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Aspects of the microdistribution of insect macrobenthos in a forest stream in Hong Kong

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With 15 figures and 1 table in the text

Abstract

An investigation of the microdistribution of 47 benthic insect taxa across the width of a shaded riffle reach of Tai Po Kau Forest Stream, New Territories, Hong Kong, was undertaken during the summer of 1977. Certain taxa were confined to midstream areas whilst others showed no obvious trends in this respect. Closely related species were frequently spatially isolated indicating a possible mechanism for avoiding interspecific competition. Species richness of the benthos was maximal at sites between the banks and midstream areas. Such localities were transitional with respect to their physical characteristics and had sediments comprised of a wide range of grain sizes. There was no relationship between species richness and macroinvertebrate abundance, nor between either of these variables and mean sediment grain size. On the basis of this study it is probable that areas of stream bed with the greatest degree of physical heterogeneity will support the most diverse assemblage of benthic fauna, although this pattern may be altered by life cycle events. However, in view of the often contradictory findings of investigations concerned with factors influencing the microdistribution of benthic invertebrates, further research is required before any such generalizations can be widely and uncritically applied.

Introduction

The distribution of benthic macroinvertebrates in lotic environments can be considered on two levels. Firstly, in terms of the locations at which these animals are found along the course of a particular habitat, i.e. how they are zoned, and secondly, their distribution within a given reach of the stream or river under study. The latter category is termed microdistribution and will be considered here with respect to the macrobenthos of a single shaded riffle reach of Tai Po Kau Forest Stream, New Territories, Hong Kong.

Cummins (1975) has stated that of the range of factors to which benthic macroinvertebrates respond, current flow, sediment type and the availability of food constitute the parameters of primary significance in determining microdistributional patterns. Other variables such as light and shade (Hughes 1966;

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THORUP 1966) as well as biological interactions (PECKARSKY 1979) may play a lesser part in determining microdistribution patterns but, on the basis of published information, it is apparent that substrate (PERCIVAL & WHITEHEAD 1929; CUMMINS 1964; THORUP 1966; CUMMINS & LAUFF 1969; CRISP & CRISP 1974; DE MARCH 1976; MINSHALL & MINSHALL 1977), current (PHILIPSON 1954, 1969; PHILLIPSON 1956; EDINGTON 1968; PHILIPSON & MOOREHOUSE 1976) and food-generally detritus (EGGLISHAW 1964, 1969; ULFSTRAND 1968; HYNES 1970) – are of primary importance. While certain other factors such as temperature, water chemistry and the presence of pollutants are known to affect macroinvertebrate distribution, these probably determine the occurrence or absence of a particular taxon in a given stretch of water rather than its distribution within that locality (ULFSTRAND 1967).

Numerous laboratory and field investigations have been undertaken in order to determine which environmental factors influence or control the microdistribution of particular taxa, thus leading to the correlation of microdistribution and abundance of faunal elements with various specific physicochemical or biotic factors. Such evidence is, however, inherently weak (CUMMINS 1975) since the relationship studied may not be direct. DUDGEON (1982 a) has demonstrated that the characteristics of the bottom sediments varied in a predictable way across the width of Tai Po Kau Forest Stream. Some differences in the standing stock of periphyton and, to a lesser extent, allochthonous detritus were also noted (DUDGEON 1982 b) and, in view of the importance of these parameters in determining macroinvertebrate abundance, some variation in the composition of the benthic fauna across the width of the stream was anticipated. Significantly, sediment characteristics showed the most consistent across-stream variation in the study area and are considered by some authors (e. g. BISHOP 1973) to be the primary factor determining macroinvertebrate distribution.

While current velocities in Tai Po Kau Forest Stream show marked changes over small areas, they were frequently relatively slight close to the stream bed (DUDGEON 1982 a). Moreover, most benthic invertebrates are restricted to boundary layers of marginal flow by morphological or ethological adaptations (NIELSON 1951; JAAG & AMBÜHL 1963) which generally isolate them from the full force of the current. Although current is important in providing stream invertebrates with fresh water which enables them to carry out gaseous exchange ("physiological enrichment", s. s. RUTTNER 1963), it is unlikely to be of great significance in determining the microdistribution of lotic macrobenthic taxa except in a few specialized microhabitats or in the case of net-spinning and filter-feeding taxa (PHILIPSON 1954, 1969; PHILLIPSON 1956).

The effects of substrate type and the associated food particles are of direct and immediate relevance to freshwater benthic animals, and it is unlikely that it will be possible to isolate the separate influences of these factors. The use of artificial substrates (e.g. MINSHALL & MINSHALL 1977) may lead to some generalizations concerning the importance of particle size in controlling the microdistribution of lotic macrobenthos, but in-stream effects, such as the accumulation of detritus on samplers (ULFSTRAND 1968; MINSHALL & MINSHALL 1977), complicate the findings of such investigations. For such reasons, no attempt was made in the present study to isolate the effects of different environmental variables on different taxa but, instead, changes in the distribution of various species across the width of the study reach were considered in view of what is already known about the characteristics of the stream bed (DUDGEON 1982a, b). Previously, only one brief study has been concerned with the distribution of fauna across the width of a stream (HIGLER 1975) although it has been stated that benthic invertebrates in temperate streams increase in numbers and diversity over the sequence of increasing particle sizes from sand through to large stones (SPRULES 1947; MACKAY 1969; CRISP & CRISP 1974). As mean sediment grain size increased across the width of Tai Po Kau Forest Stream reaching a maximum in the central portions (DUDGEON 1982a), the present investigation provided an opportunity to collect preliminary data which could be used to determine whether any relationship between mean particle size and macroinvertebrate abundance and diversity existed in a tropical freshwater environment.

Methods

Due to inherent variability in the distribution of lotic macrobenthos, largely resulting from the complex mosaic of substrate types and current velocities encountered even in first-order streams, the collection of representative samples has been a critical problem in running water ecology. It has been calculated (NEEDHAM & USINGER 1956; CHUTTER 1972) that it would take an impractically large number of samples to obtain statistically significant figures on total numbers at a 95 per cent level of confidence with the use of a standardized sampler on a visually homogeneous river segment. However, less extensive sampling is required to ascertain which of the commoner species are present. NEEDHAM & USINGER (1956) have stated that 3 square foot samples should normally provide representatives of the principal elements of the benthic fauna, whilst CHUTTER & NOBLE (1966) consider that sampling 0.3 m^2 of a stony riffle should be satisfactory for normal purposes. Due to the tendency of the benthos to show clumped distribution, the pooling of a number of small collections from within a sampling reach will provide a more accurate picture of faunal composition and abundance than one or two large samples from a single microhabitat.

The least biased form of sampling within the habitat at each site is random sampling. However due to the association of certain benthic taxa with particular sediment types it is important that samples should be collected from each subdivision of the study reach. Consequently a form of stratified random sampling (CUMMINS 1966, 1975; COFFMAN et al. 1971), based around the fact that maximum flow and sediment grain size are found in the central portion of the stream channel and the inverse at the margins, with transect samples taken at random locations along the stretch of water under investigation, can be employed in order to obtain representative collections of the benthic taxa. Generally local factors will determine how truly random the collection of such samples can be, and will also influence the number of transects. However, the number of samples in each transect should be multiples of the following arrangement: one sample at each bank, one in the centre of the stream and one on each side of this in an intermediate position between the midstream and bankside sites. These five samples constitue a transect and should include all major faunal variations occurring as a result of physical changes across the study reach.

In the present investigation the size of the habitat dictated the number of samples which could be taken without causing undue damage to the environment. On each biweekly visit five 0.1 m^2 samples were taken from a single shaded riffle reach of Tai Po Kau Forest Stream over the period May 1977 to May 1979. Detailed descriptions of the study area are presented elsewhere (DUDGEON 1982c) and only a small sample of the data accumulated as a result of the two year sampling programme will be considered here. The total area sampled in Tai Po Kau Forest Stream on each visit was greater than the area which CHUTTER & NOBLE (1966) stated had to be sampled in order to obtain a satisfactory collection of the macrobenthos. Thus within the constraints imposed by available man power and the need to avoid excessive damage of the habitat, the sampling was considered to be adequate.

In sampling of any kind in lotic environments it is important to ensure that the benthos deep in the substratum (COLEMAN & HYNES 1970; BISHOP 1973; HYNES et al. 1974, 1976; POOLE & STEWART 1976) is sampled adequately and, consequently, in the present investigation sampling extended down to the bed rock layer. It is probable that failure to appreciate the hyporheic fauna contributes to the high variability between samples from apparently homogeneous localities (e.g. NEEDHAM & USINGER 1956). While nets of various types have been used to sample lotic macrobenthos they are not generally suitable for instances where collections must be taken down to bed rock level and, moreover, the dimensions of the net mesh employed profoundly affects the composition of the resulting collection (ZELT & CLIFFORD 1973). For such reasons a special sampler was used in the present investigation comprising a clear perspex box fitted with a foam rubber skirt which, when pressed against the stream bottom produced a water-tight seal. The height of the box was sufficient to ensure that the top of the apparatus protruded above the water surface in the deepest parts of the study reach. A similar sampler has been used by COFFMAN et al. (1971).

Once the sampling area was isolated, all of the substratum and associated material in the enclosed area, down to the level of bed rock, was removed with a trowel; animals and fine material in the water column were recovered using a fine meshed (200 µ) net. Immediately after collection samples were preserved in 5 per cent neutralized formalin to prevent deterioration of the biological material which takes place rapidly in Hong Kong's high ambient temperatures. Upon return to the laboratory the detrital and faunal components of the samples were separated from the inorganic elements by flotation using a saturated solution of sea salt. The floating material was decanted through a 200 µ mesh net, washed and preserved in a mixture of 9 parts of 70 per cent ethanol to one part 5 per cent neutralized formalin. The extraction of the faunal component of the sample from the detrital element was carried out by mixing toluene with the preserved sample. The lipid molecules in the cuticles of the insect nymphs and larvae in the collections were attracted to the organic molecules so that the animals were held on the interface between the two liquids. They were then drained off, washed and preserved. The process was repeated until no more animals were extracted. Material remaining after flotation and extraction procedures was routinely checked to ensure that any animals which were too dense to float due to heavy cases were included in the samples.

Samples from bankside (sites 1 and 5), intermediate (sites 2 and 4) and mid-stream (site 3) areas were analysed separately. Although a considerable amount of information concerning faunal microdistribution in Tai Po Kau Forest Stream was available only a small proportion of this, covering a period of gradually increasing stream discharge between May and August 1977, is presented here. Four sets of samples were collected over this interval and for the more abundant taxa the density of individuals at each site across the width of the stream is shown for each sampling date. For rarer taxa, density values for all samples at each site were combined with the resultant values expressed as numbers per metre^2.

Due to the lack of reliable taxonomic information on the freshwater macroinvertebrates of Hong Kong it was rarely possible to assign specific names to any of the animals collected. Instead, individuals were identified to the lowest taxonomic rank possible and, in cases where there appeared to be more than one closely related species in the same taxonomic rank, distinct morphotypes were assigned letters and numbers by way of designation. Work is presently underway to determine the specific status of these taxa.

Results

A list of the taxa considered in this study is shown in Table 1. For reasons of taxonomic simplicity dipterous larvae were not considered and some rarer taxa were omitted entirely as insufficient specimens were collected for meaningful analysis of their microdistribution patterns to be undertaken. The microdistribution of individual taxa across the study reach is shown in Figs. 1–15.

Table 1. A list of the insect macrobenthic taxa considered in the present study.

- Ephemeroptera
  - Baetidae
    - *Baetis* T_1, T_2, T_3, T_4
    - *Pseudocloeon* T_1, T_2
  - Heptageniidae
    - *Ecdyonurus* T_1, T_2
    - *Epeorus* T_1
  - Leptophlebiidae
    - *Choroterpes* T_1
    - *Habrophleboides gillesi* PETERS 1963
    - *Isca* T_1
    - *Thraulus* T_1
  - Ephemerellidae
    - *Ephemerella* T_1, T_2
  - Caenidae
    - *Caenis* T_1
  - Ephemeridae
    - *Ephemera* T_1
- Odonata
  - Eupheaidae
    - *Euphea decorata* (SELYS)
- Plecoptera
  - Perlidae
    - Perlidae genus indet. T_4
- Trichoptera
  - Glossosomatidae
    - *Agapetus* T_1
  - Philopotamidae
    - *Chimarra* T_1
  - Stenopsychidae
    - *Stenopsyche* T_1
  - Hydropsychidae (Macronematinae)
    - *Macronema* T_1
    - *Polymorphanisis* T_1
  - Hydropsychidae (Hydropsychinae)
    - *Hydropsyche* spp.
    - *Cheumatopsyche* T_1, TdB
    - Hydropsychidae genus indet. T_1
  - Psychomyiidae
    - *Psychomyia* T_1
    - *Xiphocentron* T_1
  - Polycentropidae
    - *Polycentropus* T_1
    - *Pseudoneureclipsis* TA_1, TA_2, TA_3
    - *Ecnomus* T_1
- Coleoptera
  - Dytiscidae
    - cf. *Cybister* sp.
  - Hydrophilidae
    - cf. *Enochrus* sp.
    - Hydrophilidae genus indet. T_1
  - Helodidae
    - *Helodes* sp.
  - Psephenidae
    - *Psephenus* sp.
    - *Eubrianax* sp.
    - *Psephenoides* sp.
  - Elmidae
    - *Stenelmis* sp.
    - cf. *Limnius* sp.
    - cf. *Zaitzevia* sp.
    - Elmidae genus indet. T_1
    - Elmidae genus indet. T_2

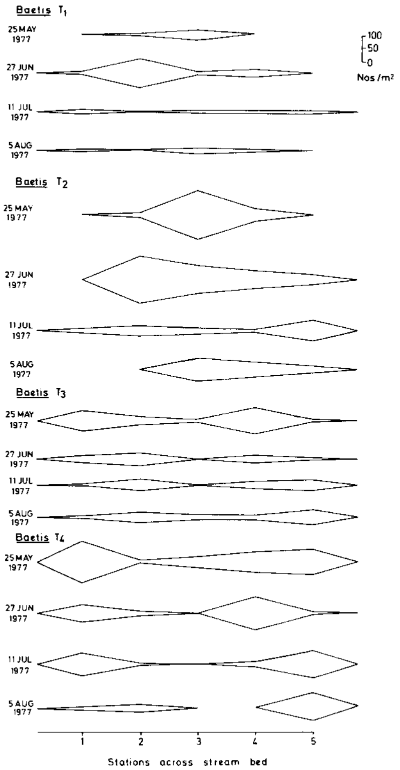

Fig. 1. Kite diagrams showing the distribution across the width of Tai Po Kau Forest of *Baetis* spp. (Ephemeroptera: Baetidae) Stream during the summer of 1977.

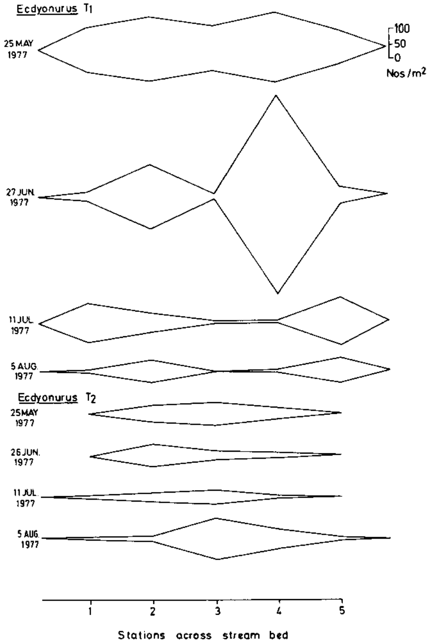

Fig. 2. Kite diagrams showing the distribution of *Ecdyonurus* T_1 and *Ecdyonurus* T_2 (Ephemeroptera: Heptageniidae) across the width of Tai Po Kau Forest Stream during the summer of 1977.

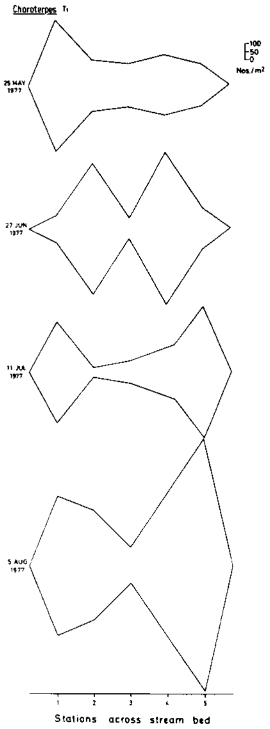

Fig. 3. Kite diagrams showing the distribution of *Choroterpes* T_1 (Ephemeroptera: Leptophlebiidae) across the width of Tai Po Kau Forest Stream during the summer of 1977.

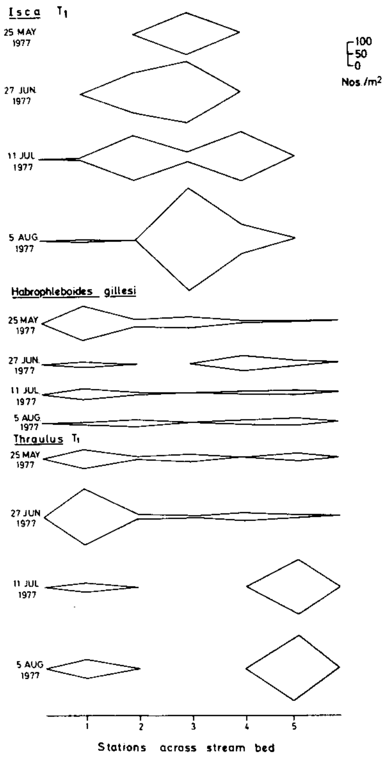

Fig. 4. Kite diagrams showing the distribution of *Isca* T$_1$, *Habrophleboides gillesi* and *Thraulus* T$_1$ (Ephemeroptera: Leptophlebiidae) across the width of Tai Po Kau Forest Stream during the summer of 1977.

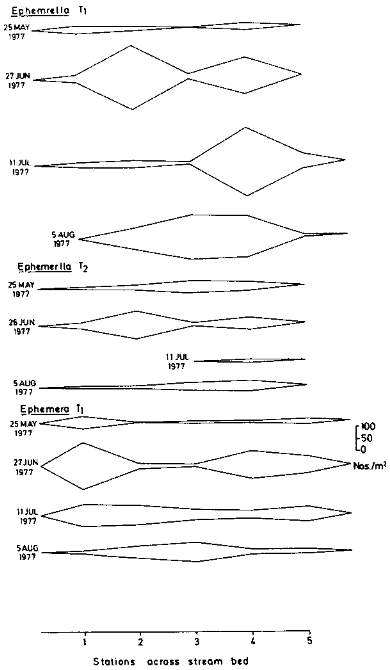

Fig. 5. Kite diagrams showing the distribution of *Ephemerella* T$_1$ and *Ephemerella* T$_2$ (Ephemeroptera: Ephemerellidae) and *Ephemera* T$_1$ (Ephemeroptera: Ephemeridae) across the width of Tai Po Kau Forest Stream during the summer of 1977.

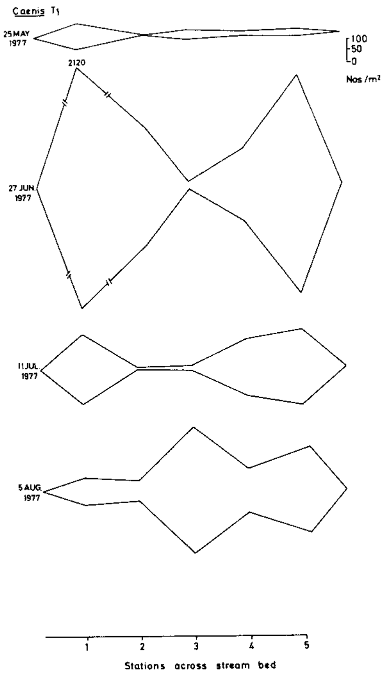

Fig. 6. Kite diagrams showing the distribution of *Caenis* T$_1$ (Ephemeroptera: Caenidae) across the width of Tai Po Kau Forest Stream during the summer of 1977.

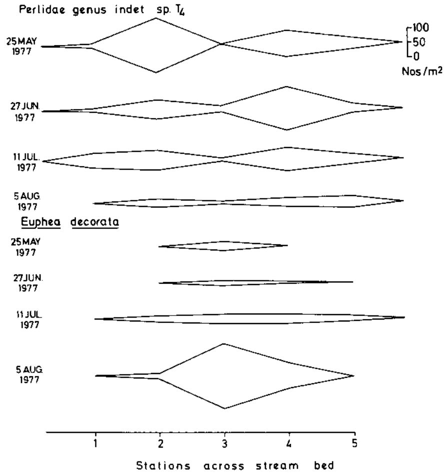

Fig. 7. Kite diagrams showing the distribution of Perlidae genus indet. T_4 (Plecoptera: Perlidae) and *Euphea decorata* (Odonata: Eupheaidae) across the width of Tai Po Kau Forest Stream during the summer of 1977.

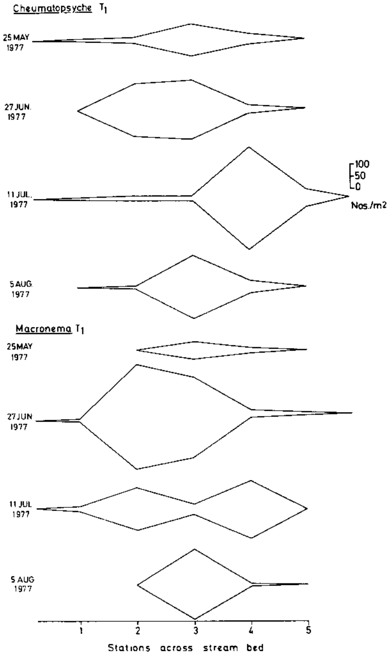

Fig. 8. Kite diagrams showing the distribution of *Cheumatopsyche* T_1 and *Macronema* T_1 (Trichoptera: Hydropsychidae) across the width of Tai Po Kau Forest Stream during the summer of 1977.

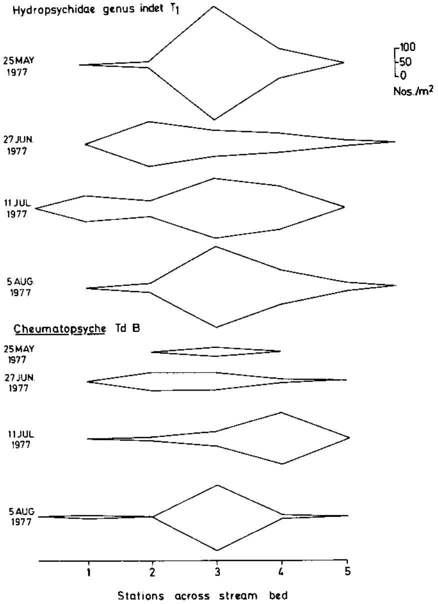

Fig. 9. Kite diagrams showing the distribution of Hydropsychidae genus indet. T_1 and *Cheumatopsyche* TdB (Trichoptera: Hydropsychidae) across the width of a riffle reach of Tai Po Kau Forest Stream during the summer of 1977.

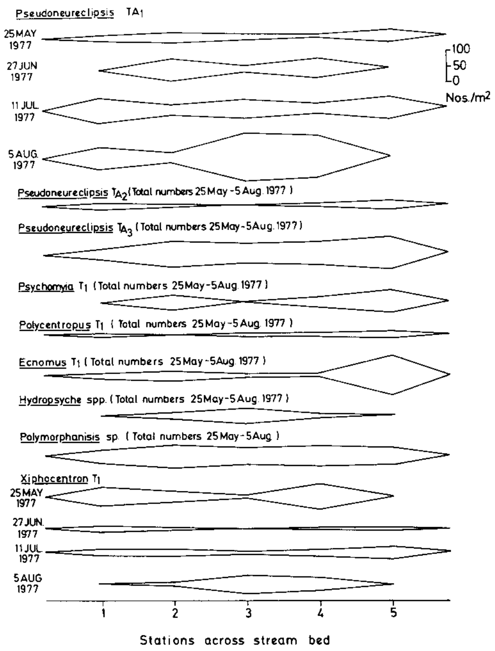

Fig. 10. Kite diagrams showing the distribution of various trichopteran taxa across the width of Tai Po Kau Forest Stream during the summer of 1977.

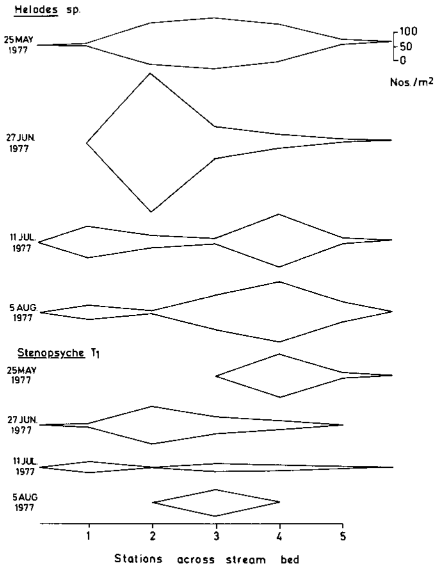

Fig. 11. Kite diagrams showing the distribution of *Stenopsyche* T_1 (Trichoptera: Stenopsychidae) and *Helodes* sp. (Coleoptera: Helodidae) across the width of Tai Po Kau Forest Stream during the summer of 1977.

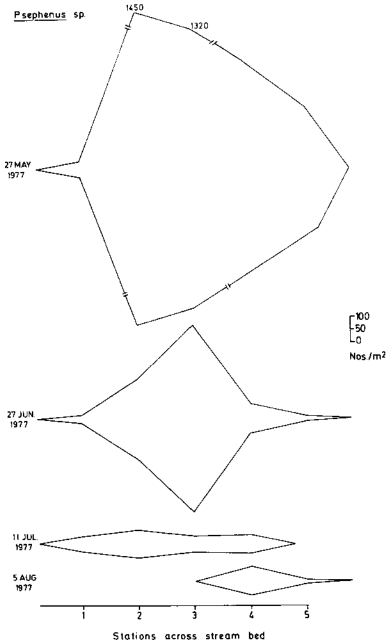

Fig. 12. Kite diagrams showing the distribution of *Psephenus* sp. (Coleoptera: Psephenidae) across the width of Tai Po Kau Forest Stream during the summer of 1977.

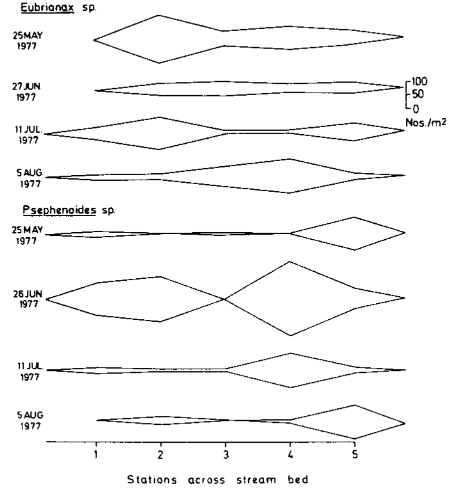

Fig. 13. Kite diagrams showing the distribution of *Eubrianax* sp. and *Psephenoides* sp. (Coleoptera: Psephenidae) across the width of Tai Po Kau Forest Stream during the summer of 1977.

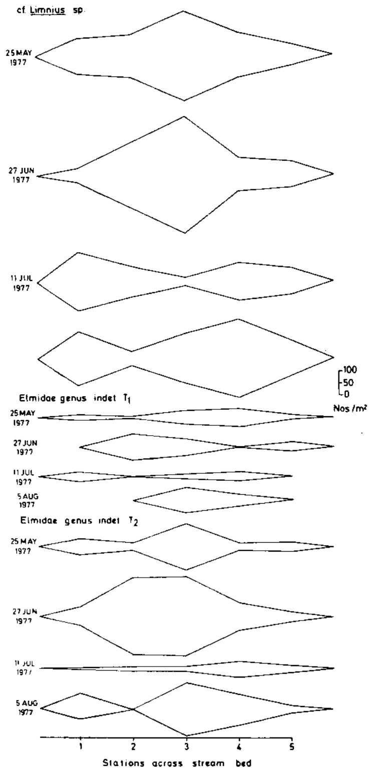

Fig. 14. Kite diagrams showing the distribution of elmid larvae (Coleoptera: Elmidae) across the width of Tai Po Kau Forest Stream during the summer of 1977.

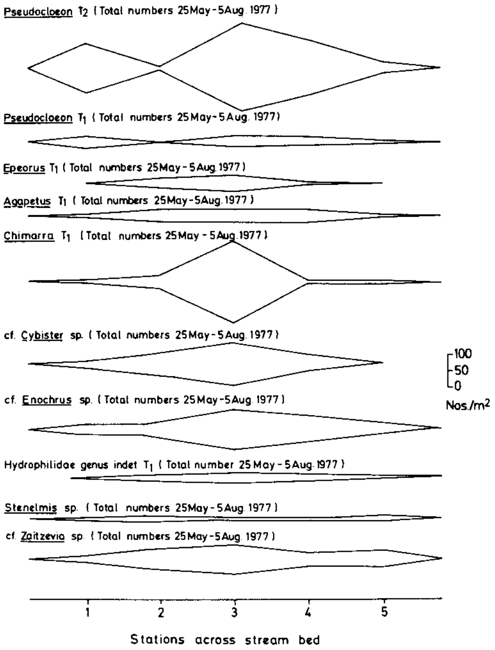

Fig. 15. Kite diagrams showing the distribution of a variety of insect taxa (Ephemeroptera, Trichoptera, Coleoptera) across the width of Tai Po Kau Forest Stream during the summer of 1977.

Trends in the distribution of invertebrate taxa across the width of the stream bed could be recognized, and these can be classified into a number of types as follows:

a) Those taxa which were most abundant in the central portion of the stream, i.e. site 3 (*Ecdyonurus* T_2, *Epeorus* T_1, *Isca* T_1, *Euphea decorata,* Hydropsychidae genus indet. T_1, *Cheumatopsyche* TdB, *Cheumatopsyche* T_1, *Hydropsyche* spp., *Chimarra* T_1, cf. *Enochrus* sp., cf. *Cybister* sp. and Elmidae genus indet. T_2).

b) Those taxa which were most abundant at the bankside sites, i.e. sites 1 and 5 (*Baetis* T_4, *Ephemera* T_1, *Caenis* T_1, *Choroterpes* T_1, *Thraulus* T_1, *Habrophleboides gillesi, Pseudoneureclipsis* TA_2 and *Ecnomus* T_1).

c) Those taxa which were most abundant in the intermediate zones between the stream banks and the midstream area, i.e. sites 2 and 4 (*Baetis* T_3, *Ecdyonurus* T_1 and Perlidae genus indet. T_4).

d) Those taxa which were most abundant in the intermediate and central areas (that is they were not common at the bankside sites) but showed no definite preference for either one of these areas, i.e. sites 2, 3 and 4 (*Baetis* T_1, *Baetis* T_2, *Ephemerella* T_1, *Ephemerella* T_2, *Macronema* T_1, *Stenopsyche* T_1, *Agapetus* T_1, *Helodes* sp., *Psephenus* sp., *Eubrianax* sp., Elmidae genus indet. T_1 and cf. *Zaitzevia* sp.).

e) Those taxa which did not show consistent patterns of spatial variation across the width of the stream (*Pseudocloeon* T_1, *Pseudocloeon* T_2, *Polymorphanisis* sp., *Psychomyia* T_1, *Xiphocentron* T_1, *Pseudoneureclipsis* TA_3, *Polycentropus* T_1, *Psephenoides* sp., cf. *Limnius* sp., *Stenelmis* sp. and Hydrophilidae genus indet. T_1).

There was a general trend towards a change in the distribution of some taxa as the discharge volume of the stream increased from May through August. As 1977 was a drought year in Hong Kong, these months, which would normally have been marked by heavy rain leading to severe spates in Tai Po Kau Forest Stream, were periods of only moderate rainfall and consequently the increase in discharge volume was gradual and relatively small. Some of those taxa which were associated with the bankside sites became noticeably restricted to these areas during the latter part of the study when discharge volume was comparatively high (e.g. *Thraulus* T_1, *Choroterpes* T_1 and *Baetis* T_4). Similarly the numbers of certain taxa inhabiting the central portions of the stream bed were reduced, or their range became more restricted, as a result of increasing discharge (e.g. *Ecdyonurus* T_1, *Psephenus* sp., Elmidae genus indet. T_1 and cf. *Limnius* sp.). In contrast, the distribution of *Caenis* T_1 changed from that of a predominately bankside species in June to that of a midstream species in August. This change was associated with the occurrence of large numbers of young nymphs in the midstream areas, current aided dispersion during periods of high discharge apparently spreading large numbers of small individuals over all parts of the stream bed.

Changes in the abundance of *Macronema* T_1 and *Psephenus* sp. were also due to life cycle events. The large numbers of *Psephenus* sp. in May were associated with the presence of many small larvae and available information suggests that the adult beetles oviposit in late spring or early summer. Similarly the peak in numbers of *Macronema* T_1 was related to the presence of large numbers of small larvae. *Macronema* T_1 has been provisionally associated with adults described by Mc LACHLAN as *Macronema lautum*. Significantly adults of *M. lautum* were collected from riparian vegetation close to the study reach during the month of May in 1977, 1978, 1979 and 1981.

Discussion

The generally accepted "erosion-deposition" concept of MOON (1939) implies that the mean grain size of stream sediments increases from the bankside to the midstream areas of a stream bed. A previous study (DUDGEON 1982a) has shown this to be the case in a riffle reach of Tai Po Kau Forest Stream and in view of the influence of substrate type upon the distribution of stream macrobenthos, characteristic microdistribution patterns across the width of the stream would be expected for many benthic taxa. The elucidation of such patterns formed part of the present study. Certain workers (SPRULES 1947; MACKAY & KALFF 1969; CRISP & CRISP 1974) have suggested that the diversity and abundance of the macrobenthos increases with the mean grain size of stream sediments. Considering available data on the sediments of Tai Po Kau Forest Stream, this study provided an opportunity to test the theory that there are more macroinvertebrate individuals and taxa inhabiting (midstream) coarse sediments than (bankside) finer sediments.

Although over 130 taxa have been recorded from the study area only 47 were included in the present investigation. Of these certain species showed clear preferences for sites close to the bank while others inhabited midstream areas. 12 taxa showed no preference in this respect including such common animals as members of the genus *Pseudocloeon*. Clearly these animals were affected by factors which did not vary regularly across the width of the stream and variables such as light and shade (THORUP 1966; HUGHES 1966) competition, predation, etc. may have been important.

Preference for the middle of the stream was more marked in some taxa than in others. For instance, most Hydropsychinae were confined to site 3, the midstream station, whilst the related Macronematinae were found at both the midstream and intermediate sites. This difference may reflect the filter-feeding habits of these net-spinning trichopterans. *Macronema* T_1 (cf. *M. lautum*) has a very fine meshed capture net of similar dimensions to that of *Macronema carolina* in North America (WALLACE 1975; WIGGINS 1977). In contrast, the nets of Tai Po Kau Hydropsychinae are relatively coarse, as is the case in North American representatives of this subfamily (WALLACE 1975). On this basis it would be expected that

Macronema would be less numerous in the most central portion of the stream as the swift current speed prevailing in such sites (DUDGEON 1982a) would damage or rupture the fine capture net. Conversely, the coarse nets of the Hydropsychinae would be more resistant to damage from high flow rates and, indeed, would need to filter a comparatively greater volume of water in order to obtain sufficient quantites of large suspended particles to meet their metabolic needs. Interestingly, *Chimarra* T_1, like most other Philopotamidae (WALLACE & MALAS 1976), has a net composed of very small rectangular mesh but is typically found in the middle of Tai Po Kau Forest Stream. Unlike the Hydropsychinae which generally favour microhabitats exposed to the flow of the current, *Chimarra* T_1 lives underneath stones and is thus protected from the full force of the current. A further filter-feeding trichopteran, *Stenopsyche* T_1 (cf. *S. angustata* MARTYNOV), occurs at the intermediate and midstream sites but like *Macronema* T_1 is not very abundant at site 3. As *Stenopsyche* T_1 has a coarse meshed capture net the degree of spatial isolation between this species and the Hydropsychinae can be seen as a way of reducing competition for food. In contrast the mesh size of the nets of *Macronema* T_1 and *Stenopsyche* T_1 show no overlap, so that while these species may occupy the same microhabitats on the stream bed they are unlikely to compete for food. The investigations of WALLACE (1975) and MALAS & WALLACE (1977) suggest that lotic trichopterans commonly show differential mesh size as a way of reducing interspecific competition for food.

In view of the potential for competition between closely related taxa living in the same reach of water, it is interesting to examine the microdistribution of genera where more than one species was known to occur within the study area. Such comparisons can be made with the ephemeropteran genera *Baetis, Ecdyonurus* and *Ephemerella. Ecdyonurus* T_1 and *Ecdyonurus* T_2 showed some differentiation in their spatial distribution with the former species being most abundant at sites 2 and 4 whilst *Ecdyonurus* T_2 was commonest at the midstream site. In the genus *Baetis, Baetis* T_1 and *Baetis* T_2 were abundant in the intermediate and midstream sites while *Baetis* T_4 was most common close to the banks. *Baetis* T_3 was most frequently encountered at sites 2 and 4 but not at site 3 thus reducing its distributional overlap with *Baetis* T_1 and *Baetis* T_2. Although the distribution patterns of the two latter species were similar, *Baetis* T_1 has a slimmer and more streamlined body shape than *Baetis* T_2. This suggests that a further microhabitat segregation, not revealed by this investigation, could exist between these two species.

While there was no direct evidence of habitat segregation between the two species of *Ephemerella* recorded from the study reach, evidence collected during other investigations of Tai Po Kau Forest Stream indicates that *Ephemerella* T_2 is characteristically associated with accumulations of allochthonous detritus while *Ephemerella* T_1 was less commonly found on such material. At the family level, some signs of habitat partitioning can be seen from an examination of the microdistribution of four genera of leptophlebiid mayfly nymphs. *Isca* T_1 was clearly separated from the other three genera by its occupation of the centre of the stream; such a habitat is also suggested by the species' streamlined body form and attachment of the gills to the underside of the abdomen. In contrast, the three remaining genera, *Thraulus*, *Choroterpes* and *Habrophleboides*, were confined to the bankside sites. Undue competition between these genera is probably reduced by differences in feeding habits, the head capsule of *Habrophleboides gillesi* being more similar to that of a baetid nymph than those of the flatter *Thraulus* and *Choroterpes*. Avoidance of competition between the latter two genera is a matter for speculation although the body form and large filamentous gills of *Thraulus* T_1 suggest that it is a burrowing species. Evidence of habitat segregation among other groups of macroinvertebrates in the study area is incomplete and, in the case of the Coleoptera, so little is known about the ecology of these animals in Asia that any enlargement upon the basic information presented above would be inappropriate.

Certain workers have suggested that the abundance and diversity of benthic macroinvertebrates will be greater in stream sediments with large mean particle size than in those with smaller mean particle size. If this hypothesis applies in Tai Po Kau Forest Stream, site 3 should have a greater density and diversity of macroinvertebrates than sites 1, 2, 4 and 5. 12 taxa, or approximately 25 per cent of those investigated, were found in their highest densities at site 3. This may be a reflection of the stability of boulder microhabitats (DE MARCH 1976) which form the dominant part of the midstream sediments. While 12 taxa did not show any particular distribution pattern across the stream, 8 taxa were restricted to the bankside areas. Thus on the basis of the distribution patterns of 47 common taxa in Tai Po Kau Forest Stream, slightly more taxa showed a preference (as determined by the site at which they attained maximum abundance) for station 3, where the sediments were coarsest, than any other single area of the stream bed. However when the total number of taxa occurring at each site grouping are totalled, sites 2 and 4 had the greatest diversity. The richness of these intermediate sites may be a reflection of substrate heterogeneity in these transitional microhabitats due to the varying proportions of fine and coarse particles that are represented (DUDGEON 1982a). On this basis it is probable that mean particle size is less important than substrate heterogeneity in determining the species richness of a particular sediment patch. As substrate characteristics are of profound importance in determining benthic macroinvertebrate abundance (e.g. CUMMINS 1966; THORUP 1966; BISHOP 1973) it is reasonable to assume that a sediment containing a range of grain sizes would support a greater variety of animals than one containing particles of a single size category.

Results from Tai Po Kau Forest Stream do not support the findings of SPRULES (1947), PENNACK & VAN GERPEN (1947), MACKAY & KALFF (1969) and CRISP & CRISP (1974) concerning the relationship between benthic species diversity and increasing particle size. Significantly, in an investigation of the distribution of macrobenthos across the width of a European stream HIGLER (1975) found most taxa in a sample collected close to the bank. However, in the absence of information on substrate characteristics it is not clear how his findings compare with those of the present study. On the basis of previously published work (e.g. MacKay & Kalff 1969; Hynes 1970; Reice 1974; Allan 1975), as well as the findings of the present study, it is apparent that the degree of heterogeneity of the particle sizes within a sediment patch may be an important factor influencing the species diversity of the associated benthic fauna. From the remarks of Allan (1975) concerning the preferences of different taxa for particular substrate particle sizes, it is obvious that those sediment patches with the widest range of grain diameters should yield the greatest variety of species. Such is apparently the case in Tai Po Kau Forest Stream as intermediate sites 4 and 2, which have the greatest species diversity, have been shown to have heterogeneous sediment characteristics representing a transition between the extremes seen in midstream and bankside areas (Dudgeon 1982a). It should be noted, however, that Wise & Molles (1979) did not record significantly higher numbers of species on mixed introduced substrates when compared with those of more homogeneous particle size. The reason for this difference is not apparent.

Patterns of species richness across the width of Tai Po Kau Forest Stream were not reflected in changes in the abundance of the total macroinvertebrate taxa considered, and there was no evidence of consistent across-stream trends in this parameter. The observations of Sprules (1947) and MacKay & Kalff (1969) relating to increased abundance of macroinvertebrates on large particles in North American stream sediments do not seem to apply to the study reach. It seems appropriate, therefore, to echo the remarks of Minshall & Minshall (1977) who stated that there is a need to re-examine certain generalizations about organism-substrate relationships in streams. Indeed it should be emphasized that, in common with the present study, very few investigations have included all components of the macrobenthic fauna in analyses of microdistribution patterns. The calamoceratid trichopteran larvae and atayid shrimps which could not be included in the present study due to their specialized microhabitat preferences are normally found close to the stream banks. Such omissions doubtless led to an underestimate of macrobenthos diversity at the bankside sites. Similar comments can also be made regarding the exclusion of Diptera (due to taxonomic considerations), as chironomid and tipulid larvae were frequently abundant in depositional areas close to the stream margins. These remarks have particular relevance in view of the findings of Wise & Molles (1979) cited above.

It seems clear that the exclusion of certain taxonomically complex groups (Coleoptera, Chironomidae, etc.) and the profusion of studies based on sampling programmes which have ignored the hyporheic fauna, has created a situation where much of our knowledge of lotic fauna is based upon only the systematically well-known invertebrates which are associated with boulder and cobble substrates. It is desirable for future work to include more studies upon less well-known groups in order to introduce some balance into our knowledge of lotic invertebrates. Only after such investigations have been undertaken can broadly based generalizations, which will apply to a wide range of running waters, be set down with any degree of certainty.

In conclusion, some possible explanations for the lack of trends in macroinvertebrate abundance across the width of Tai Po Kau Forest Stream should be considered. As the numbers of macroinvertebrates did not vary consistently at one site or area of the stream bed it is unlikely that the patterns of abundance simply reflected increased current speed or stream discharge volume over the duration of the study. A contributing factor may have been the exclusion of certain groups which may have been of numerical importance (such as the Chironomidae); this point has been referred to above. The recruitment of young larvae and nymphs of *Psephenus* sp., *Macronema* T_1 and *Caenis* T_1 appeared to be associated with high values of total macroinvertebrate densities at some sites. For example, at site 3 on 27 June and 5 August 1977 large numbers of individuals of these three taxa contributed significantly to the observed pattern of greatest macroinvertebrate density in the centre of the stream. However, life cycle events such as recruitment are unlikely to contribute to all of the spatial variation in faunal densities observed. In view of the fact that substratum itself is a multi-variable factor and will act in a synergistic way with such parameters as food availability and type, current velocity and so on to control macroinvertebrate microdistribution patterns, it is probable that the lack of regular trends in faunal abundance across the width of the stream reflects within-site (or within-sediment patch) microhabitat variability resulting from the interaction of a variety of environmental parameters.

Summary

The microdistribution of 47 macroinvertebrate taxa across the width of a shaded riffle reach in Tai Po Kau Forest Stream has been studied. Certain taxa were restricted to different areas of the stream bed, some being confined to bankside regions whilst others were typical of midstream reaches. About one quarter of the taxa showed no obvious trends in distribution across the study area. An examination of the microdistribution of a number of closely related taxa in the study area indicated that a degree of spatial isolation existed between those species which were expected to compete for resources. Where two such taxa overlapped, morphological variations or differences in feeding behaviour seemed to provide reasonable explanations for their coexistence. Examples of such taxa were the ephemeropteran family Leptophlebiidae and genera *Baetis*, *Ecdyonurus* and *Ephemerella*, as well as a number of net-spinning trichopterans.

Species richness of macroinvertebrates varied across the width of the stream and was maximal at sites between the banks and the middle of the bed. Such sites were transitional with respect to their sediment characteristics and, due to their heterogeneity, were able to support a variety of macroinvertebrate taxa. There was no relationship between species richness and total macroinvertebrate numbers which varied unpredictably both temporally and spatially. Some variation reflected recruitment of certain common taxa and may have indicated within-site heterogeneity. In view of the often contradictory findings of other studies of

macroinvertebrate distribution present in the literature, further investigation of factors controlling the diversity and abundance of lotic macrobenthos is required before any widely applicable generalizations can be made about this topic.

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