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Seasonal dynamics of invertebrate drift in a Hong Kong stream

DAVID DUDGEON

Department of Zoology, The University of Hong Kong, Hong Kong

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(With 6 figures in the text)

Drift samples were taken with paired nets on 19 occasions over a 12-month period in Tai Po Kau Forest Stream (TPKFS), Hong Kong. Mean drift density (± 1 S.E.) was $277{\cdot}9 \pm 25{\cdot}0$ individuals 100 m^{-3}; peaks in density were apparent during autumn and spring. One hundred and two taxa were recovered from the drift, and the total number of taxa drifting was positively related to water temperatures. Over 99% of the aquatic animals collected in drift samples were insects, 10 taxa of which constituted 67·3% of the entire catch. Baetid mayflies dominated the composition of the drift, comprising 40·4% of individuals caught.

Seasonal changes in the drift of individual taxa were evident, reflecting significant relationships between drift densities and water temperature: *Simulium* T_1 (Diptera), *Anisocentropus maculatus* (Trichoptera) and *Amphinemura chui* (Plecoptera) drifted most in winter, whereas *Chimarra* T_1, *Polymorphanisus astictus* (Trichoptera), *Helodes* #1 and cf. *Rhantus* sp. (Coleoptera) were most numerous in summer. Drifting mayflies showed spring (*Indobaetis* sp., *Cinygmina* T_1, *Serratella* T_2), autumn (*Baetiella* sp., *Pseudocloeon* T_2), or spring and autumn (*Baetis* nr *pseudofrequentus*) peaks which were not clearly related to water temperature. In only two cases (*A. maculatus* and *P. astictus*) was TPKFS drift seasonality associated with life-cycle events. Overall, there was no evidence of community-level trends in the periodicity of stream drift in this seasonal tropical habitat.

Contents

Introduction

Drift, the downstream transport of benthic animals in running waters, has been widely studied and is the subject of extensive reviews (Waters, 1972; Muller, 1974; Brittain & Eikeland, 1988). Invertebrate drift dynamics are characterized by changes during the course of a single day, as well as between seasons. Diel periodicity is generally manifested by an increase in drift during the night, especially just after sunset, and the pattern seems to apply across all latitudes (Brittain & Eikeland, 1988). The seasonal dynamics of drift are more variable: in temperate regions drift is usually least during the winter (e.g. McLay, 1968; Clifford, 1972; Cloud & Stewart, 1974; O'Hop & Wallace, 1983), whereas in subtropical streams winter peaks (Cowell & Carew, 1976), late-spring peaks

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(Soponis & Russell, 1984) or a lack of periodicity (Benke, Hunter & Parrish, 1986; Allan *et al.*, 1988) have been reported. Data from the tropics are scarce (Brittain & Eikeland, 1988), but a distinct seasonal pattern there may be lacking (Bishop, 1973; Hynes, 1975).

Hong Kong has a seasonal tropical climate, and benthic communities are influenced by variations in temperature and rainfall over an annual cycle (Dudgeon, 1988*a*). It was with the expectation that such seasonality would influence drift dynamics that the present study was undertaken. The results add basic information to the little that is known of riverine ecology in the Oriental tropics and permit comparisons with better-known stream communities elsewhere.

Materials and methods

The study was undertaken in a shaded riffle reach of Tai Po Kau Forest Stream (TPKFS), New Territories, Hong Kong (22° 7′ N, 113° 5′ E), from July 1983 to June 1984 inclusive. The waters of this unpolluted stream are slightly acidic and poor in dissolved minerals; the bottom sediments are coarse and poorly sorted but show marked across-reach gradients, being finer closer to the bank. An account of previous investigations of the ecology of the stream macrobenthos, and a description of the study site, are given by Dudgeon (1987).

The drift samplers used were essentially the same as those described by Field-Dodgson (1985), although the mouthpiece of each of the paired nets was circular (16·6 cm internal diameter) instead of rectangular. Each collecting net was 1·7 m long and constructed of 220 μm mesh. It was slipped over the rear of the mouthpiece and secured with an aluminium hose clamp.

Nineteen duplicated samples were collected during the 12-month study. On each occasion, 2 nets fished the stream for a timed period (varying from 11 to 13·8 h) from dusk until dawn. The sampling duration in winter was thus slightly longer than in summer. Samples were not taken during daylight as most taxa in this and other streams show night-time drift peaks (Dudgeon, 1983; Brittain & Eikeland, 1988). The nets were positioned in shallow water (< 20 cm deep) so that the bulk of the water column was sampled. This should have reduced under-sampling of taxa tending to drift near to the water surface or stream bed. Current speed was estimated by timing the passage of a leaf suspended in the water column over a known distance. Water temperatures were taken at the beginning and the end of sampling; temperature data presented here are the medians of these 2 readings.

Drift densities were expressed in terms of numbers of animals 100 m^{-3}. In order to reduce the effects of spates on drift densities (see Brittain & Eikeland, 1988), each pair of samples was collected following a period of several days without rain. However, heavy rain just before dawn on 6 June 1984 did cause a marked increase in drift densities, and the summer monsoon precluded collection of replacement samples around this date. Clogging and backwash from one of the paired nets was recorded on 2 occasions. Catches from these nets have not been included in the data presented.

Results

A total of 9883 individuals and 102 taxa (excluding terrestrial insects) were recovered from the drift samples. A taxon was a genus or morphospecies in all groups but Chironomidae (which were separated into subfamilies) and water mites (Hydrachnellae). Only seven taxa (two caridean shrimps, water mites, a water snake and four species of fish larvae), comprising 0·6% of the individuals caught, were not aquatic insects.

The mean (±1 S.E.) number of drifting taxa per collection date over the study period was 48·5 ± 1·8, falling to a minimum (33) on 29 December 1983. The highest total of 59 was recorded on three occasions (Fig. 1). Changes in the number of drifting taxa reflected water temperatures: the mean stream temperature was 20·1 ± 1·1 °C, but temperatures fell to 10·5 °C in December 1983, and were highest (25·8 °C) in August 1983 (Fig. 1). A univariate regression of prevailing

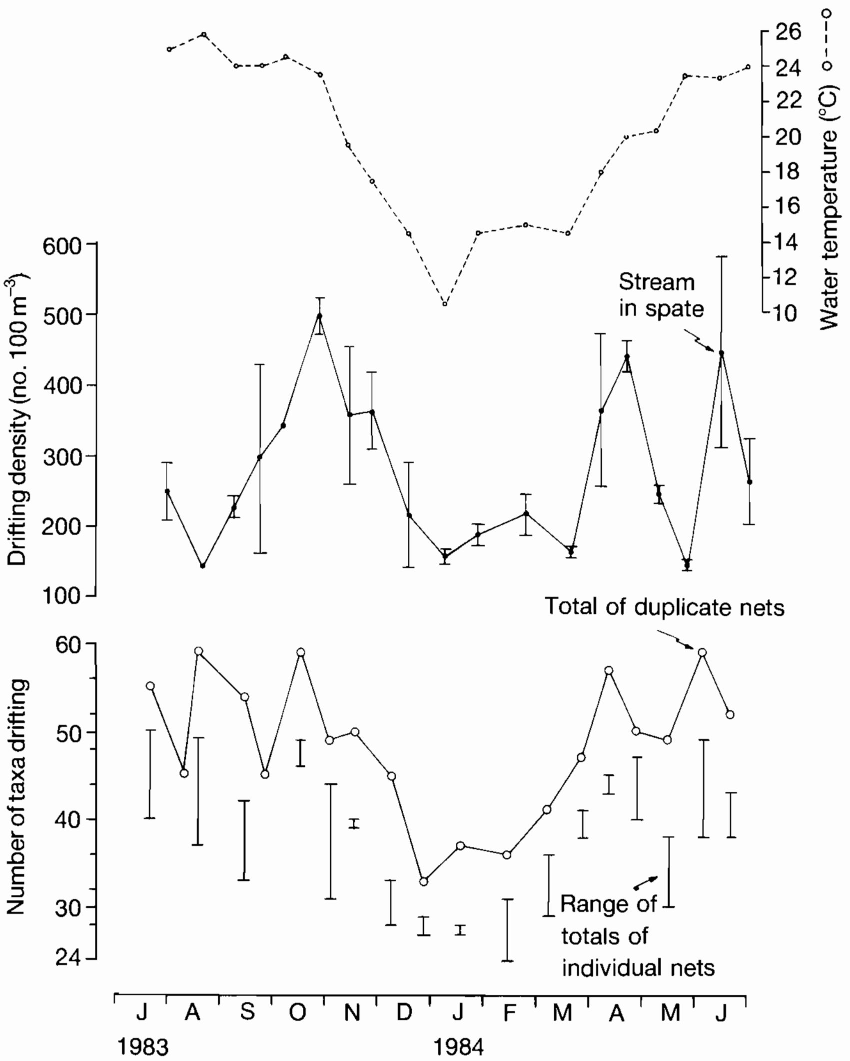

FIG. 1. Drift density (no. 100 m^{-3}; median and range) and number of taxa drifting (total taxa on each date and range of values of individual nets) in Tai Po Kau Forest Stream, Hong Kong. Data based on 19 sets of samples from paired drift nets between July 1983 and June 1984. Water temperatures at the time of sampling are also shown.

temperature versus total number of taxa drifting on each date was highly significant ($r=0{\cdot}739$, $P=0{\cdot}0003$, $n=19$).

Mean drift density over the study was $277{\cdot}9 \pm 25{\cdot}0$ individuals 100 m^{-3}. Leaving aside an increase in drift density on 6 June 1984 which was associated with rising stream discharge volume during heavy rain, peaks in density (400–500 individuals 100 m^{-3}) were apparent during autumn and spring (Fig. 1). Univariate stepwise regressions yielded no significant relationship between drift densities and prevailing temperatures or temperatures on preceding sampling dates. This result was unaffected by exclusion of the 6 June data. There was, however, a significant (and not

TABLE I

Drift composition in Tai Po Kau Forest Stream, Hong Kong: relative abundance of the 10 most numerous taxa in 1983–84 samples

Taxa		Relative abundance (%)
Pseudocloeon T_2	(Ephemeroptera: Baetidae)	16·0
Baetis nr *pseudofrequentus*	(Baetidae)	9·3
Simulium T_1	(Diptera: Simuliidae)	8·6
Orthocladiinae	(Diptera: Chironomidae)	8·5
Indobaetis sp.	(Baetidae)	5·0
Baetiella sp.	(Baetidae)	4·6
Chironominae	(Chironomidae)	4·2
Serratella T_2	(Ephemeroptera: Ephemerellidae)	4·1
Helodes #1	(Coleoptera: Helodidae)	4·0
Amphinemura chui	(Plecoptera: Nemouridae)	2·8

unexpected) relationship between drift densities and the number of taxa drifting ($r=0{\cdot}628$, $P=0{\cdot}004$, $n=36$).

Baetid mayflies (nine species) dominated the composition of the drift, comprising 40·4% of all individuals caught. *Pseudocloeon* T_2 was the most abundant species, making up 16·0% of the total catch. Chironomidae constituted 15·6% and Simuliidae 8·6% of drifting animals. Table I lists the 10 most abundant taxa in declining rank order; together they comprised 67·3% of total drift.

Seasonal changes in the drift densities of individual taxa were evident, and significant relationships between log transformed densities ($X'=\log[X+1]$) and water temperature were recorded. Among the Diptera, *Simulium* T_1 was most numerous during the cooler months from November through March ($r=-0{\cdot}552$, $P=0{\cdot}0005$, $n=36$), when it constituted approximately 20% of total drift (Fig. 2). Seasonality was not obvious among Orthocladiinae and Chironominae (data not presented here), reflecting the fact that these taxa comprised several species, each of which may have had its own distinct seasonal drift pattern (Soponis & Russell, 1984). In addition, the 220 μm-mesh drift nets used in this study would have permitted the passage of first- and second-instar chironomids, thus distorting the composition of samples (Storey & Pinder, 1985; Williams, 1985).

In contrast to the seasonal changes in *Simulium* T_1 drift density, *Pseudocloeon* T_2 were abundant in summer and autumn and were especially numerous in September through November (Fig. 3). During this peak period, *Pseudocloeon* T_2 made up over 30% of the total drift. The seasonality of drift among other Baetidae varied considerably according to species. Like *Pseudocloeon* T_2, *Baetiella* sp. was most numerous in drift samples during the autumn (Fig. 4). Drift densities of *Baetis* nr *pseudofrequentus* Muller-Liebenau peaked during autumn (October and November) and spring (March and April), while *Indobaetis* sp. was most abundant in spring drift samples. Among non-baetid mayflies, *Cinygmina* T_1 (Heptageniidae) also showed a springtime drift peak (Fig. 5); a similar periodicity was weakly exhibited by *Serratella* T_2 which drifted throughout the year. There were no significant relationships between water temperature and drift densities of any mayflies.

Trichoptera larvae were poorly represented in the TPKFS drift samples and comprised <6% of the total catch. Among the more abundant species, *Chimarra* T_1 (Philopotamidae) drift densities showed a winter decline (Fig. 5), and were positively related to water temperature ($r=0{\cdot}442$,

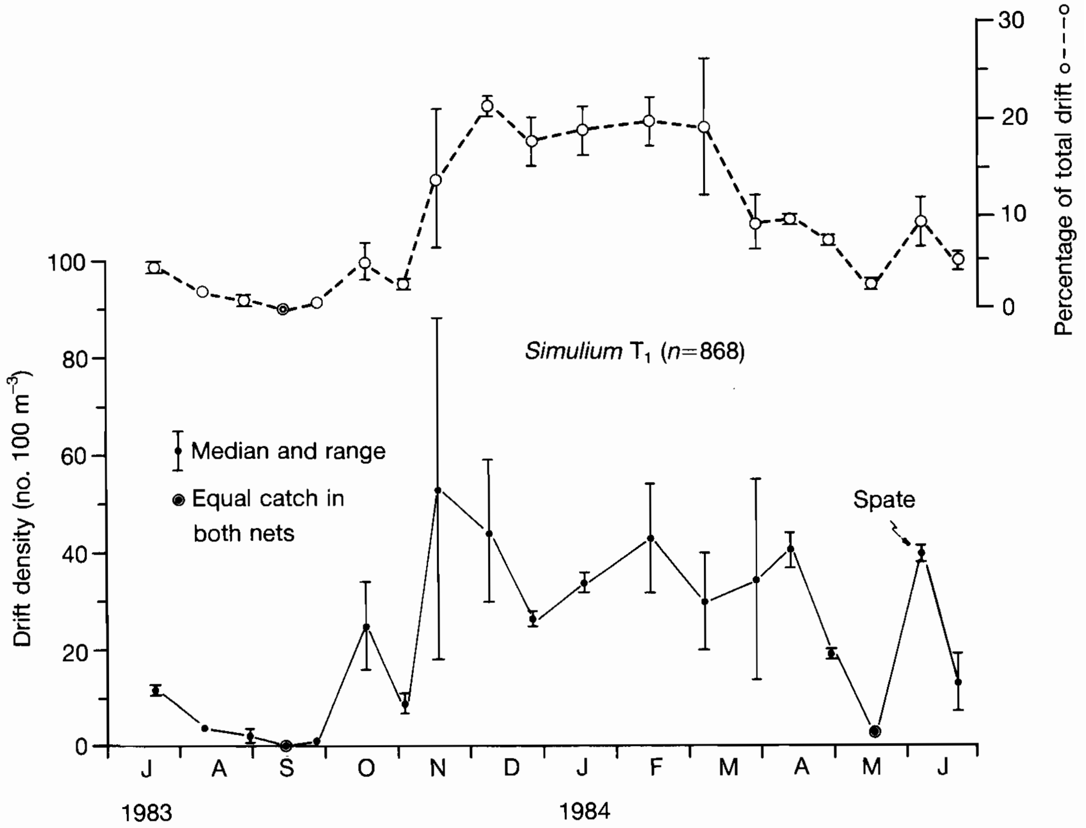

FIG. 2. Drift density (no. 100 m^{-3}; median and range) of *Simulium* T_1 larvae in Tai Po Kau Forest Stream (July 1983–June 1984). The percentage contribution of this species to the total number of animals drifting is also shown.

$P=0{\cdot}0069$, $n=36$). By contrast, drift of *Anisocentropus maculatus* Ulmer (Calamoceratidae) was negatively correlated with temperature ($r=-0{\cdot}607$, $P=0{\cdot}0001$, $n=36$). Densities were highest between November and March, and these caddisflies were not recorded between May and August (inclusive). Only first-instar larvae of *Polymorphanisus astictus* Navas (Hydropsychidae: Macronematinae) were found in drift samples; they were taken in summer and were most numerous during June and July. A significant relationship with water temperature was recorded ($r=0{\cdot}347$, $P=0{\cdot}038$, $n=36$).

Amphinemura chui (Wu) was the most numerous drifting stonefly, comprising >90% of the plecopteran catch. Seasonal periodicity was manifested by a winter peak in drift (Fig. 6), and densities increased significantly as temperatures fell ($r=-0{\cdot}581$, $P=0{\cdot}0002$, $n=36$). Among the Coleoptera, families which were well represented in the stream benthos (e.g. Elmidae and Psephenidae) were scarce in drift samples. *Helodes* #1 and larvae of the dytiscid beetle cf. *Rhantus* sp., however, were exceptions to this generalization. *Helodes* #1 drifted most readily during the summer, whereas cf. *Rhantus* sp. attained highest drift densities during July and August and was not recorded in drift samples between November and April. Drift of both species was significantly related to temperature ($r=0{\cdot}636$ and $0{\cdot}593$, respectively, $P\leq0{\cdot}0001$, $n=36$).

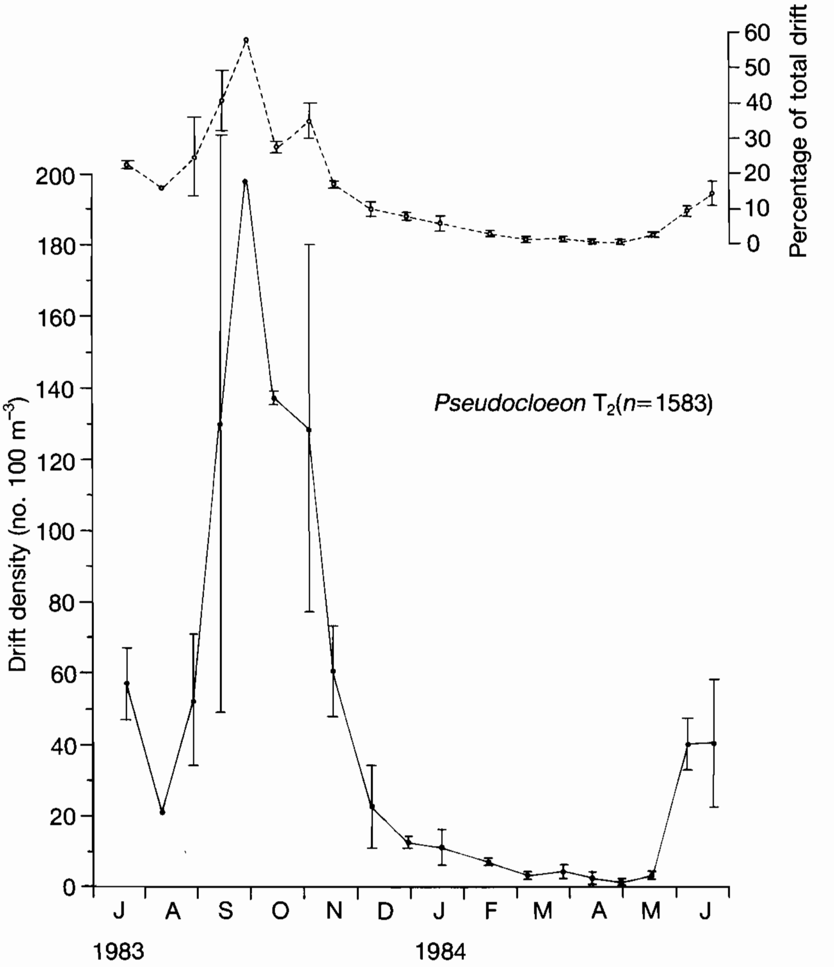

FIG. 3. Drift density (no. 100 m^{-3}; median and range) of *Pseudocloeon* T_2 larvae in Tai Po Kau Forest Stream (July 1983–June 1984). The percentage contribution of this species to the total number of animals drifting is also shown.

Discussion

Drift densities in TPKFS were well within the range of values recorded for temperate and subtropical streams (Waters, 1972; Allan *et al.*, 1988; Brittain & Eikeland, 1988). The composition of samples seemed, however, relatively diverse, although it must be emphasized that 10 out of the 102 taxa collected made up almost 70% of the total catch. Such diversity may reflect the duration of drift collections, because sampling throughout the night (as in the present study) will lead to more diverse catches than sampling for a shorter period immediately after dusk (e.g. Cowell & Carew, 1976; Benke *et al.*, 1986; Allan *et al.*, 1988). However, levels of taxonomic resolution employed by different investigators—especially with regard to Diptera (e.g. Benke *et al.*, 1986 versus Allan *et al.*, 1988)—profoundly affect records of the diversity of drifting animals and

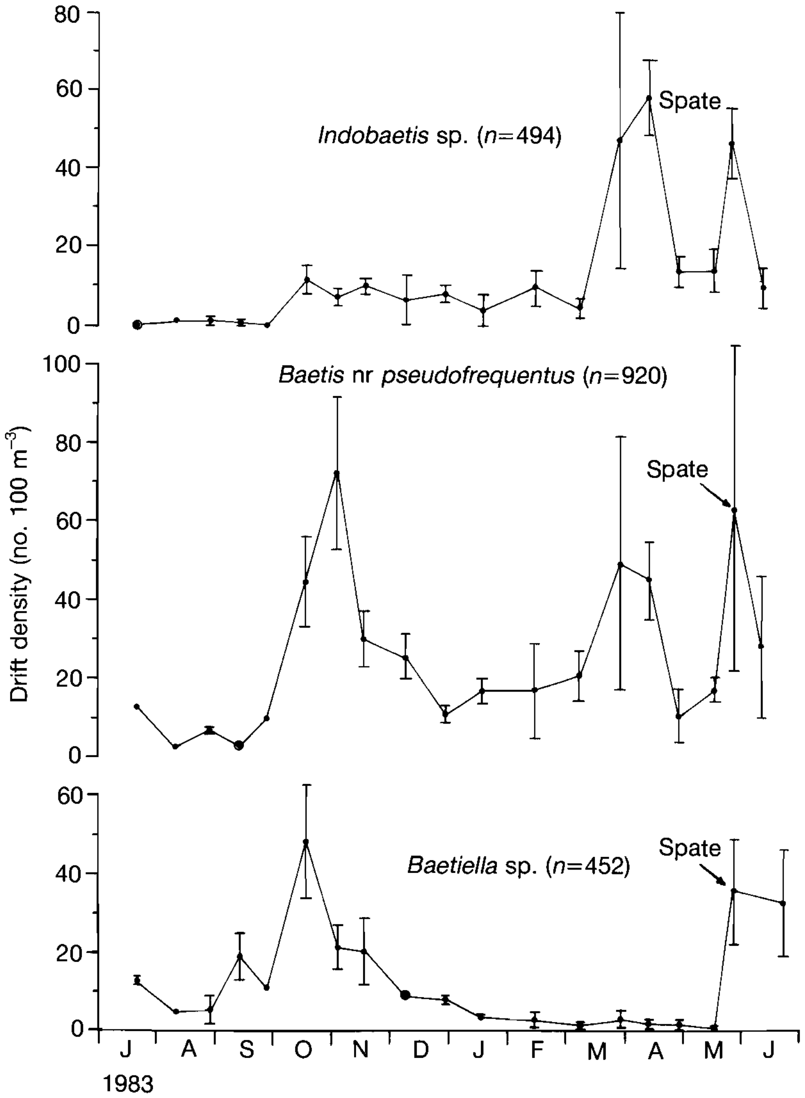

FIG. 4. Drift densities (no. 100 m^{-3}; median and range) of three species of baetid mayflies in Tai Po Kau Forest Stream (July 1983–June 1984).

thereby confound inter-habitat comparisons. Nevertheless, it was clear that the overall composition of TPKFS drift was broadly comparable with that of other tropical streams (e.g. Bishop, 1973; Hynes, 1975), and the observation that a few abundant taxa comprised a high proportion of the drift seems typical (Cowell & Carew, 1976). These studies also indicate that Baetidae are a major part of the drift in a variety of tropical and subtropical streams, although there may be local deviations from this pattern (Benke *et al.*, 1986).

Data on the constitution of TPKFS benthos (Dudgeon, 1988*c* and unpubl. obs.) indicate that drift composition is not simply a reflection of bottom communities. Hydropsychid caddisflies

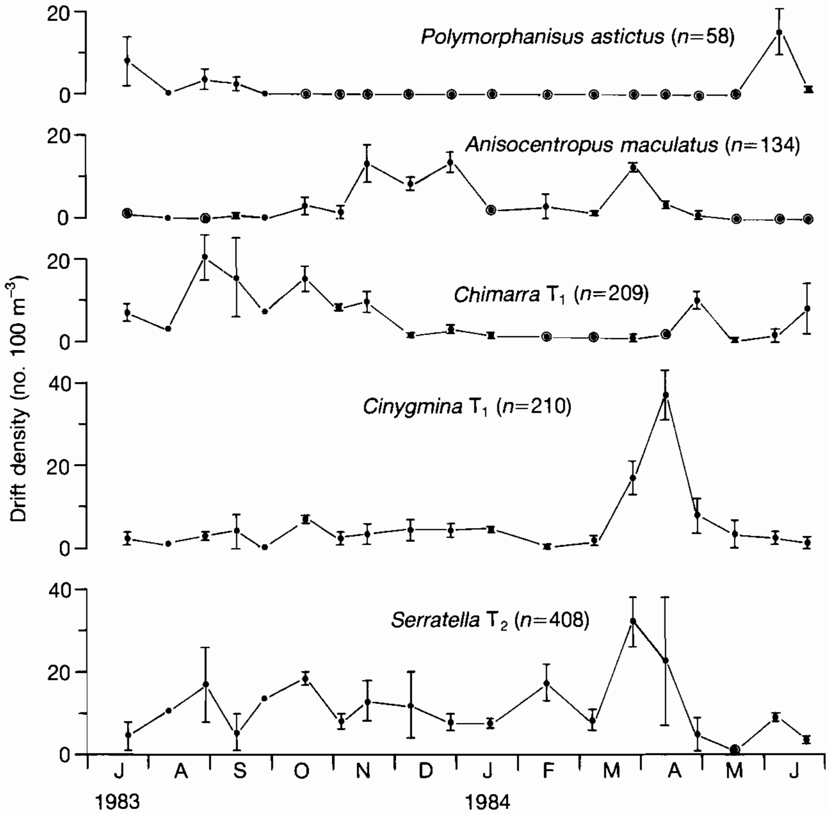

FIG. 5. Drift densities (no. 100 m^{-3}; median and range) of two mayfly and three Trichoptera species in Tai Po Kau Forest Stream (July 1983–June 1984).

(especially *Cheumatopsyche* spp.) and leptophlebiid mayflies are major components of the benthos which were scarce in drift samples. Elmid and psephenid beetles were likewise under-represented. This result highlights the fact that drift is largely a result of behavioural mechanisms and that individual taxa differ in their propensity to abandon the stream bed.

Seasonal peaks in total drift density occurred in autumn and spring, while the number of taxa drifting was significantly related to water temperature and was highest in the summer. As Cowell & Carew (1976) noted, total drift densities were not clearly related to temperature but seemed to increase when the stream cooled in autumn and warmed during spring. Whereas changing water temperatures could have triggered drifting behaviour, other factors, such as photoperiod (e.g. shorter summer nights) or phases of the moon (Hynes, 1975), might have influenced the observed pattern. Shading of the study reach by riparian forest would, however, have reduced any depressant effect of moonlight on drift. Changes in discharge volume are also unlikely to have produced the observed seasonal pattern because stream flow declined steadily during the autumn and winter dry season until the onset of the summer monsoon in June.

The possibility that a single explanation might account for changes in total drift density over the study period gains little support from data on seasonal patterns of drift among individual taxa.

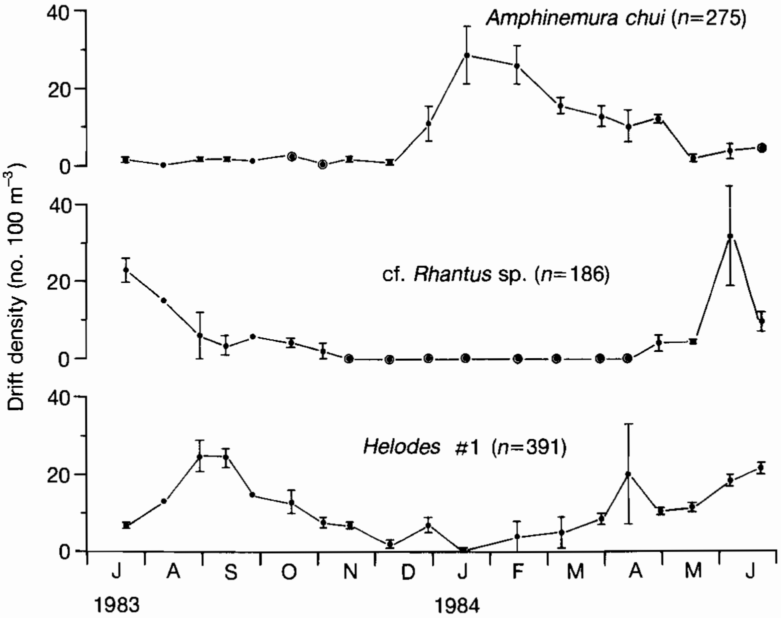

FIG. 6. Drift densities (no. 100 m^{-3}; median and range) of the stonefly *Amphinemura chui* and larvae of two Coleoptera species in Tai Po Kau Forest Stream (July 1983–June 1984).

Simulium T_1, *Anisocentropus maculatus* and *Amphinemura chui* showed winter peaks; *Chimarra* T_1, *Polymorphanisus astictus*, *Helodes* #1 and cf. *Rhantus* sp. were most numerous in summer drift samples, whereas other taxa exhibited spring (*Indobaetis* sp., *Cinygmina* T_1, probably *Serratella* T_2), autumn (*Pseudocloeon* T_2, *Baetiella* sp.), or both spring and autumn (*Baetis* nr *pseudofrequentus*) peaks. It is notable that drift densities in species with summer or winter peaks were significantly related to water temperatures, but that the effects of changing water temperatures varied between taxa. No direct relationship between water temperature and the drift of any mayfly taxa could be detected.

Polymorphanisus astictus and *Anisocentropus maculatus* drift comprised mainly first-instar larvae and was associated with recruitment (Dudgeon, 1988*b* and unpubl. obs.). Drift of other taxa involved a range of instars and could not be linked with known periods of emergence or oviposition. An understanding of the significance of drift will require investigations of the population dynamics, life cycles and interactions of the main components of TPKFS benthos. Such work is in progress.

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