

Predicting the Colonization Cycle of Aquatic Invertebrates¹

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Abstract. The components of the colonization cycle for aquatic invertebrates (drift, upstream movement within the stream, and female flight direction) were quantified for a small Pennsylvania stream. Diel periodicities were evident for both aquatic and terrestrial drift. A regression predicted a linear relation between the proportion of benthos in the drift and the degree of upstream female flight. Accordingly, insects commonly occurring in the drift (Chironomidae, *Baetis* spp., *Ephemera invaria*) showed significant upstream flight of females, whereas those rarely found in the drift (*Glossosoma intermedium* and *G. nigrior*, Psychodidae, *Hydroptila* spp. and *Ochrotrichia wojcickyi*, *Sialis* spp.) did not show significant upstream flight of females. Organisms without a winged adult stage (*Gammarus minus*, Turbellaria) showed a greater degree of upstream movement in the stream. Upstream movement in the stream compensated for only 2.6% of the total aquatic drift in July.

The drift of benthic invertebrates is often observed in running water (review in Müller 1974; Waters 1972). Some studies have suggested that more organisms drift over a unit area of bottom than are actually present in that area (Bishop & Hynes 1969; Elliott 1965a, 1967; Pearson & Franklin 1968; Townsend & Hildrew 1976; Ulfstrand 1968; Waters 1962). This drift characteristically exhibits diel variation (Tanaka 1960; Waters 1962), as well as seasonal variation (Bishop & Hynes 1969).

Downstream displacement of benthic invertebrates often is accompanied by upstream movement within the stream (Bishop & Hynes 1969; Elliott 1971; Hughes 1970; Hultin 1968; Hultin, Svensson & Ulfstrand 1969; Minckley 1964) or by upstream flight of adult females, which is often described as a compensatory recolonization mechanism (Müller 1954). Alternatively, Waters (1961, 1966) did not consider upstream movement necessary, because overproduction occurred in upstream reaches of the stream.

There have been few previous attempts to examine the relation between drift and its compensatory mechanisms in the same system. Therefore, the goal of this study was to concurrently investigate drift, upstream movement in the stream, and the flight direction of adults.

MATERIALS AND METHODS

Study Site

Slab Cabin Run is about 6 km southwest of State College, Centre County,

¹Contribution 6473 of the Pennsylvania Agricultural Experiment Station. We thank the following specialists for their determinations: R.O. Brinkhurst (Oligochaeta); G.W. Byers (Tipulidae); L.E. Canterbury (Sialidae); L.C. Ferrington (larval Chironomidae); O.S. Flint & E.C. Masteller (Trichoptera); P.M. Grant (Ephemereillidae); C.J. Hillson (algae); W.N. Harman (*Physa heterostropha*); J.R. Holsinger (*Gammarus minus*); D.J. Klemm (*Helobdella stagnalis*); J.P. Kramer (*Empoasca fabae*); D.K. Morihara (Baetidae); T.M. Peters (Dixidae); R. Seward (adult Chironomidae); H.J. Teskey (*Chrysops ater* and *Limnophora*); R.D. Waltz (Collembola); W.W. Wirth (Ceratopogonidae). T. Gerlach, K.C. Kim, J. Miller, E. Paul, and B. Wildman gave generous technical assistance and J.L. Watkins granted permission to conduct the research on his property. D.E. Arnold, E.L. Cooper, and F.M. Williams reviewed the manuscript. Funding was provided in part by a National Wildlife Federation Fellowship awarded to the senior author.

Pennsylvania. The watershed is underlain by Carboniferous limestones and dolomite, making Slab Cabin Run a hard-water and highly productive stream with a rich flora of periphytic algae and trailing grasses. Yearly ranges for major chemical and physical characteristics follow: alkalinity, 66-112 mg/liter as CaCO_3 ; pH, 7.2-7.5; and specific conductance, 225-335 $\mu\text{mhos/cm}$. The study site was 35 m long and composed of one pool (5 m long) at the upper end followed by a riffle of moderate gradient. The study site had a mean depth of 0.15 m and a mean width of 4.1 m. The stream flowed through old fields and had a limited canopy.

Benthic Sampling

Benthic numbers were estimated by a stratified random sampling design (Elliott 1977). The study site (150 m^2) was divided into three strata: pool, riffle, and grass areas (grass islands and trailing grasses). Each stratum was further subdivided into 0.1 m^2 units and mapped, and random sampling sites were selected within each stratum. Eight 0.1 m^2 samples were collected with a stovepipe sampler equipped with a Nitex^a collecting net (mesh size, 500 μm)—two from pool areas, five from riffle areas, and one from grass areas. Benthos was collected on 16 July and 18 September 1981, and preserved in 75% ethanol. Samples were sorted under 4 \times magnification and identified to the lowest taxonomic rank practical. Voucher specimens were deposited in the Frost Entomological Museum, The Pennsylvania State University.

Drift Sampling

Drift samples were collected for 24-hour periods on 15-16 July and 17-18 September 1981. Seven drift nets were placed at the base of the study area covering the entire width of the stream. The mouth of each net was 30.5 cm square. Each net was equipped with 60 cm of Nitex (mesh size, 500 μm) attached to a steel frame by 25 cm of reinforced canvas. Samples were divided into 11 two-hour and 2 one-hour periods. The 2 one-hour periods corresponded to 2000-2100 and 2100-2200 (all times are given as Eastern daylight-saving time). Treatment of invertebrates in the drift was the same as that of organisms in the benthos. Stream velocity was measured with a Gurley pygmy current meter accurate to 0.015 m/sec and average stream discharge was calculated for July (7084 $\text{m}^3/24 \text{ h}$), and September (5443 $\text{m}^3/24 \text{ h}$). Drift density was calculated as the number of organisms drifting past a particular point per 24 h per m^3 . Biomass of drifting algae (*Ulothrix* sp. and *Oscillatoria* sp.) and adherent debris collected during September was quantified after drying to constant weight at 100°C.

Sampling Upstream Movement Within The Water Column

We quantified upstream movement of invertebrates in the stream by placing three drift nets in reverse position across 43% of the stream width. These nets were placed 5 m below the drift nets. To insure that organisms would remain in the nets, rocks sterilized with formalin were placed in the bottom of each net to serve as attachment areas. In addition, vaseline was applied to the net frames to discourage entry of invertebrates from upstream. Nets were emptied at the end of the 24-h sampling period on 16 July 1981.

Sampling Upstream Flight Of Adults

Winged adults were collected with a bilateral Malaise trap (original design described by Malaise 1937). The trap was 2.2 m high and 4.4 m wide, and was modified so that upstream and downstream collections were separated. The Malaise trap was positioned across the stream, 20 m below the drift nets. Canisters were emptied every 4 h on 15-16 July and 17-18 September and every 24 h on 18-22 September. Adults not emerging during those times were collected during a portion of their respective emergence periods: *Sialis* spp., 15-18 May 1982; and *Ephemerella invaria* (Walker), 8-10 June 1982. In addition, a portable car-vacuum was used to remove insects from the netting on 17-22 September. Aquatic adults were individually identified; all terrestrials were treated as a single group. A Chi-square test of significance of a binomial proportion was used to test differences in flight patterns.

^aUse of trade names does not imply government endorsement of commercial products.

RESULTS

Benthos

The benthic collections from July and September contained 6833 and 7417 invertebrates, respectively (Table 1). Collections for each 24 h period included seven orders of insects (23 families in July and 20 in September) and seven noninsect groups.

Chironomids were the most abundant organisms in the benthos samples. Identifications of adults and larvae indicated that at least 21 species were represented (*Conchapelopia* spp., *Corynoneura* sp., *Cricotopus trifascia* gr. sp., *Cricotopus* sp. 1 and 2, *Eukiefferiella* cf. *brevicalcar* or *clypeata* gr. sp., *E.* cf. *devonica* gr. sp., *Heterotrissocladius marcidus* gr. sp., *Micropsectra* sp., *Pagastia* sp., *Parametrioctenemus* sp., *Paraphaenocladus* sp., *Polypedilum* sp., *Prodiamesa* cf. *olivacea* (Meigen), *Psectrotanytus* sp., *Rheocricotopus* sp., *Stictochironomus* sp., *Sympotthastia* sp., *Synorthocladus semivirens* (Kieffer), *Tvetenia* cf. *bavarica* gr. sp., *Zavreliomyia* sp.). Numbers of chironomids were similar in both July and September samples, despite considerable preemergence activity during the July collections. Second in order of abundance was the amphipod *Gammarus minus* Say, which varied little between the two samples (2593/m² in July and 2556/m² in September). Other important taxa collected in the benthos were *Helobdella stagnalis* (L.), *Physa heterostropha* Say, *Limnophora* sp., Turbellaria, and Oligochaeta (*Tubifex tubifex* Müller and *Limnodrilus hoffmeisteri* Claparède).

Differences were evident between pool, riffle, and grass collections. Most *Helobdella stagnalis* and Oligochaeta, but no trichopterans were collected from pool areas. The obvious contagious dispersions of these taxa and of many others apparently led to the exclusion of several taxa from either the July or September samples, e.g., *Dixa* sp. nr. *inextricata-johansenni* in July. This is not a reflection of the absence of these taxa, but rather a result of the inherent problems in benthic sampling designs.

Upstream Movement In The Stream

Nine taxa were captured in the upstream traps in July, including six families of insects (Table 2). A total of 80 organisms were captured in the three nets, corresponding to a total estimate of 184. Mesh size of the nets necessitated a minimum size limit of 3.5 mm for chironomids.

To determine what fraction of the downstream drift was compensated for, we included the aquatic stages of all taxa collected in the drift in the compensation calculations. Thus, of the 7017 totally aquatic stages drifting downstream, upstream movement in the stream compensated for only 2.6%. Individual compensation of taxa ranged from 0.9% to 1400% (Table 2).

Drift Composition

Among the major taxa represented in drift collections (Table 1), the Chironomidae were the most abundant in both July and September. With the inclusion of pupae and adults (preemergent forms), total numbers of chironomids were 28271 in July and 11593 in September. Preemergent forms accounted for nearly 79% of all drifting aquatics in July and 62% in September. Other important taxa in the drift in July were *Gammarus minus*, *Dixa* sp. nr. *inextricata-johansenni*, and *Sigara alternata* (Say); and in September, *Limnophora* sp. and *Physa heterostropha*. A number of organisms represented in the benthos were scarce in the drift: *Glossosoma intermedium* (Klapálek), *G. nigrior* Banks, *Hydroptila concimilis* Morton, *H. rono* Ross, *Ochrotrichia wojcickji* Blickle, *Cheumatopsyche* spp., *Chrysops ater* Macquart, *Sialis* spp., *Helobdella stagnalis*, Turbellaria, and *Bezzia* sp. Drifting algae and adherent debris amounted to 32.7 g/24 h.

Contributions of terrestrial forms to the drift were substantial during both sampling

TABLE I

Major invertebrate taxa collected in Slab Cabin Run, Pennsylvania, July and September 1981.

Taxon and month	Benthos (No./m ² ±1 SE) ^a	Drift density (No./m ³ /24 h) ^a	No. of females flying upstream	No. of females flying downst.
Chironomidae				
July	4507.5±3844.4	0.393	2336	824 ^b
Sept	4688.8±3329.1	0.312	1337	719 ^b
Baetis spp.				
July	95.0±229.2	0.054	4	3 ^d
Sept	65.0±125.9	0.116	27	4 ^b
Glossosoma intermedium and G. nigrior				
July	25.0±30.7	0.000	2	0 ^d
Sept	71.3±171.4	0.000	30	30 ^d
Psychodidae				
July	6.3±14.1	0.000	120	119 ^d
Sept	2.5±7.1	0.000	90	94 ^d
Hydroptila consimilis, H. rono and Ochrotrichia wojcickyi				
July	3.8±8.1	0.000	83	90 ^d
Sept	7.5±11.6	0.002	83	58 ^c
Dixa sp. nr. inextricata- johansenni				
July	—	0.007	4	0 ^d
Sept	5.0±7.6	0.004	10	2 ^d
Hemerodromia spp.				
July	1.3±3.5	0.000	4	13 ^d
Sept	35.0±44.1	0.004	8	8 ^d
Sialis spp.				
July	2.5±7.1	0.000	—	—
Sept	17.5±19.8	0.000	—	—
May	—	—	6	17
Chrysops ater				
July	30.0±13.1	0.000	—	—
Sept	55.0±40.4	0.000	—	—
Ephemerella invaria				
Sept	11.3±20.3	0.093	—	—
June	—	—	196	14 ^b
Sigara alternata				
July	2.5±4.6	0.010	—	—
Sept	6.3±14.1	0.005	—	—
Limnophora sp.				
July	35.0±34.2	0.007	—	—
Sept	193.8±198.6	0.040	—	—
Gammarus minus				
July	2592.5±3189.1	0.136	—	—
Sept	2557.5±3392.0	0.503	—	—
Physa heterostropha				
July	21.3±24.2	0.001	—	—
Sept	71.3±65.8	0.011	—	—
Helobdella stagnalis				
July	243.8±369.2	0.001	—	—
Sept	733.8±948.2	0.001	—	—

^aOnly larval and nymphal stages; ^bUpstream flight significant (P<0.01); ^cUpstream flight significant (P<0.05); ^dUpstream flight not significant (P>0.05).

TABLE II

Numbers of invertebrates moving upstream within the water column versus numbers drifting in a small Pennsylvania stream (July).

Taxon	Estimated no. moving upstream	No. of aquatic forms drifting	Compensation (%)
<i>Gammarus minus</i>	128	961	13.3
Dytiscidae	2	111	1.8
<i>Baetis</i> spp.	5	385	1.3
Turbellaria	14	1	1400
Chironomidae	26	2781	0.9
Hydracarina	2	16	12.5
<i>Hydroptila</i> sp.	5	2	250
<i>Antocha</i> sp.	2	1	200

periods and accounted for 17.0% of the total drift in July and 10.7% in September. In July collections, 67% of the terrestrials were composed of Collembola and the potato leafhopper, *Empoasca fabae* (Harris). Of the total *E. fabae*, 98.8% were males. The Collembola included three species, *Neanura muscorum* (Templeton), *Agrenia bidenticulata* (Tullberg) - an aquatic species, and *Lepidocyrtus paradoxus* Uzel; *L. paradoxus* contributed more than 99% in July and nearly 92% in September.

Diel Periodicity Of The Drift

Nearly all major aquatic taxa collected in drift samples showed diel periodicity. The nocturnal pattern of the aquatic taxa followed the light-dark cycle (Figs. 1b & 2b). Dusk and dawn fell at 2042 and 0553 in July, and at 1916 and 0655 in September. A large peak in movement coincided with dusk, followed by a smaller peak just before dawn - the bigeminus pattern of Waters (1965). The larger peak in July (2000-2200) was largely due to the preemergence activity of chironomids. Peaks for nymphs and larvae were higher in the September collections. The drift patterns of the aquatics did not appear to follow the periodicity of the water or air temperature.

The pattern of occurrence of the terrestrial component was diurnal in July and September. The activity patterns for terrestrials did not follow the light-dark cycle directly. Rather, the greatest drift followed changes in air temperature (Figs. 1c,d & 2c,d). Peak air temperatures and occurrence of the terrestrial peak did not coincide, but there was a general trend of rising numbers and temperature throughout the day in both months. Maximum numbers of terrestrials occurred before dusk in both samples; numbers dropped off sharply after dusk. *Empoasca fabae* (July) and Collembola (July and September) showed distinct peaks before dusk (Fig. 3).

Individual taxa of aquatics displayed a wide range of nocturnal patterns (Fig. 4). The chironomid larvae (July) followed an alternans pattern (Waters 1965, Fig. 5a). Chironomid collections in September were atypical of most aquatic invertebrates; numbers were high in both day and night collections (Fig. 5b). Peaks in preemergence activity were clearly present in both samples of chironomids (Figs. 5a,b). The predatory chironomid tribe, Pentaneurini (*Conchapelopia* spp., *Zavreliomyia* sp.), peaked between 2000 and 2200 in September (Fig. 5c). *Baetis* spp. (*B. brunneicolor* McDunnough, *B. flavistriga* McDunnough, *B. tricaudatus* Dodds) followed an alternans pattern in July (Fig. 4f), and a bigeminus pattern in September (Fig. 4l). *Gammarus minus* remained at high levels throughout the night in July without any obvious pattern (Fig. 4e), but had a pattern similar to that of *Baetis* spp. (September sample) in September (Fig. 4k). Although numbers were low (especially in September), the drift of both *Sigara alternata* and *Dixa* sp. nr. *inextricata-johansenni* increased at night (Figs. 4c,d,i,j). Both

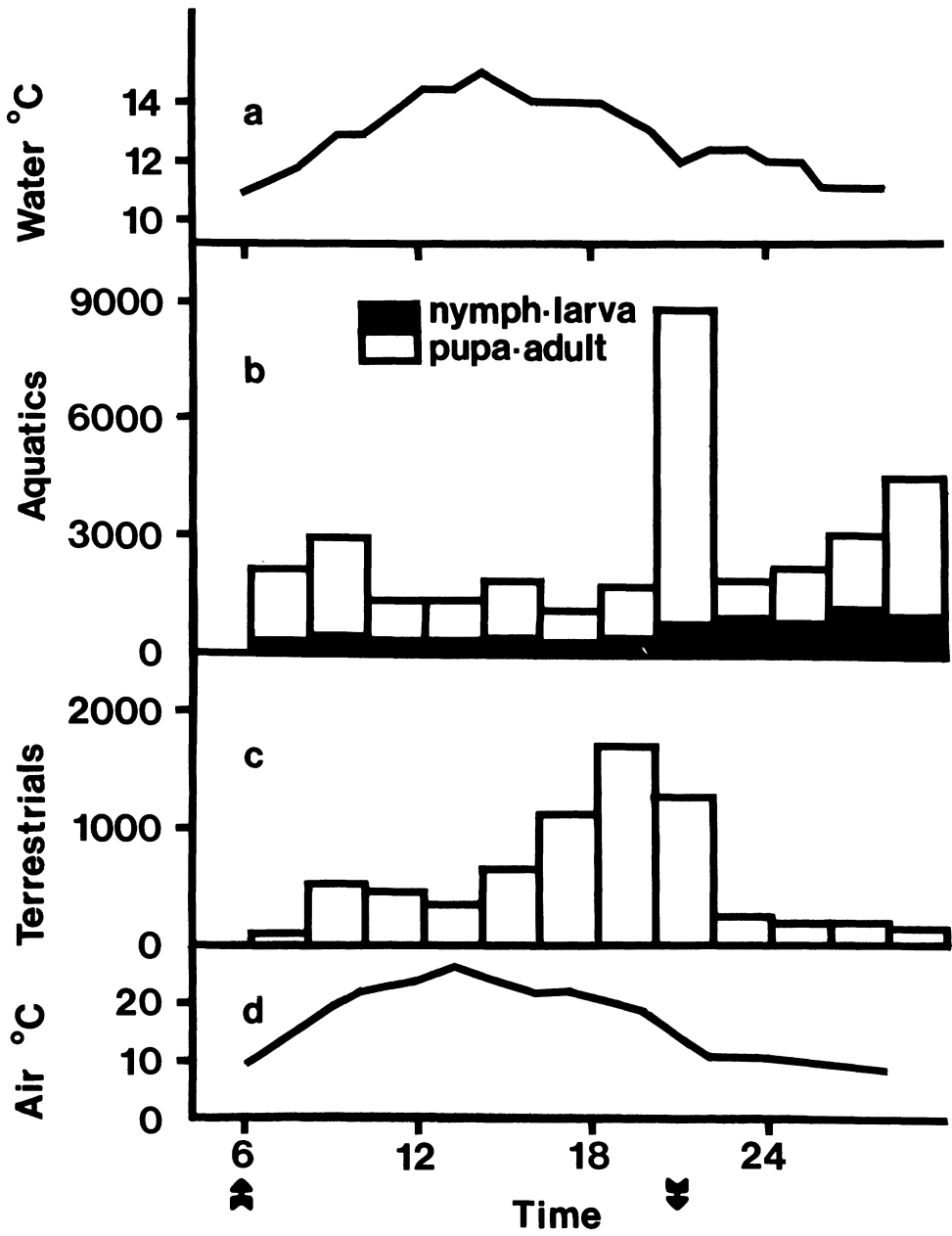


Fig. 1. July diel periodicities. a) water temperature, b) drift of aquatic nymphs, larvae, pupae and adults, c) terrestrial drift, d) air temperature. Arrows indicate dawn (↑) and dusk (↓).

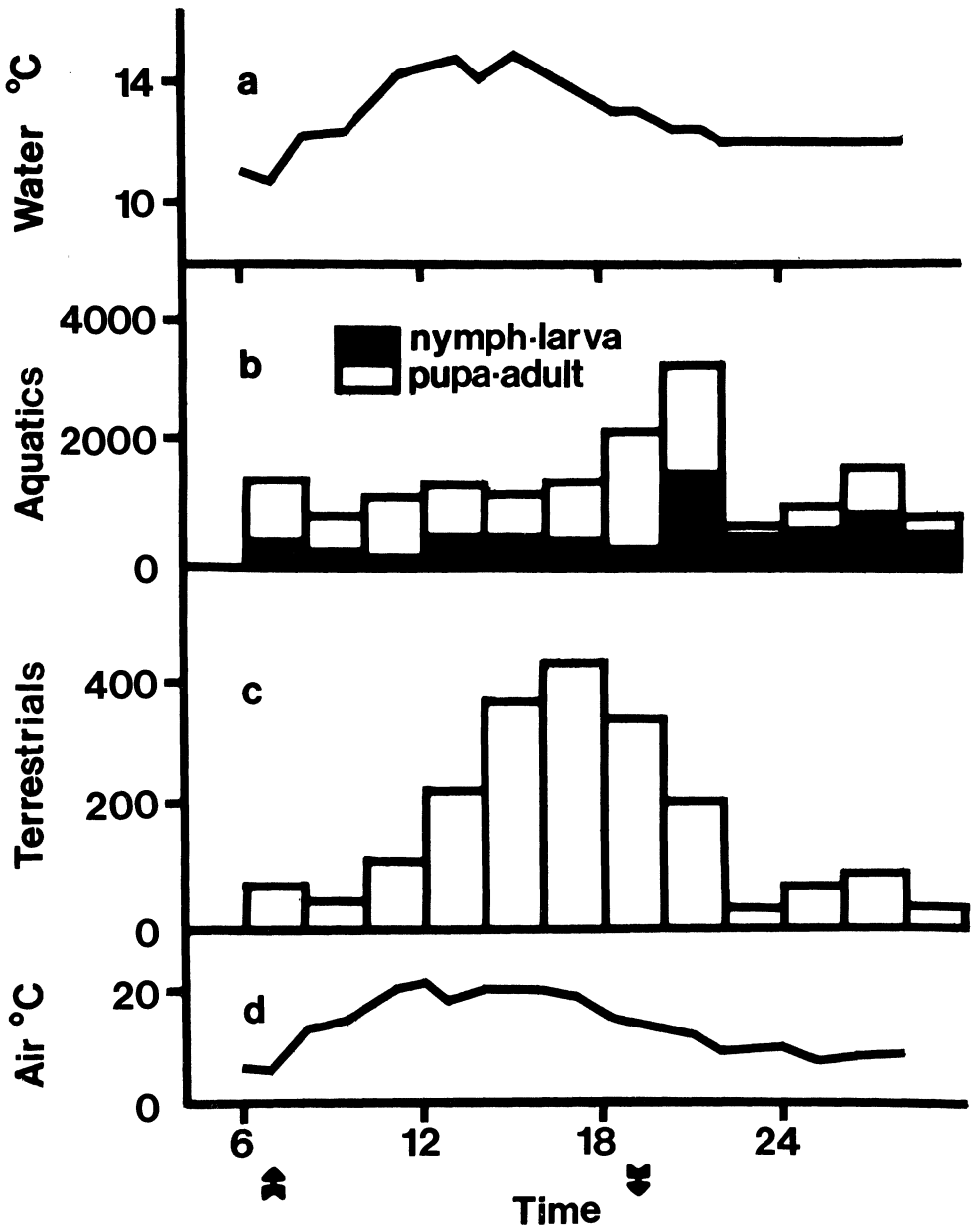


Fig. 2. September diel periodicities. a) water temperature, b) drift of aquatic nymphs, larvae, pupae and adults, c) terrestrial drift, d) air temperature. Arrows indicate dawn (↑) and dusk (↓).

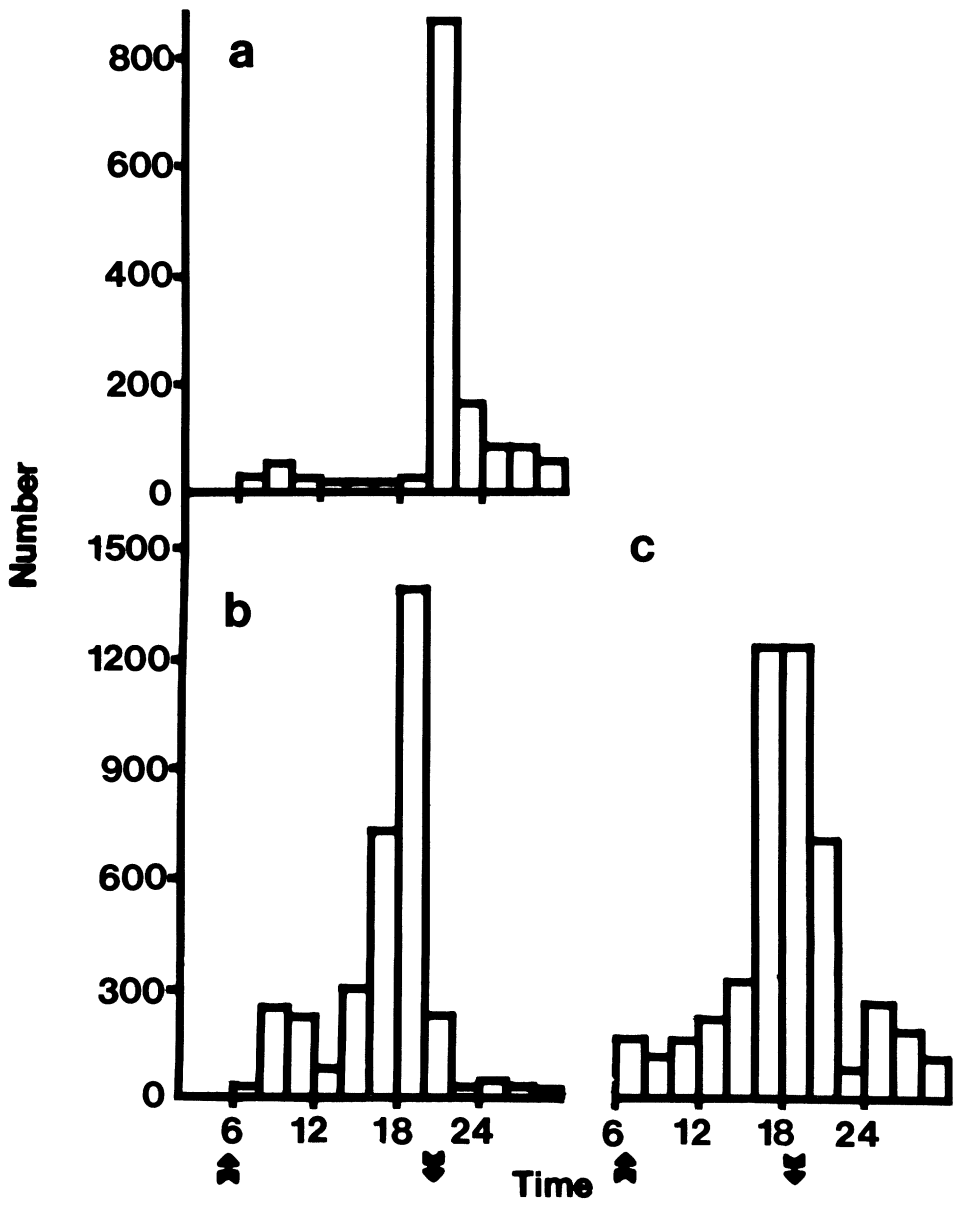


Fig. 3. Diel periodicities for terrestrial drift. a) *Empoasca fabae* (July), b) *Collembola* (July), c) *Collembola* (September). Arrows indicate dawn (↑) and dusk (↓).

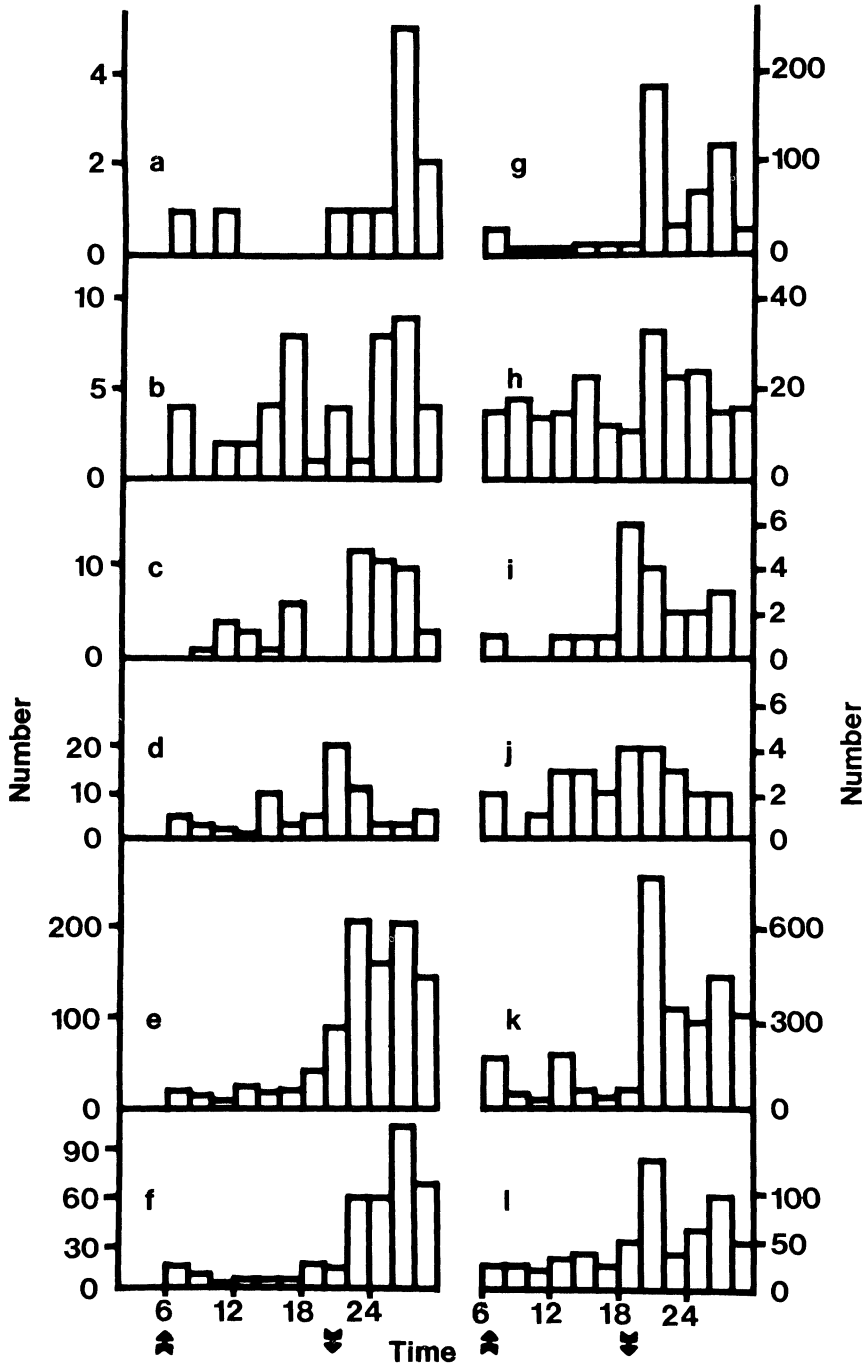


Fig. 4. Diel periodicities for aquatic drift. July: a) *Drunella cornutella* (McDunnough), b) *Limnophora* sp., c) *Dixa* sp. nr. *inextricata-johansenni*, d) *Sigara alternata*, e) *Gammarus minus*, f) *Baetis* spp.; September: g) *Ephemera invaria*, h) *Limnophora* sp., i) *Dixa* sp. nr. *inextricata-johansenni*, j) *Sigara alternata*, k) *Gammarus minus*, l) *Baetis* spp. Arrows indicate dawn (↑) and dusk (↓).

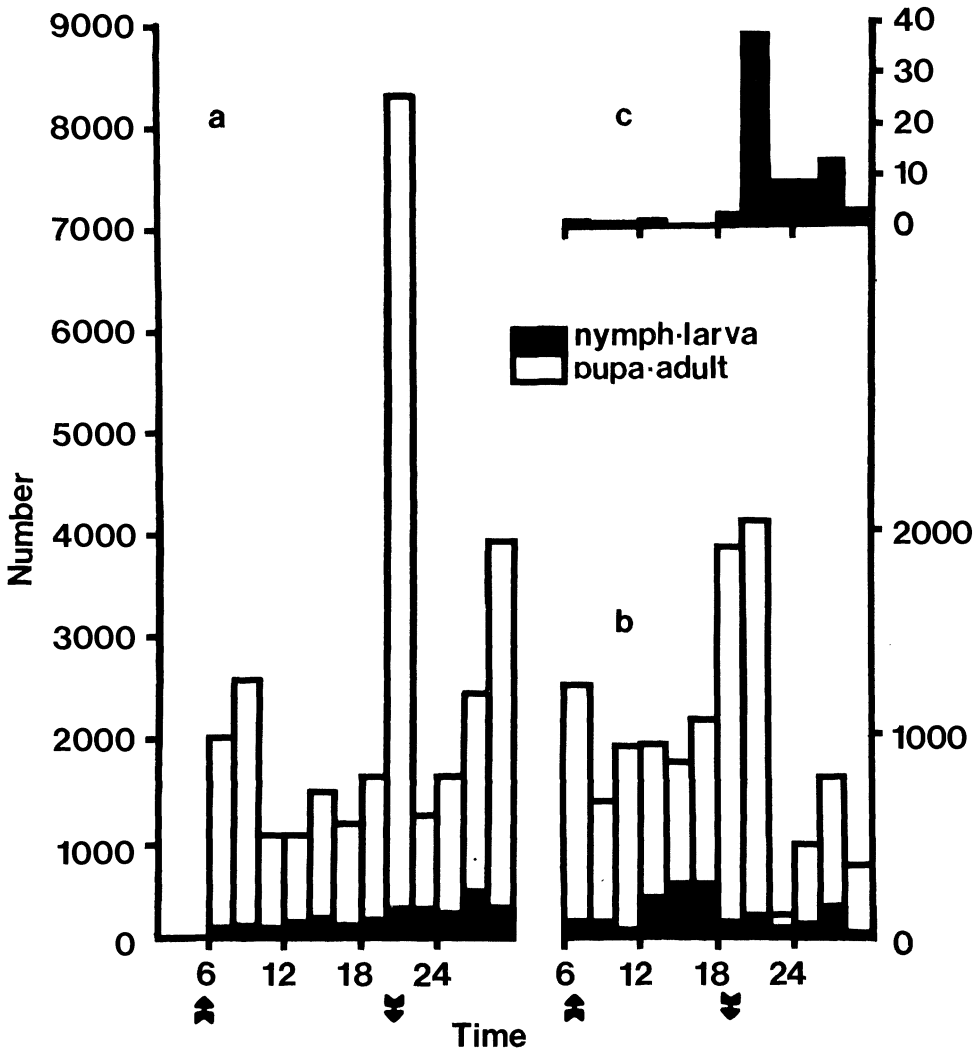


Fig. 5. Diel periodicities for chironomid drift. a) July, b) September without tribe Pentaneurini, c) tribe Pentaneurini, September. Arrows indicate dawn (↑) and dusk (↓).

Limnophora sp. and *Drunella cornutella* were sparse in July (Figs. 4a,b). *Ephemerella invaria* followed a bigeminus pattern in September, whereas numbers of *Limnophora* sp. remained high throughout the night (Figs. 4g,h).

Upstream Flight Of Adults

Captures in the Malaise trap included members of 13 aquatic families in July and 16 in September (Table 1). Significant upstream flight was demonstrated for several taxa: chironomids (July and September), *Baetis* spp. (September), *Hydroptila* spp. and *Ochrotrichia wojcickyi* (September), *Dixa* sp. nr. *inextricata-johansenni* (September), and *Ephemerella invaria* (June). No significant upstream flight was observed in either month for *Glossosoma intermedium* and *G. nigrior*, *Hemerodromia* spp., or Psychodidae.

Quantification Of The Colonization Cycle

To quantify the relation between net upstream flight of females and the drift, we applied a regression involving a \log_{10} transformation; it has as the dependent variable the ratio of females flying upstream to those flying down, and as the independent variable the proportion of benthos in the drift (P), defined as $P = xD(100)/X - xD$, where x = drift density, X = benthic density, and D = average stream depth (Elliott 1965b). The regression included the major taxa from Table I for which flight data were available. Data for the *Simulium vittatum* complex (July and September separately; Adler, Kim & Light 1983) and *S. tuberosum* complex (July and September separately; Adler & Light, unpubl. data) from this study site were also included in the regression. The regression (Fig. 6) was significant ($P < 0.005$), 51% of the variability in net upstream flight of females being accounted for by the proportion of benthos in the drift.

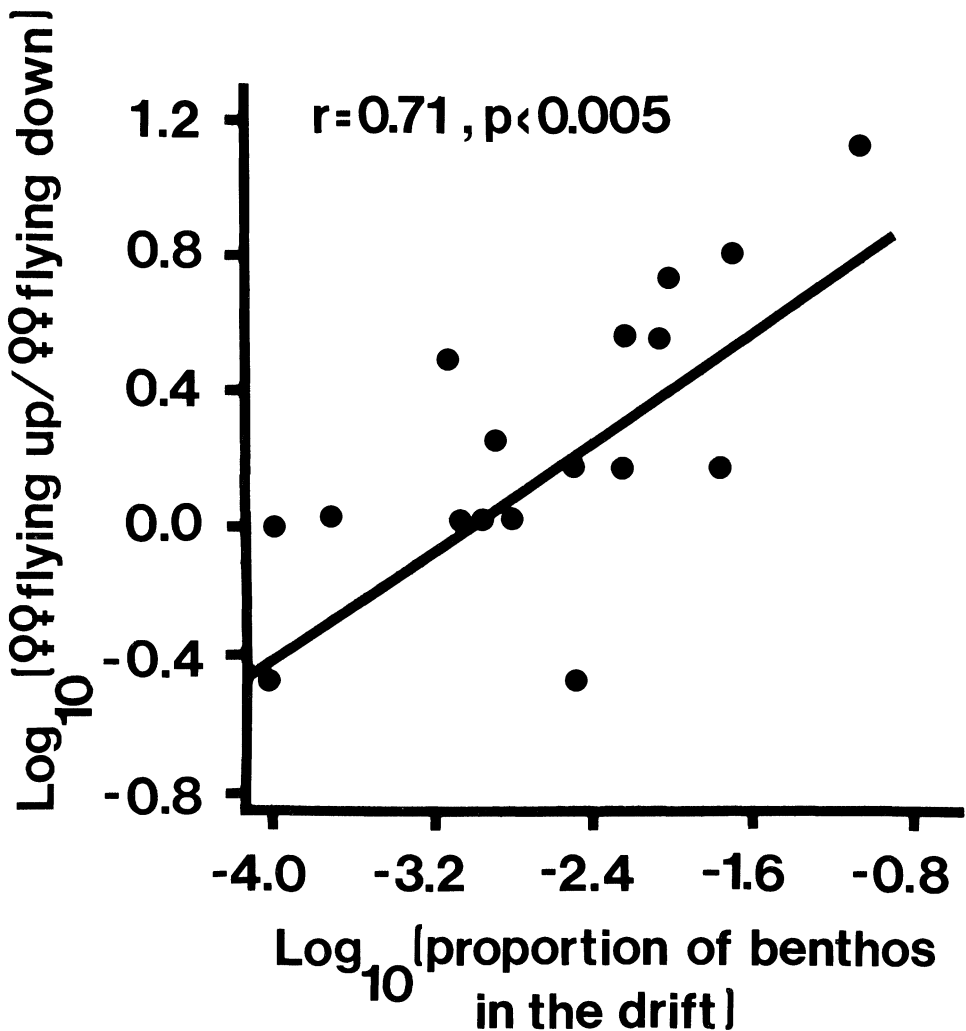


Fig. 6. Relation between the ratio of females flying upstream to those flying downstream and the proportion of benthos in the drift.

DISCUSSION

Drift

Aquatic drift, whether passive or active, occurs to some degree in the life history of most aquatic organisms. Well-defined drift rhythms, when present in these organisms, indicate a continual and predictable downstream displacement. The diel periodicities found in this study are in accordance with those found in other studies (Tanaka 1960; Waters 1962). For short-lived or univoltine organisms, the displacement distance may be short. In long-lived or semivoltine organisms, however, the distance traveled downstream may be long. The consequences of this displacement are not always favorable; large pools may become areas of decomposition for drifting organisms (Bailey 1966; Dendy 1944; Waters 1962), or pollution outflows may cause mortality.

Upstream Movement Within The Water Column

Aquatic organisms have the capacity to move upstream within the water column, thereby compensating for downstream drift. However, the number moving upstream is small when compared with the number drifting downstream. Bishop and Hynes (1969) found only 6.5% compensation of the drift in numbers and 4% compensation in weight, and Elliott (1971) found 7-10% compensation in summer and 30% in winter. Data from the present study indicate that only 2.6% compensation occurred. Predictably, organisms that are solely aquatic throughout their life cycle show one or more of several characteristics: 1) little tendency to drift, e.g., turbellarians and *Hellobdella stagnalis* in the present study; 2) a greater tendency for upstream movement, e.g., *Gammarus minus* in our study and other gammarid species (Hughes 1970; Hultin 1968; Minckley 1964); 3) a parasitic relationship, e.g., Hydracarina (Schmidt 1969); or 4) phoresy, e.g., algae (Stewart, Millinger & Solon 1970).

Upstream Flight Of Adults

Other organisms that have a winged adult stage may compensate for drift by flying upstream to mate and deposit their eggs. Although a population might be able to maintain itself in a particular area of stream by random movements alone, the individuals of the population are the units of selection. Therefore, females that fly upstream for oviposition should be favored, since they are insuring continuation of their genes in a favorable habitat. The tendency for upstream flight should therefore be most highly developed in the species most prone to drift (Hultin et al. 1969; Madsen, Bengtson & Butz 1973).

At the other extreme, organisms such as certain Trichoptera and certain Plecoptera that do not drift in large proportion (Madsen et al. 1973; Müller 1974), need not show a strong tendency for upstream flight. Undoubtedly, there is wide variation in upstream flight tendencies, as there is in drift tendencies. Accordingly, we developed a regression as a means of predicting the degree of upstream flight based on the proportion of benthos in the drift at an instant of time. In practice, deviations from the predicted regression line might be attributed to insufficient sampling, particularly of the benthos, and to overriding environmental factors such as strong winds (Bishop & Hynes 1969; Elliott 1967). The behavior of the species may also be an important factor. *Sialis* spp., which oviposit on overhanging vegetation (Canterbury & Neff 1980), might be expected to fly to such areas. In our study, overhanging vegetation was concentrated below the Malaise trap, and as expected, we observed predominant downstream flight of the sialids.

Characterization of female flight patterns has received considerable attention since Müller (1954) advanced the colonization cycle hypothesis. Most of the work has been concerned with trends at the population level and has largely ignored the individual. The earliest and perhaps best quantification of flight patterns is that of Roos (1957), who found significant upstream flight of females of lotic Trichoptera, Plecoptera, Ephemeroptera, and the dipteran families Simuliidae and Chironomidae. All of these taxa had at least 70% upstream flight of females. Our analysis (Chi-square) of his data

indicates that organisms he characterized as lentic or rheo-indifferent showed no such upstream trend. Roos (1957) also stated that for *Cheumatopsyche lepida* Pict. and *Rhyacophila nubila* Zett., females flying upstream carried predominantly mature eggs and those displaying no directional preference carried immature eggs. Lehmann (1970), on the basis of indirect evidence, arrived at similar conclusions for *Philopotamus montanus* (Donovan), and hypothesized that gravid females fly upstream. Pearson (1970), using artificial oviposition sites in a Utah stream, determined that egg masses of *Oligophlebodes sigma* Milne were concentrated near the headwaters and suggested that this was an evolutionary mechanism, concentrating eggs in areas relatively safe from the effects of anchor-ice and floods. In other studies, Waters (1968) observed upstream flight of adult *O. sigma*; Russev (1972a, b) found 21 species of mayflies in the lower Danube that flew predominantly upstream; Elliott (1969) found predominant upstream flight for *Sericostoma personatum* Spence; and Bengtson et al. (1972), working in a Danish stream, described upstream flight of mayflies and stoneflies. Müller and Mendl (1980) documented upstream flight of the plecopteran *Leuctra digitata* Kempny. They described high drift rate in a coastal stream near the Bothnian Sea, nymphal maturation in brackish water, and subsequent compensatory upstream flight of adults. Madsen et al. (1973) concluded that Plecoptera that are subject to displacement by the current (*Brachyptera risi* (Mort.)) displayed upstream flight of females, whereas those protected from the current (*Nemoura* sp.) did not.

We have demonstrated that the degree of upstream flight of female aquatic invertebrate species can be predicted from the respective tendencies of the immatures to drift. As the proportion of benthos in the drift increases, so does the degree of upstream flight.

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