four diel (24 h) studies were made seasonally employing hourly sample intervals. Paired sampling, with nets side-by-side, was used on all dates except the 24 h collections when a single net was used.

After each drift sampling, one to three benthic samples were collected from each of three habitats (riffle, pool and aquatic vegetation) in the vicinity of the drift nets. Standing crop of the riffle was determined with a 0·1 m^2 Surber net; pool benthos was sampled with a 15·2 × 15·2 cm Ekman dredge; and a hand-grab of *Vallisneria neotropicalis* was taken for faunal analysis. All samples were preserved in 10% formalin.

Drift and benthic samples were taken to the laboratory and organisms were separated from the detritus, counted, and preserved in 80% ethanol. The *Vallisneria* samples were washed to remove attached invertebrates, blotted, and dried for 24 h at 60°C before weighing. Densities of organisms on the *Vallisneria* were recorded as numbers per gram dry weight of plant. Numbers of organisms (x) in the drift, benthic, and *Vallisneria* samples were transformed using $\log_{10}(x+1)$ to meet basic assumptions of statistical procedures (see Pearson & Franklin, 1968; Reisen & Prins, 1972).

Most of the aquatic invertebrates were identified to species; terrestrial insects were discarded. Slides of larval Chironomidae were made with the techniques given by Beck (1968). Mayflies were measured from the front of the head to the base of the cerci, and trichopterans were measured from the apex of the frons to the base of the anal leg.

Water temperature, dissolved oxygen concentration and current velocity were measured concurrently with drift sampling. Temperature was measured with a mercury thermometer. Dissolved oxygen concentration of water collected in the riffle was determined using the azide modification of the Winkler method (American Public Health Association, 1965). Current velocity was estimated by timing the passage of a rubber bulb through a measured distance of riffle. Notes also were taken in the field on weather conditions, cloud cover, and moon phase.

Least-square, stepwise, multiple regression analyses were used to determine the influence of independent variables on drift rates of total organisms and the predominant taxa. All independent variables were examined for significant multicolinearity.

Results

Composition of the benthos and drift

The benthic fauna of Blackwater Creek was dominated by Diptera (39·2%), Coleoptera (29·3%), Ephemeroptera (17·0%) and Trichoptera (10·7%) which comprised 96·2% by number of the total population (Table 1). However, the three habitats sampled (riffle, pool, and aquatic vegetation) differed markedly in density and composition.

The mean annual standing crop in the riffle (435·5/m²) was significantly greater ($P<0{\cdot}05$) than that of the pool (242·2/m²). Statistical comparisons of riffle and pool densities with the *Vallisneria* were not possible because of differences in sampling techniques. However, the comparatively small size of the *Vallisneria* samples (hand-grab) indicates that the total density of organisms on the weed was much greater than in the other habitats; mean density on the *Vallisneria* was 130·5 organisms/g dry wt of plant.

Stenelmis fuscata Blatchley was the most abundant organism in both the riffle and pool with mean densities of 117·8/m² and 101·6/m², respectively. *Simulium* sp. was the predominant form on the *Vallisneria*, comprising 79·5%, with a mean density of 103·8/g dry wt. The predominant mayflies (*Baetis* and *Stenonema*) and the trichopteran, *Cheumatopsyche* sp. were most abundant in the riffle, whereas the other mayflies (*Caenis*, *Ephemerella*, and *Hexagenia*) and the dragonfly naiads (Odonata) occurred in greater abundance in the pool. Chironomids were abundant in all three habitats (Table 1).

Most of the taxa in the benthos occurred in the drift, but relative frequencies differed markedly. Six abundant taxa comprised 87% of the total drift (Table 1). These organisms, in order of relative abundance, were: *Baetis intercalaris* McDunnough, *Cheumatopsyche* sp., *Stenelmis fuscata* Blatchley, Chironomidae, *Stenonema exiguum* Traver and *Simulium* sp. Of the remaining 19 taxa identified, none comprised more than 2·3% of the drift.

Seasonal comparisons of total drift

Paired sampling was used for seasonal drift collections to estimate the variability and a paired *t*-test (Steel & Torrie, 1960) was used to compare annual means. The difference between nets was not significant ($P<0{\cdot}01$) so data from the two nets were combined. Drift rates were recorded as numbers of organisms per m² of drift net straining surface per hour (no./m².h); conversion to the actual number of organisms collected during the 2-h sample period can be made by dividing by 6·25 on routine sampling dates (two nets fished) and by 12·5 on dates of 24-h sampling (1 net fished). Conversion of our data to rates per unit of stream discharge (i.e. numbers per day per m³/s) recommended by Waters (1972) or 'drift density' (number of individuals passing a given point per unit volume) used by Bishop (1973) can be made utilizing current velocities given in Fig. 1.

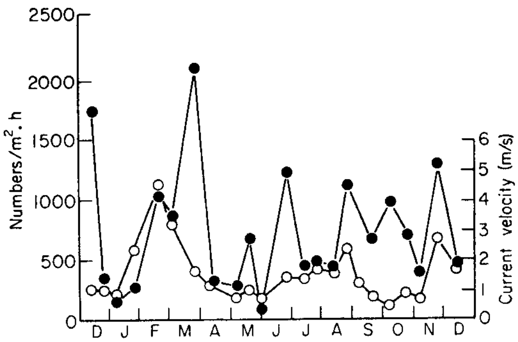

Fig. 1. Seasonal comparisons of total drift (2 h samples starting 15 min after sunset) (●) and current velocity (○) in Blackwater Creek, Florida. December 1971 to December 1972.

Drift rates of total organisms ranged from 100 to 2125/m².h and averaged 737/m².h on an annual basis (drift densities in terms of number drifting past a given point per h per m³/s ranged from 117 to 1750 and averaged 568; numbers per m³ ranged from 0·03 to 0·49 and averaged 0·16). Major peaks in the drift rates (Fig. 1) occurred in December (1750/m².h) and March (2125/m².h) while smaller peaks occurred in late June (1237/m².h), late August–early October (987 to 1131/m².h) and November (1331/m².h). Drift rates were low in late December and January, and, with the exception of the late June peak, tended to be low during the warmer months of April to late August.

Simple correlation coefficients were calculated between total drift and some factors previously shown to influence drift (current velocity, dissolved oxygen concentration, water temperature, and mean benthic abundance). Current velocity yielded the highest correlation ($r=0{\cdot}34$) but it was not significant ($P>0{\cdot}05$) and there was little evidence of catastrophic drift (Fig. 1). Correlation coefficients for the other three variables were $-0{\cdot}11$, $0{\cdot}09$, and $-0{\cdot}06$, respectively and were nonsignificant. Stepwise, multiple regression analyses of these variables also was nonsignificant; the multiple correlation coefficient (R) was 0·396 and accounted for only 15·7% of the variability in total drift.

Table 1. Mean benthic densities in three habitats and percent composition of the drift in Blackwater Creek, Hillsborough County, Florida for the year December 1971 to December 1972

Taxon	Mean benthic densities in three habitats* Riffle (No./m²)	Pool (No./m²)	*Vallisneria* (No./g dry wt)	Percent of total drift†
Stenonema exiguum Traver	72·2	6·2	0·0	8·8
Stenonema interpunctatum (Say)	17·8	1·5	0·0	2·2
Stenonema smithae Traver	T‡	0·0	0·0	T
Baetis intercalaris McDunnough	35·5	3·8	1·0	35·2
Caenis hilaris (Say)	3·2	13·5	0·0	2·3
Ephemerella hirsuta Berner	0·5	7·7	0·0	0·1
Hexagenia munda Traver	0·0	5·8	0·0	0·0
Total Ephemeroptera	129·2	38·5	1·0	48·6
Aphylla williamsoni (Selys)	0·0	1·4	0·0	0·0
Gomphus pallidus Rambur	0·0	7·7	0·0	0·0
Epicordula regina Selys	0·9	0·0	0·0	T
Macromia taeniolata Rambur	0·5	1·5	0·0	0·1
Total Odonata	1·4	10·6	0·0	0·1
Ranatra buenoi Hungerford	0·0	1·4	0·0	0·0
Rhagovelia choreutes Hussey	0·0	0·0	0·0	1·4
Mesovelia mulsanti White	0·0	0·0	0·0	0·5
Limnogonus hesione (Kirkaldy)	0·4	0·0	0·0	1·3
Total Hemiptera	0·4	1·4	0·0	3·2
Cheumatopsyche sp.	89·5	15·3	8·9	14·6
Polycentropus sp.	0·0	0·0	0·0	0·1
Total Trichoptera	89·5	15·3	8·9	14·7
Corydalus cornutus (Linnaeus)	10·0	1·9	0·2	0·2
Total Megaloptera	10·0	1·9	0·2	0·2
Stenelmis fuscata Blatchley (larvae)	97·3	91·1	0·1	4·8
Stenelmis fuscata Blatchley (adults)	20·5	9·5	0·3	6·5
Peltodytes oppositus Roberts (adults)	0·9	0·0	0·0	1·8
Dineutus discolor Aube (larvae and adults)	0·0	0·0	0·0	1·9
Hydroporus sp. (larvae)	0·0	0·0	0·0	0·1
Bidessus sp. (larvae and adults)	0·9	0·0	0·0	0·1
Hydrobius sp. (larvae)	0·0	0·0	0·0	0·1
Berosus sp. (larvae)	0·0	0·0	0·0	0·1
Noteridae (adults)	0·0	0·0	0·0	0·1
Total Coleoptera	119·6	101·6	0·4	16·0
Unknown Pyralidae	1·8	0·0	0·3	0·2
Total Lepidoptera	1·8	0·0	0·3	0·2
Simulium sp.	24·1	23·1	103·8	5·9
Chironomidae§	59·5	49·8	15·9	11·1
Total Diptera	83·6	72·9	119·7	17·0
Totals	435·5	242·2	130·5	100·0

* Based on total of twenty-two sampling dates.
† Based on 2128 organisms collected from 2-h sample periods on twenty-two dates.
‡ T = less than 0·1 organism/m² or 0·1%.
§ Includes in order of relative abundance: *Polypedilum halterale* (Coquillett), *Rheotanytarsus* sp., *Tanytarsus* sp., *Conchapelopia* sp., *Cricotopus* sp., *Polypedilum illinoense* (Malloch), *Thienemanniella* sp., unknown Pentaneurini, *Glyptotendipes* sp., *Chironomus* sp., and *Cryptochironomus* sp.

Seasonal and diel patterns of the predominant taxa in the drift

Ephemeroptera. Baetis intercalaris was the most abundant organism in the drift comprising 35·2% of the total drift. Moreover, comparisons of Figs. 1 and 2 suggest that seasonal changes in the drift of this organism accounted for much of the variability in the total drift. Drift rates of *B. intercalaris* ranged from 6 to 887 organisms/m².h and

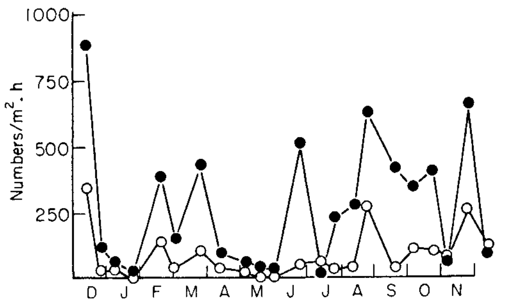

Fig. 2. Seasonal drift rates (2 h samples starting 15 min after sunset) of *Baetis intercalaris* (●) and *Stenonema* spp. (○) in Blackwater Creek, Florida. December 1971 to December 1972.

peaks occurred at 2- to 3-month intervals (Fig. 2). Large numbers of last instar exuviae were collected in the drift nets on 28 March, 25 July, and 3 October 1972, indicating emergences at these times. However, the interval between samples was too large to determine the total number of broods or generations per year.

The drift rate of *B. intercalaris* was correlated positively with riffle density of the species ($r = 0{\cdot}57$) and mean size of drifting nymphs ($r = 0{\cdot}46$); both correlations were significant at the 5% level. In contrast, simple correlations between *Baetis* drift rate and current velocity ($r = 0{\cdot}23$), water temperature ($r = 0{\cdot}09$) and dissolved oxygen concentration ($r = 0{\cdot}09$) were not statistically significant.

Stepwise, multiple regression and correlation analyses were then used to determine the combined effects and significance of the above variables on the drift rate of *B. intercalaris*. Riffle density and mean size of drifting nymphs yielded a multiple correlation of $R = 0{\cdot}67$ and accounted for 45% ($R^2 = 0{\cdot}449$) of the variability observed in the drift rate. Addition of the other three variables (current velocity, water temperature, and dissolved oxygen concentration) did not appreciably increase either value; for all five variables $R = 0{\cdot}71$ and $R^2 = 0{\cdot}513$.

B. intercalaris exhibited a marked night-active periodicity in drift rate. In all four diel studies peak drift rates, 700- to 800-fold greater than daytime levels, occurred within 1 h of sunset (Fig. 3). The December series showed a typical bigeminus pattern (major peak following sunset and a secondary peak before dawn). In June, high drift rates occurred for 4 h after sunset, while in March and October, drift was high for only 1 h after sunset. The October series was not complete, however, as sampling was discontinued when large numbers of cattle entered the stream.

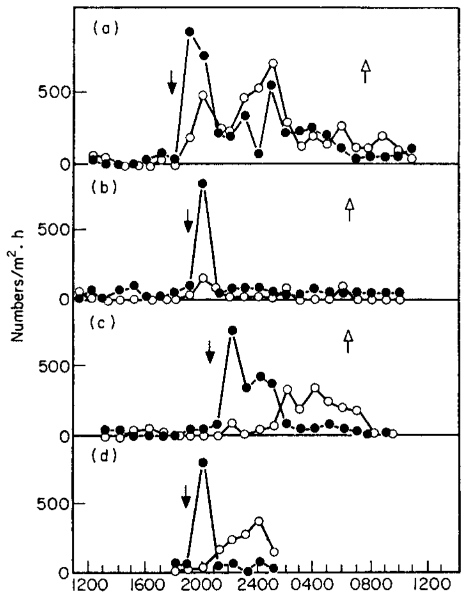

Fig. 3. Diel periodicity in the drift of *Baetis intercalaris* (●) and *Stenonema* spp. (○) in Blackwater Creek, Florida. Sunset and sunrise are indicated by arrows. (a) 13–14 Dec. 1971; (b) 28–29 May 1972; (c) 27–28 June 1972; (d) 23–24 Oct. 1972.

Stenonema exiguum and *S. interpunctatum* (Say) comprised 11·1% of the total drift. Drift rates of these species ranged from 0 to 350/m^2.h with peaks coinciding with the *Baetis intercalaris* peaks (Fig. 2). Large numbers of adults (primarily *S. exiguum*) were observed in late March, April and September. Drift of *Stenonema* correlated positively with the mean size of drifting nymphs ($r = 0{\cdot}69$) and riffle density ($r = 0{\cdot}51$). Correlations with current velocity ($r = 0{\cdot}30$), dissolved oxygen ($r = 0{\cdot}15$) and water temperature ($r = -0{\cdot}05$) were not significant. The R^2 multiple correlation value indicated that 63% of the variability in *Stenonema* drift rate was accounted for by mean size of drifting nymphs and riffle density ($R = 0{\cdot}79$). For all five independent variables $R = 0{\cdot}82$ and $R^2 = 0{\cdot}679$.

Diel periodicity in the drift rate of *Stenonema* differed on all four sampling dates (Fig. 3). In December, *Stenonema* drifted in a typical alternans pattern (secondary peak in the early part of the night and a major peak prior to dawn). In March, following a major emergence, drift was negligible. The June series showed drift beginning approximately 4 h after sunset, and then continuing throughout the night at comparable levels. In October, drift began 1 h after sunset and gradually increased to a peak 4 h later.

The only other mayfly to occur in the drift in appreciable numbers was *Caenis hilaris* (Say). However, this species only was found regularly in the drift from September to November when rates between 100 and 200/m².h were recorded.

Trichoptera. Cheumatopsyche sp. was the second most abundant organism in the drift comprising 14·6% of the total. The drift rate was highly variable throughout the year with alternating periods of high and low drift at 1–2-month intervals (Fig. 4). Maximum drift occurred in May and June (387/m².h) while minimum values were recorded in winter and early spring. The drift rate of *Cheumatopsyche* correlated significantly with mean size of drifting larvae (r = 0·71), riffle density (r = 0·49), and water temperature (r = 0·43). These three variables accounted for 62% of the variability in the drift rate (R^2 = 0·618 and R = 0·78). Correlations with current velocity (r = 0·15) and dissolved oxygen concentration (r = 0·01) were not significant and did not increase the multiple correlation coefficient appreciably.

Two patterns of night-active periodicity were observed in the drift of *Cheumatopsyche* sp. The December and June series showed bigeminus patterns with the major peak (400 to 500/m².h) 1–2 h after sunset and the secondary peak (200/m².h) 4–5 h later. Drift continued through the night tapering off with the approach of sunrise. In March and October drift was relatively constant (25 to 100/m².h) throughout the night.

Coleoptera. The riffle beetle, *Stenelmis fuscata*, was the only colepteran appearing regularly in the drift. Both larvae and adults were present and together comprised 11·3% of the total drift. Larvae were found in the drift at all times of the year except during late summer and early fall (Fig. 4). Adults occurred throughout the year but were most abundant in the fall months when larvae were present in low numbers, both in the drift and in the benthos. The drift rate of larvae did not correlate significantly with any of the variables measured (current velocity, dissolved oxygen, water temperature or mean size). Drift of adults correlated positively ($P < 0{\cdot}05$) with the density of adults in the riffle and pool (r = 0·40).

The diel periodicity of larvae and adults of *S. fuscata* was highly variable. In December and October, larvae were night-active and drifted in low concentrations (<50/m².h) throughout the night. In March, drift increased to 100/m².h immediately after sunset, peaked at 225/m².h 3 h later, and then decreased to daytime levels. Drift was low in June (<50/m².h) except for the 2 h period just before sunrise when it increased to 225/m².h. Day-active drift (midafternoon) of larvae, with rates up to 100/m².h, was observed in both March and June.

Adults of *S. fuscata* were entirely night-active. In December, June and October drift peaked shortly after sunset with values ranging from 125 to 225/m².h. In December and October, drift was low during the remainder of the night (<75/m².h, but in June, a secondary peak (bigeminus pattern) was observed 6 h after the first. Adults did not drift in March.

Diptera. The blackfly, *Simulium* sp., and five species of Chironomidae were the only dipterans found in the drift. These organisms comprised 17% of the total drift and showed marked variations in seasonal and diel periodicity.

Drift of *Simulium* larvae was restricted to the

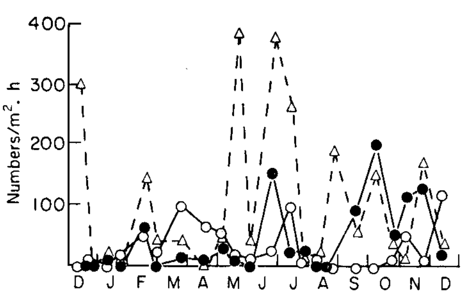

Fig. 4. Seasonal drift rates (2 h samples starting 15 min after sunset) of *Cheumatopsyche* sp. (△) and *Stenelmis fuscata* larvae (○) and adults (●) in Blackwater Creek, Florida. December 1971 to December 1972.

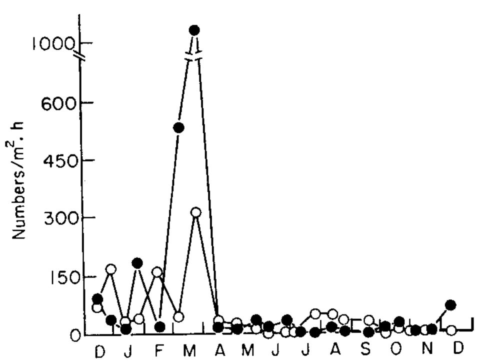

Fig. 5. Seasonal drift rates (2 h samples starting 15 min after sunset) of *Simulium* sp. (○) and Chironomidae (●) in Blackwater Creek, Florida. December 1971 to December 1972.

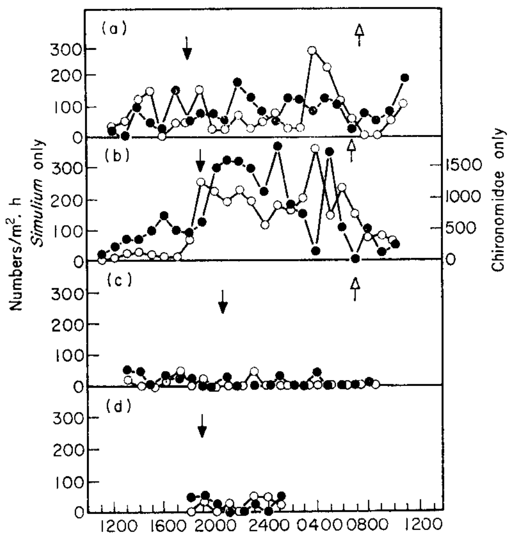

Fig. 6. Diel periodicity in the drift of *Simulium* sp. (●) and Chironomidae (○) in Blackwater Creek, Florida. Sunset and sunrise are indicated by arrows. (a) 13–14 Dec. 1971; (b) 28–29 March 1972; (c) 27–28 June 1972; (d) 23–24 Oct. 1972.

winter (December to March) and summer (July to September) months (Fig. 5). Correlation coefficients between drift rate of *Simulium* and current velocity, riffle density, density on aquatic vegetation, dissolved oxygen, and water temperature were all nonsignificant.

Diel periodicity in the drift of *Simulium* larvae was not observed in three of the four 24 h studies (Fig. 6). In June, October and December, drift occurred throughout the day and night at low levels. However, in March, marked periodicity occurred with night drift rates approximately three-fold greater than day rates; peaks (300 to 350/m².h) occurred immediately after sunset and just before sunrise.

Drift of chironomid larvae occurred primarily in the winter and early spring months (December to March) when rates as high as 1037/m².h were recorded (Fig. 5). During the rest of the year drift was low ranging from 0 to 25/m².h. *Polypedilum halterale* (Coquillett) was the only chironomid to occur regularly in the drift and comprised more than 90% of the total number of chironomids collected in the drift nets. During the spring peak, most of the drifting *P. halterale* were 3rd and 4th instar larvae.

The diel drift patterns of the chironomids were quite similar to those of *Simulium* sp. (Fig. 6). June and October series showed low (0 to 50/m².h) day and night drift rates. In December, daytime peaks averaged 150/m².h and the single nighttime peak of 300/m².h occurred just before sunrise. The March series showed a typical alternans pattern with the secondary peak (1275/m².h) immediately after sunset and the major peak (1600/m².h) approximately 2 h before sunrise.

Discussion

Insect drift in this small, southern stream was generally night-active and the major component, as in most northern streams, was mayfly nymphs (principally *Baetis intercalaris*). However, the drift rates of total organisms expressed in units of volume of stream discharge were considerably lower than those reported for northern streams (see Waters, 1969, 1972; Bishop, 1973), and marked differences in seasonal patterns were evident.

Seasonal patterns or variations in the drift have been shown to fluctuate with changes in age (life stage), growth rate, population density, and physical parameters of the stream such as water temperature and current velocity (Bishop & Hynes, 1969; Elliott, 1968; Waters, 1972). In northern streams there is an overall trend toward low drift rates during winter (Müller, 1954; Waters, 1962, 1966; Clifford, 1972a, b) with subsequent increases accompanying rising water temperature during spring and summer (Waters, 1962, 1966; Bishop & Hynes, 1969; Pearson & Franklin, 1968; Pearson & Kramer, 1972). In contrast, our data showed peak drift rates (total organisms, and most taxa) in winter and early spring with minimal values during the summer. One might attribute these differences between our study and those from northern areas to the sampling bias introduced by our 2 h samples (15 min after sunset to 2 h later) which missed the peaks of species with alternans drift patterns, but our 24 h studies showed alternans patterns for only a few species with comparatively low drift rates. Instead, we believe that different life history patterns related to the marked differences in environmental conditions (e.g., temperature, photoperiod, patterns of allochthonous import, etc.) found between northern and southern streams are probably responsible for the differences in seasonal drift patterns. The fact that first emergence of many of the species of aquatic insects in Blackwater Creek takes place in late winter or early spring, compared to late spring or early summer for similar taxa in northern habitats, tends to corroborate this hypothesis.

Our studies of the diel periodicities of the predominant taxa also showed marked seasonal variation and indicate the importance of long-term, drift studies. In subtropical and tropical streams with multivoltine species, sampling and measurement of ecological parameters at short intervals throughout the year appear to be necessary to understand the drift phenomenon.

The diel periodicity (alternans pattern) of late instars of *Polypedilum halterale* observed in this study apparently represents a new drift pattern for the family Chironomidae. Reisen & Prins (1972) noted that drift of chironomid larvae in South Carolina was crepuscular and suggested that the drift rate of immatures increased as pupation activity progressed. However, Waters (1972) cites literature indicating that most Chironomidae larvae show little propensity to drift in a diel periodicity. We plan to conduct additional studies on the factors influencing the drift of *P. halterale*.

Our preliminary studies of factors influencing behavioural drift were inconclusive; significant multiple correlations were recorded only for *Baetis intercalaris, Stenonema* spp. *and Cheumatopsyche* sp. Future plans call for increasing the number of independent variables and, in the case of multivoltine species, in depth analysis of factors influencing each generation.

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