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Life histories, production dynamics and resource utilisation of mayflies (Ephemeroptera) in two tropical Asian forest streams

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SUMMARY

1. A 2-year study of the life histories, production dynamics and resource utilisation of five mayfly species was undertaken in two forest streams in Hong Kong [Tai Po Kau Forest Stream (TPKFS) and Shing Mun River (SMR)]. *Afronurus* sp. and *Cinygmina* sp. (Heptageniidae), *Procloeon* sp. and *Baetiella pseudofrequenta* (Baetidae), and *Choroterpes* sp. (Leptophlebiidae) were abundant in both streams and contributed more than 50% of the total mayfly populations.
2. All species had asynchronous larval development with recruitment occurring throughout the year. Mean annual production (all mayflies combined) was 3.1 and 2.0 g dry weight m^{-2} $year^{-1}$ in SMR and TPKFS, respectively – the higher value at SMR reflecting greater mayfly densities – with more than 70% of production occurring during the wet season. Mayfly production varied between years, decreasing by 5% in TPKFS and 43% in SMR during 1996–97, reflecting lower densities of heptageniids relative to 1995–96. Annual biomass turnover rates (*P/B*) were high in both sites ranging from 27.2 to 94.6 in TPKFS (*Cinygmina* sp. and *Procloeon* sp.) and from 31.8 to 109.8 in SMR (*Cinygmina* sp. and *B. pseudofrequenta*).
3. Patterns of daily production in both streams showed that *Afronurus* sp., *Cinygmina* sp. and *Choroterpes* sp. were most productive during the wet season, while *Procloeon* sp. maintained high production levels throughout the year. The highest daily production of *B. pseudofrequenta* occurred during the wet season in TPKFS, but in the dry season at SMR. Temporal overlap in production and hence resource utilisation in both streams, calculated using the proportional similarity index (*PS*), ranged from 0.39 to 0.81. It was highest (0.63–0.81) between pairs of species of Heptageniidae and Baetidae, and lowest between *Choroterpes* sp. and other mayflies (0.39–0.61). No clear temporal segregation was observed among any species. However, when using the fraction of production attributable to each food, lower *PS* values were obtained for all species in both sites. In SMR, trophic segregation may have occurred between the two species pairs *Procloeon* sp.–*Cinygmina* sp. and *Procloeon* sp.–*Choroterpes* sp. ($PS = 0.17$ and 0.03, respectively).
4. A combination of production data and information on the stable isotope signature of mayflies revealed that, during both the wet and dry seasons, more than 50% of total mayfly production in TPKFS was derived from autochthonous foods. In SMR, 68% of production was supported by allochthonous foods during the wet season, and 72% by autochthonous sources in the dry season. Considering that more than 70% of the total production occurred in the wet season, the trophic basis of mayfly production in SMR is mostly allochthonous (58%) while in TPKFS it is mainly of autochthonous origin (66%).

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The year-round importance of autochthonous foods in shaded streams such as TPKFS is surprising, but the wet season contribution of allochthonous foods (especially in SMR) may have resulted from depletion of algal biomass during spates.

Keywords: autochthonous and allochthonous foods, Ephemeroptera, resource utilisation, secondary production, tropical streams

Introduction

Measurements of secondary production integrate density, biomass, survival, growth and reproduction of individual species (Benke, 1993), and provide information on their relative importance in ecosystems. The ecology of tropical streams is generally poorly known, particularly tropical Asian streams, although information from Hong Kong has accumulated in recent years (Dudgeon, 1992, 1999a and references therein). Mayflies (Ephemeroptera) are abundant and diverse in most Hong Kong streams, representing almost 30% of benthic populations (Dudgeon, 1992), but, until recently, little was known of their life histories and production. The ephemerids *Ephemera spilosa* (Hsu, 1937) and *Ephemera pictipennis* (Hsu, 1936) are univoltine (Dudgeon, 1995), but heptageniid mayflies have asynchronous development and continuous recruitment (Dudgeon, 1996). *In situ* growth studies of two heptageniids have shown that they complete at least four generations per year in Hong Kong streams (Salas & Dudgeon, 2001b). Smaller mayflies (e.g. Baetidae and Leptophlebiidae) are likely multivoltine also. One consequence of this high turnover is that even a low standing stock of mayflies may yield substantial secondary production. However, we lack reliable estimates of the magnitude of production in tropical Asian streams; neither do we have information on how production is affected by seasonal variations in discharge.

Mayflies have generally similar trophic roles (they feed principally by scraping or collecting food from surfaces); therefore, when resources are limited, we may expect them to segregate either by food type, habitat or space (Schöener, 1986). Samples collected in a stratified manner across a Hong Kong forest stream showed that the heptageniids *Paegnoides cupulatus* (Eaton, 1871), *Iron* sp. and *Epeorus* sp. were more abundant in midstream, while *Cinygmina* sp. occurred close to the banks (Dudgeon, 1996). Other mayfly species such as *Procloeon* sp., *Baetiella pseudofrequenta* (Müller-Liebenau, 1985) (Baetidae) and *Choroterpes* sp. (Leptophlebiidae) had no evident differences in microhabitat use in Hong Kong streams (Salas, 1998). Co-existing species such as these may exhibit temporal segregation in order to minimise competition for food (Vannote, 1978). Indeed, Benke & Jacobi (1994) used daily production estimates and gut content analysis to demonstrate that coexisting mayfly species in a blackwater river (U.S.A.) had staggered production schedules based on differential utilisation of common food resources over time.

Allochthonous food resources exceeded periphyton biomass by over 100 times over a 2-year period in Tai Po Kau Forest Stream (TPKFS), and spates during the wet season reduced algal biomass by up to 90% (Dudgeon, 1982). However, despite the relative abundance of allochthonous foods, a recent stable isotope study showed that mayflies make extensive use of autochthonous foods, although consumption of allochthonous foods is also important during the wet season (Salas & Dudgeon, 2001a). In order to understand how multivoltine mayflies can sustain production throughout the year in streams, where the relative abundance of food resources changes seasonally, it is necessary to determine the contribution of allochthonous and autochthonous foods to mayfly production during each season.

The present paper has the following objectives to: (1) describe the life histories of the more abundant mayfly species present in TPKFS and Shing Mun River (SMR), Hong Kong; (2) quantify their secondary production using the size-frequency and instantaneous growth methods; (3) determine the overlap in resource utilisation by coexisting mayflies in TPKFS and SMR; and (4) determine the trophic basis of mayfly production in these two forested streams using available data derived from stable isotope analysis in TPKFS and SMR (Salas & Dudgeon, 2001a) combined with daily production estimates.

Methods

Study sites

Tai Po Kau Forest Stream and SMR are located in the New Territories of the Hong Kong Special Administrative Region (SAR) of the People's Republic of China (lat. 22°17'N). Both support a diverse array of benthic invertebrates (Dudgeon, 1992). Tai Po Kau Forest Stream runs through a managed nature reserve located on the south-western shores of Tolo Harbour. The stream originates 400 m above sea level, and has slightly acidic water that is poor in dissolved minerals but high in silicates (Dudgeon, 1992). The study site, a second-order shaded stream (UTM: 50Q KK 093821), is approximately 200 m above sea level, and drains mixed secondary forest within a nature reserve. Shing Mun River is located inside Shing Mun Country Park, adjacent to Tai Po Kau Nature Reserve, with similar geology, vegetation and water chemistry to TPKFS. The SMR study site is a second-order shaded stream (UTM: 50Q KK 071788) at an altitude of approximately 100 m above sea level. Water temperature at both sites remained above 15 °C for most of the year, ranging from 13 to 29 °C with an annual mean of 20 °C. Hong Kong receives an average of 2214 mm of rainfall each year, 77% of which occurs between May and September, with approximately 18% falling during August – the wettest month. In contrast, only 6% of the total annual rainfall occurs during the rest of the year (Dudgeon & Corlett, 1994). As a result, stream discharge is strongly seasonal with spates occurring during the wet season (see Dudgeon, 1993).

The mayflies studied were present in both streams and represented more than 50% of the total mayflies collected from cobble samples (Table 1). They comprised the heptageniids *Afronurus* sp. and *Cinygmina* sp., the leptophlebiid *Choroterpes* sp. (this taxon may include two undescribed species that could not be separated in the larval stage), and the baetids, *Procloeon* sp. and *B. pseudofrequenta*. All of these species have been classified as scrapers/collectors (Dudgeon, 1992), and successfully reared to maturity in the field and/or in the laboratory on periphyton growing on stones (Salas & Dudgeon, 2001b).

Table 1 Mayfly abundance at each site shown as the percentage of the total number of mayflies collected from 60 and 100 cobbles in Tai Po Kau Forest Stream (TPKFS) and Shing Mun River (SMR), respectively, in November 1996

	Abundance in each site (%)	
Species	TPKFS	SMR
Afronurus sp.	14.0	34.0
Cinygmina sp.	13.0	17.4
Procloeon sp.	7.8	7.9
Baetiella pseudofrequenta	14.3	12.0
Choroterpes sp.	1.4	1.1
Other mayfly species	49.5	27.6

Sampling

Benthic samples for life-history investigation and secondary production estimates were obtained in TPKFS from April 1995 to April 1997 (inclusive) and in SMR from October 1995 to September 1997 (inclusive). Sampling during the wet season, mainly in July or August, was sometimes impeded due to spates. Quantitative samples were collected biweekly by randomly sampling individual cobbles in a stratified manner across each stream site. Equal numbers of cobbles (from 8 to 20 cm along the longest axis) were collected from the stream bed close to the banks on either side, and from mid-stream. A minimum of 30 cobbles were collected at any one time from each site, with an increased sampling effort (up to 90 cobbles) during the wet season (May–September) when larval densities were reduced. Individual cobbles were lifted from the stream bed into a hand net (200 μm mesh) positioned immediately downstream whereupon each cobble was thoroughly washed inside the net. Larvae collected from all cobbles at any one site on each date were pooled and preserved in 70% ethanol.

Surface area was calculated according to Graham, McCaughan & McKee (1988) by measuring length (*L*), width (*W*) and height (*H*) of each cobble (to the nearest mm) with a tape measure in the field. Surface area was obtained by applying an equation (where $r^2 = 0.96$) developed from 30 cobbles collected at TPKFS:

$$\text{Surface area (cm}^2) = 0.13\ (LW + WH + HL)$$

The equation was based on a linear regression between (*LW* + *WH* + *LH*) and the area obtained from wrapping each cobble in aluminium foil, where the weight of a unit area of aluminium foil was known.

Laboratory methods

Mayflies were identified and counted under a stereomicroscope. Density was determined as the number of individuals per m^2 cobble. Biomass was obtained by using predetermined length–mass regressions for each species (see Appendix 1), and results were expressed in mg dry weight (DW) m^{-2} cobble. Only fresh (unpreserved) animals were used for calculating length–mass regressions. Field-collected animals were identified to genus in the laboratory, and body size (head width for heptageniids; body length for other mayflies) was measured to the nearest 0.1 mm under a stereomicroscope. Several individuals (up to 10) of the same size class were placed in a preweighed aluminium foil boat, oven-dried for 24 h at 60 °C, cooled in desiccator, and weighed to the nearest 0.01 mg using a semimicro analytical balance.

Production was calculated using the size-frequency method, corrected by the length of the larval development (Benke, 1979) obtained *in situ* (Salas & Dudgeon, 2001b) and also using the instantaneous growth method (Benke, 1993) calculated as the product of mean biomass (B) and mean growth rate (g) for a sampling interval:

$$P = B \times g$$

Growth rates were predicted using growth models derived from field data (Salas & Dudgeon, 2001b). Growth rates for *Afronurus* sp., *Cinygmina* sp., *Chorotterpes* sp. and both baetids (*B. pseudofrequenta* and *Procloeon* sp.) were based on temperature-specific growth equations (see Appendix 2). The same models were used to predict the growth rate of mayflies from SMR.

To determine whether coexisting species have differences in temporal usage of resources, daily production values obtained with the instantaneous growth method for each species were used to calculate the temporal overlap in production among pairs of species at each site using the proportional similarity index (PS) (Whittaker, 1975):

$$PS_{ab} = \sum_{i=1}^{n} \min(P_{ai}, P_{bi})$$

where PS_{ab} is the proportional similarity of species a and b, P_{ai} and P_{bi} represent the proportion of production of species a and b in the ith sampling interval, and n is the number of sampling intervals (see Georgian & Wallace, 1983; Rader & Ward, 1987; Benke & Jacobi, 1994). A PS_{ab} of 1 indicates 100% overlap. As information on the food sources used by these mayflies was available (Salas & Dudgeon, 2001a), we also calculated PS values between mayfly pairs by using the fraction of production attributable to each food source.

To determine the trophic basis of mayfly production in TPKFS and SMR, stable isotope data (carbon and nitrogen) from Salas & Dudgeon (2001a) were used to estimate the proportion of autochthonous foods used by each mayfly species. By using a simple two-source mixing model, they calculated the percentage of autochthonous foods (periphyton, filamentous algae and cyanobacteria) and allochthonous material (leaf litter and fine particulate organic matter) assimilated by mayflies during each season, where the isotopic composition (carbon and nitrogen) of consumers and foods at both sites had been measured (see Salas & Dudgeon, 2001a). We obtained the production of each species during the dry (taken from November to April) and wet season (from May to October) using the daily production estimates for each species, then a mean value was obtained for each season in 1995–96 and 1996–97. The amount of production attributed to autochthonous foods (allochthonous by difference) was calculated from:

$$P_A = \%_A \times P$$

where P_A is mayfly production attributed to autochthonous foods, $\%_A$ the percentage of mayfly biomass derived from autochthonous foods during the wet or dry season, and P is mayfly production during the wet or dry seasons (mean over 2 years).

Results

Life histories

Size-frequency histograms of all species revealed a lack of obvious seasonal trends in growth in both streams (Figs 1–5). Most size classes were present throughout the year, reinforcing the observation that most Hong Kong mayflies show asynchronous development and continuous emergence (Dudgeon, 1996). Based on the presence of tiny larvae (< 0.3 mm head width), recruitment of *Afronurus* sp. in TPKFS and SMR occurred throughout the

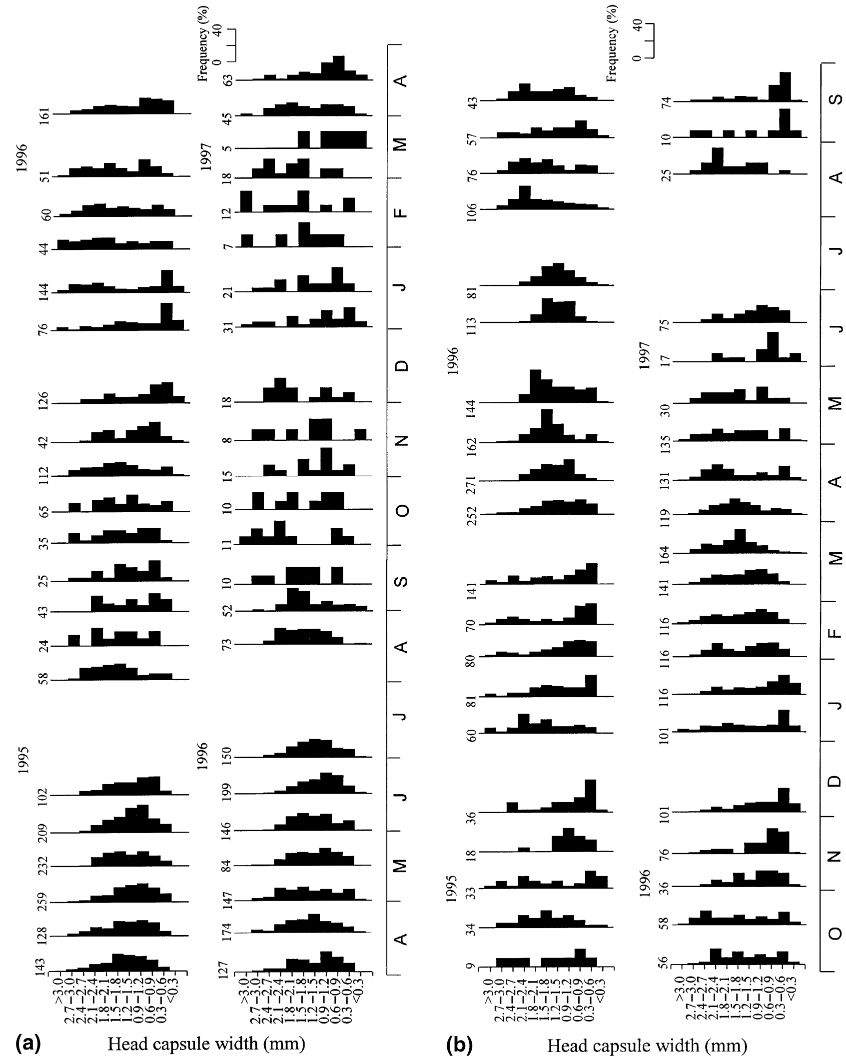

Fig. 1 Size-frequency distributions of *Afronurus* sp. in (a) TPKFS and (b) SMR during 1995–97. Empty spaces represent dates where heavy rain or spates impeded sampling. Sample size is shown besides each histogram.

year (Fig. 1a,b). Size-frequency histograms of *Cinygmina* sp. in TPKFS showed the presence of tiny larvae mainly from October 1995 to February 1996 and from May to July 1996 (Fig. 2a). In SMR, recruitment occurred mainly from October to February during both years, although small larvae were also collected during the wet season of 1997 (Fig. 2b).

Size-frequency histograms of *B. pseudofrequenta* and *Procloeon* sp. in TPKFS and SMR were likewise indicative of asynchronous larval development with year-round growth and continuous recruitment (Figs 3 & 4). Tiny larvae of *B. pseudofrequenta* and *Procloeon* sp. were present at both sites throughout both years. Size-frequency histograms of *Choroterpes* sp. revealed a lack of synchrony in larval development, as shown by the presence of most size classes throughout the study period. However, a notable decrease in abundance of *Choroterpes* sp. occurred in both streams during the dry season (Fig. 5a,b), particularly in TPKFS from November 1996 to February 1997 and in SMR from November 1995 to February 1996. Recruitment at both sites appeared to take place mostly during the wet season when small larvae (< 1.5 mm body length) were found (Fig. 5a,b). Additional recruitment periods probably occurred during the rest of the year, but may have not been detected due to low population densities (and consequent small sample sizes).

Production dynamics

Total mayfly production was 53% higher in SMR than in TPKFS, reflecting higher densities of most mayfly

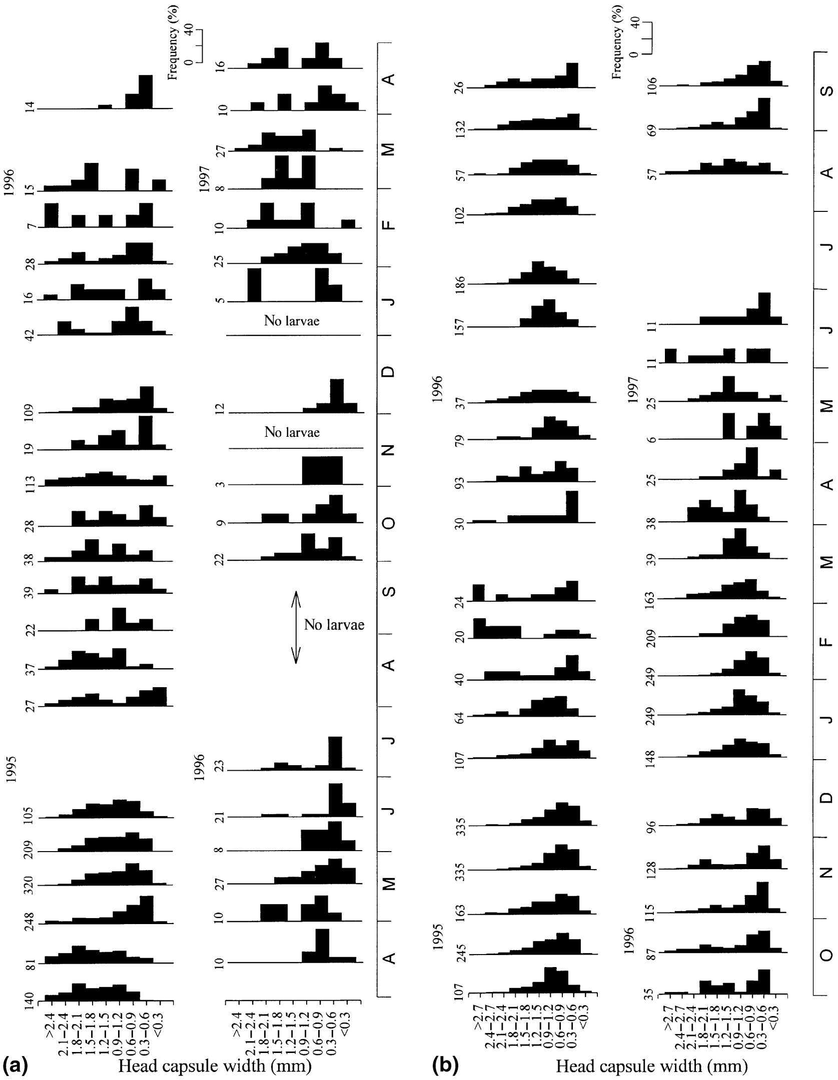

Fig. 2 Size-frequency distributions of *Cinygmina* sp. in (a) TPKFS and (b) SMR during 1995–97. Empty spaces represent dates where heavy rain or spates impeded sampling. Sample size is shown besides each histogram.

species in that site (Table 2). Heptageniids were by far the most productive mayflies, with combined production estimates for the two species exceeding 1.8 and 2.7 g DW m^{-2} $year^{-1}$ in TPKFS and SMR, respectively. *Afronurus* sp. alone accounted for more than 57% of the total mayfly production in these sites. Most mayfly species were more abundant (9–234%) in SMR, but *Procloeon* sp. maintained higher (~16%) densities in TPKFS.

Population densities and biomass of all mayfly species showed inter-year variation in both streams (Table 3). Lower estimates were recorded for most species during 1996–97, except for *Choroterpes* sp. which had higher biomass (5–35%) and densities (2–28%) during the second year of sampling. Total mayfly production during 1996–97 was 5 and 43% lower (TPKFS and SMR, respectively) than in 1995–96. This difference in total production reflected a 50% decrease in population densities of heptageniids in SMR and a 70% decrease in the abundance of *Cinygmina* sp. in TPKFS during 1996–97. The size-frequency method was only used to provide a comparison of the similarity of estimates between methods. Secondary production estimates obtained with the instantaneous growth method were 1–29% lower than values derived from the size-frequency method for heptageniids, but were generally higher (11–55%) for baetids and *Choroterpes* sp. Annual biomass turnover ratios (*P/B*) were high for all species in both streams and ranged from 27.2 (*Cinygmina* sp.; TPKFS) to 109.8 (*B. pseudofrequenta*; SMR).

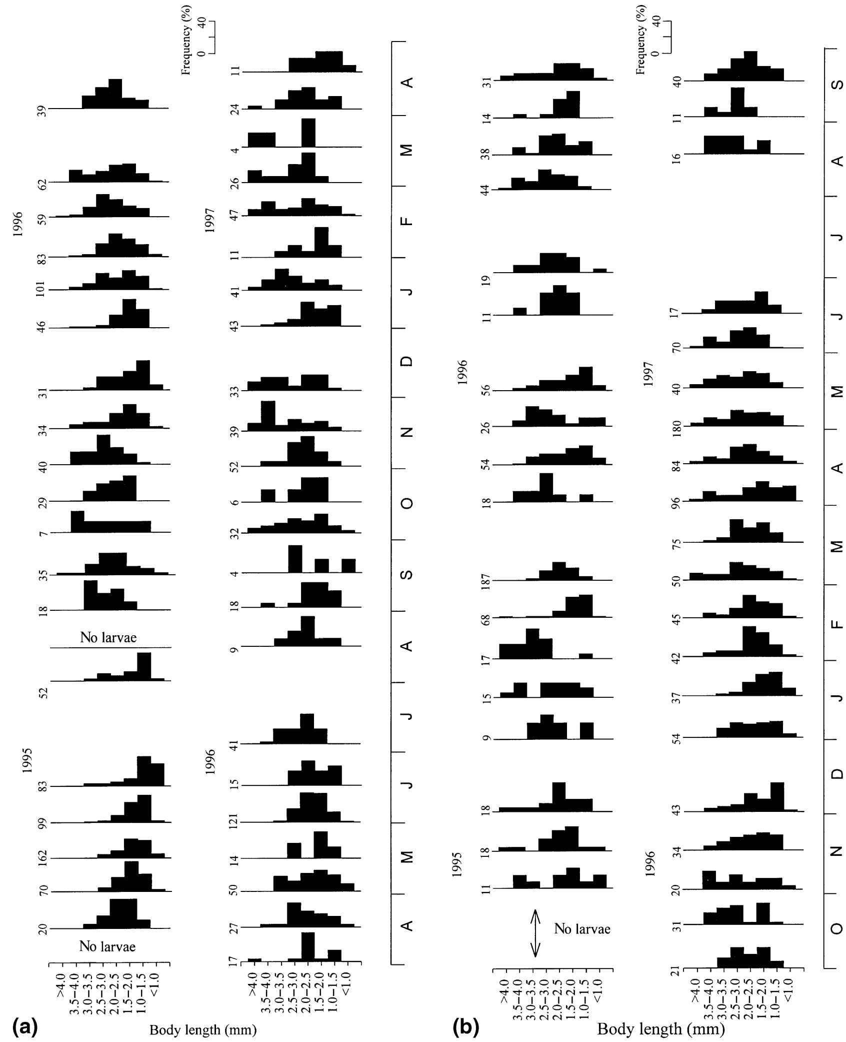

Fig. 3 Size-frequency distributions of *Procloeon* sp. in (a) TPKFS and (b) SMR during 1995–97. Empty spaces represent dates where heavy rain or spates impeded sampling. Sample size is shown besides each histogram.

All mayfly species sustained significant levels of production throughout the year, except *Choroterpes* sp. which was more abundant during the wet season (Figs 6 & 7). Most mayflies in both streams exhibited higher production during the wet season, especially the early part. Exceptions were *Procloeon* sp., which had peaks of high productivity throughout the year in both streams, and *B. pseudofrequenta* which was more productive during the dry season in SMR. *Afronurus* sp. daily production peaked in May 1996 at both sites (16 and 13 mg m^{-2} in SMR and TPKFS, respectively), while the maximum production of *Cinygmina* sp. occurred during July 1996 in SMR, and during May 1995 in TPKFS (9.5 and 3.5 mg m^{-2}, respectively). Daily production of *B. pseudofrequenta* peaked during June 1995 in TPKFS (0.3 mg m^{-2}) but in November 1996 in SMR (1.6 mg m^{-2}). *Procloeon* sp. exhibited three periods of high productivity in TPKFS (>0.6 mg m^{-2}): two during the dry season (March and November 1996) and one in the wet season (June 1996). In SMR, a maximum of 0.7 mg m^{-2} was recorded during May 1997. Production of *Choroterpes* sp. peaked during June 1996 (2.9 and 1.6 mg m^{-2} in SMR and TPKFS, respectively).

Temporal overlap and the trophic basis of production

The temporal overlap of production (*PS*) among pairs of mayfly species was approximately 30% higher in SMR than in TPKFS, with mean annual *PS* values ranging between 0.39 and 0.71 in TPKFS and between 0.44 and 0.81 in SMR (Table 4). Only two pairs of species in TPKFS had *PS* values exceeding 0.6, compared with six species pairs in SMR (italic

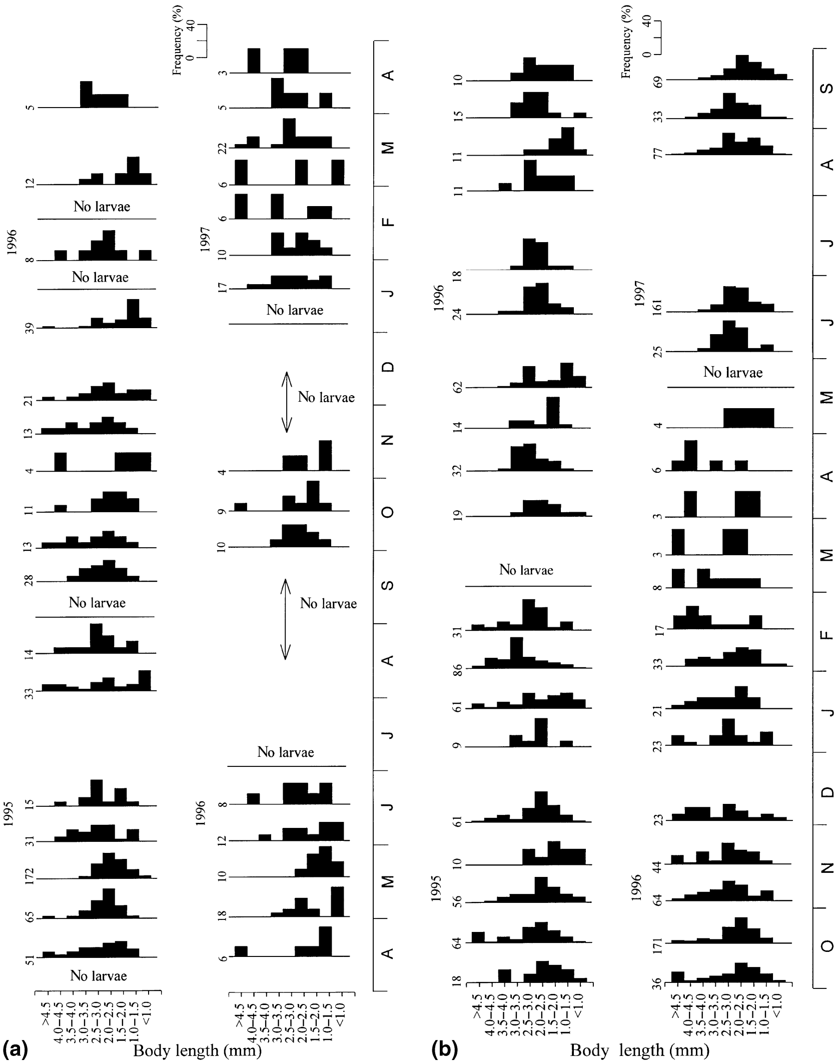

Fig. 4 Size-frequency distributions of *B. pseudofrequenta* in (a) TPKFS and (b) SMR during 1995–97. Empty spaces represent dates where heavy rain or spates impeded sampling. Sample size is shown besides each histogram.

values in Table 4). The highest values (>0.7) were obtained between species of *B. pseudofrequenta* and *Cinygmina* sp. and *Procloeon* sp. and *Afronurus* sp., while the lowest similarity index was generally found in species pairs that included *Choroterpes* sp. When the overlap between species was calculated using the fraction of production attributable to each food source, *PS* values ranged from 0.4 to 0.67 in TPKFS (up to 20% lower than when using production data only), while in SMR they varied between 0.03 and 0.57 (Table 5). Although most *PS* values in SMR were 11–45% lower than those calculated in Table 4, two pairs of species had similarity values which decreased by more than 70%: *Procloeon* sp.–*Cinygmina* sp. ($PS = 0.17$) and *Procloeon* sp.–*Choroterpes* sp. ($PS = 0.03$).

Total annual mayfly production in SMR depended greatly (58%) on allochthonous foods, while in TPKFS, 66% of mayfly production was derived from autochthonous foods. However, seasonal differences in the importance of allochthonous/autochthonous foods were observed in both streams. During the dry season, 72 and 99% of total mayfly production depended on autochthonous foods in SMR and TPKFS, respectively (Table 6). However, during the wet season, 56% of total mayfly production in TPKFS was attributed to autochthonous foods, while in SMR only 32% was derived from autochthonous sources.

At the individual species level, more than 90% of mayfly production was derived from autochthonous foods in both streams during the dry season, except for *Choroterpes* sp. and *Cinygmina* sp. in SMR where

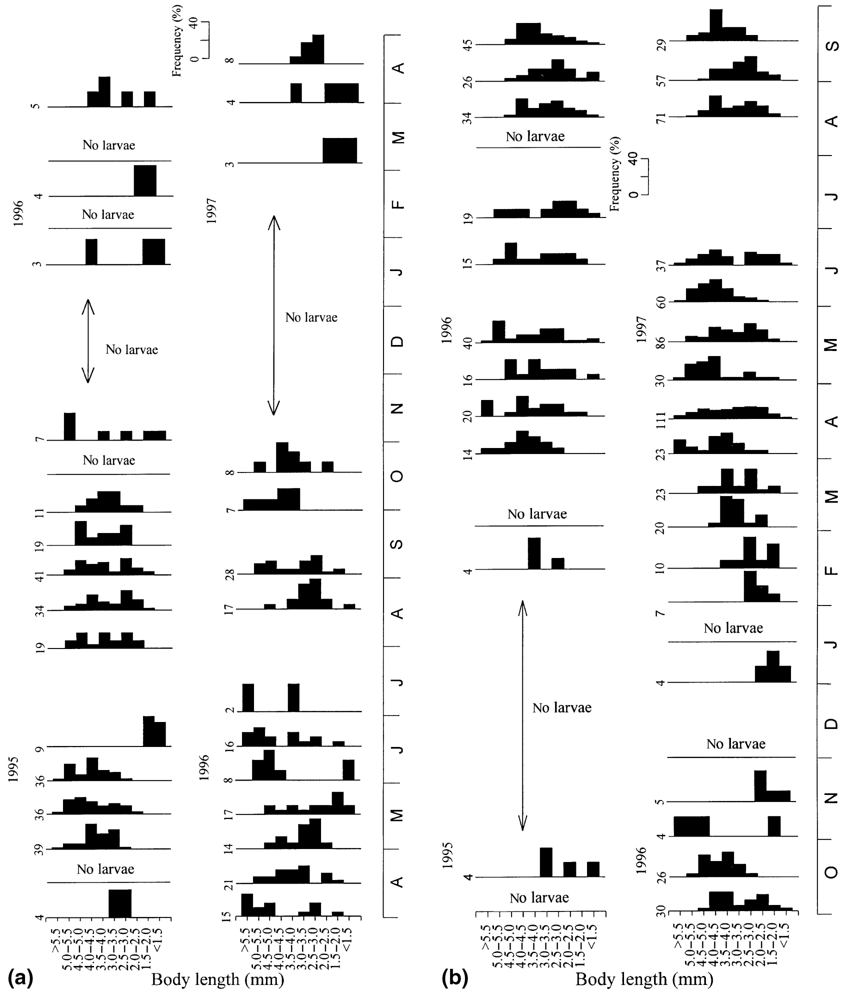

Fig. 5 Size-frequency distributions of *Choroterpes* sp. in (a) TPKFS and (b) SMR during 1995–97. Empty spaces represent dates where heavy rain or spates impeded sampling. Sample size is shown besides each histogram.

more than 60% of production depended on allochthonous sources (Table 6). During the wet season, 30–100% of production of individual species was attributed to allochthonous foods, except for *Procloeon* sp. which used autochthonous sources exclusively. Inter-stream differences in the use of resources were observed between conspecifics during the wet season; for example, the production of *Cinygmina* sp. and *Choroterpes* sp. was based entirely on allochthonous sources in SMR but had at least a 30% contribution from autochthonous foods in TPKFS.

Discussion

All Hong Kong mayflies studied exhibited asynchronous development with most size classes present throughout the year. Life-history interpretations have been confirmed by the larval development time of these species measured *in situ* at TPKFS, where heptageniids could complete up to four generations, baetids at least eight, and *Choroterpes* sp. up to six generations per year (Salas & Dudgeon, 2001b). Temperate heptageniids normally have univoltine life histories (Clifford, 1982), although some species have been reported to complete two generations per year (Benke & Jacobi, 1986; Jacobi & Benke, 1991). Baetids can have uni-, bi- or multivoltine life cycles (Clifford, 1982; Fisher & Gray, 1983), while leptophlebiids have non-seasonal uni- or bivoltine life histories (Huryn & Wallace, 1987; Dieterich & Anderson, 1995; Huryn, 1996). Interpretations of field data support the occurrence of three or more generations each year in three leptophlebiid species (*Jappa* spp.) from a river in Queensland (Australia) where the water temperature remained above 18 °C for most of the year (Campbell, 1995).

Table 2 Mean annual density (*D*, no. of individuals m^{-2} cobble), secondary production using the instantaneous growth method (*P*, mg DW m^{-2} cobble) of five mayfly species in two Hong Kong streams during 1995–97 and percentage of total production (%) contributed by each species

	Tai Po Kau Forest Stream			Shing Mun River		
Mayfly species	*D*	*P*	%	*D*	*P*	%
Afronurus sp.	81.3	1530.9	73.5	88.5	1827.8	57.4
Cinygmina sp.	30.0	287.8	13.8	100.2	880.6	27.6
Procloeon sp.	39.3	100.7	4.8	34.0	104.3	3.3
Baetiella pseudofrequenta	11.9	33.7	1.6	32.9	159.5	5.0
Choroterpes sp.	8.1	128.9	6.2	16.8	214.2	6.7
Total	170.6	2082.0		272.4	3186.4	

Table 3 Secondary production estimates for mayflies in two Hong Kong streams during 1995–97 using the instantaneous growth method and the size-frequency method (in parenthesis). Values shown as dry mass

	1995–96				1996–97			
	Density (no. m^{-2})	Biomass (mg m^{-2})	Production (mg m^{-2} $year^{-1}$)	*P/B*	Density (no. m^{-2})	Biomass (mg m^{-2})	Production (mg m^{-2} $year^{-1}$)	*P/B*
Tai Po Kau Forest Stream								
Afronurus sp.	82.4	49.3	1431.6 (1601.1)	29.0	80.3	41.7	1630.2 (1481.9)	39.1
Cinygmina sp.	46.2	15.7	482.9 (486.2)	30.7	13.8	3.4	92.8 (107.2)	27.2
Procloeon sp.	41.1	1.0	88.0 (64.3)	88.0	37.6	1.2	113.5 (69.5)	94.6
Baetiella pseudofrequenta	15.3	0.5	44.2 (28.7)	88.4	8.5	0.3	23.2 (15.7)	77.3
Choroterpes sp.	7.1	2.0	88.3 (58.7)	44.1	9.1	2.7	169.6 (75.3)	62.8
Total			2135.0 (2239.0)				2029.3 (1749.6)	
Shing Mun River								
Afronurus sp.	119.0	69.3	2405.5 (2528.4)	34.7	58.1	37.7	1250.2 (1210.8)	33.2
Cinygmina sp.	133.0	36.3	1198.1 (1250.5)	33.0	67.4	17.7	563.0 (606.3)	31.8
Procloeon sp.	35.5	1.0	99.5 (61.5)	99.5	32.5	1.1	109.2 (61.6)	99.3
Baetiella pseudofrequenta	34.8	1.5	143.2 (76.2)	95.4	31.1	1.6	175.8 (73.1)	109.8
Choroterpes sp.	16.6	3.9	225.7 (124.9)	57.8	17.0	4.1	202.7 (128.6)	49.4
Total			4072.0 (4041.5)				2300.9 (2080.4)	

Despite a tendency to complete more generations per year, total annual production of individual mayfly species in the Hong Kong forest streams were within the range of production estimates reported elsewhere (see review by Benke, 1993). In both streams, more than 70% of total mayfly production occurred during the wet season. The high productivity of most species during this period resulted from the combination of elevated biomass and warm water temperatures (24–29 °C), while the production sustained by *Procloeon* sp. in TPKFS and *B. pseudofrequenta* in SMR during the dry season reflected high biomass during that period. Although we only calculated the production of the five more abundant mayfly species in both sites, these estimates represent 56 and 71% of the total mayfly production in TPKFS and SMR, respectively.

Our production estimates are per unit of habitat surface area (per cobble area) and therefore habitat specific. This makes it difficult to compare our data with production estimates in the literature. The annual production of *Afronurus* sp. (1.5 and 1.8 g m^{-2} $year^{-1}$ in TPKFS and SMR) was higher than values recorded for most heptageniids on snags in southern United States rivers (Benke *et al*., 1984; Benke & Jacobi, 1994) where mean water temperatures (20 °C) were similar to the Hong Kong sites, and production estimates were at the high end of published values. Annual production of Hong Kong baetids (*Procloeon* sp. and *B. pseudofrequenta*) were

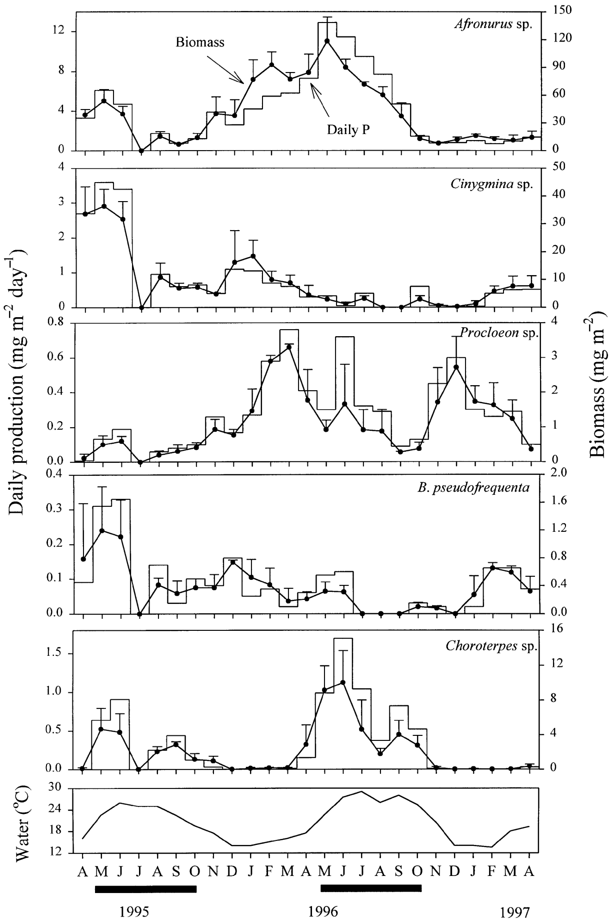

Fig. 6 Mean daily production (histograms) and biomass (●, mean ± SE), from two to four consecutive sampling dates, of five mayfly species collected biweekly in TPKFS during 1995–97. Units are per m^2 cobble area. Horizontal black bars represent the wet season.

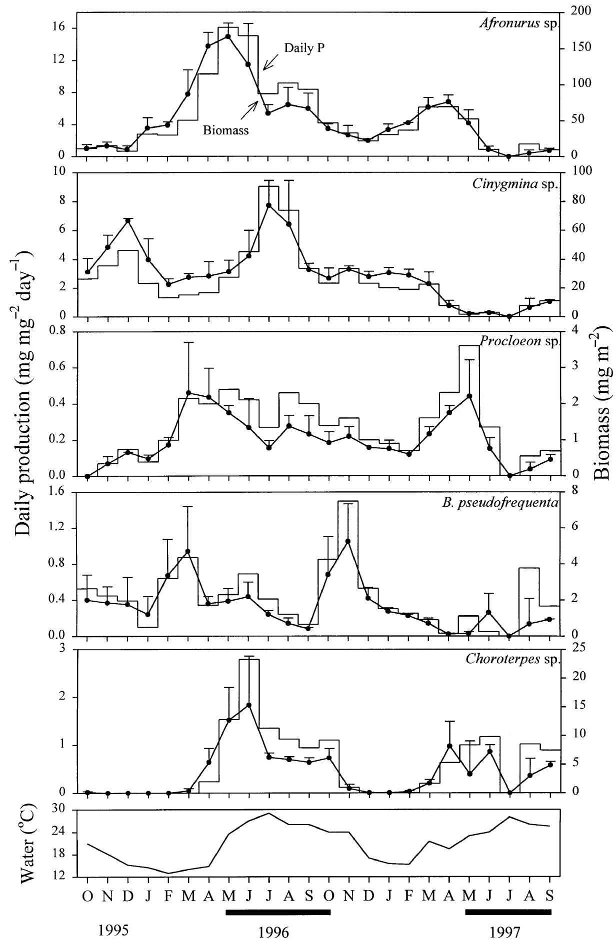

Fig. 7 Mean daily production (histograms) and biomass (●, mean ± SE), from two to four consecutive sampling dates, of five mayfly species collected biweekly in SMR during 1995–97. Units are per m^2 cobble area. Horizontal black bars represent the wet season.

lower than reported for baetids on snags in the United States (Benke & Jacobi, 1994) and in a Victorian (Australia) river (Marchant, 1986), but higher than estimates for *Baetis* sp. in Neotropical Costa Rica (Ramirez & Pringle, 1998). Similarly, production estimates for Hong Kong *Choroterpes* sp. were lower than for *Choroterpes mexicanus* in the Brazos River, Texas (McClure & Stewart, 1976) and the leptophlebiids *Atalonella* spp. and *Atalophlebioides* sp. 4 in Victoria (Marchant, 1986), but higher than for *Thraulodes* sp. and *Leptohyphes* sp. from Costa Rica (Ramirez & Pringle, 1998). Total mayfly production measured in both TPKFS and SMR (2.0 and 3.0 g m^{-2} year^{-1}, respectively) were lower than values reported for Ephemeroptera (14 species) from snags in the United States (20–42 g m^{-2} year^{-1}; Benke & Jacobi, 1994), but higher than for mayflies in an Australian and a Costa Rican river (0.7–1.0 g m^{-2} year^{-1}; Marchant, 1986; < 0.1 g m^{-2} year^{-1}; Ramirez & Pringle, 1998).

Inter-year variations in production were observed in both Hong Kong streams, with lower mayfly production in 1996–97. Such differences were related to variations in annual population densities. Annual standing stocks of most species were higher during 1995–96, while during the second year of sampling a 23 and 39% decrease was recorded in TPKFS and SMR, respectively. The lower 1996–97 densities reflected declines in heptageniid abundance. Similar inter-year variations in heptageniid abundance were reported by Dudgeon (1996) in TPKFS during the period 1977–79. Although there is no clear explanation

Table 4 Overlap of production between pairs of mayfly species in two Hong Kong streams during 1995–97, calculated as the proportional similarity index (PS_{ab}). Values represent mean PS with annual estimates for the period 1995–96 and 1996–97 shown in parentheses. Mean values equal or higher than 0.6 are in italics

Species number	1	2	3	4
Tai Po Kau Forest Stream				
Afronurus sp.	–			
Cinygmina sp.	0.51 (0.58; 0.44)	–		
Procloeon sp.	*0.70* (0.81; 0.60)	0.46 (0.43; 0.49)	–	
Baetiella pseudofrequenta	0.54 (0.57; 0.51)	*0.71* (0.75; 0.67)	0.50 (0.45; 0.56)	–
Choroterpes sp.	0.54 (0.38; 0.69)	0.49 (0.59; 0.40)	0.39 (0.26; 0.51)	0.54(0.66; 0.41)
Shing Mun River				
Afronurus sp.	–			
Cinygmina sp.	*0.68* (0.66; 0.71)	–		
Procloeon sp.	*0.81* (0.82; 0.79)	*0.66* (0.71; 0.61)	–	
Baetiella pseudofrequenta	0.57 (0.65; 0.49)	*0.63* (0.62; 0.64)	*0.60* (0.68; 0.52)	–
Choroterpes sp.	0.57 (0.61; 0.53)	0.44 (0.48; 0.39)	*0.61* (0.55; 0.66)	0.44 (0.51; 0.37)

Table 5 Proportional similarity (PS_{ab}) between pairs of mayfly species in two Hong Kong streams during 1995–97, based upon the fraction of production attributable to each food type. $PS_{ab} = \Sigma \min(P_{ai}, P_{bi})$, where P_{ai} is the fraction of food type *i* used by species *a*, and P_{bi} is the fraction used by species *b*. Food types were autochthonous and allochthonous foods

Species number	1	2	3	4
Tai Po Kau Forest Stream				
Afronurus sp.	–			
Cinygmina sp.	0.50	–		
Procloeon sp.	0.64	0.38	–	
Baetiella pseudofrequenta	0.51	0.67	0.40	–
Choroterpes sp.	0.49	0.43	0.32	0.47
Shing Mun River				
Afronurus sp.	–			
Cinygmina sp.	0.44	–		
Procloeon sp.	0.53	0.17	–	
Baetiella pseudofrequenta	0.57	0.38	0.46	–
Choroterpes sp.	0.36	0.39	0.03	0.24

for these inter-year variations, differences in the intensity of monsoonal rains between years appears to affect the abundance and production of other species of mayflies (Dudgeon, 1999b); rainfall during 1996–97 was 38% higher than in the previous year. Benthic populations increase during periods of stable water flow, and decrease after spates in rivers in Malaysia (Bishop, 1973) and elsewhere in tropical Asia (Dudgeon, 1999a). Because few studies elsewhere have measured production in consecutive years, the factors causing inter-year variation in production are obscure. However, Benke & Jacobi (1994) reported a twofold increase in mayfly production on snags during their second year of sampling, which was attributed mostly to a shift in species composition and increased turnover rates rather than due to biomass changes. In the present study, the abundance of heptageniids decreased during the second year, but total mayfly biomass and turnover rates were similar between years. This accords with Dudgeon (1999b), who showed that the production of species living in depositional habitats (i.e. *Afronurus* sp.) declined with an increase in stream discharge, while production of rheophilic taxa (e.g. *Epeorus* and *Iron*) increased.

Annual biomass turnover rates (or *P/B* ratios) of Hong Kong mayflies were generally higher than values reported in the literature, but within the range predicted for tropical species (Benke & Jacobi, 1986). Heptagenid *P/B*s ranged from 27.2 to 39.1, baetids from 77.3 to 109.8, and *Choroterpes* sp. (Leptophlebiidae) from 44.1 to 62.8. Elsewhere, Marchant (1986) reported annual *P/B* ratios of 9–14 for *Baetis* sp. from a Victorian river, while a *P/B* of 18.7 was measured by Huryn & Wallace (1987) in a North Carolina mountain stream. An annual *P/B* ratio of 64 was estimated for *Baetis quilleri* from a desert stream in Arizona (Fisher & Gray, 1983), while Benke & Jacobi (1994) calculated a maximum *P/B* ratio of 95.7 for *Baetis ephippiatus* on snags in Georgia. The highest published annual turnover rate for any heptageniid was measured for *Stenonema* sp. in the same river (*P/B* = 17.4; Benke & Jacobi, 1994). Based on these values, the Hong Kong *P/B* estimates exceed most reports in the literature for baetids and heptageniids. Likewise records of *P/B*

Table 6 Mean production (P, mg DW m^{-2}) of mayflies from two Hong Kong streams during the period 1995–97 obtained using the instantaneous growth method. $P_{All,\ Au}$ is production attributed to allochthonous (All) and autochthonous foods (Au) calculated from stable isotope data (Salas & Dudgeon, 2001a). Wet season: May–October; dry season: November–April

	Wet season		Dry season	
	P_{All}	P_{Au}	P_{All}	P_{Au}
Tai Po Kau Forest Stream				
Afronurus sp.	530.6	703.4		332.0
Cinygmina sp.	131.1	80.3		63.2
Procloeon sp.		55.4		47.9
Baetiella pseudofrequenta	12.9	11.0	2.1	6.1
Choroterpes sp.	39.3	79.7		
Total	713.9	929.8	2.1	449.2
Shing Mun River				
Afronurus sp.	834.8	629.8		391.3
Cinygmina sp.	532.8		223.9	110.3
Procloeon sp.		75.8		25.7
Baetiella pseudofrequenta	46.5	44.6		66.6
Choroterpes sp.	237.0		2.9	1.5
Total	1651.1	750.2	226.8	595.4

ratios for leptophlebiids do not exceed 17 (McClure & Stewart, 1976; Marchant, 1986; Huryn & Wallace, 1987; Ramirez & Pringle, 1998), and the Hong Kong figures appear to be the highest so far reported. High water temperatures at the sites (maximum 29 °C; annual mean 20 °C) and small body size of the mayflies studied (maximum length < 10 mm) contributed to these elevated *P/B* ratios. Because of their fast turnover rates, Hong Kong mayflies sustain continuous secondary production that would not be expected on the basis of their relatively low biomass (<50 mg DW m^{-2}). High turnover rates and production can be predicted to occur in other tropical Asian streams.

Production estimates as well as biomass and density values have been previously used to determine overlap in resource utilisation by mayflies and caddisflies (Georgian & Wallace, 1983; Rader & Ward, 1987; Benke & Jacobi, 1994). Although we found generally high temporal overlaps in production for most species in both sites, lower similarities were observed when considering the fraction of production attributed to each food type. This was most evident for two pairs of species in SMR: *Procloeon* sp.–*Cinygmina* sp. and *Procloeon* sp.–*Choroterpes* sp. Although these pairs had high temporal overlap in production ($PS > 0.6$), they appeared to segregate at the trophic level. According to stable isotope analysis, *Procloeon* sp. feeds exclusively on autochthonous foods throughout the year, while *Cinygmina* sp. and *Choroterpes* sp. mainly feed on allochthonous foods (Salas & Dudgeon, 2001a). However, for most mayfly species there was a lack of temporal and trophic segregation, which was not surprising given that all species are multivoltine and present throughout the year. The Hong Kong overlap values were within the range reported for mayflies in a northern Colorado stream and in the Ogeechee River (Rader & Ward, 1987; Benke & Jacobi, 1994) and might reflect the fact that food resources do not limit mayflies under normal conditions. In TPKFS, at least, allochthonous foods are abundant throughout the year (Dudgeon, 1982), although spates (during wet season rains) can drastically reduce periphyton biomass and wash out macroinvertebrates.

The trophic basis of mayfly production had a strong seasonal component. During the dry season 72–99% of total mayfly production was based on autochthonous foods, while in the wet season (when periphyton biomass decreases) 44–69% of mayfly production was derived from allochthonous sources. Seasonal changes in the use of terrestrial and aquatic food sources have been reported for stream benthos elsewhere. Huryn *et al*. (2001) found that terrestrial carbon supported macroinvertebrate biomass during summer (reflecting growth that occurred during the winter), while aquatic carbon was more important in autumn (reflecting growth that occurred during the summer). In the present study, more than 70% of total mayfly production occurred during the wet season. When the contribution of each food source to the total production was calculated the trophic basis of mayfly production in SMR depended mostly (58%) on allochthonous sources but, in TPKFS, was based mainly on autochthonous foods (66%). This difference can be explained in part by the increased production of two species in SMR that were heavily dependent (65–100%) on allochthonous foods, i.e. more than 75% of *Cinygmina* sp. and more than 80% of *Choroterpes* sp. production occurred during the wet season.

The importance of autochthonous foods for macroinvertebrate production in forest streams is unexpected, but has been reported elsewhere. Mayer & Likens (1987) showed that benthic algae were an important component in the diet of an abundant caddisfly larvae, in a New Hampshire forest stream. While, Huryn & Wallace (1985) found that diatom consumption accounted for 58% of the annual production of *Goerita semata* (Trichoptera) in a southern Appalachian Mountain stream. Similarly, Smock & Roeding (1986) found that algae could support from 15 to 31% of macroinvertebrate production even in fully canopied headwater streams. These values compare with the highest values of 42% of total mayfly production derived from autochthonous sources in SMR and 66% in TPKFS. The present study is the first to show the seasonal contribution of allochthonous/autochthonous foods to mayfly production in tropical Asian streams. As mayflies are a major component of benthic macroinvertebrates communities in Hong Kong streams, these results have implications for stream production as a whole. However, it remains to be seen whether autochthonous foods play an important role in the production of other macroinvertebrates and fishes in these forested streams.

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Appendix 1 Linear regression equations for several mayfly species relating dry weight (mg) to body dimensions (mm). Body dimensions measured as head width (HW) or body length (BL) (from Salas, 1998)

Species	Regression equation	*n*	r^2	*P*
Afronurus sp.	ln DW = −2.1 + 2.9 ln HW	13	0.95	< 0.001
Cinygmina sp.	ln DW = −2.0 + 2.8 ln HW	24	0.91	< 0.001
Baetiella pseudofrequenta	ln DW = −5.9 + 2.8 ln BL	12	0.97	< 0.001
Procloeon sp.	ln DW = −6.0 + 2.8 ln BL	15	0.93	< 0.001
Choroterpes sp.	ln DW = −6.0 + 3.3 ln BL	16	0.78	< 0.001

Appendix 2 Regression equations of daily growth rate (g, mg mg^{-1} day^{-1}) and water temperature (T, °C) in TPKFS during 1996–97 (from Salas & Dudgeon, 2001b)

Species	Growth equation	*n*	r^2	*P*
Afronurus sp.	$g = -0.01 + 0.005\ T$	38	0.29	< 0.001
Cinygmina sp.	$g = 0.005 + 0.004\ T$	25	0.39	< 0.001
Baetidae*	$g = 0.06 + 0.01\ T$	36	0.23	< 0.01
Choroterpes sp.	$g = -0.2 + 0.015\ T$	13	0.77	< 0.0001

**Baetiella pseudofrequenta* and *Procloeon* sp. combined.