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Drift patterns in a high Andean stream

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Abstract

The drifting of invertebrates was sampled for six 24-hour periods from September 1976 to July 1977 in a small stream of the paramo of the Ecuadorian Andes. The composition of the drift is similar to that of the benthos, though percentages may differ markedly. Drift is relatively constant throughout the year, except in March when unusually high rates were noted; at this same period a marked reduction in the benthos was also observed. Diel periodicities in the drift are unclear, although on the whole drift is more important during the daytime; when individual data series are analyzed, weak patterns of day or night drifting can be recognized in some groups. The input of insects through drift from the small streams is thought to be an important source of food for the salmonid fish inhabiting the larger torrents.

Introduction

An extensive literature has now been accumulated on downstream drift in running water habitats (Waters 1972), but the bulk of it is from arctic and temperate latitudes. Only three studies from tropical regions are known to us (Bishop 1973; Hynes 1975; Elouard & Lévêque 1977) and these indicate that the classic features of drift are also prevalent under equatorial conditions; all three investigations were conducted however in warm tropical areas of Asia and Africa.

During an extended stay in Ecuador by the senior author, we have taken the opportunity to make a preliminary examination of the drifting of invertebrates in a cold tropical habitat, a small stream flowing in the paramo of the Andes, at an altitude of some 3000 m.

The study site

The stream chosen for this study is a small tributary of the Rio Matadero, a headwater river of the Rio Santiago drainage, and hence of the Amazon. It is situated at approximately 20 km northwest of the city of Cuenca in the republic of Ecuador (79°09'W; 2°48'S). The stream originates in a small crater lake Laguna Verde Cocha at an altitude of some 4000 m and flows down an abrupt slope into a wide glacial valley where it reaches Rio Matadero at 3300 m. The surrounding vegetation is a typical paramo association of grasses and shrubs. The mean annual water temperature, as well as the mean monthly temperatures, are of the order of 9 °C; extreme temperatures measured during the year were 5.5° and 13°. A more detailed description of the stream and of its benthic fauna is available elsewhere (Turcotte & Harper 1982); it will suffice here to recall that the stream is small (discharge 13–30 l s^{-1}), the climate cool and wet (Fig. 1), and the benthic fauna relatively rich and diverse (Tables 1 and 2). There are no fish in the stream, though trout (*Salmo gairdneri* Richardson) are common in the main river.

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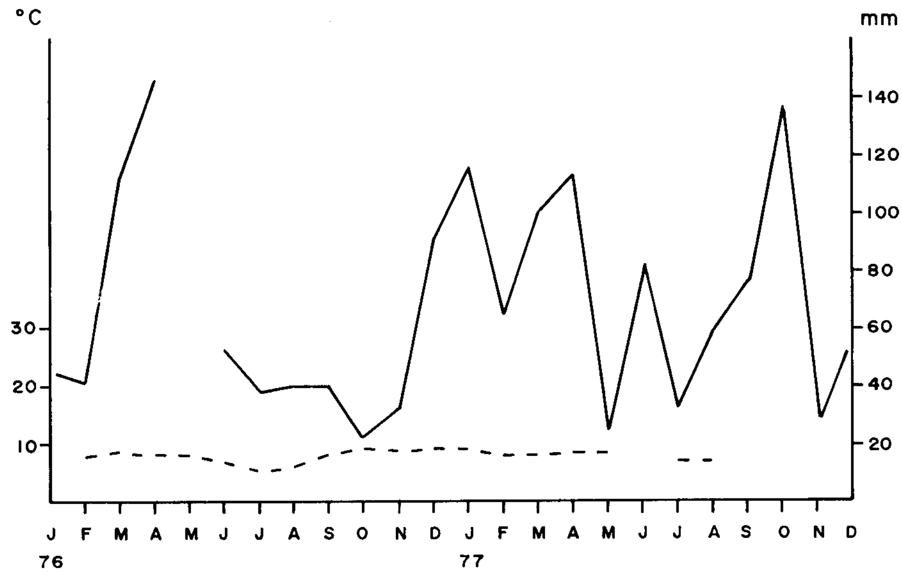

Fig. 1. Climogram of monthly precipitations and mean temperatures recorded at the Matadero weather station near the study site.

Methods

The stream was sampled for drifting invertebrates just before its junction with the Rio Matadero; at that point, the stream drops over a shallow embankment into the main river and it is possible with a large net to filter the whole water flow. The net we used was approximately 1 m wide and had a mesh-size of 200 μm.

Once a month from August 1976 to July 1977 a 24 hour sampling program was conducted; usually the net was emptied four times during this period, at mid-day, at sunset, at midnight and at dawn, which is once every 6 hours in this photoperiodically stable environment. In May and in July 1977 however, the net was emptied 16 times a day, every 1.5 hours.

For the present discussion we have analyzed six

Table 1. General composition of the drift (N/24 h) and comparison (%) with the benthos.

	Sep.	Dec.	Jan.	Mar.	May	Jul.	% drift–% benthos
Turbellaria	19	13	27	30	5	14	0.63– 3.02
Nematoda	11	6	6	67	8	1	0.58– 2.35
Hirudinea	2	–	–	1	1	–	0.02– 0.07
Oligochaeta	240	282	304	1 135	573	160	15.50– 19.87
Gastropoda	–	–	–	50	115	103	1.55– 0.19
Pelecypoda	–	–	–	1	4	2	0.04– 0.04
Copepoda	22	37	33	394	41	16	3.14– 19.44
Ostracoda	141	111	14	95	66	19	2.58– 1.67
Amphipoda	42	26	96	321	350	179	5.87– 1.73
Hydracarina	756	529	475	2 071	1 162	460	31.58– 25.35
Insecta	915	524	820	2 674	1 027	673	38.41– 24.19
Subtotal	2 148	1 528	1 775	6 839	3 352	1 627	100.00–100.00
Terrestrial inv.	476	370	395	1 084	518	481	16.14
Total	2 624	1 898	2 170	7 923	3 870	2 108	100.00

Table 2. Aquatic insects in the drift (N/24 h) and comparison with the benthos.

	Sep.	Dec.	Jan.	Mar.	May	Jul.	% drift–% benthos
Ephemeroptera							
Baetis	123	47	76	237	58	122	10.00– 5.01
Baetodes	49	21	32	44	14	31	2.88– 0.22
Atalonella	10	–	4	8	5	5	0.48– 1.19
Odonata	–	–	–	–	1	–	0.01– 0.02
Plecoptera							
Claudioperla	27	3	14	4	1	3	0.78– 0.49
Anacroneuria	44	8	11	11	34	13	1.82– 2.64
Trichoptera							
Oxyethira	24	43	40	333	20	55	7.76– 3.02
Ochrotrichia	58	8	14	98	40	18	3.56– 1.62
Neotrichia	32	11	3	5	22	28	1.52– 0.39
Dibusa	5	–	–	5	3	1	0.21– 0.03
Alisotrichia	–	–	2	2	1	2	0.11– 0.89
Nectopsyche	12	1	3	12	6	7	0.62– 1.57
Magellomyia	37	8	16	31	19	12	1.85– 4.80
Atopsyche	38	8	23	21	30	13	2.01– 1.31
Hydropsychidae	1	–	1	–	1	–	0.05– 0.23
Helicopsychidae	2	–	–	–	–	–	0.03– 0.08
Phylloicus	4	1	1	3	2	2	0.20– 0.06
Brachycentridae	1	–	–	3	–	–	0.06– 0.07
Coleoptera							
Elmidae	22	13	18	36	16	18	1.85–12.04
Helodidae	10	9	10	8	44	52	2.01– 0.40
Dytiscidae	2	1	6	3	5	–	0.26– 0.05
Psephenidae	–	–	–	–	–	–	0.00– 0.07
Diptera							
Psectrotanypus	37	5	84	265	141	25	8.40– 0.90
Zavrelimyia	4	6	2	4	10	12	0.57– 0.42
Podonomus	16	18	6	22	6	3	1.07– 5.07
Podonominae	–	–	3	24	–	2	0.44– 1.93
Cricotopus	119	114	153	377	114	88	14.55–19.06
Limnophyes	2	5	28	58	43	18	2.32– 8.98
Pseudosmittia	1	–	–	1	–	–	0.03– 0.06
Krenosmittia	–	–	–	–	–	–	0.00– 0.03
Psectrocladius	–	–	–	–	–	–	0.00– 0.01
Brillia	–	–	–	–	–	–	0.00– 0.06
Smittia	–	–	–	–	1	–	0.01– 0.18
Thienemanniella	–	–	–	–	–	–	0.00– 0.13
Corynoneura	–	1	–	5	–	–	0.09– 0.29
Eukiefferiella	–	1	–	2	1	–	0.06– 0.00
Eurycnemus	–	–	–	–	–	1	0.01– 0.00
Ortho. genus A	6	–	–	–	–	–	0.09– 0.17
Ortho. genus B	–	–	–	1	–	1	0.03– 0.08
Ortho. genus C	2	14	4	8	13	1	0.03– 0.13
Ortho. genus D	–	–	–	–	–	–	0.00– 0.04
Ortho. genus E	–	–	–	–	1	–	0.01– 0.00
Ortho. genus F	–	–	–	–	4	–	0.06– 0.01
Ortho. genus G	1	–	–	–	–	–	0.01– 0.03
Ortho. genus H	–	–	–	–	–	–	0.00– 0.07
Heterotrissocladius	–	–	1	1	–	–	0.03– 0.00
Pseudochironomus	15	3	10	156	94	7	4.39–14.35
Micropsectra	6	1	17	131	31	3	2.88– 4.28
Rheotanytarsus	–	–	–	–	1	–	0.01– 0.00
Polypedilum	1	–	–	–	–	–	0.01– 0.08
Harnischia	–	–	–	–	–	–	0.00– 0.01

Table 2. (Continued).

	Sep.	Dec.	Jan.	Mar.	May	Jul.	% drift–% benthos
Cryptochironomus	–	–	–	1	–	–	0.01– 0.02
Endochironomus	–	–	–	–	–	–	0.00– 0.12
Paralauterborniella	–	–	–	1	–	–	0.01– 0.00
Chironominae	–	–	–	–	–	–	0.00– 0.05
Gigantodax	40	33	55	108	21	7	4.21– 0.67
Simulium	10	3	8	17	11	3	0.84– 0.18
Simuliidae	–	–	–	–	–	–	0.00– 0.01
Ceratopogonidae	5	3	2	14	7	2	0.50– 2.13
Tipulidae	13	8	2	33	14	7	1.16– 0.65
Psychodidae	6	11	14	9	30	13	1.25– 0.10
Empididae	2	–	2	16	2	–	0.33– 0.59
Ephydridae	11	15	13	38	1	–	1.18– 0.37
Muscidae	–	–	2	2	4	–	0.12– 0.05
Dixidae	4	1	–	1	4	2	0.18– 0.00
pupae	113	92	140	515	151	77	16.40– 2.50

data series, that of every second month except that the series from December was substituted for that of November (when sampling was perturbed by cattle passing through the stream).

Composition of the drift

The species composition of the drift samples is very similar to that of the benthos (Tables 1 and 2); the relative abundances are however different. A few taxa were collected in the drift but not in the benthos (*Eukiefferiella, Eurycnemus, Heterotrissocladius,* Dixidae), and very few from the benthos were not recovered at least once from the drift (*Psectrocladius, Brillia, Thienemaniella, Harnischia, Endochironomus,* etc.). In all cases, these are rare species in the habitat, and their absence can be explained by chance.

By comparing the percentages of each taxon in the drift and in the benthos, one can assess its tendency to drift; many groups, such as the Platyhelminthes, the Nematoda, the Annelida, and the Copepoda are underrepresented in the drift; all these animals are known to be poor drifters, though we would have expected many more Copepoda, given the high densities they sometimes reach in the benthos (Turcotte & Harper, 1982). The other groups, particularly the insects, are well represented in the drift. Within the insect groups (Table 2), the tendency to drift varies as well; the Trichoptera and the Ephemeroptera are relatively more numerous in the drift, while the Plecoptera, the Coleoptera and the Diptera are relatively more abundant in the benthos.

Among the Ephemeroptera, as could be expected, the current-loving *Baetis* and *Baetodes* play a relatively more important role in the drift than the more lentic *Atalonella.*

Similarly within the Plecoptera, *Claudioperla* is more liable to drift than *Anacroneuria.*

In the Trichoptera, the free-living *Atopsyche* and the micro-caddisflies (Hydroptilidae) are important components of the drift, whereas the Leptoceridae and the Limnephilidae in their stone cases are not.

The relatively high abundance of the Helodidae (Coleoptera) in the drift is surprising, since they are uncommon in the benthos; by contrast, the Elmidae which are the dominant beetles drift relatively little.

Among the Diptera, many of the uncommon families (such as the Psychodidae and the Tipulidae) were more important in the drift than in the benthos, whereas the dominant Chironomidae were on the whole less represented in the drift. Exception must be made however of the pupae which are always abundant. The tendency to drift varies also among genera; thus *Psectrocladius* appears relatively more common in the drift, while others, such as *Podonomus, Cricotopus* and *Pseudochironomus,* are so in the benthos.

Winged insects and terrestrial invertebrates make up an average of 16% of the drifting animals (Table 3); these are either freshly emerged aquatic insects,

Table 3. Terrestrial organisms collected in the drift (N/24 h).

	Sep.	Dec.	Jan.	Mar.	May	Jul.	%
Oligochaeta	–	–	–	3	3	2	0.24
Isopoda	–	–	–	3	–	–	0.09
Arachnida	6	7	13	14	16	8	1.93
Myriapoda	–	–	7	–	–	–	0.21
Protura	1	–	–	–	–	–	0.03
Diplura	–	–	–	2	–	–	0.06
Collembola	36	147	86	154	45	41	15.31
Thysanura	1	2	–	7	–	–	0.30
Orthoptera	–	–	–	–	–	1	0.03
Psocoptera	–	1	1	3	3	1	0.27
Thysanoptera	1	2	–	7	1	–	0.33
Homoptera	76	79	52	437	130	23	23.98
Heteroptera	–	3	–	1	2	4	0.30
Hymenoptera	18	23	5	22	18	9	2.86
Coleoptera	8	4	2	22	7	4	1.41
Lepidoptera	–	1	–	2	5	–	0.24
Neuroptera	–	–	–	1	–	–	0.03
Diptera	329	101	229	406	288	388	52.38
Total	476	370	395	1084	518	481	

spent females of aquatic species, or insects and invertebrates (spiders, springtails and Homoptera) blown into the water from the riparian vegetation.

Density of the drift

As the net filtered all the water flowing in the stream, it is possible to estimate the number of animals drifting down into the main river each day; this estimate varies from 1898 to 7923 for an average of 3433 (N = 6, Fig. 2). Bishop (1973) gives values of 7 000 to 40 000 for a headwater section of the Malayan river Sungai Gombak, but this was a slightly larger stream.

If the data are converted to numbers per cubic meter of water, the densities vary from 0.85 to 3.28 and compare favorably with other estimates made in the tropics (1.56–1.79 in Malaya (Bishop 1973); 0.1–1.9 in Ghana (Hynes 1975); 0.03–0.49 in Florida (Cowell & Carew 1976)). Indeed they are of the same order of magnitude as in a temperate system, where drift densities only rarely exceed 10 (Bishop 1973).

Seasonal variations

The composition of the drift (Fig. 3) varies

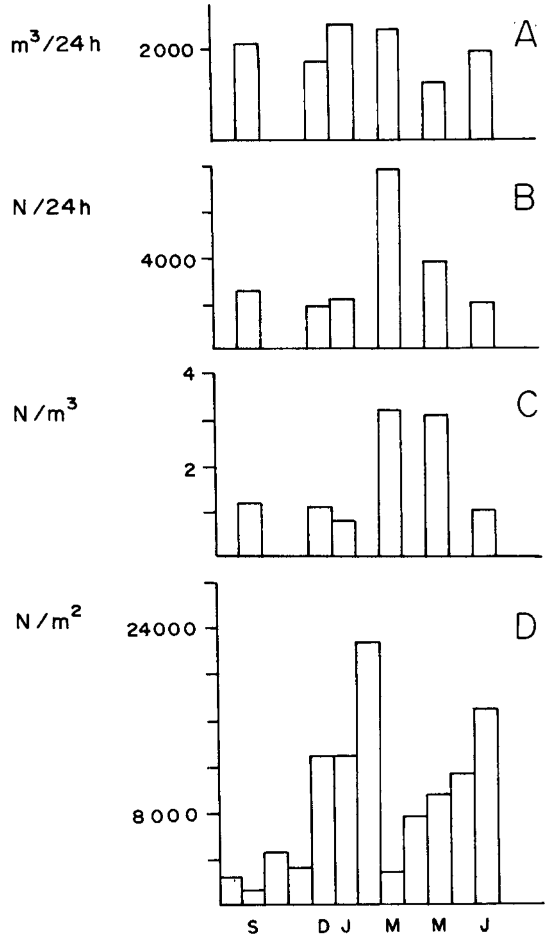

Fig. 2. Flow (A), drift (B and C) and benthos (D) throughout the year.

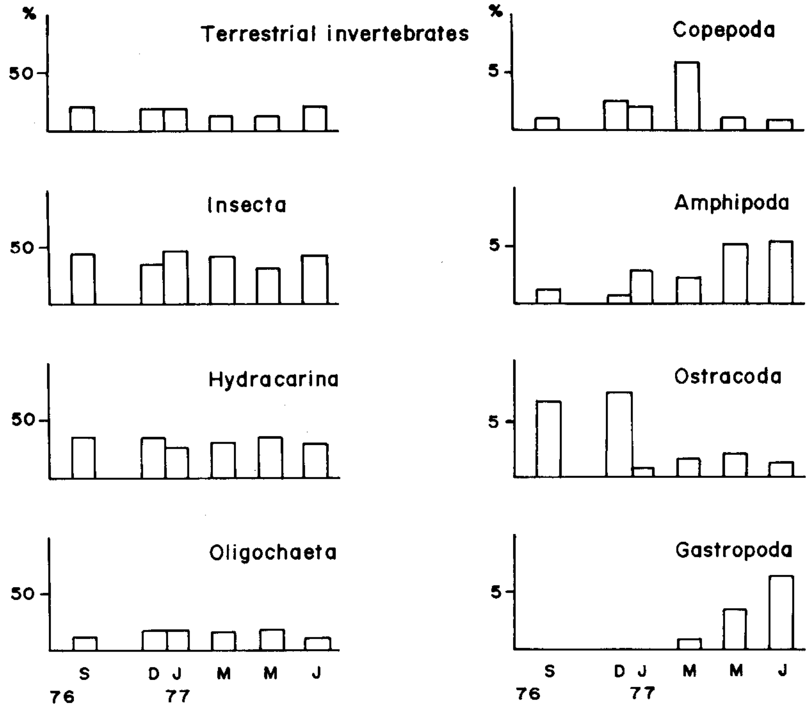

Fig. 3. Relative importance (%) of each major taxon in the six drift samples.

relatively little during the course of the year, as does that of the benthos (Turcotte & Harper 1981). The insects (30–46%), the terrestrial invertebrates (13–23%), the watermites (26–36%), and the oligochetes (9–18%) are always the main components. Other groups, such as the ostracods, the amphipods, and the gastropods, are more sporadic and tend to gain importance in some months. Among the insects, dipteran pupae, *Baetis, Cricotopus* and *Psectrocladius* are the dominant taxa.

The intensity of the drift does however vary somewhat during the year. The numbers of animals drifting per day are relatively constant from one sampling data to the next (1 800–3 900), except in March when there is an exceptionally high number (7 923); it is perhaps noteworthy to recall that in March an important decrease was observed in the benthos by comparison with the previous month (of nearly one order of magnitude) and is thought to be due to spates (Turcotte & Harper 1982); this is not inconsistent with high drift rates in the March sample.

When expressed as numbers per unit volume, the drift rates are similar in most months, except (as could be expected) in March, but also surprisingly in May; the flow rates were then relatively low and no immediate cause of this high number of drifting animals is seen.

Figure 2 shows the corresponding values of the drift and of the benthos; no simple correlation is evident, but perhaps too few series of data were taken and analyzed. If Neveu's (1974) calculation is computed from these data, it appears that at any one time only a small fraction of the fauna is actually in the drift; for instance in September, the density of the benthos was estimated at 1 254 animals m^{-2} and the drift at 1.24 animals m^{-3}; as 1 m^3 of water covers approximately 5 m^2 of bottom, it appears that only 0.02% of the fauna is drifting at any one moment.

Diel periodicity

The circadian variations in the drift are illustrated both by the four 4-sample series and the two 16-sample series.

When total drift is taken into account (Fig. 4), no

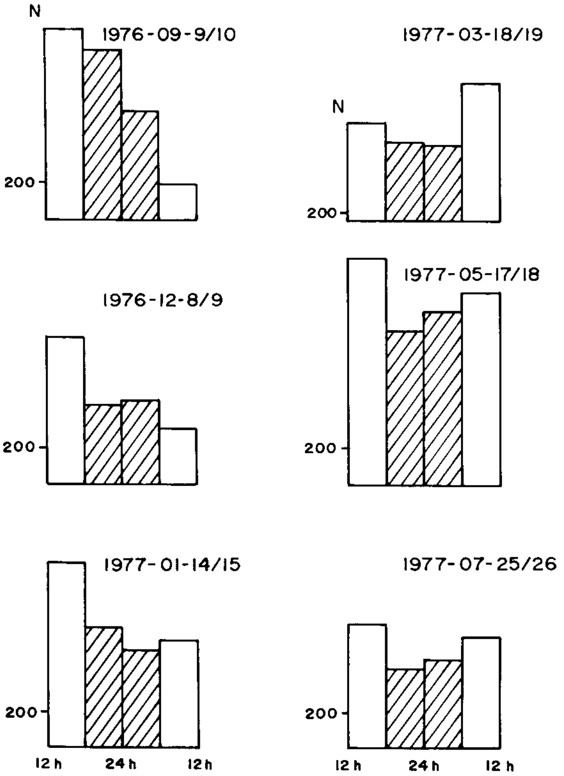

Fig. 4. Diel periodicity of the total drift in the six samples (N/24 h).

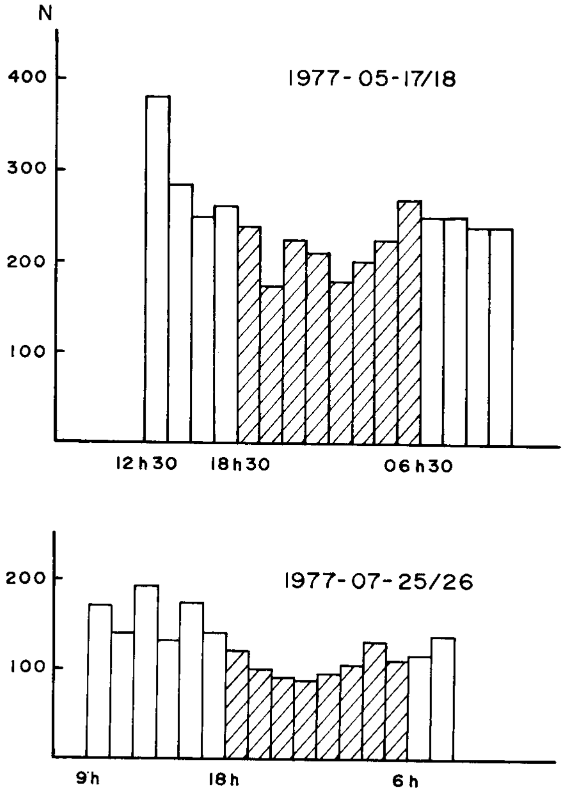

Fig. 5. Diel periodicity of the total drift in the May and July samples (N/24 h).

constant pattern seems to recur in the six data series. Unexpectedly the maximum drift is always observed in the daytime. The phenomenon is even clearer in the 16-sample series (Fig. 5). The same observations can be made on the major taxa (Fig. 6) and in no case is the maximum at night, even in groups such as *Baetis* which are universally known as night-active.

If single series are considered (Figs. 7 and 8), obscure patterns can be recognized: *Baetodes, Magellomyia, Ochrotrichia, Psectrotanyous, Pseudochironomus,* dipteran pupae, and terrestrial invertebrates are predominantly day-drifters; *Baetis, Anacroneuria, Neotrichia,* and in one instance *Oxyethira* are more abundant in the night samples; others, such as *Atopsyche, Cricotopus, Limnophyes,* and the Simuliidae, show no marked periodicity. In all cases the patterns are not clearcut, and obviously vary much from one month to the next.

Discussion

As Waters (1972) has pointed out, there does not exist a particular drift fauna and most benthic organisms will at one time or another be picked up in the drift. However the tendency to drift differs considerably from one group to the next, and this is evident when one compares the relative densities of each taxon in the benthos and in the drift. In our stream, as elsewhere, the active swimming animals, such as *Baetis,* are much more likely to drift than others which are sluggish or weighted down by a stone case.

The terrestrial component of the drift is important both by the numbers and the variety of animals it comprises. Hynes (1975), in an African stream, had observed a terrestrial component of less than 1%, most of it made up of ants; Bishop (1973), on the other hand, collected large numbers of terrestrial invertebrates drifting in a Malayan river; other

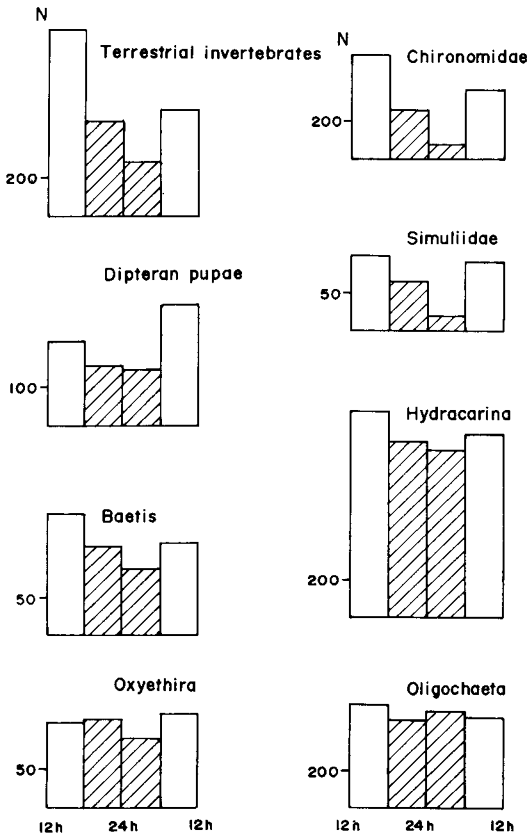

Fig. 6. Diel periodicity in the drifting of major taxa (N/24 h). September, December, January and March samples pooled.

authors (Cowell & Carew 1976; Elouard & Lévêque 1977) do not mention terrestrial animals, perhaps because they were relatively insignificant in their data-series.

It is not easy to distinguish in our stream between background drift (a simple dislodging of the animals by the current) and true drift (a behavioral action of the animal). Hynes (1975) has argued that true drift should be less important in the tropics where single-species populations are never large due to the high diversity of the stream communities. This situation does apply to our stream in which diversity is not particularly high compared to other systems; nonetheless there is little evidence of true drift in response to high densities, but perhaps our observations are still too fragmentary. Catastrophic drift (as a consequence of scouring of the bottom by spates) has also been set forth as an explanation of the high drift rates during rainy periods; indeed Van Someren (1952) observed large numbers of *Baetis* and Simuliidae being carried down by rapid waters in Kenya. The only instance in our observations when such a phenomenon could have occurred was in March; the drift was sampled after a period of extended rain; in fact, although flow rates were not unusually strong, the drift rates were quite high and there was a marked reduction in the benthos from the previous month. As well, many forms not usually found in large numbers in the drift (*Oxyethira, Micropsectra, Gigantodax,* etc.) were particularly abundant.

The absence of a simple correlation between the benthos and drift values is not surprising since similar observations were made nearly everywhere else (Müller 1966; Elliott 1967; Bishop & Hynes 1969). Drift is thus not a simple index of the benthos which generates it (Elliott & Minshall 1968). The drift rates we observed are within the usual ranges and require no special discussion.

The absence of a clear daily periodicity in the drift in our stream is perhaps our most interesting observation. Since Tanaka (1960) described diel variations in the composition and the intensity of the drift, similar patterns have been observed again and again the world over, in tropical latitudes (Bishop 1973; Hynes 1975; Elouard & Lévêque 1977) as well as elsewhere. We had expected a much more distinct variation between day and night, particularly within groups such as *Baetis* which usually show such unmistakable patterns. In Hynes' (1975) data series, many do not exhibit very clear periodicities, but in all cases the absence of pattern could be related to clear moon-lit nights. In our stream this cannot be the case as the stream was clouded over or fogged in on most sampling dates. The phenomenon obviously requires further study to find out if it is widespread in cold tropical habitats or whether our data are atypical.

The insects drifting down from small streams such as ours into the mainstream must provide an important source of food for the fish living there, especially since salmonids are dependent on drift for their nutrition (Elliott 1973). Since the major streams in the high Andes are subject to much flushing due to spates, the continuous inflow of invertebrates from dozens of small tributaries must represent a major contribution to the trophic structure of the system. As an example, it can be estimated that the small stream we studied con-

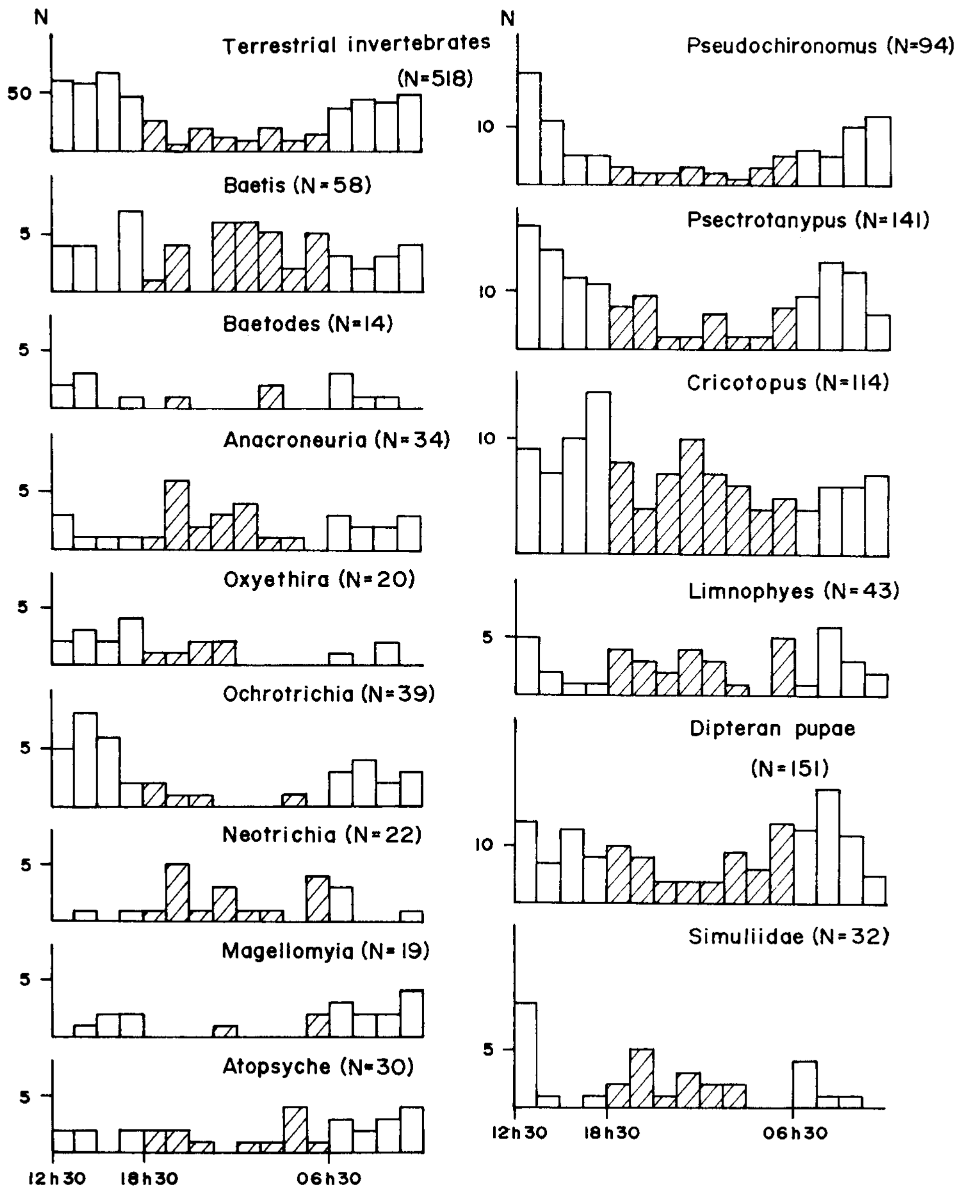

Fig. 7. Diel periodicity in the drifting of major taxa in the May sample (N/24 h).

tributed during the year some 600 000 m^3 of water to the mainstream together with some 1.2 million animals.

Further study is indeed warranted of the structure and the functioning of high altitude tropical streams in order to correct the current concepts of stream ecosystem which are based too exclusively on northern temperate rivers which are perhaps in many regards atypical. Furthermore, tropical streams are devoid of the many and interdependent environmental cues that so obscure the controlling factors in temperate running water ecosystems.

Summary

1. The composition of the drift in a small stream in the paramo of Ecuador is similar to that of the

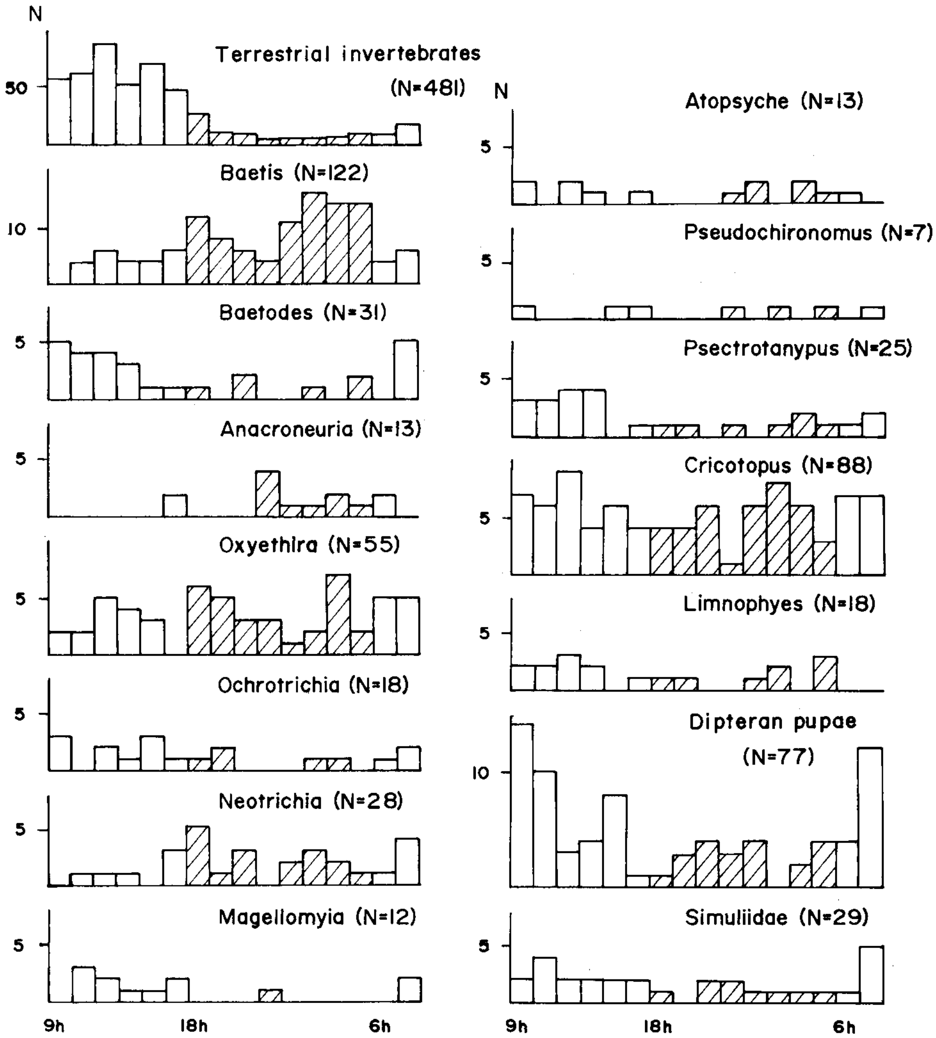

Fig. 8. Diel periodicity in the drifting of major taxa in the July sample (N/24 h).

benthos, though relative frequencies of the various groups often differ. Insects, watermites and oligochaetes are the major components; among the insects, the Ephemeroptera *(Baetis)*, the Trichoptera *(Oxyethira, Ochrotrichia)*, and the Diptera *(Psectrotanypus, Cricotopus, Pseudochironomus, Gigantodax)* are the dominant taxa.

2. Terrestrial invertebrates and insects represent an average of 16% of the drifting animals. The major groups are Arachnida, Collembola and Homoptera blown into the stream from the surrounding paramo grasses and bushes.

3. An average of 3 433 (1 898–7 923) invertebrates drift down the stream into the main river each day; this represents some 0.85–3.28 invertebrates per cubic meter of water. These values are of the same order of magnitude as thoses measured in other tropical streams.

4. The composition of the drift varies little over the course of the year, and drift rates were similar in most months, except towards the end of the rainy season (March and May).

5. Few diel patterns are apparent in the drift; surprisingly, on the whole, there is more drifting during the day than during the night. Few species exhibit a clear periodicity and there is much variation from one month to the next.

6. Drift is a means by which many invertebrates

are transferred from the numerous small streams into the torrential rivers where they are a potentially important source of food for the fish (trout) which have been introduced there.

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