DETERMINANTS OF THE DISTRIBUTION AND ABUNDANCE OF LARVAL EPHEMEROPTERA (INSECTA) IN HONG KONG RUNNING WATERS

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ABSTRACT

The mayflies of Hong Kong are poorly known with only nine species recorded from the territory. This paper lists 47 OTUs (putative species) in eight families, and considers factors determining the distribution and abundance of common species in two lotic habitats. The Baetidae was the most diverse family, occurring widely in running waters; Heptageniidae and Leptophlebiidae were also well represented but generally restricted to upper-course unpolluted sites. In the Lam Tsuen River patterns of mayfly longitudinal distribution and abundance were a result of the combined effects of river discharge volume (a reflection of seasonal rainfall) and organic pollution. Regression analysis of the relationship between environmental parameters and mayfly abundance revealed that the major predicting variables were pollution-related. There were interspecific differences within genera with regard to major predictors in best-fit models, and species restricted to upstream sites were negatively associated with pollution-related parameters. Microdistribution patterns in Tai Po Kau Forest Stream were generally explained by regressions including sediment characteristics as predictive variables, although standing stocks of chlorophylls were sometimes useful predictors. It was concluded that the mayfly fauna of Hong Kong is to a great extent the product of anthropogenic influences, i.e. organic pollution of lotic habitats by agricultural wastes.

INTRODUCTION

Little is known of the natural history of Hong Kong freshwaters. This is surprising in view of the importance of rivers and stream draining into reservoirs as a major source of water supplies. The potential diversity of freshwater fauna is high as Hong Kong lies in an area of transition between the tropical Oriental fauna and the temperate faunas of China and Japan. The local Trichoptera comprise approximately 65 species belonging to 36 genera in 19 families, incorporating primarily Oriental elements with little Palaearctic representation (Dudgeon 1987). The mayflies of Hong Kong are incompletely known but include species which are widespread in southern China (*Paegnoides cupulatus* (Eaton): Heptageniidae) and/or the Oriental region (*Procloeon harveyi* Kimmins: Baetidae; *Ephemera (Ephemera) pulcherrima* Eaton and *E. (E.) serica* Eaton: Ephemeridae), as well as species which have only been recorded from within the territory (*Ecdyonurus herklotsi* Hsu and *Heptagenia ngi* Hsu: Heptageniidae; *Cryptopenella fascialis* Gillies and *Habrophlebioides gilliesi* Peters: Leptophlebiidae). Preliminary studies have indicated that a diverse assemblage of mayflies inhabit Hong Kong streams and rivers (Dudgeon 1982d, e, 1983a, 1984a, b), although limited knowledge of Oriental Ephemeroptera larvae coupled with the uncertain status or limits of some baetid and heptageniid genera have hindered identification of these animals.

This paper includes a brief account of the composition of the local mayfly fauna, and considers

I.C. Campbell (ed.) Mayflies and Stoneflies, 221–232.

data from investigations of the Lam Tsuen River and Tai Po Kau Forest Stream, New Territories, Hong Kong. Information on the longitudinal and seasonal distribution patterns of common taxa, as well as analysis of the factors determining both longitudinal zonation and microdistribution of these animals, is presented.

STUDY AREAS

Hong Kong is situated 250 km south of the Tropic of Cancer (latitude 22°7′–22°9′N, longitude 113°52′–14°30′E) on the southern coast of the People's Republic of China adjoining Guangdong Province. The landscape comprises the southern end of an eroded mountain chain of Jurassic origin, made up of folded and metamorphosed volcanic and granitic rocks with local sedimentary outcrops. A rise in sea level following the last glaciation has resulted in a drowned coastline with former mountain tops represented by small offshore islands, the highest peak attaining 958 m. Consequently, Hong Kong lacks an extensive coastal plain and much of the land area comprises steep hillsides supporting grassland and low scrub on thin podsols. Only in sheltered valleys does forest obtain, the restricted lowland being given over to agriculture (7% of total land area) or to urbanization (17% of land area and increasing).

The climate is tropical monsoon with mild dry winters (February mean minimum – 15.2°C) and hot wet summers (July mean maximum – 31.6°C). Most of Hong Kong's average rainfall of 2225 mm falls in summer resulting in increased stream flow volume and sediment loads.

Lam Tsuen River

Investigations of seasonal patterns of ephemeropteran longitudinal distribution and abundance were undertaken at six sites along the Lam Tsuen River (LTR) which runs from southwest to northeast across the central New Territories. Increasing organic pollution of the river has been observed in recent years (for details see Dudgeon 1983c, 1984a, b) reflecting intensified livestock rearing (pigs, ducks and chickens) in the watershed. Until recently, such activities affected only the middle and lower course of the river, and the data presented herein (derived from a 1978-1979 study) predate deterioration of the upper reaches.

The two uppermost sampling sites, draining sparsely populated scrubland, indicate the "natural" LTR hydrology. Waters were soft and slightly acidic (pH 6.8-7.0) rich in silicates (4.0-8.2, $\bar{x}$ = 6.13 mg l^{-1}), but relatively poor in phosphates (0.04-0.62, $\bar{x}$ = 0.24 mg l^{-1}), nitrites (0.00-0.05, $\bar{x}$ = 0.02 mg l^{-1}) and nitrates (0.03-0.23, $\bar{x}$ = 0.10 mg l^{-1}). Dissolved oxygen concentrations always exceeded 8.0 mg l^{-1} ($\bar{x}$ = 8.9 mg l^{-1}) and biological oxygen demand (BOD_5) was less than 2.85 mg O_2 l^{-1} ($\bar{x}$ = 1.13 mg O_2 l^{-1}). Seston loads were 0.10 to 0.55 mg l^{-1} ($\bar{x}$ = 0.38 mg l^{-1}). Water temperatures along the river ranged between 17.5 and 30.0°C during the study.

Tai Po Kau Forest Stream

Mayfly microdistribution was investigated in a shaded riffle reach (altitude 200 m, slope 6%) of Tai Po Kau Forest Stream (TRKFS), New Territories. The stream waters were soft and slightly acidic, generally poor in nutrients with low conductivity (Dudgeon 1982a). Distinct across-stream gradients in sediment characteristics were apparent (Dudgeon 1982b) and standing stocks of allochthonous detritus were high, exceeding periphyton biomass by 100 times (Dudgeon 1982c). The benthic community was species-rich and exhibited a heterotrophic metabolism (P:R = 0.17) (Dudgeon 1983b).

MATERIALS AND METHODS

Longitudinal zonation and abundance

Lam Tsuen River samples were collected from six riffle sites; site 1 was a boulder-strewn headwater torrent while site 6, in the lower course, was characterised by extensive macrophyte growth. Hydrological parameters were measured at the time of benthic sampling according to standard procedures (APHA 1975, Dudgeon 1982a). Stratified quantitative samples of the benthos were taken at each site (Dugeon 1984a gives details) in June, September and December 1978 and March 1979, corresponding to the onset of the wet season (June), the latter stages of the wet season (September), and the middle and end of the dry season (December and March respectively). Mayflies were sorted to the highest taxonomic level possible (using letters and numbers to designate morphotypes within taxonomic units) and counted. In addition to hydrological parameters, sediment grain size statistics (mean grain size, sorting coefficient, skewness and kurtosis) were calculated according to Folk and Ward (1957) and Folk (1966) Dudgeon 1982b gives details); the organic content of fine ($< 500\ \mu$m) sediments was determined from weight loss after ignition for two hours at 550°C.

Microdistribution

Tai Po Kau Forest Stream samples were taken (during summer 1977) on a stratified basis with effort divided equally between five stations; two stations by the stream banks (one by each bank), one in the centre of the stream, and two samples in intermediate positions. Different microhabitats arising as a result of across-stream physical changes (see Dudgeon 1982b, c) were thereby sampled according to their relative frequency of occurrence across the riffle. The perspex box sampler employed enclosed an area of 1000 cm^2 and bore a foam rubber skirt around the base which made a seal with the uneven stream bed. All sediments and associated material in the enclosed area, down to the level of parent rock, were scooped out; animals and fine material in the water column were recovered with a 200 μm mesh net. The detrital and faunal components of the sample were separated from the inorganic fraction by flotation in brine. Arthropods were separated from detritus on a toluene –70% ethanol interface, identified as far as possible and counted. The allochthonous detritus was dry-weighed and ashed to give estimates of standing stocks of coarse particulate organic material (CPOM) and total detritus. The periphyton associated with a single stone of known surface area from each sample unit was estimated using a trichromatic chlorophyll technique; phaeophytins were also determined (see Vollenweider 1974, Dudgeon 1982c). Sediment statistics and the organic content of cores taken adjacent to each benthic sample were analysed as indicated above.

Statistical methods

The relationship between mayfly abundance and environmental parameters for each station in LTR and for each sample at TPKFS were examined by calculating multiple regression equations for each mayfly species of the form:

$$Y = a + b_{Y1}X_1 + b_{Y2}X_2 + b_{Y3}X_3 + \ldots$$

where $X_1, X_2, X_3\ldots$ refer to separate independent variables (which need not be uncorrelated with each other), in this case environmental parameters; b_{Yi} is the regression coefficient of Y (mayfly abundance) on variable X_i. In LTR dissolved oxygen, nitrites, nitrates, phosphates, BOD_5, to tal seston, suspended organic matter (SOM), sediment statistics and fine sedimentary organic matter were used as independent variables (or predictors); parameters such as pH, temperature, conductivity and silicates showing little inter-site variation (Dudgeon 1984a) were not included. TPKFS independent variables were sediment statistics, fine sedimentary organics, total detritus, CPOM, chlorophyll *a*, *b* and *c*, total chlorophylls and phaeophytins. Stepwise multiple regressions of Y on various combinations of $X_1, X_2, X_3\ldots$ were undertaken to obtain a minimum of unexplained residual variance in terms of the smallest number of independent variables by dropping potential independent variables that did not remove a significant independent portion of the variation in Y. *F* ratios (variation in Y accounted for by variation in X/residual variation) were used to test whether a significant portion of the variation in Y had been explained by the regression, and changes in the significance level (P value) of the *F* ratio were used as an indication of the explanatory power of combinations of the variables X_1, X_2, X_3....

The coefficient of determination (r^2) was calculated for each regression according to Walpole & Myers (1978), and 100 r^2% was used to indicate the proportion of the variation in Y which could be accounted for by the linear relationship with X (or X_1). This calculation assumes a bivariate normal distribution of variables, consequently data were $\log_{10}$ transformed prior to analysis, thereby also minimising difficulties associated with fitting regression lines to curved functions of Y on X. In order to avoid complications with zero counts, 0.01 was added to counts of mayfly population density before $\log_{10}$ transformation ($X' = \log^{10}(X + 0.01)$, Makiya *et al.* 1982). Percentage data (fine sedimentary organics) were normalised by an $X' = \log_{10}(X + 0.5/100.5 - X)$ transformation. As LTR site 6 samples yielded no mayflies (although some specimens were associated with trailing riparian roots and grasses), this site was excluded from the regression analyses; all other LTR sites and all TPKFS samples were included in the analyses regardless of the incidence of zero counts for certain species.

It should be emphasised that the independent variables employed in regression analysis may have been correlated with each other (e.g. skewness, kurtosis and the sorting coefficient of sediments were correlated) or with environmental factors not measured. In consequence, the parameters which best explain the abundance of a given species may not necessarily be the actual factors which cause the observed pattern of distribution and abundance (Shiozawa 1986). Nevertheless, the set of independent variables in a best-fit regression model do give an indication of the parameters of a habitat in which a particular species is likely to occur. In this sense such parameters can be considered as "determinants" of distribution and abundance.

RESULTS

Faunal composition

Prior to 1982, nine species in four ephemeropteran families were known from Hong Kong (Hubbard 1986). Following quantitative collections of larvae from lotic habitats, the total can be raised to 47 species or OTUs (Operational Taxonomic Units) (Table 1). This number is conservative in that it assumes that all larvae of previously recorded species are included in the collections (i.e. that, for example, *Isca* T_1 is the larva of *Isca* (*Isca*) *purpurea* Gillies). Eight families are included in the Hong Kong Ephemeroptera fauna; one of these, the Prosopistomatidae, is a new record for China (Gui 1985, Dudgeon, unpubl. obs.). The generic total of 26 is provisional pending clarification of the status of *Cryptopenella* (see Kluge 1984) and *Centroptella* (R.D. Waltz, pers. comm.), as well as establishment of limits and larval characters for the *Epeorus*/*Iron* genera (or subgenera) in Asia (see Tomka and Zurwerra 1985, Zurwerra *et al.* 1986). Note that larvae of *Paegnoides cupulatus* (Eaton) were previously referred to *Thalerosphyrus* by Dudgeon (1982e, 1983a, 1984a, b). Additional corrections of this nature are listed in Table 1.

Longitudinal zonation and abundance

Seasonal changes in LTR hydrology during 1978-79 apparently had a direct influence on mayfly zonation patterns. Phosphates, nitrates, nitrites, SOM and BOD_5 levels were generally higher in the middle and lower course than upstream (sites 1 and 2). Conditions at site 3 depended upon the season, with high levels of phosphates, nitrates, nitrites and BOD_5 prevailing during the dry season. Thus in March 1979, site 3 closely resembled downstream sites with respect to hydrology. By contrast, during the wet season this site was more closely akin to the headwaters (Dudgeon 1984a).

Sediment characteristics also showed spatial and temporal trends. Mean grain size and sediment sorting coefficient decreased downstream

Table 1. A provisional list of Hong Kong mayfly taxa, including corrections to previously published designations

Baetidae
- *Baetis* T_1, T_2, T_3, T_4, T_5, T_6, T_7, T_8
- *Pseudocloeon* T_2, T_3, T_D
- *Baetiella* T_1
- *Platybaetis* T_1 (= cf. *Baetiella*, Dudgeon 1983a)
- *Procloeon harveyi* Kimmins
- *Centroptilum* T_x, LT
- *Cloeon* sp.

Oligoneuriidae
- *Isonychia* sp. (probably *I. kiangsinensis* Hsu)

Heptageniidae
- *Compsoneuriella* T_1, T_2 (= *Compsoneuria* and *Ecdyonurus*, Dudgeon 1982d, e; 1983a; 1984a, b)
- *Ecdyonurus herklotsi* Hsu
- *Epeorus (Iron)* T_1
- *Epeorus* T_2
- *Afronurus* (= *Cinygmina*?) sp.
- *Paegnoides cupulatus* (Eaton) (= *Thalerosphyrus* t_1, Dudgeon 1982e; 1983a; 1984a, b)

Leptophlebiidae
- *Choroterpes (Euthraulus)* T_c, T_H (previously included under *Choroterpes* T_1, Dudgeon 1982d; e; 1983a; 1984a, b)
- *Choroterpes (Euthraulus)* L_1
- *Cryptopenella fascialis* Gillies
- *Isca (Isca) purpurea* Gillies
- *Habrophlebioides gilliesi* Peters
- *Thraulus* T_1 (nr. *T. bishopi* Peters and Tsui)

Ephemerellidae
- *Serratella* T_2, L_2 (= *Ephemerella*, Dudgeon 1982d; e; 1984a, b)
- *Teloganodes* sp.
- *Ephemerellina* T_1 (= *Ephemerella* T_1, Dudgeon 1982d, e; 1983a; 1984a, b)

Caenidae
- *Caenodes* T_1, T_2 (= *Caenis*, Dudgeon 1982d, e; 1983a; 1984a, b)
- *Caenis* L_2, L_3

Ephemeridae
- *Ephemera (Ephemera) pulcherrima* Eaton
- *E. (E.) serica* Eaton
- *Ephemera (E.)* sp. (probably *E. (E.) spilosa Navàs*) (= *Ephemera* T_1, Cudgeon 1982d)
- *E. (Aethephemera) pictipennis* Ulmer (= *Ephemera* T_2, Dudgeon 1983a)

Prosopistomatidae
- *Prosopistoma* sp.

(i.e. the sediments were better sorted), reflecting a greater proportion of fine particles in middle and lower course river deposits. Skewness increased downstream as the fine "tails" of the sediments became more developed and the "peaked-ness" of the particle-size distribution was reduced (raising kurtosis values to approach unity). Scouring of fine particles from the river bed during the summer wet season lead to more poorly sorted sediments of larger mean grain size in the middle course, but declining flow volume in December through March allowed re-establishment of downstream trends in sediment grain-size statistics (Dudgeon 1984a). A slight downstream increase in sedimentary organics was observed, with a tendency towards an overall decline throughout the river during the summer monsoon. Greatest levels of sedimentary organics were recorded in the middle and lower course at the end of the dry season.

Thirty mayfly species were recorded from the LTR; 21 of these were numerous and were recorded from at least two stations. Downstream trends in species richness were not matched by changes in abundance with little correlation between standing stock and species richness (Fig. 1). Only at site 4 during the dry season was a fall in combined abundance paralleled by decreased species representation; this observation was attributable to waste discharge from a newly established duck farm. A wider range of families and genera were represented in the upper course, and this trend was most marked in the dry season when mayflies had been eliminated from site 5. Only Caenidae and Baetidae persisted at sites 3 and 4 throughout the year; Leptophlebiidae were present from the headwaters to station 5 in the wet season, but by the late dry season were restricted to sites 1 and 2 (Fig. 1). Heptageniiidae and Ephemerellidae were confined to sites 1–3, and were numerous at sites 1 and 2 only.

Several of the 14 baetids recorded from LTR displayed distinctive longitudinal zonation patterns (Fig. 2). *Baetiella* T_1, *Baetis* T_1 and *Baetis* T_2 were mostly confined to stations 1 and 2; *Baetis* L_7 and *Pseudocloeon* L_3 by contrast were restricted to sites 3–5, while *Baetis* L_8 was not recorded

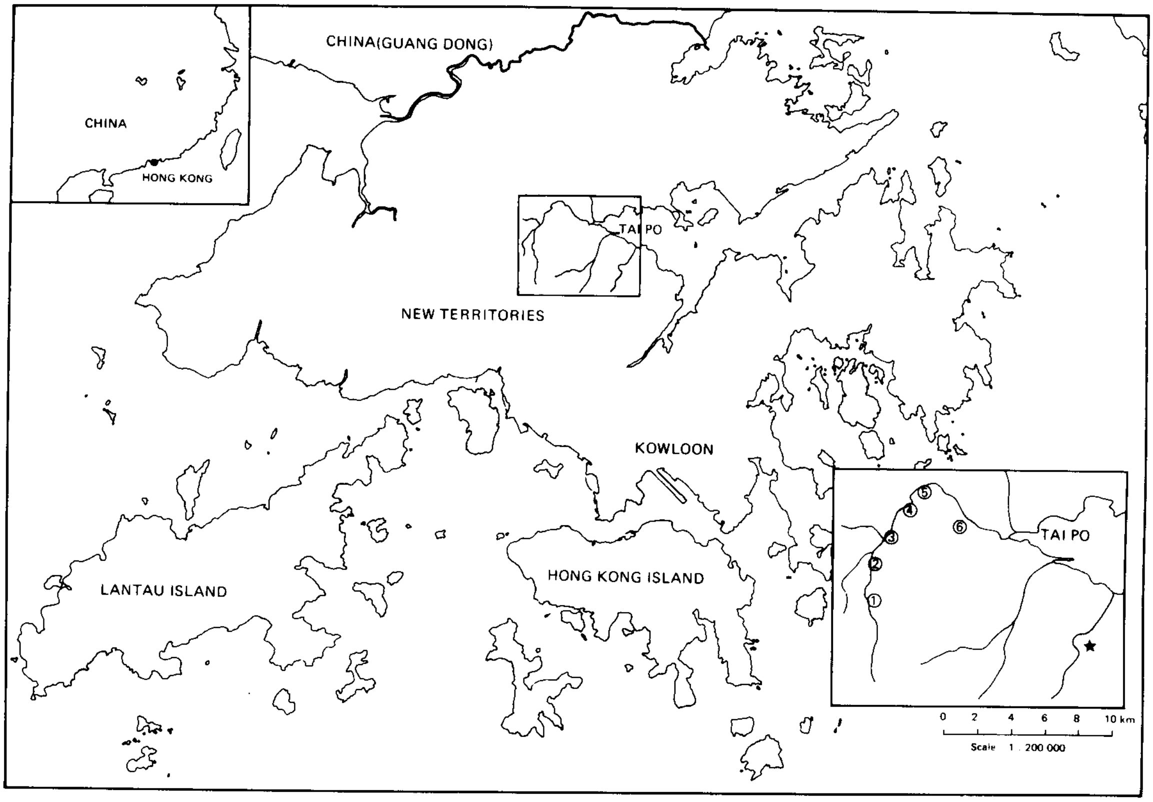

Fig. 1. A map showing the location of Hong Kong, the study area and the study sites. The star marks Tai Po Kau forest stream and the numbers the sites on Lam Tsuen River.

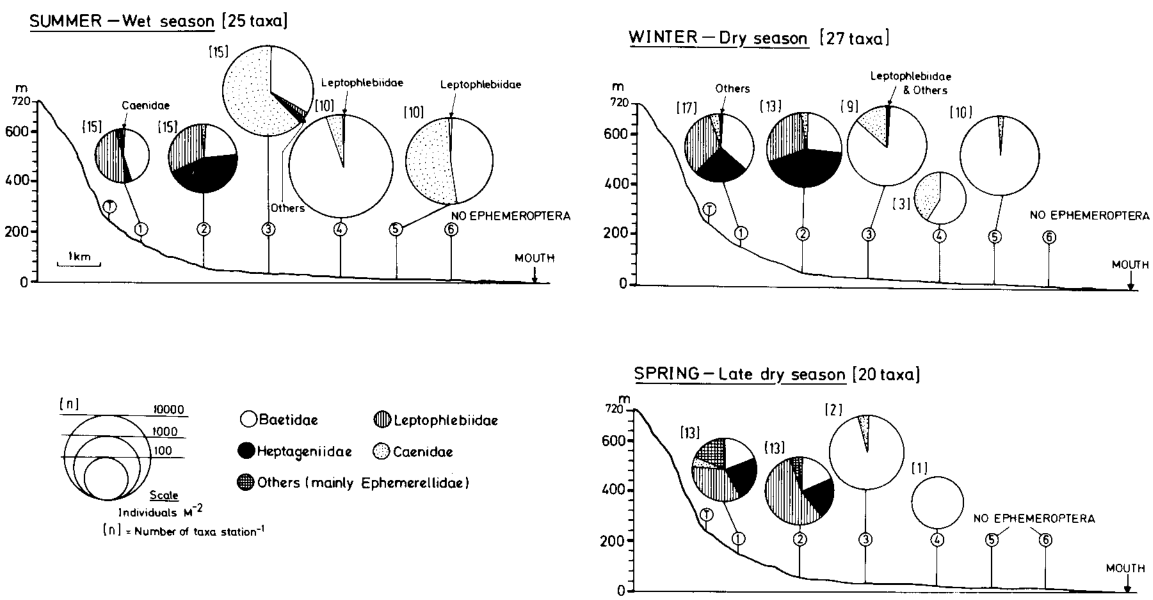

Fig. 2. Seasonal changes in the distribution and abundance of ephemeropteran families along the Lam Tsuen river, Hong Kong.

at site 1 despite its abundance downstream. Only *Baetis* T_3 was present at all sites where mayflies were found, and was highly numerous (over 35000 individuals m^{-2}) at site 4. *Centroptilum* L_1 was recovered from benthic samples at site 5 only; elsewhere in LTR this species was associated with trailing roots and grasses beside the river banks. LTR caenids likewise showed interspecific differences in longitudinal distribution (Fig. 3). *Caenodes* T_1 was found at sites 2 and 3 (also at site 1 in the dry season), whilst *Caenodes* T_2 extended downstream to site 4. *Caenis* L_2 and *Caenis* L_3 were not present upstream of site 3, and were the only caenids at site 5 where they attained combined densities in excess of 5000 individuals m^{-2}.

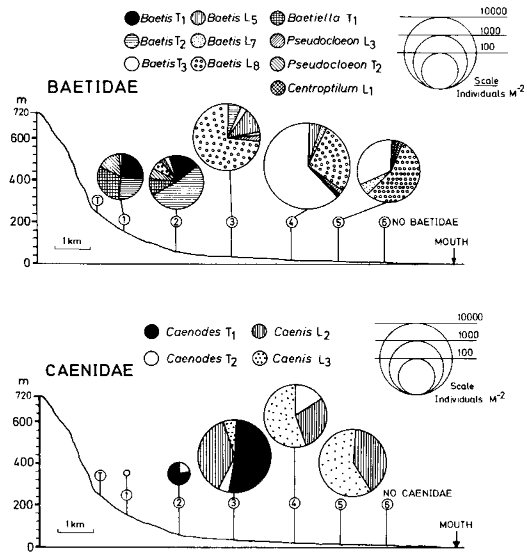

Fig. 3. The distribution and abundance of common Baetidae and Caenidae along the Lam Tsuen River, Hong Kong, in September 1978.

Microdistribution

Trends in the mean abundance of 14 common Ephemeroptera larvae (of a total of 31 recorded

Table 2. The abundance (mean numbers m^{-2} ± 95% confidence limits) of mayflies at five sites across the width of Tai Po Kau Forest Stream

	1	2	3	4	5
Baetidae					
Baetis T_1	10.6 ± 4.1	30.4 ± 6.9	20.4 ± 5.6	12.5 ± 4.4	2.5 ± 2.0
Baetis T_2	5.0 ± 2.8	60.4 ± 9.7	102.5 ± 12.6	47.5 ± 8.6	37.4 ± 7.6
Baetis T_3	32.5 ± 7.1	42.7 ± 8.1	7.5 ± 3.4	45.7 ± 8.4	30.9 ± 6.9
Baetis T_4	85.8 ± 11.5	17.7 ± 5.2	10.0 ± 3.9	32.3 ± 7.1	82.5 ± 11.3
Leptophlebiidae					
Thraulus cf. *bishopi*	110.9 ± 13.1	7.7 ± 3.5	10.0 ± 3.9	7.5 ± 3.4	137.4 ± 14.6
Isca T_1	5.0 ± 2.8	90.4 ± 11.8	227.6 ± 18.8	82.5 ± 11.3	5.4 ± 2.9
Habrophlebioides gilliesi	60.0 ± 9.6	17.8 ± 5.3	10.3 ± 4.0	25.0 ± 23.8	20.6 ± 5.6
Choroterpes (*Euthraulus*) spp.	622.5 ± 31.0	470.6 ± 27.0	190.3 ± 17.2	680.1 ± 32.4	725.9 ± 33.5
Heptageniidae					
Compsoneuriella T_1	85.4 ± 11.5	152.8 ± 15.4	45.1 ± 8.3	245.0 ± 19.5	110.9 ± 13.1
Compsoneuriella T_2	5.0 ± 2.8	47.5 ± 8.6	75.9 ± 10.8	35.4 ± 7.4	2.6 ± 2.0
Ephemerellidae					
Serratella T_1	20.4 ± 5.6	102.5 ± 12.6	52.9 ± 9.1	157.5 ± 15.6	17.2 ± 5.2
Ephemerellina T_2	10.6 ± 4.1	35.6 ± 7.4	22.7 ± 5.9	35.2 ± 7.4	2.8 ± 2.1
Caenidae					
Caenodes T_1	607.5 ± 30.6	142.2 ± 14.8	157.9 ± 15.6	1182.5 ± 16.8	397.2 ± 24.8
Ephemeridae					
Ephemera (*Ephemera*) sp.	85.4 ± 11.5	37.5 ± 7.6	35.6 ± 7.4	42.3 ± 8.1	42.5 ± 8.1

Table 3. Results of regression analysis of Baetidae in Lam Tsuen River samples

	Variables	Coefficient of determination ($100r^2\%$)	*F* ratio	d.f.	*P*	*b* values
Baetiella T_1	NO_2	89.8	149.51	1,22	<0.0005	−2.26
Baetis T_1	NO_2	88.3	127.74	1,22	<0.0005	−2.26
Baetis T_2	NO_3	78.2	61.12	1,22	<0.0005	−3.16
Baetis T_3	Seston, PO_4	47.9	7.35	2,21	<0.005	+3.91, −2.69
Baetis T_5	Sorting	20.9	4.50	1,22	<0.05	−5.24
Baetis T_6	Sedimentary organics	25.5	7.53	1,22	<0.025	−3.23
Baetis T_7	Sedimentary organics BOD_5, NO_2	58.0	9.20	3,20	<0.0005	−4.00, 1.25, 0.73
Baetis T_8	NO_2	46.1	14.56	1,22	<0.001	+2.07
Pseudocloeon T_2	Sedimentary organics	21.2	5.92	1,22	<0.05	−4.02
Pseudocloeon T_3	Sedimentary organics	23.7	6.82	1,22	<0.025	−4.14

species) across the width of TPKFS are shown in Tables 2-4, where sites 1 and 5 were near the banks, site 3 was mid-stream, and sites 2 and 4 were intermediately situated. Within the Baetidae (Table 2), *Baetis* T_1 and *Baetis* T_2 attained greatest abundance midstream, this trend being slightly more apparent for the numerous *Baetis* T_2. *Baetis* T_4, by contrast, was abundant close to the banks while *Baetis* T_3 was frequent at bankside and (particularly) intermediate sites.

The Leptophlebiidae likewise varied in across-stream microdistribution (Table 2), with *Isca* T_1 largely confined to midstream and *Thraulus cf. bishopi* mostly inhabiting bankside sites. *Habrophlebioides gilliesi* was also scarce in midstream, while the *Choroterpes (Euthraulus)* spp. microdistribution pattern was poorly defined reflecting the difficulty of distinguishing larvae of different TPKFS species within the subgenus *Euthraulus*.

Of the remaining common taxa, *Compsoneuriella* T_2 (Heptageniidae) generally occupied midstream sites (Table 2), although only a small proportion of the more numerous *Compsoneuriella* T_1 which were collected came from this site. *Caenodes* T_1 and *Ephemera (Ephemera)* sp. were slightly more numerous close to the stream banks, but there was considerable intersample variation in population densities at all sites. Ephemerellidae

Table 4. Results of regression analysis of Heptageniidae, Leptophlebiidae, Ephemerellidae and Caenidae from Lam Tsuen River samples

	Variables	Coefficient of determination ($100r^2\%$)	*F* ratio	d.f.	*P*	*b* values
Compsoneuriella T_1	NO_3	67.6	45.84	1,22	<0.005	−2.17
Compsoneuriella T_2	BOD_5	80.2	89.09	1,22	<0.0005	−2.66
Epeorus (*Iron*) T_2	NO_2	82.6	104.21	1,22	<0.0005	−1.73
Choroterpes (*Euthraulus*) spp.	BOD_5	81.4	96.53	1,22	<0.0005	−2.62
Isca T_1	BOD_5	83.0	107.26	1,22	<0.0005	−2.90
Serrtella T_2	NO_2	68.4	47.52	1,22	<0.0005	−1.63
Caenodes T_2	BOD_5	31.5	10.14	1,22	<0.005	−1.62
Caenis L_2	Sedimentary organics, NO_3, NO_2	100.0	78015.5	3,20	<0.0005	+4.55, +1,19, +1.78
Caenis L_3	NO_2, sedimentary organics	54.6	12.61	2,21	<0.0005	+1.27, −4.85

were generally least abundant close to the banks, and most numerous at sites 2 and 4. Again, however, the microdistribution patterns of *Serratella* T_2 and *Ephemerellina* T_1 were obscured by high intersample variation in population densities.

Determinants of distribution and abundance

Regression analysis of mayfly population densities (dependent variable) on environmental parameters (independent variables or predictors) for LTR species gave mixed results, but in most cases some degree of explanation (as indicated by the significance of F ratios and the coefficient of determination, r^2) was possible. Of 21 species tested, only *Caenodes* T_1 and *Choroterpes* (*Euthraulus*) L_1 had no significiant predictor variables. The organic content of fine sediments and the nitrite concentration of river water were the most common best-fit predictor variables for LTR Baetidae (Table 3), although nitrates, seston load and sediment sortedness were also significant. Baetids responded negatively to increased sedimentary organics, but the response, if any, to seston load was positive. *Baetis* L_8 was favoured by increasing nitrite concentrations although the abundance of upper course species (*Baetis* T_1, *Baetis* T_2, and *Baetiella* T_1) declined with elevated nitrite or nitrate levels.

Water quality was also a major determinant of heptageniid and leptophlebiid abundance (Table 4). Numbers of *Compsoneuriella* T_1, *Compsoneuriella* T_2 and *Epeorus* T_1 were inversely related to nitrate, nitrate and BOD_5 loading, while *Isca* T_1 and *Choroterpes* (*Euthraulus*) spp. (excluding *Choroterpes* [*Euthraulus*] L_1) declined as BOD_5 increased. *Serratella* T_2 and *Caenodes* T_2 were similarly influenced by nitrites and BOD_5 (Table 4). *Caenis* L_2 and *Caenis* L_3, which were numerous in the middle and lower course, differed in their responses to habitat parameters. *Caenis* L_2 was favoured by increased sedimentary organics, nitrates and nitrites, while *Caenis* L_3 abundance responded positively to nitrites but numbers declined as sedimentary organics increased.

A surprising result of the LTR regression analysis was the extent to which variations in abundance of individual mayfly species could be explained by models containing a single environmental predictor. In only two species did best-fit models include two parameters, a further two species incorporating three predictors. Also of interest was the poor predictive or explanatory power of sediment grain size statistics; in addition phosphates and total seston were (together) only significant predictors for a single species.

A similar tendency for best-fit models to include a single predictor was apparent for TPKFS mayfly samples, although five out of 12 regressions included two predictors (Tables 5 and 6). No best-fit models included three predictors, and *Baetis* T_3 and *Serratella* T_2 had no significant predictor variables. By contrast with predictors of

Table 5. Results of regression analysis of Baetidae and Leptophlebiidae from Tai Po Forest Stream samples

	Variables	Coefficient of determination ($100r^2\%$)	F ratio	d.f.	P	b values
Baetis T_1	Skewness, chlorophyll c	19.2	4.29	1,18	<0.05	+2.65, −5.57
Baetis T_2	Skewness	32.0	8.46	1,18	<0.01	+3.57
Baetis T_4	Sorting	32.8	8.78	1,18	<0.005	−3.35
Thraulus cf. *bishopi*	Sorting, CPOM	69.6	19.47	2,17	<0.0005	−3.56, −4.43
Isca T_1	Sorting	51.7	19.29	1,18	<0.0005	+5.78
Choroterpes (*Euthraulus*) spp.	Sorting, skewness	42.2	6.21	2,17	<0.01	−5.20, +4.48
Habrophlebioides gilliesi	Kurtosis, chlorophyll b	41.9	6.13	2,17	<0.01	+21.4, +3.07

Table 6. Results of regression analysis of Heptageniidae, Ephemerellidae, Caenidae and Ephemeridae from Tai Po Forest Stream samples

	Variables	Coefficient of determination ($100r^2\%$)	*F* ratio	d.f.	*P*	*b* values
Compsoneuriella T_1	Chlorophyll *a*, sorting	26.0	4.77	2,17	<0.025	$+1.56$, -1.48
Compsoneuriella T_2	Skewness	55.1	22.06	1,18	<0.0005	$+4.46$
Ephemerellina T_1	Sedimentary organics	33.4	9.02	1,18	<0.01	-5.01
Caenodes T_1	Total chlorophyll	32.8	8.78	1,18	<0.01	-4.05
Ephemera (*Ephemera*) sp.	Mean particle size, Chlorophyll *b*	78.7	23.78	2,17	<0.0005	$+0.57$, $+3.33$

longitudinal zonation patterns, sediment statistics were important predictors of microdistribution. Chlorophylls were included in best-fit models of *Compsoneuriella* T_1 and *Caenodes* T_1 abundance, in addition to serving as secondary predictors for three species. Sedimentary organics were important for *Ephemerellina* T_1 alone while total detritus or CPOM standing stocks were generally unimportant, CPOM serving as a secondary predictor for *Thraulus cf. bishopi* only. As in LTR, there were interspecific differences in mportant predicting variables within genera. This observation was in agreement with differences in across-stream microdistribution of *Baetis* spp. and *Compsoneuriella* spp.

DISCUSSION

Of the 47 species/OTUs in eight families of Hong Kong Ephemeroptera, the Baetidae were the most diverse. This reflects the wide range of baetid habitat preferences, from standing water (*Cloeon*) to torrential streams (*Baetiella*), in addition to considerable intrageneric differences in longitudinal zonation and microdistribution patterns. The latter is emphasized by best-fit regression models which revealed interspecific differences in predictor parameters and, for Baetis, interspecific differences (positive or negative) in responses to the same parameters (e.g. nitrites). Similar comments apply to Caenidae which were widely distributed in LTR. Like Baetidae, the Hong Kong Heptageniidae and Leptophlebiidae were species-rich, but both were largely restricted to the upper course of streams and rivers. The negative relationship between the abundance of species of these families and nitrate, nitrite or BOD_5 loadings is a strong indication of truncation of longitudinal distribution by organic pollution. Indeed, the confinement of mayflies with similar predictors to upper LTR during the dry season, when pollution loads increase as flow volume declines, supports this supposition. The importance of pollution is further indicated by declining overall species richness below LTR site 3 during the dry season, compared to the downstream spread of species after the river has been flushed out by summer monsoonal rains.

An extensive literature has documented the relationship between water quality and mayfly presence, absence or abundance (e.g. Roback 1974, Williams 1980), but it is often unclear how a particular parameter may affect the distribution of any one species. This aspect is complicated by different degrees of response to pollution by larvae of different genera or species (Roback 1974). A direct toxic effect of nitrites is possible in certain cases whilst high biological oxygen demand may lead to night-time oxygen sags causing acute respiratory stress for sensitive species. However, it should be emphasized that the predictor variables in best-fit models may not be direct determinants of abundance as they could be correlated with unmeasured parameters. For example, the positive relationship between *Caenis* L_3 or *Baetis* L_8 abundance and nitrite concentration may have involved an indirect interaction through increased food availability; unfortunately the importance or details of such processes are virtually unknown (Wiederholm 1984).

The point to be made here is that the longitudinal distribution of mayflies in LTR, and by implication other Hong Kong rivers, is a consequence of organic pollution. Dumping untreated animal waste and farmyard debris into rivers has a direct effect on the nutrient levels, BOD_5, seston characteristics and sedimentary organic content (Dudgeon 1984a), and it is these parameters which (directly or indirectly) determine the abundance of LTR mayflies. Significantly, factors unaffected by organic pollution (sediment grain-size statistics) have, with a single exception, no influence on LTR mayfly abundance.

A point related to organic pollution is the notable absence of Ephemeroptera characteristic of larger rivers from the Hong Kong fauna. Genera such as *Neopotamanthodes, Neopotamanthus, Potamanthodes, Rhoeanthus* (Potamanthidae), *Ephoron* (Polymitarcyidae), *Angenesia* (Palingeniidae) and *Potamanthellus* (Neoephemeridae), although known from China (Gui 1985, Dudgeon unpubl. obs.), may be excluded by a shortage of suitable habitat due to the restricted area of coastal plain. However river pollution is also likely to have played a part.

Preliminary investigations of TPKFS mayflies indicated that sediment characteristics were important determinants of microdistribution. Across-stream gradients in grain-size statistics (Dudgeon 1982b) apparently influenced species abundance across the study reach, and interspecific differences in microdistribution could be related to differences in the parameters included in best-fit regression models. The importance of sediment characteristics in determining the microdistribution of aquatic insects is well known (e.g. Cummins & Lauff 1969, Minshall and Minshall 1977, Minshall 1984), both grain size and sediment heterogeneity (sortedness, skewness and kurtosis) comprising important aspects of the substrate "template". The importance of sedimentary organic material is less clearly established, since although sometimes serving as a food source it may also reduce pore space, blanket the surface of the bed and impede movement, respiration and feeding (Minshall 1984). An excess of decaying organic particles can lead to reduction in oxygen concentrations (especially at night) and this may account for the negative relationship between certain LTR baetids and sedimentary organics. TPKFS sedimentary organics reduced the abundance of *Ephemerellina* T_1 but the mechanisms of this interaction are unclear.

Surprisingly in view of the heterotrophic community metabolism of TPKFS (Dudgeon 1983b), neither sedimentary organics, allochthonous detritus nor CPOM were positively associated with increased mayfly abundance. By contrast, the standing stock of periphyton (as chlorophylls) was a predictor of abundance for certain species. While these data may reflect factors determining the abundance of a few specialised algivores, detrital standing stocks exceeded TPKFS periphyton biomass by over 100 times. Perhaps all patches are well endowed with detrital food and/or substrate so that detritus-related parameters would have little or no influence on mayfly abundance within the study reach. A similar lack of association has been documented by Minshall and Minshall (1977) and Peckarsky (1980) when the amounts of detritus were in excess of the insects' requirements.

The present regression analysis of insect microdistribution in TPKFS is drawn from a series of samples taken during one summer. It is preliminary in the sense that it does not include seasonal effects. Data are now being collected to extend the analysis over a two year period, which will allow development of more robust models of the determinants of microdistribution of TPKFS mayfly larvae.

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