

# The life history, secondary production and micro-distribution of *Ephemera* spp. (Ephemeroptera: Ephemeridae) in a tropical forest stream

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With 2 figures and 1 table in the text

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**Abstract:** The ecology of ephemerid mayflies was investigated in Tai Po Kau Forest Stream (TPKFS), New Territories, Hong Kong, over a two-year period. Quantitative benthic samples of larvae were taken from different microhabitats within stream riffles on 45 occasions, and combined with light-trap captures of adults, were used as a basis for investigating life-history patterns and estimating secondary production. Two species, *Ephemera* (*Ephemera*) *spilosa* and *E. (Aethephemera) pictipennis* were collected, of which the former was more abundant (mean densities  $\pm$  95 % confidence limits =  $11.06 \pm 1.48$  versus  $0.48 \pm 0.26$  indiv.  $m^{-2}$ ). Larvae of *E. (E.) spilosa* were patchily distributed. Mean densities in microhabitats close to the stream banks, where sediments were relatively fine grained, were  $>50\%$  greater than those in midstream; however, this difference was not statistically significant. Both ephemerids were univoltine in TPKFS, but emergence of adult *E. (A.) pictipennis* was highly synchronized (in April), while *E. (E.) spilosa* emerged later over a more extended period (mainly May–July). Annual production of *E. (E.) spilosa* (in terms of ash-free dry weight, AFDW) in the study reach was estimated at  $24.26 \text{ mg AFDW } m^{-2}$  using the size-frequency method; the dry-weight (DW) annual production estimate was  $37.28 \text{ mg DW } m^{-2}$ . Densities of *E. (A.) pictipennis* were too low to allow reliable production estimates. Production: biomass ratios for *E. (E.) spilosa* were 3.79 (AFDW) and 3.67 (DW), and within the range of values reported for ephemerids elsewhere.

## Introduction

The ephemeropteran family Ephemeridae has an almost cosmopolitan distribution and, by comparison with other geographical regions, the number of Asiatic species is high (MCCAFFERTY 1973). Two ephemerid genera have been

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recorded from China: *Ephemera* L. and *Eatonigenia* ULMER (HSU 1936 a, 1936 b, 1937; ZHANG 1988). The latter is known from Hainan Island in southern China only (ZHANG 1988), while *Ephemera* is relatively speciose and widely distributed (HSU 1936 a, 1936 b, 1937). Ephemeroidea are common in lotic habitats throughout Asia, including the islands of Taiwan and the Philippines (MCCAFFERTY 1973), and the larvae burrow in sandy stream sediments. Despite their prevalence and diversity, investigations of ephemeroidea ecology in Asia have been confined largely to Japan (e.g. GOSE 1970, KURODA et al. 1984, TAKEMON 1985, WATANABE & KURODA 1985, BAN & KAWAI 1986, BAN 1988, TAKEMON 1990); a paper reporting research undertaken by BALASUBRAMANIAN et al. (1992) in India being the single exception.

The present study is an account of the life history, microdistribution and production of Ephemeroidea in a Hong Kong forest stream. An attempt was made to estimate secondary production because this parameter integrates survival, growth and voltinism in a single figure, and indicates the success of a population and its functional importance in the ecosystem (BENKE 1984, 1993). Despite this, there are few data on secondary production from tropical streams (BENKE 1993), and there is a general paucity of information on benthic production in Asia (DUDGEON 1995).

## Materials and methods

The work reported upon here is part of on-going research on the trophic dynamics of the macrobenthos in Tai Po Kau Forest stream (TPKFS; latitude 22° 09' N), New Territories, Hong Kong. DUDGEON (1992) has provided a summary of this work and DUDGEON (1992, p. 21–27) gives a detailed description of the study site which is a third-order, unpolluted, nutrient-poor forest stream. Sediments constituting the stream bed are, in general, coarse grained, poorly-sorted and leptokurtic (DUDGEON 1992, p. 21–24 and references therein), with a positive skew towards large particles. Substrate characteristics change across the stream bed with increasing proportions of fine particles in sediment patches close to the banks. Spates associated with summer monsoonal rains scour the stream bed and wash fine particles downstream thereby reducing interpatch heterogeneity. Across-stream gradients in particle size and sediment characteristics are re-established as discharge volumes decline upon the onset of the dry season when sediment heterogeneity is restored (DUDGEON 1992, p. 21–24).

Two species of *Ephemera* were present in TPKFS. They comprised a single species in the subgenus *Ephemera* L. – *Ephemera* (*Ephemera*) *spilosa* NAVAS (re-described by HSU 1937) – and a representative of the subgenus *Aethphemera* MCCAFFERTY & EDMUNDS – *Ephemera* (*Aethphemera*) *pictipennis* MCLACHLAN (see HSU 1937b). Hong Kong ephemeroidea identified as *E. (E.) spilosa* also resemble the more widespread and better known *E. (E.) serica* EATON rather closely (W. L. PETERS, Florida A & M University, pers. comm.). The name *E. (E.) spilosa* is used herein, but confirmation of the identity of this species must await a reexamination of all Chinese *Ephemera* since

“... there has always been an obvious lack of consistency in species descriptions of Ephemeridae in general, making species comparisons difficult” (HUBBARD 1983). Adult *E. (A.) pictipennis* are large and distinctive, while small larvae of the two subgenera can be distinguished easily by virtue of the strongly asymmetric mandibular tusks of *Aethephemera* (the right tusk is smaller). Although the subgenus *Aethephemera* was established initially on the basis of larval characteristics only (MCCAFFERTY & EDMUNDS 1973, HUBBARD 1983), the features of the adults are now known (BALASUBRAMANIAN et al. 1991). The association of larval and adult *Aethephemera* in TPKFS was confirmed by the simultaneous collection of larval exuviae and emerging adults.

Life-history observations and production estimates of *Ephemera* spp. were based upon samples taken from a single, shaded riffle of TPKFS between May 1977 and May 1979 (inclusive). Quantitative collections were made at approximately two-week intervals using a box sampler (COFFMAN et al. 1971) which enclosed 0.1 m<sup>2</sup> of stream bed. Samples were taken in multiples of five in a stratified basis across the stream (one at each bank, one in midstream, and two between the banks and midstream) in an attempt to ensure that different substrate patches were sampled in relation to their relative abundance. Animals from these collections were used to estimate production. Additional individuals from five further samples, collected from the midstream portion of another riffle situated 100 m upstream, were used as an aid to interpret life-history patterns. This involved investigation of the age/size-structure of sample populations of each species by dividing them into 0.5-mm size groups on the basis of head-capsule width. Larvae of both species were insufficiently abundant to permit construction of size-frequency histograms on a sample-by-sample basis. Accordingly, larvae were grouped according to month of collection over the two-year study, allowing the construction of 12 histograms for the months of January to December (see also DUDGEON 1989 a). Note that this approach assumes that there is no year-to-year variation in voltinism, but a concurrent study of the damselfly *Euphaea decorata* SELYS in TPKFS (DUDGEON 1989 b) did not uncover any differences in life-history patterns between 1977–78 and 1978–79.

Data on flight periods of adult ephemerids were obtained from collections made by three ultra-violet light traps situated beside TPKFS. Traps were operated simultaneously throughout the night at irregular intervals (but at least monthly) on 23 occasions from July 1983 to June 1984 inclusive (DUDGEON 1988 gives details). Insects were trapped into alcohol and sorted in the laboratory under a dissecting microscope. Equal sampling effort was employed on each occasion that the traps were operated, and thus counts of the number of mayflies caught over the sampling period could be used to give an indication of seasonal patterns of adult emergence. It is assumed that life-history patterns in 1977–79 (when larval development was followed) matched those in 1983–84 (when adults were trapped).

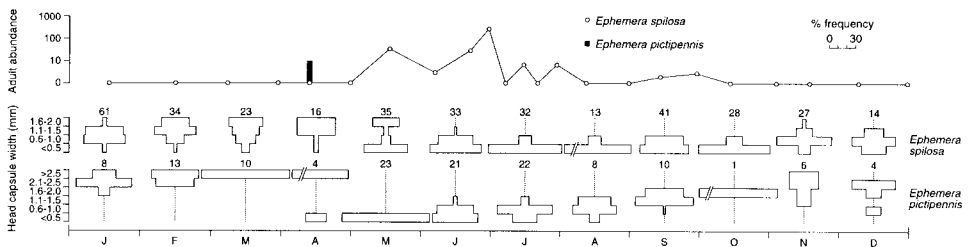
Information on changes in the size composition of larval populations of *E. (E.) spilosa*, the more abundant ephemerid in TPKFS, were combined with data from light-trap catches and used as a basis for production estimates by the size-frequency method (BENKE 1984). Here a knowledge of the cohort production interval (CPI; i.e. the mean length of the aquatic stage relative to a full year) is essential, because the initial production estimate must be corrected if the CPI is significantly greater or less than one year. Animals collected from the second (upstream) riffle were not included in calcula-

tions leading to production estimates because they were collected from midstream microhabitats only, and their inclusion would have biased standing-stock estimates for the stream bed as a whole. The calculations involved in the size-frequency method are detailed by BENKE (1984), while DUDGEON (1989b) gives an example of such calculations for the damselfly *Euphaea decorata* in TPKFS. The relationship between size and biomass of *E. (E.) spilosa* larvae of different sizes was elucidated by oven-drying groups of similar-sized animals to constant dry weight (DW), ashing them at 450 °C for one hour, and then reweighing them to obtain ash-free dry weight (AFDW).

## Results

*Ephemera (E.) spilosa* was the more abundant of the two Ephemeridae in TPKFS, with mean densities ( $\pm 95\%$  confidence limits) of  $11.06 \pm 1.48$  indiv.  $m^{-2}$  compared to densities of  $0.48 \pm 0.26$  indiv.  $m^{-2}$  for *E. (A.) pictipennis*. Monthly size-frequency histograms for populations of both species in TPKFS are shown in Fig. 1. Despite rather small sample sizes, the histograms reveal that both species were univoltine, with *E. (A.) pictipennis* showing a more restricted period of recruitment and more synchronous larval growth than *E. (E.) spilosa*. Although *E. (E.) spilosa* larvae of the smallest size category were present in all months, peak recruitment took place in summer, and full-grown larvae (which did not appear in the population until November) were relatively abundant from February until May when a new generation of recruits appeared (Fig. 1).

The seasonal incidence of adults in light-trap catches strongly supported the supposed univoltinism of *Ephemera* spp. (Fig. 1). Adult *E. (A.) pictipennis* were captured by light traps on 12 April 1984, and were not taken at any other time. A seasonal study of drift in TPKFS (DUDGEON 1990) yielded exuviae of final-instar larvae of this species in April only. Records of adult mayflies captured by hand nets during 1979 (DUDGEON, unpubl. observ.), when TPKFS



**Fig. 1.** Size-frequency histograms for *Ephemera (Ephemera) spilosa* and *Ephemera (Aethephemera) pictipennis* larvae from Tai Po Kau Forest stream. The numbers beside each histogram refer to sample size. Seasonal trends in abundance of adult Ephemeridae, as indicated by light-trap catches, are also shown (note logarithmic scale).

was visited at least once every two weeks, showed that *E. (A.) pictipennis* was collected on 12 April of that year only. *Ephemera (E.) spilosa* adults were relatively common around TPKFS in 1983–84, and were most abundant in light-trap catches during May, June and July, although a few individuals were collected in August, September and early October. Records of captures of adult mayflies around TPKFS in 1979 show that *E. (E.) spilosa* was present from late April to July.

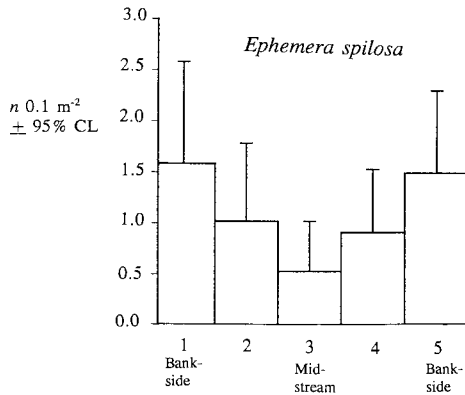
Log dry weight (DW, mg) and ash-free dry weight (AFDW, mg) were strongly correlated with head-capsule width ( $x$ ) of *E. (E.) spilosa* (AFDW  $r=0.968$ ,  $P<0.001$ ,  $y=-1.539 + 1.123 x$ ; DW  $r=0.977$ ,  $P<0.001$ ,  $y=-1.890 + 1.518 x$ ) and, when combined with information on population densities, size distribution and voltinism (or CPI) of these larvae in TPKFS, provided a basis for calculating secondary production. Based on a knowledge of the life-history of *E. (E.) spilosa* in TPKFS (Fig. 1), a CPI of one was used in production calculations. As Table 1 shows, annual production was estimated at 24.26 mg AFDW  $m^{-2}$  (37.28 mg DW  $m^{-2}$ ), and production : biomass ( $P : B$ ) ratios were 3.79 (AFDW) and 3.67 (DW).

The microdistribution patterns of *E. (E.) spilosa* across TPKFS were characterised by a considerable degree of variation in population densities within microsites (due in part to the number of samples which lacked larvae) with concomitantly high 95 % confidence limits around values of mean density (Fig. 2). Larvae were generally more numerous at bankside microsites 1 and 5 than at microsites 2, 3 and 4 in mid-stream, and mean densities at the banks were at least 1.5 times higher than in midstream. Densities at microsite 3 were approximately one third of those at the banks. Despite these microdistributional trends, one-way analysis of variance (ANOVA) on log-transformed density data did not yield a significant difference in abundance among microsites ( $F_{4,212} = 1.97$ ,  $P=0.099$ ).

Stepwise multiple-regression analysis was employed to account for the microdistribution patterns of *E. (E.) spilosa* in TPKFS. Larval densities were the dependent variable, and periphyton, detrital standing stocks and sediment grain-size statistics (particle size, sorting, skewness and kurtosis) measured in

**Table 1.** Production statistics for *Ephemera (Ephemera) spilosa* (Ephemeridae) in Tai Po Kau Forest Stream, Hong Kong, 1977–1979, calculated by the size-frequency method and based on a total of 45 sets of samples (including those without animals).  $D$  = mean density ( $n m^{-2}$ );  $B$  = mean biomass (mg AFDW  $m^{-2}$ );  $P$  = annual production (mg AFDW  $m^{-2} y^{-1}$ ). Figures in parentheses are in dry weight (mg) units for comparison.

|                              | $D$   | $B$             | $P$              | $P : B$        |
|------------------------------|-------|-----------------|------------------|----------------|
| <i>Ephemera (E.) spilosa</i> | 11.06 | 6.40<br>(10.16) | 24.26<br>(37.28) | 7.58<br>(7.34) |



**Fig. 2.** Mean population densities ( $n\ 0.1\ m^{-2}$ )  $\pm$  95% confidence limits (CL) for *Ephemera* (*Ephemera*) *spilosa* larvae at five microsites across Tai Po Kau Forest Stream, 1977–1979. Microsites 1 & 5 were beside the banks, 3 in midstream, and 2 & 4 were in intermediate positions.

each sampling unit constituted the independent variables (see DUDGEON 1989b for details). None of the independent variables – nor any combination of them – explained a statistically-significant proportion of the variation in *E. (E.) spilosa* abundance.

## Discussion

*Ephemera (E.) spilosa* and *E. (A.) pictipennis* were both univoltine in TPKFS. Adult emergence of the latter species took place during April and showed marked synchrony. The timing of emergence prior to the onset of the summer monsoon could be interpreted as an adaptation to reduce spate-induced mortality of large larvae as has been suggested for Odonata and certain Trichoptera in Hong Kong (DUDGEON 1992, p. 46–50). Alternatively, or in addition, such synchrony could be viewed as increasing the probability of finding a mate or a means of satiating predators, thereby reducing the predation rates on individual mayflies (SWEENEY & VANNOTE 1982). In Japan, *Ephemera* spp. are typically univoltine and may have synchronized emergence (GOSE 1970, KURODA et al. 1984, WATANABE & KURODA 1985, BAN & KAWAI 1986, TAKEMON 1990), but semivoltinism can occur if stream temperatures are low (GOSE 1970). Indeed, two or even three-year life cycles (in England and Sweden, respectively: WRIGHT et al. 1981, SVENSSON 1977) have been reported for *E. danica* MÜLLER in Europe.

The timing of ephemeraid emergence is related to stream temperatures in Japan, and recruitment of *E. japonica* MCLACHLAN and *E. strigata* EATON

takes place earlier in the lower (warmer) course of Japanese streams than in the upper reaches (GOSE 1970, WATANABE & KURODA 1985). There is evidence that *E. japonica* and *E. strigata* populations in some Japanese streams are bimodal comprising two groups (KURODA et al. 1984, BAN & KAWAI 1986) which may be the result of cohort splitting due to delayed hatching of eggs (BAN & KAWAI 1986). A similar, complex situation is seen in the life histories of North American Ephemeridae (*Hexagenia* spp.) owing to the combination of a protracted flight period, the presence of multiple cohorts, delayed hatching of eggs, and considerable individual variation in growth rate (HEISE et al. 1987, CORKUM & HANES 1992).

Unequivocal evidence of bivoltinism is still lacking for Japanese *Ephemera* spp. (despite suggestions to the contrary: e.g. KURODA et al. 1984), and a recent view is that the *E. strigata* (at least) is univoltine despite the presence of population bimodality (BAN 1988). Given that Hong Kong *Ephemera* spp. can complete only one generation per year, and that larval growth rates are temperature dependent (see above; also SWEENEY 1984, CORKUM & HANES 1992), it is unlikely that Japanese ephemerids are bivoltine because this would imply that they can achieve faster growth and development rates than the Hong Kong species despite living in a cooler, more seasonal environment. In tropical south India, *E. (A.) nadinae* MCCAFFERTY lacks the clear seasonal cycle of development seen in Hong Kong or Japan, and larval growth is asynchronous with adults emerging throughout the year (BALASUBRAMANIAN et al. 1992). These authors assert that *E. (A.) nadinae* is multivoltine but the size-frequency histograms that they present (BALASUBRAMANIAN et al. 1992, p. 74) merely display asynchronous growth and give no hint as to voltinism. On the basis of the data presented, this ephemerid could be univoltine with asynchronous larval growth and development.

The life-histories of Hong Kong ephemerids are rather simple, with only *E. (E.) pilosa* showing evidence of prolonged recruitment (relative to *E. (A.) pictipennis*). This lack of complexity could reflect strong selective pressure for adult emergence before the height of the summer monsoon (rainfall peaks in August when 18% of the annual total is recorded; DUDGEON 1992, p. 40), but other factors (e.g. temperature, photoperiod; reviewed by SWEENEY 1984) could also influence life histories in Hong Kong's seasonal tropical climate. Both temperature and photoperiod have been shown to affect growth and survivorship of *Hexagenia* spp. in laboratory rearing trials (CORKUM & HANES 1992). It should be stressed that there are no data on egg-development times for the Hong Kong ephemerids, but given that TPKFS temperatures during and after adult emergence and oviposition exceeded 20 °C (reaching a high of 26 °C), the hatching period would be quite short. FRIESEN et al. (1979) report that *Hexagenia rigida* MCDUNNOUGH hatch in 10 days or less at 24 °C, but egg-development time lengthens markedly at low temperature ( $\leq 16$  °C).

Production estimates for *Ephemera strigata* in pool microhabitats of the Niugawa River, Japan, were 4.25 g wet weight m<sup>-2</sup> (GOSE 1970), but restriction of sampling to pools and the use of wet-weight units confound comparison with the results of the present study. In North America, *Hexagenia* spp. occupy lakes and large rivers where conditions differ greatly from the stony stream habitats of *Ephemera* spp. in Asia. Nevertheless reported *P*:*B* ratios (2.8–4.4; WATERS 1977) are similar to the values calculated for *E. (E.) spilosa* (3.79 in AFDW units) in TPKFS. The *P*:*B* ratio (wet-weight units) for Japanese *E. strigata* was 2.4 (GOSE 1970), reflecting cooler water temperatures (winter lows of 4 °C) than prevail in TPKFS (winter lows  $\geq 10$  °C; DUDGEON 1992, p. 38). Where *P*:*B* ratios of <2 are reported in the literature, the ephemerids involved are slow-growing, semivoltine species (e.g. *E. vulgata* L.; MORGAN et al. 1980, p. 298) unlike univoltine *E. (E.) spilosa* TPKFS.

The microdistribution of *E. (E.) spilosa* was characterised by a trend towards greater (although not statistically-significant) abundance close to the stream banks. There, sediments were relatively fine-grained and contained more sand than in midstream (DUDGEON 1992, p. 21–24), and would have provided suitable habitat for burrowing Ephemeridae. Other mayflies in TPKFS have distinctive species-specific gradients in abundance across the stream: among the Leptophlebiidae, for example, *Isca (Isca) purpurea* GILLIES is most abundant in midstream while *Thraululus* sp. is confined to bankside microsites (DUDGEON 1992, p. 24–26). However, microdistribution patterns may be complicated by ontogenetic changes, and BAN (1988) reports that *E. strigata* in Japanese streams migrates from riffles to pools during larval growth. There is no evidence that Hong Kong ephemerids undertake such migrations.

There is a close relationship between prothoracic leg morphology and the oxygen consumption of ephemerids which influences species-specific selection of sediment particle sizes for burrowing (WAUTIER & PATTEE 1955, ERICKSEN 1963, 1964). These relationships may scale up to influence ephemerid distribution in nature (ERICKSEN 1964) such that microdistribution can be correlated with sediment characteristics. Nevertheless, multiple-regression models including environmental variables (such as sediment statistics) in TPKFS failed to account for a statistically-significant proportion of the variation in *E. (E.) spilosa* densities. High variance in mayfly densities may have concealed responses of larval abundance to the independent variables. Such variance may, in turn, be linked to the seasonal scouring of the stream bed by spates during the summer monsoon (DUDGEON 1992, p. 40).

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