Chinese Journal of Oceanology and Limnology
Vol. 25 No. 1, P. 106-115, 2007

DOI: 10.1007/s00343-007-0106-9

Life history, secondary production and trophic basis of two dominant mayflies in a subtropical stream of China*

YAN Yunjun (闫云君)**, LI Xiaoyu (李晓宇)
(*College of Life Science and Technology, Huazhong University of Science and Technology, Wuhan 430074, China*)

Received July 19, 2005; revision accepted Nov. 10, 2006

Abstract Mayflies constitute a major part of macroinvertebrate biomass and production in lotic ecosystems, and play an important role in material cycle and energy flow. There are more than 250 species of mayflies in rivers and streams of China. In order to learn their ecological functions, an investigation on life cycle, production and trophic basis of dominant species of mayflies in a second-order branch of Hanjiang River basin, Hubei, China was carried out during June 2003 to June 2004. The results showed that the dominant mayfly species *Epeorus* sp. and *Caenis* sp. developed two generations per year; in term of *Epeorus* sp., pupation mainly occurred in spring and then from late summer to early autumn, while *Caenis* sp. pupated in spring and autumn. The abundance and biomass of the *Epeorus* sp. population peaked twice (1 226 ind/m^2, 3.142 5g/m^2) in April and June. *Caenis* sp. also had two peaks (307ind/m^2, 1.590 g/m^2), but in February and June. Cohort production and cohort P/B ratio of *Epeorus* sp. were 161.009 g/m^2 wet weight and 7.7, respectively, and annual production and P/B ratio were 267.46g/m^2.a wet weight and 15.4, respectively; cohort production and P/B ratio of *Caenis* sp. were 26.7995g/m^2 wet weight and 4.7, its annual production and P/B ratio were 53.60 g/m^2.a wet weight and 9.4, respectively. For *Epeorus* sp., the proportions contributing to secondary production of the main food types were: amorphous detritus, 33.46%; fungi, 10.83%; vascular plant detritus, 1.80%; diatoms, 53.90%; for *Caenis* sp., the proportions were 70.79%, 6.90%, 3.52% and 18.77%, respectively.

Key word：Macrozoobenthos; mayfly; secondary production; *Epeorus* sp; *Caenis* sp; Heizhuchong Stream

1 INTRODUCTION

Macroinvertebrates are very important in material cycle and energy flow of a fluvial ecosystem as well as in the biomonitoring of ecological health, and more and more studies have been conducted on this group. Recently, the literature about life history, production and trophic basis of riverine macroinvertebrates has grown considerably. The development of the River Habitat Template (Townsend and Hildrew 1994) elicited a new interest on life history traits such as voltinism (Usseglio-Polatera et al., 2000), size (Statzner et al., 1997) and timing of development, and tried to find relationships between these changes and differences in physical habitat (Sanchez and Hendricks, 1997; Robinson and Minshall, 1998). Knowledge about secondary production dynamics of river macroinvertebrates has been also enriched remarkably. Production is a composite of population parameters such as individual growth rate, survivorship, development time and biomass that provide a measure of population function in the processing of an ecosystem (Benke, 1993). Besides, secondary production also can be used to relate population dynamics to other processes in an ecosystem. There were several papers that tried to relate secondary production of some populations and communities with water chemistry (Griffith et al., 1994), temperature (Morin and Bourassa, 1992), habitat quality (Dudgeon, 1999), food resources (Wallace et al., 1997), position in food web (Grubaugh et al., 1997), land use mode (Sanchez and Hendricks, 1997), or other human impacts (Whiles and Wallace, 1995).

* Supported by the NSFC (No.30270278).
** Correspondence author: yanyunjun@tom.com

A major theme in ecosystem ecology has been the description and analysis of food webs (Polis, 1994). For a long time, ecologists attempted to define linkages through qualitative food web diagrams, and thence to measure energy flow along major pathways in ecosystems. However, most trophic dynamics studies used qualitative energy flow approach, they all suffer a common problem that they cannot provide quantitative measure of detailed food web linkages. Since 1980, Benke et al (1980, 1984, 1997) have done a good job on quantitative food web analysis.

It is a great help for us to quantitatively analyze trophic linkage and its strength of dominant species before start to construct a quantitative food web diagram to illustrate the complexity of trophic linkage and dominance of certain feeding pathway. The main purposes of this work were (1) to describe life history and to estimate secondary production of the two dominant mayflies *Epeorus* sp. and *Caenis* sp. in a second-order stream in the middle part of China; (2) to analyze the trophic basis of the secondary production; and (3) to assess the difference or similarity in secondary production and trophic basis of these species by comparison with other studies.

The Heizhuchong Stream drains a small catchment (52 km^2) located in the northwest mountainous part of Nanzhang County, Hubei Province, China (Fig.1). The climate in the zone is sub-tropical, with mean monthly temperature ranging between 4.2℃ (January) and 28.3℃ (August) during 2003–2004. The main land uses are pine and maple forestry, and rice and wheat plantations. Human population is relatively low (about 50 000 inhabitants). The township of Nanzhang County situates at the middle reach of the stream with several sewage outlets.

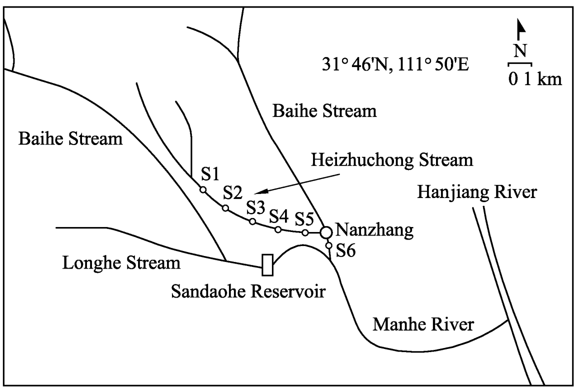


Fig.1 Heizhuchong Stream and distribution of sampling sites

From upper to lower reaches of Heizhuchong Stream, we chose 6 types of habitats for quantitative sampling. Station 1 (S_1) lay in the middle of the stream with big round rocks, Station 2 (S_2) in the inner part of a weir with cobble substratum, Station 3 (S_3) in the middle of a peacefully flowing section with gravel-sand bottom, Station 4 (S_4) at the side of the riparian with aquatic macrophytes and snags, Station 5 (S_5) in the middle of a riffle, Station 6 (S_6) at the lower reach with a sewage outlet ca 100 m upstream.

Due to strong self-purification of the stream, water quality is quite good at S_1 to S_5, and a little polluted at site S_6. Limnological details of the river water during the study period are listed in Table 1.

2 MATERIALS AND METHODS

Quantitative benthic samples were collected monthly from June 2003 to June 2004. At each site, 3 random replicates were taken with a Surber net (area 0.09 m^2, mesh size 250 μm), and preserved in 10% formalin. In laboratory, invertebrates were sorted, identified and counted under a binocular microscope. Head width and body length of each specimen were measured to the nearest 50 μm using a micrometer. Individual wet weights of *Epeorus* sp. and *Caenis* sp.

Table 1 Main physical and chemical characteristics of Heizhuchong Stream (The parameters with annual ranges in parentheses were measured monthly during 2003–2004)

Parameter	Value
Elevation (m)	450
Drainage area (ha)	6906
Channel width (m)	10–12
Water temperature (℃)	15.4 (4.2–28.3)
pH	7.4 (6.8–8)
Conductivity (μS/ cm)	228.6 (191–293)
Oxygen (mg/L)	11.6 (9.7–14.8)
Oxygen saturation (%)	108.7 (100–126)
Periphyton (g/m^2)	24.3 (3.4–92.1)
CPOM* (g/m^2)	20.4 (10.3–56.7)

* Crude particulate of organic materials

were estimated from a length–weight regression model constructed using nymphs from the study sites. Secondary production was determined with the size-frequency method (Hynes and Coleman, 1968) modified by Hamilton (1969) and Benke (1979). Here we used generation number (b) instead of 365/CPI so that the generation was easy to distinguish, and ignored the correction factor Pe/P, because data were not available, and little error was produced (Hamilton, 1969; Menzie, 1980).

We used diet analysis to estimate consumption of various food sources by following the method of Benke and Wallace (1980, 1997), and analyzed gut contents of the two mayfly species during 3 seasons, spring (March–May), summer (June–Sept.), and autumn (Oct.–Dec.). Each time we dissected guts of 3 to 4 individual animals, suspended the contents in distilled water, filtered the contents onto a membrane filter, placed them onto a microscope slide, and cleared them with immersion oil. We made 5 to 7 slides for each species in each season, and quantified gut contents by measuring the relative areas of 6 diet categories (amorphous detritus, fungi, vascular plant detritus, diatoms, filamentous algae, and animal material) on the filters (Cummins, 1973) using a compound microscope equipped with a video image analyzer. We used the method of Benke and Wallace (1980, 1997) to estimate the relative contribution of each food type to secondary production.

3 RESULTS

3.1 Population dynamics

***Epeorus* sp.** Fig. 2a shows the annual variations of standing stock of *Epeorus* sp. population. Abundance of the population reached its peak in July with the density of 122 6 ind/m^2, and biomass of the population had two prominent peaks, the main one occurred in April at 3.1425 g/m^2, the second one occurred in July at 2.691 7 g/m^2. In October, biomass declined to its lowest level, and in December the abundance was the least.

***Caenis* sp.** Abundance of the population had two peaks; one was in February with the density of 194 ind/m^2, the other in July at 307 ind/m^2. Biomass peaked in February of 1.590 0 g/m^2. In November, the population declined to lowest level, but with the arrival of reproduction period next year, the population recovered swiftly (Fig.2b).

3.2 Life history

***Epeorus* sp.** Its population developed two generations in one year. Adults mainly emerged from February to March, followed by mating and spawning. Hatching of larvae reached its peak in April, and after a 4-month development, these larvae pupated in July to September. Their descendants would emerge again in February to March next year. Nevertheless, there

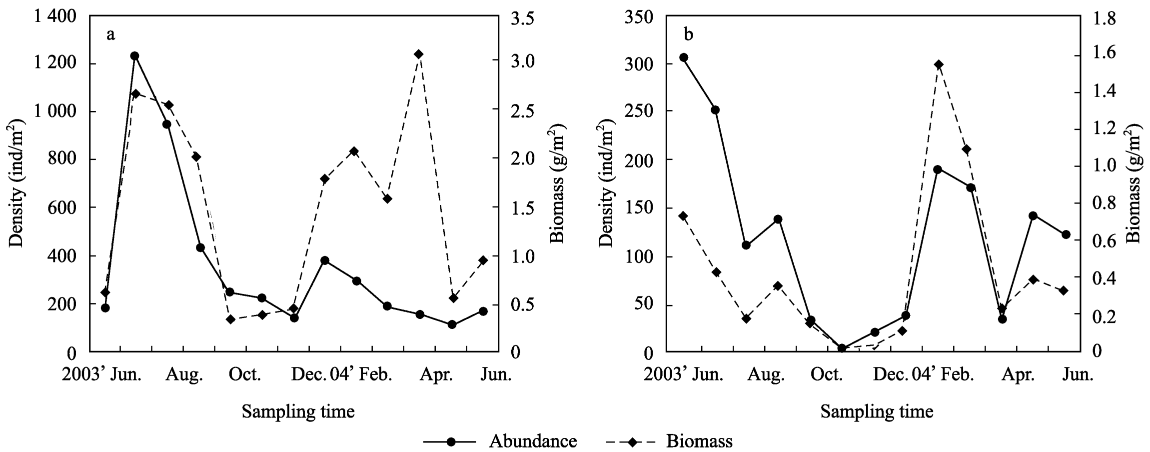


Fig. 2 Annual variations of standing stock of *Epeorus* sp. (a) and *Caenis* sp. (b) in Heizhuchong Stream

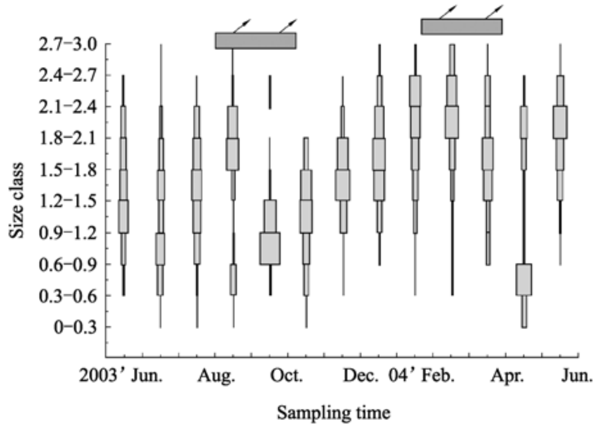


Fig.3 Monthly instar frequency distributions for *Epeorus* sp. in Heizhuchong Stream

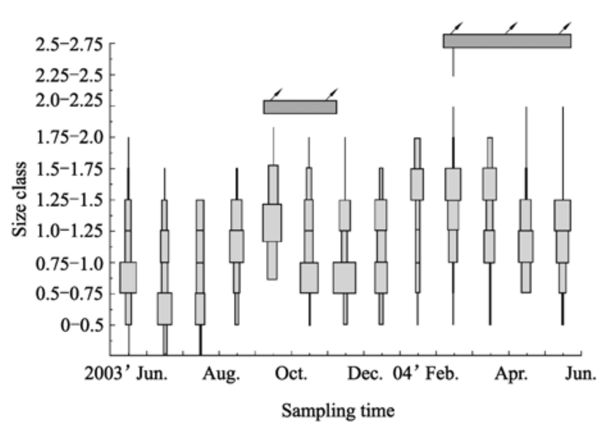


Fig.4 Monthly size frequency distributions for *Caenis* sp. in Heizhuchong Stream

was a little overlap between the two generations (Fig.3).

***Caenis* sp.** This species also developed two generations during a year (Fig.4). Adults mainly emerged from March to April, then mating and spawning occurred, reproduction continued for several months. The larvae began emergence again in October to November. Adults mated and spawned immediately. Hatching occurred in November and December, and emergence takes place during March to May the next year.

3.3 Relationship of length and mass

The length (L, mm)—mass (Ww, g wet wt) equation obtained was:

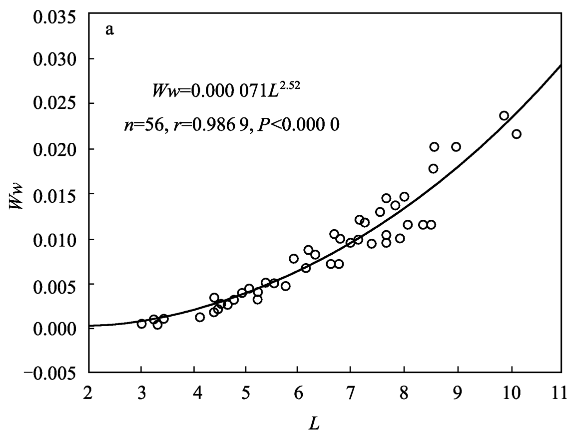
Epeorus sp., $Ww=0.000071L^{2.52}$ ($n=56$, $r=0.986\,9$, $P<0.000\,0$)

Caenis sp., $Ww=0.036L^{2.94}$ ($n=64$, $r=0.991\,8$, $P<0.000\,0$).

The details are presented in Fig.5.

3.4 Secondary production

***Epeorus* sp.** Through the use of size–frequency method, cohort production was estimated at 161.009 g/m^2 wet weight and annual production at 322.018 g/m^2.a wet weight; and cohort P/B ratio was 7.7, annual P/B ratio 15.4. Other production parame



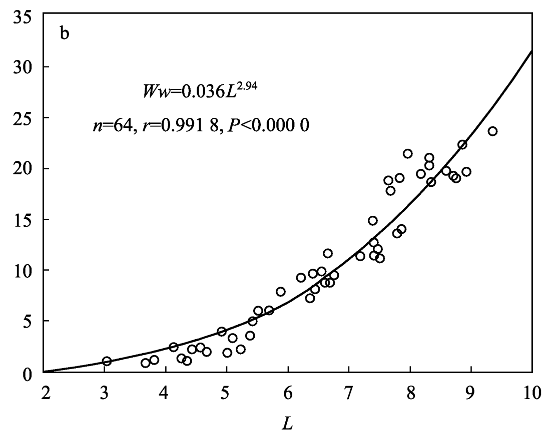


Fig.5 Relationship between body weight (Ww, g wet wt) **and body length** (L, mm) **for *Epeorus* sp. (a) and *Caenis* sp. (b) in Heizhuchong Stream**

ters are presented in Table 2.

Caenis sp. Calculated cohort production was 26.799 5 g/m^2 wet weight and annual production was 53.599 0 g/m^2 wet weight. Cohort and annual P/B ratio was 4.7and 9.4, respectively (Table 3).

Table 2 Annual production (g/m^2 wet wt) **of *Epeorus* sp. in Heizhuchong Stream estimated by size-frequency method**

Size group (mm)	Density (No./m^2)	Mean wt (g)	Biomass (g/m^2)	No. loss (No./m^2)	Mean wt at loss (mg)	Wt loss (g/m^2)	Production (g/m^2)
0-2	274.1	0.0003	0.0822	-1651.8	0.0006	-0.9911	-9.911
2-4	1925.9	0.0013	2.5037	175.9	0.0025	0.4400	4.400
4-6	1750	0.0048	8.4000	1131.5	0.0065	7.3548	73.548
6-8	618.5	0.0088	5.4428	520.4	0.0119	6.1928	61.928
8-10	98.1	0.0160	1.5696	74.1	0.0208	1.5413	15.413
10-12	24	0.0270	0.648	9.2	0.0376	0.3459	3.459
12-14	14.8	0.0523	0.7740	5.5	0.0585	0.3218	3.218
14-16	9.3	0.0654	0.6082	3.7	0.0749	0.2771	2.771
16-18	5.6	0.0857	0.4799	1.9	0.0993	0.1887	1.887
18-20	3.7	0.1151	0.4259	3.7	0.1161	0.4296	4.296
Standing stock= 20.9343					Cohort production =161.009		
Cohort production×2 Annual production=322.018							
Cohort P/B= 7.7 Annual P/B= 15.4							

Table 3 Annual production (g/m^2 wet wt**) of *Caenis* sp. in Heizhuchong Stream estimated by size-frequency method**

Size group (mm)	Density (No./m^2)	Mean wt (mg)	Biomass (g/m^2)	No. loss (No./m^2)	Mean wt at loss (mg)	Wt loss (g/m^2)	Production (g/m^2)
1-2	27.8	0.1978	0.0055	-227.80	0.3422	-0.0780	-0.7016
2-3	255.6	0.5921	0.1513	-192.50	0.9444	-0.1818	-1.6362
3-4	448.1	1.5064	0.6750	44.40	2.1101	0.0937	0.8432
4-5	403.7	2.9556	1.1932	187.00	3.9717	0.7427	6.6844
5-6	216.7	5.3372	1.1566	96.30	6.7755	0.6525	5.8723
6-7	120.4	8.6013	1.0356	53.70	10.5979	0.5691	5.1220
7-8	66.7	13.0580	0.8710	40.80	15.3928	0.6280	5.6522
8-9	25.9	18.1451	0.4700	22.20	20.8242	0.4623	4.1607
9-10	3.7	23.8989	0.0884	3.7	24.1004	0.0892	0.8025
Standing stock =5.6466				Cohort production = 26.7995			
Cohort production×2= Annual production = 53.5990							
Cohort P/B= 4.7 Annual P/B=9.4							

Table 4 The percentages of foregut food contents of the two mayflies; proportion of annual production attributable to various food types is shown in parentheses below each value

Taxa	No.of guts examined	Amorphous detritus	Fungi	Vascular plant detritus	Diatom	Filament algae	Animal material
Epeorus sp.	12	60.40	3.91	3.25	32.44	0.01	0.00
		(33.46)	(10.83)	(1.80)	(53.90)	(0.01)	(0.00)
Caenis sp.	11	85.52	1.67	4.25	7.56	0.00	0.00
		(70.79)	(6.90)	(3.52)	(18.77)	(0.00)	(0.00)

3.5 Food consumed and their contribution to production

Gut contents of 12 individuals of *Epeorus* sp. and 11 *Caenis* sp. were examined (Table 4). The analyses showed that two species consumed a large portion of amorphous detritus, constituting 60.40% and 85.52% of their diets, and contributing 33.46% (107.75 g/m^2) and 70.79% (37.94 g/m^2) to their secondary production. Diatoms were the second major food type, averaging 32.44% and 7.56% of the diets, contributing 53.90% (173.57 g/m^2) and 18.77% (10.06 g/m^2) to the production in average. Fungi were not abundant, taking 3.91% and 1.67% respectively, contributing merely 10.83% (34.87 g/m^2) and 6.90% (3.70 g/m^2) to the production. Vascular plant detritus composed 3.25% and 4.25% of the gut contents, and contributed 1.80% (5.80 g/m^2) and 3.52% (1.89 g/m^2) to the production. Filamentous algae and animal materials were not encountered in gut contents of *Caenis* sp., filamentous algae occupied 0.01% of the diet of *Epeorus* sp.

Table 5 Comparison of secondary production and P/B ratio with other mayfly studies

Species	P (mgDW/m^2)	P/B	Habitat (Location)	Source
C. luctuosa	6349.81	15.98	Mediterranean semiarid stream (Murcia, Spain)	A. Perán, J. Velasco and A. Millan, 1999
C. amica	445.05	13.00	Experimental ponds (Virginia, U.S.A.)	Christman and Voshell, 1992
C. amica	676	12.72	Experimental stream (Alabama, U.S.A.)	Rodgers, 1982
C. simulans	4200	4.20	Cold/mesic plains stream (Minnesota, U.S.A.)	MacFarlane and Waters, 1982
Caenis spp.	82.10	59.1	In the Ogeechee River (Georgia, U.S.A.)	Benke and Jacobi, 1994
C. rivulorum	30	/	Experimental stream (Dorset, UK)	Welton et al., 1982
C. luctuosa	76	7.9	Reach 7 (northern Spain)	González J. M., A. Basaguren and J. Pozo, 2001
C. luctuosa	93	7.1	Reach 9 (northern Spain)	González J. M., A. Basaguren and J. Pozo, 2001
C. amica	400	13.0	Experimental pond (Virginia, USA)	Christman and Voshell, 1992
C. horaria	539	10.2	Woodland pond (Geneva, Switzerland)	Oertli, 1993
C. simulans	560	4.4	Plains stream (Minnesota, USA)	MacFarlane and Waters, 1982
Caenis sp.	206	10.1	Experimental stream (Alabama, USA)	Rodgers, 1982
Caenis sp.	271	11.5	Experimental stream (Alabama, USA)	Rodgers, 1982
Caenis sp.	676	12.7	Experimental stream (Alabama, USA)	Rodgers, 1982
Caenis sp.	10183.81*	9.4	Heizhuchong Stream, Hubei, P. R. China	This study, 2005
Afronurus sp.	2405.5	34.7	Shing Mun River (Hong Kong)	M. Salas and D. Dudgeon, 2003
Cinygmina sp.	1198.1	33.0	Shing Mun River (Hong Kong)	M. Salas and D. Dudgeon, 2003
Procloeon sp.	99.5	99.5	Shing Mun River (Hong Kong)	M. Salas and D. Dudgeon, 2003
Baetiella pseudofrequenta	143.2	95.4	Shing Mun River (Hong Kong)	M. Salas and D. Dudgeon, 2003
Choroterpes sp.	225.7	57.8	Shing Mun River (Hong Kong)	M. Salas and D. Dudgeon, 2003
H. limbata	4688	4.09	Blackwater Creek (central Florida, USA)	Lobinske R.J., A. Ali and I. J. Stout, 1996
H. limbata	3.123	4.59	Rock Springs Run (central Florida, USA)	Lobinske R. J., A. Ali and I. J. Stout, 1996
Hb. lauta	198.5	9.6	A northern Spain stream	González J. M., A. Basaguren and J. Pozo, 2003
Hd. confusa	412.6	5.7	A northern Spain stream	González J. M., A. Basaguren and J. Pozo, 2003
Epeorus sp.	61183.42*	15.4	In the Heizhuchong Stream, Hubei, P. R. China	This study, 2005

*Ratio of wet wt and dry wt (Yan, 1999)

4 DISCUSSION

4.1 Life cycle

Mayflies show a remarkable variation in life history at species level. Temperature, food, habitat and photoperiod are factors causing the observed variability. In most species the total day-degree is the major growth regulator (Benke, 1993; Huryn and Wallance, 2000).

The life cycles of many *Caenis* populations seem quite flexible. About half the *Caenis* life cycles summarized by Clifford (1982) were univoltine, mainly univoltine winter, while the other half were multivoltine, mainly bivoltine winter–summer. A typical case is *Caenis luctuosa*, displaying a considerable degree of life cycle flexibility throughout its distribution range. It has been reported as univoltine in high latitudes and mountain areas (Mol, 1983), while in Central Europe it is bivoltine with a winter and a summer generation (Landa, 1968). In Britain, Elliot et al. (1988) described both univoltine and bivoltine cycles. Hall et al. (2001) observed four generations with shorter development times (90–210 days) in Bear Brook of Hubbard Brook Experimental Forest in the United States. A similar flexibility was also found in *C. horaria* and many of the Baetidae species (Brittain, 1982). Flexibility in the number of generations per year may be a response to thermal differences between habitats at different latitudes or altitudes (Ward and Stanford, 1982; Benke, 1993).

In this study area, we observed a bivoltine winter–summer cycle of *Caenis* sp., coinciding with the *Caenis* species reported by Landa (1968), McClure and Stewart (1976) and Elliot et al. (1988), and documented in details by Huryn and Wallance (2000). The Heizhuchong Stream runs among mountains (altitude>400m). It bears similar inhabiting circumstances, such as water temperature (annual mean <16°C), food quality, and time available for development of mayfly species in the above mentioned streams. This may explain partly why *Caenis* sp. and *Epeorus* sp. develop two generations a year in the middle area of China.

4.2 Secondary production

There exist many estimates of mayfly production including a few ones for genus *Caenis*. The estimated annual production in our study is the highest among the values ever reported for *Caenis* species (Perán, et al., 1999; Christman and Voshell, 1992; Rodgers, 1982; MacFarlane and Waters, 1982; Benke and Jacobi, 1994; Welton et al., 1982; González, et al., 2001, 2003; Oertli, 1993; Salas and Dudgeon, 2003; Lobinske, et al., 1996) (for details see Table 5). This is probably due to the relatively higher densities (average 4 724 ind/m^2 and 1 569 ind/m^2) and bigger size of the two mayflies. Furthermore, in Heizhuchong Stream we found fewer predators (only a species of crab *Sinopotamon* sp.), richer food resources and more diverse micro-habitats, which imply that the mayflies confront less predaceous pressure and occupy more food and spatial resources. All these aid the mayfly species to grow bigger in size and reproduce larger population.

Annual P/B ratios of the mayfly species in the Heizhuchong Stream were moderate among the published data in Table 5. Annual P/B ratios of most studies were within the range of 4 to 16 (Perán, et al., 1999; Christman and Voshell, 1992; Rodgers, 1982; MacFarlane and Waters, 1982; González, et al., 2001, 2003; Oertli, 1993; Lobinske, et al., 1996), much lower than those reported by Benke and Jacobi (1994) for three *Caenis* species (*C. diminuta, C.hilaris* and *C. macafferti*) in a subtropical Blackwater Stream and Salas and Dudgeon (2003) for five mayfly species in a tropical stream (Shing Mun River), Hong Kong. These high annual P/B values are mainly due to rapid development of the insects with multiple cohorts and smaller individual size (Benke et al., 1984; Benke, 1993, Huryn and Wallance, 2000; Salas and Dudgeon, 2003), and have also been found in streams in hot and desert region of the United States (Fisher and Gray, 1983; Gaines et al., 1992). According to Waters (1977) and Benke (1993), P/B ratios of bivoltisms are roughly within the scope of 7 to 14, ours are also near or within this range.

4.3 Food consumption and their contribution to production

Measuring the trophic basis of production is useful because gut content analyses alone could be misleading since assimilation efficiencies vary with food types (Benke and Wallace 1980, 1997). Our results indicate that about 33.46% of *Epeorus* sp. production, and 70.79% of *Caenis* sp. production were attributable to detritus, even though this food source has the lowest assimilation efficiency of the five food types present in larval guts. Owing to relatively higher assimilation efficiency, diatoms accounted for about 53.90% of *Epeorus* sp. production, and 18.77% of *Caenis* sp. production, despite comprising only 32.44% of larval diet of *Epeorus* sp. and 7.56% of larval diet of *Caenis* sp. As a result of the low quality diet, a large portion of the total amount of food consumed was egested as detritus, which will subsidize other taxa (Benke and Wallace, 1980; Vannote et al., 1980; Fisher and Gray, 1983; Wallace and Webster 1996; Johnson et al., 2000; Hall et al., 2001).

So far, there are few studies on the trophic basis of production of *Epeorus* sp. and *Caenis* sp., a direct comparison cannot be made, but compared with other reported mayfly species of the same functional feeding group, our results are reasonable. Wallace, et al. (1997) reported *Isonychia*, *Baetis*, *Heptagenia*, *Stenonema* in Ogeechee River and Black Creek also consumed a large portion of amorphous detritus, constituting more than 80% of their diets, and contributed the largest proportion of their production. Benke and Jacobi (1994) showed in Ogeechee River, amorphous detritus contributed 69.7% to the production of *Baetis* spp., 78.3% of *Heptagenia* sp., 53.4 % of *Stenonema* spp., 51.1% of *Ephemerella* spp., 76.9% of *Eurylophella* sp., 65.9% of *Caenis* spp., 65.9% of *Tricorythodes* sp., and 96.3% of *Isonychia*; diatoms contributed the second most to the production of *Baetis* spp. at 26.1%, *Stenonema* spp. at 23.4%, *Caenis* spp. at 11.5%, and *Tricorythodes* sp. at 11.5%; fungi and vascular plant detritus contribute much less proportion to the production for all mayfly species except for *Ephemerella* spp.(vascular plant detritus contributed 28.4%). Johnson et al. (2000) reported amorphous detritus comprised >80% of the diet in all seasons and accounted for 70% of total production in a permanently inundated wetland. Hall et al (2001) reported amorphous detritus and leaf detritus contributed 42.8% and 42.2% to the production of *Baetis,* 34.8% and 40.6% of *Epeorus*, and 28.8% to 64.4% of *Eurylophella* in Bear Brook of Hubbard Brook Experimental Forest in the United States. Similarly, Salas and Dudgeon (2003) found in the wet season 44%–69% of mayfly production was derived from allochthonous detritus in a tropical forest stream (Shing Mun River), Hong Kong in the south of China.

To the best of our knowledge, this is the first study on secondary production and trophic basis of mayfly in rivers and streams in inner land of China. The lack of information regarding structure and function of macrozoobenthos in riverine ecosystems in China is vastly surprising. Several factors may be directly responsible for this lack, including the difficulty in quantitative sampling, the additional time and effort required for secondary production estimates and diet analysis, and scarcity of hydrobiologists working on rivers and streams in China, but the most important indirect reasons were the lack of grants and the inadequate public consciousness on the health of river ecosystems. However, rivers and streams play very important roles in our social and economic construction and development, especially in view of more and more huge dams being built cross Changjiang (Yangtze) River and its big tributors, and the problem of river pollution and shortage of drinkable water are worsening, it is extremely urgent that much more research effort should be directed to a better understanding of riverine ecosystem function in China. This is especially true given the recent concerns regarding sustainable development and scientific strategy of development.

5 ACKNOWLEDGEMENTS

The authors wish to thank our postgraduate students Guo Daoyi, Li Qin, Shu Zhengyu, Liu Wenshan, Liu Hui, Zhou Wei and Zeng Shuhua for hard field work. Special thanks are expressed to professor Liu Jiankang for his valuable comments on the manuscript.

Reference

Benke, A. C., 1993. Baldi Memorial Lecture: Concepts and patterns of invertebrate production in running waters. *Verhandlung der Internationale Vereinigung für theoretische und angewandte Limnologie* **25**: 15-38.

Benke, A. C. and D. I. Jacobi, 1994. Production dynamics and resource utilization of snag-dwelling mayflies in a blackwater river. *Ecology* **75**: 1219-1232.

Benke, A. C. and J. B. Wallace, 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. *Ecology* **61**:108-118.

Benke, A. C. and J. B. Wallace, 1997. Trophic basis of production among riverine caddisflies: implications for food web analysis. *Ecology* **78**:1 132-1 145.

Benke, A. C., 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. *Limnology and Oceanography* **24**: 168-171.

Benke, A. C., T. C. Arsdall, and D.M. Gillespie and F. K. Parrish, 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. *Ecological Monographs* **54**(1): 25-63.

Brittain. J. E., 1982. Biology of mayflies. *Annual Review of Entomology* **27**: 119-147.

Christman, V. D. and J. R. Voshell, 1992. Life history, growth and production of Ephemeroptera in experimental ponds. *Annual of Entomological Society of America* **85**: 705-712.

Clifford, H. F., 1982. Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. *Quaestionae Entomologicae* **18**: 15-90.

Covich, A. P., M. A. Palmer and T. A. Crowl, 1999. The Role of Benthic Invertebrate Species in Freshwater Ecosystems. *BioScience* **49** (2): 119-127.

Cummins, K. W., 1973. Trophic relations of aquatic insects. *Annual Review of Entomology* **18**:183-206.

Dudgeon, D., 1999b. Patterns of variation in secondary production in a tropical stream. *Archiv für Hydrobiologie* **144**: 271-281.

Elliot, J. M., U. H. Humpesch and T. T Macan, 1988. Larvae of the British Ephemeroptera: a key with ecological notes. Scientific Publictions of Freshwater Biological Association. 49.

Fisher, S. G. and L. J. Gray, 1983. Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. *Ecology* **64**: 1 217-1 224.

Gaines, W. L., C. E. Cushing and S. D. Smith, 1992. Secondary production estimates of benthic insects in three cold desert streams. *Great Basin Naturialist* **52**: 11-24.

Georgian, T. and J. B. Wallace, 1983. Seasonal production dynamics in a guild of periphyton-grazing insects in a southern Appalachian stream. *Ecology* **64**:1 236-1 248.

Gonz´alez, J. M., A. Basaguren and J. Pozo, 2001. Life history and production of *Caenis luctuosa* (Burmeister) (Ephemeroptera, Caenidae) in two nearby reaches along a small stream. *Hydrobiologia* **452**: 209-215.

González, J. M., A. Basaguren and J. Pozo, 2003. Life history, production and coexistence of two Leptophlebiid mayflies in three sites along a Northern Spain stream. *Archiv, für Hydrobiologie* **158**(3): 303-316.

Griffith, M. B., S. A. Perry and W. B. Perry, 1994. Secondary production of macroinvertebrate shredders in headwater streams with different baseflow alkalinity. *Journal of North American Benthology Society* **13**: 345-356.

Graubaugh, J. W., J. B. Wallace and E. S. Houston, 1997. Production of benthic macroinvertebrate communities along a southern Appalachian river continuum. *Freshwater Biology* **37**: 581-596.

Hall, R. O., Jr, G. E. Likens and H. M. Malcom, 2001. Trophic basis of invertebrate production in 2 streams at the Hubbard Brook Experimental Forest. *Journal of the North American Benthological Society* **20**(3): 432-447.

Hamilton, A. L., 1969. On estimating annual production. *Limnology and Oceanography* **14**: 771-782.

Huryn, A. D. and J. B. Wallance, 2000. Life history and production of stream insects. *Annual Review of Entomology* **45**: 83-110.

Hynes, H. B. N. and M. J. Coleman, 1968. A simple method of assessing the annual production of stream benthos. *Limnology and Oceanography* **13**: 569-573.

Johnson, B. R., D. C. Tarter, and J. J. Hutchens, 2000. Life history and trophic basis of production of the mayfly *Callibaetis fluctuans* (Walsh) (Ephemeroptera: Baetidae) in a mitigated wetland, West Virginia, USA. *Wetlands* **20**(2): 397-405.

Landa, V., 1968. Development cycles of central European Ephemeroptera and their interrelations. *Acta Entomology of Bohemoslov* **65**: 276-284.

Lobinske, R. J., A. Ali and I. J. Stout, 1996. Life history and productivity of *Hexagenia limbata* (Ephemeroptera: Ephemeridae) and selected physico-chemical parameters in two tributaries of the Wekiva river, central Florida. *Florida Entomologist* **79**(4): 543-551.

Macfarlane, M. B. and T. F. Waters, 1982. Annual production by caddisflies and mayflies in a western Minnesota plains stream. *Canadian Journal of Fishery and Aquatic Sciences* **39**: 1 28-1 635.

Majecki, J., M. Grzybkowska and R. Reddy, 1997. Density, production and life cycle of Brachycentrus subnubilus Cuttis (Trichoptera: Brachycentridae) in a lowland river, Central Poland. *Hydrobiologia* **354**:51-56.

Mantel, S. K. and D. Dudgeon, 2004. Dietary variation in a predatory shrimp *Macrobrachium hainanense* (Palaemonidae) in Hong Kong forest streams. *Archiv für Hydrobiologie* **160**: 305-328.

McClure, R. G. and K. W. Stewart, 1976. Life cycle and production of the mayfly *Choroterpes* (*Neochoroterpes*) *mexicanus* Allen (Ephemeroptera: Leptophlebiidae). *Annual Entomological Society of America* **69**:134-144.

Menzie, C. A., 1980. A note on the Hynes method of estimating secondary production. *Limnology and Oceanography* **25**(4): 770-773.

Mol, A. W., 1983. *Caenis lactea* (Burmeister) in the Netherlands (Ephemeroptera: Caenidae). *Entomology of Berichten* **43**: 119-123.

Morin, A. and N. Bourassa, 1992. Modeles empiriques de la production annuelle et du rapport P/B d'invertebres benthiques d'eau courtante. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 532-539.

Oertli, B., 1993. Leaf litter processing and energy flow through macroinvertebrates in a woodland pond (Switzerland). *Oecologia* **96**: 466-477.

Perán, A., J. Velasco and A. Millán, 1999. Life cycle and secondary production of *Caenis luctuosa* (Ephemeroptera) in a semiarid stream (Southeast Spain). *Hydrobiologia* **400**: 187-194.

Polis, G. A., 1994. Food webs, trophic cascades and community structure. *Australian Journal of Ecology* **19**: 121-136.

Robinson, C. T. and G. W. Minshall, 1998. Macroinvertebrate communities, secondary production, and life history patterns in two adjacent streams in Idaho, USA. *Archiv für Hydrobiologie* **142**: 257-281.

Rodgers, E. B., 1982. Production of Caenis (Ephemeroptera: Caenidae) in elevated water temperatures. *Freshwater Invertebrate Biology* **1**: 2-16.

Salas, M. and D. Dudgeon, 2003. Life histories, production dynamics and resource utilisation of mayflies (Ephemeroptera) in two tropical Asian forest streams. *Freshwater Biology* **48**:485-499.

Sanchez, M. and A. C. Hendricks, 1997. Life history and secondary production of Cheumatopsyche spp. In a small Appalachian stream with two different land uses on its watershed. *Hydrobiologia* **354**:127-139.

Statzner, B., K. Hoppenhaus, M. F. Arens and P. Richoux, 1997. Reproductive traits, habitat use and templet theory: a synthesis of world wide data on aquatic insects. *Freshwater Biology* **38**: 109-135.

Townsend, C. R. and A. G. Hildrew, 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biology* **31**:265-275.

Usseglio-Polatera, P. and H. Tachet, 1994. Theoretical habitat templets, species traits, and species richness: Plecoptera and Ephemeroptera in the Upper Rhône River and its floodplain. *Freshwater Biology* **31**: 357-375.

Usseglio-Polatera, P., M. Bournaud and P. Richoux, 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshwater Biology* **43**: 175–205.

Vannote, R., G. W. Minshall, K. W. Cummins, J. R. Sedell and C. E. Cushing, 1980. The river continuum concept. *Canadian Journal of Fishery and Aquatic Sciences* **37**: 130-137.

Wallace, J. B.and J. R. Webster, 1996. The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology* **41**:115-139.

Wallace, J. B., A. C. Benke, A. H. Lingle and K. Parsons, 1987. Trophic pathways of macroinvertebrate primary consumers in subtropical blackwater streams. *Archiv für Hydrobiologie（Supplement）* **74**: 423-451.

Wallace, J. B., S. L. Eggert, J. L. Meyer and J. R. Webster, 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* **277**: 102-104.

Ward, J. V. and J. A. Stanford, 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* **27**: 97-117.

Waters, T. F., 1977. Secondary production in inland waters. In: A. Macfadyen, ed. Advances in Ecological Research Vol. 10, Academic Press, 91-164.

Welton, J. S., M. Ladle and J. A. B. Bass, 1982. Growth and production of five species of Ephemeraptera larvae from an experimental recirculating stream. *Freashwater Biology* **12**: 103-122.

Whiles, M. R. and J. B. Wallace, 1995. Macroinvertebrate production in a headwater stream during recovery from anthropogenic disturbance and hydrological extremes. *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 2 402-2 422.

Yan, Y. and Y. Liang, 1999. A study of dry-to-wet weight ratio of aquatic macroinvertebrates. *Journal of Huazhong University of Science and Technology (Science Edition)*, **27**(9): 61-63. (in Chinese with English abstract)