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Secondary Production and Its Trophic Basis of Two Mayfly Species in a Subtropical Stream of China

key words: Macrozoobenthos, production, *Epeorus sinensis*, *Caenis nigropunctata*, Heizhuchong stream

Abstract

During June 2003 to June 2004, an investigation on life cycle, production and trophic basis of two species of mayfly in a second-order river of Hanjiang River Basin, Hubei, China was conducted. The results showed *Epeorus sinensis* UMLER and *Caenis nigropunctata* WU both developed two generations a year. The mean annual production and P/B ratio of *E. sinensis* were 9.154 g m^{-2} a^{-1} dry weight and 16.0, and those of *C. nigropunctata* were 1.554 g m^{-2} a^{-1} and 9.6, respectively. For *E. sinensis*, the proportions contributing to secondary production of the main food types were: amorphous detritus 33.46%, fungi 10.8%, vascular plant detritus 1.8%, diatoms 53.9%; for *C. nigropunctata*, the proportions were 70.8%, 6.90%, 3.5% and 18.8%, respectively. Compared with those species reported in North America and Europe, although land use mode and local climate were greatly different in China, life history and trophic basis of the mayflies seemed roughly similar, yet secondary production appeared to be much higher.

1. Introduction

Mayflies constitute a major part of macroinvertebrate biomass and production in freshwater habitats (BRITTAIN, 1982), and play an important role in material cycle and energy flow in water ecosystem (COVICH *et al.*, 1999). By now, more and more studies were conducted on this group (CLIFFORD, 1982; BENKE, 1984; BENKE and JACOBI, 1994; LOBINSKE *et al.*, 1996; GONZÁLEZ *et al.*, 2001, 2003). These studies mainly focused on life cycle, secondary production and its trophic basis, and the relating food web analysis in subtropical and temperate areas in North America and Europe. However, until now there are only few reports available on this group in Asia, even fewer in China (SALAS and DUDGEON, 2003). As known to all, there are more than 300 species of mayflies in Asia, and over 250 species in China, among which many are endemic species. They also distribute nearly in all lentic and lotic water bodies, especially abounding in rivers and streams, and contribute significantly to ecological processes. But which definite kind of function they exert in Asian and Chinese rivers and streams is still unknown, and there is no comparison to show to what extent their functions are similar or different from their counterparts reported in North America and Europe.

The main purposes of this work were (1) to describe life history of the two dominant mayfly *Epeorus sinensis* UMLER and *Caenis nigropunctata* WU in a second-order stream in

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the middle part of China, (2) to estimate their secondary production, (3) to determine the trophic basis of secondary production, and (4) to compare with those species reported in North America and Europe, so as to assess their similarity/difference in continental scale.

2. Materials and Methods

2.1. Study Area

The Heizhuchong stream drains a small catchment (52 km^2) located in the northwest mountainous part of Nanzhang County (31°70′ N, 111°81′ E), Hubei Province, P.R. China (Fig. 1). The climate in the zone is subtropical, with mean monthly temperature ranging between 4.2 °C (January) and 28.3 °C (August) during 2003–2004. There are usually floods during summer (May to mid-July), and droughts between late July to October each year, which means that climate is highly variable in summer and autumn. The main land uses are pine, maple forestry and rice and wheat plantations. Human population is relatively low (about 50000 inhabitants). The township of Nanzhang County situates at the middle reach of the stream with several sewage outlets.

From the upper to the lower reach of Heizhuchong stream we chose six types of habitats for quantitative sampling. Station 1 (S_1) lied in the middle of the stream with big round rocks, station 2 (S_2) in

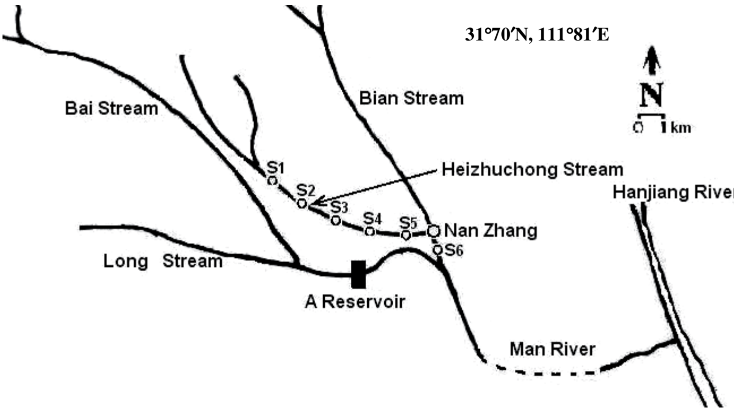

Figure 1. Heizhuchong stream and distribution of sampling sites.

Table 1. Main physical and chemical characteristics of Heizhuchong stream. Those parameters with annual ranges in parentheses were measured monthly during 2003–2004.

Elevation (m)	450 (ca 350–550)
Drainage area (km^2)	52
Channel width (m)	10–12
Water temperature (°C)	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 dry wt /m^2)	20.4 (10.3–56.7)

* crude particulate of organic materials.

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 meters upstream. Preliminary calculations showed that the relative proportions of the above habitats were roughly equal within the sampled sections, so we assume that such habitats play equal roles in the stream function.

Limnological details of the river water during the study period are listed in Table 1.

2.2. Sampling and Analysis

Quantitative benthic samples were collected monthly from June 2003 to June 2004. At each site, four random replicates were taken with a Surber net (area 0.09 m^2, mesh size 250 μm), and preserved in 10% formalin. In the 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 dry weights of *Epeorus sinensis* UMLER and *Caenis nigropunctata* WU were estimated from a length–weight regression model constructed using nymphs from the study sites. Secondary production was determined by the size-frequency method (HYNES and COLEMAN, 1968) with the modifications by HAMILTON (1969) and BENKE (1979).

We used diet analyses 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.) from S_1, S_2, S_3 and S_4. Each time we dissected guts of 11 to 15 individual animals in different size, 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 15 to 17 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) and WALLACE *et al.* (1987) to estimate the relative contribution of each food type to secondary production.

The data were analyzed using a 2-way analysis of variance (ANOVA).

3. Results

3.1. Population Dynamics

Figure 2a shows the annual variations of standing stock of *E. sinensis* population. Abundance of the population reached its peak in July 2004 with the density of 1226 ind/m^{-2}, and biomass of the population had two prominent peaks, the main one occurred in April 2003 at 3.14 g m^{-2}, the second was in July at 2.69 g m^{-2}. In October, biomass declined to its lowest level, and in December abundance was the fewest.

Abundance of *C. nigropunctata* population had two peaks, one was in February with the density of 194 ind m^{-2}, the other in July of 307 ind m^{-2}. Biomass peaked in February of 1.59 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).

Abundance and biomass of the two mayflies were significantly different ($P < 0.05$, $F = 7.2368$, $df = 12$ and $P < 0.01$, $F = 13.2653$, $df = 12$). Abundance and biomass of *C. nigropunctata* with respect to sampling site and time are also significantly different ($P < 0.01$, $F = 5.4428$, $df = 48$ and $F = 2.7267$, $df = 48$; $P < 0.01$, $F = 4.1508$, $df = 48$ and $F = 3.0584$, $df = 48$). Also the abundance of *E. sinensis* with respect to sampling site and time was significantly different ($P < 0.05$, $F = 2.6308$, $df = 48$ and $P < 0.01$, $F = 4.5778$, $df = 48$). Neither in *C. nigropunctata* nor in *E. sinensis* was an interaction between time and sampling site.

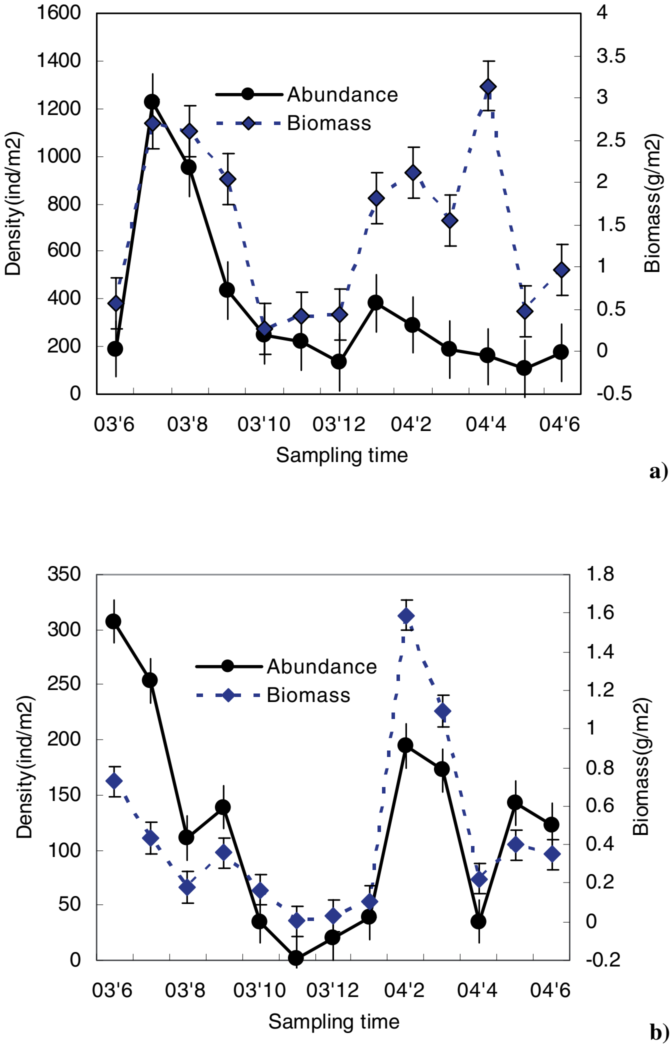

Figure 2. Annual variations of standing stock of *E. sinensis* (a) and *C. nigropunctata* (b) in Heizhuchong stream (± Standard error).

3.2. Life History

The *E. sinensis* 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 four months, these larvae developed into adult in July to September. Their descendants will emerge again in February to March next year. Nevertheless, there was a little overlap between the two generations (Fig. 3).

C. nigropunctata also completed two generations during a year (Fig. 4). Adults mainly emerged from March to April, then mating and spawning, reproduction continued for sev-

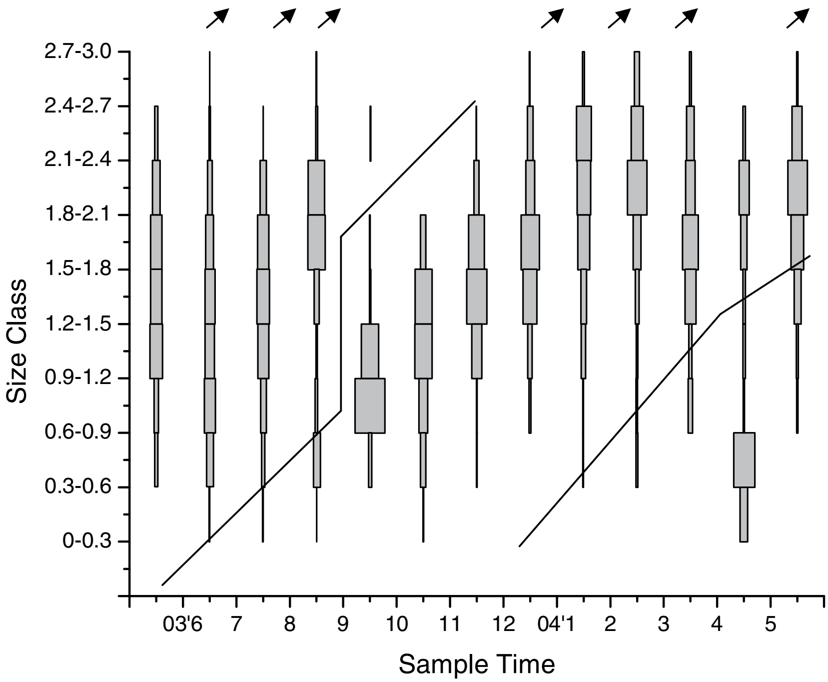

Figure 3. Monthly instar frequency distributions for *E. sinensis* in Heizhuchong stream.

eral months. The larvae began emergence again in October to November. Adults mated and spawned immediately, hatching occurred in November and December, emergence will take place during March to May the next year.

3.3. Annual and Cohort Production

The best correlation between size and weight was achieved using exponential equations that did not differ between sites ($P > 0.1$, $F = 1.6473$, d$f = 105$).

Thus, all morphometric data were pooled and one equation was calculated for both mayflies, respectively:

$$E.\ sinensis,\ Wd = 0.0135L^{2.52}\ (n = 56,\ r = 0.9869,\ p < 0.0000)$$

$$C.\ nigropunctata,\ Wd = 0.0068L^{2.94}\ (n = 64,\ r = 0.9918,\ p < 0.0000)$$

Where *Wd* is dry weight (mg) and *L* is body length (mm).

Estimated with size-frequencies, cohort and annual production and P/B of *E. sinensis* and *C. nigropunctata* are presented in Table 2: The mean cohort and annual production of *E. sinensis* were 4.577 g m^{-2} a^{-1} and 9.154 g m^{-2} a^{-1} and mean P/B (cohort/annual) was 8.0 and 16.0. Therefore, for *E. sinensis*, the rank of productivity of micro-habitats is $S_1 > S_2 > S_3 > S_4 > S_5 > S_6$.

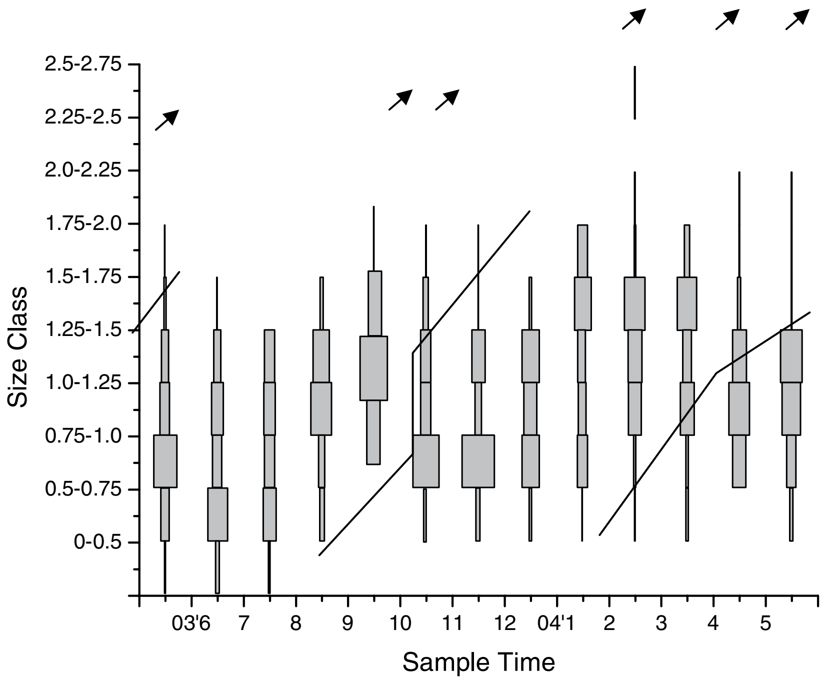

Figure 4. Monthly size frequency distributions for *C. nigropunctata* in Heizhuchong stream.

The mean cohort and annual production of *C. nigropunctata* were 0.777 g m^{-2} a^{-1} and 1.554 g m^{-2} a^{-1} and mean P/B (cohort/annual) was 4.8, 9.6, respectively. Thus, for *C. nigropunctata*, the rank of productivity of micro-habitats is $S_1 > S_5 > S_3 > S_4 > S_2 > S_6$ (Table 2). Note the exchange between S_5 and S_2 in this row.

Based on the estimated production of all sites the mean annual production and P/B ratio for the two mayflies were: for *E. sinensis,* 9.154 g m^{-2} a^{-1} and 16.0; for *C. nigropunctata*, they were 1.554 g m^{-2} a^{-1} and 9.6.

Table 2. Annual productions (g dry wt/m^2 a) of *E. sinensis* and *C. nigropunctata* for each sampling site in Heizhuchong stream by size-frequency method.

Sampling site	***E. sinensis***		***C. nigropunctata***	
	P (Cohort/Annual)	**P/B (Cohort/Annual)**	**P (Cohort/Annual)**	**P/B (Cohort/Annual)**
1	14.040/28.080	8.4/16.8	2.228/4.456	5.1/10.2
2	4.948/9.896	7.7/15.4	0.464/0.928	4.7/9.4
3	3.478/6.956	7.2/14.4	0.645/1.290	4.2/8.4
4	2.474/4.948	7.8/15.6	0.628/1.256	4.9/9.8
5	2.331/4.662	7.5/15.0	0.662/1.324	4.5/9.0
6	0.191/0.382	7.0/14.0	0.034/0.068	5.3/10.6
Mean	4.577/9.154	8.0/16.0	0.777/1.554	4.8/9.6

Although these two mayflies coexist in all their habitats, production of *E. sinensis* was approximately 6-fold that of *C. nigropunctata*, which suggests that *E. sinensis* plays a much greater role in ecological processes than *C. nigropunctata* in the stream.

3.4. Food Consumed and Their Contribution to Production

Gut contents of 12–15 individuals of *E. sinensis* and 11–14 individuals of *C. nigropunctata* in different size were examined for each season (Table 3). The analyses showed that both *E. sinensis* and *C. nigropunctata* consumed a large portion of amorphous detritus, constituting 60.4% and 85.52% of their diets, and contributing 33.46% (107.75 g m^{-2}) and 70.8% (37.94 g m^{-2}) to their secondary production. Diatoms were the second important food type, averaging 32.44% and 7.56% of their diets, average contributing 53.90% (173.57 g m^{-2}) and 18.8% (10.06 g m^{-2}) to their production. Fungi were not abundant in the guts of the two mayflies, comprising of 3.91% and 1.67% of the gut contents, merely contributing 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 3.5% (1.89 g m^{-2}) to the production. Filament algae and animal materials were not encountered in gut contents of *C. nigropunctata*, filament algae occupied 0.01% of the diet of *E. sinensis*.

Table 3. Percentage of foregut food contents of the two mayflies; percentage proportion of annual production attributable to various food types is shown in parentheses below each value (± Standard error).

Taxa	**No. guts examined**	**Amorphous Detritus**	**Fungi**	**Vascular Plant Detritus**	**Diatoms**	**Filament Algae**	**Animal Material**
E. sinensis	12–13–15	60.4 ± 5.3 (33.4)	3.9 ± 0.6 (10.8)	3.25 ± 0.74 (1.80)	32.44 ± 3.21 (53.90)	0.01 ± 0.00 (0.01)	0.00 (0.00)
C. nigropunctata	11–12–14	85.5 ± 7.0 (70.8)	1.7 ± 0.3 (6.9)	4.25 ± 1.04 (3.52)	7.56 ± 1.35 (18.77)	0.00 (0.00)	0.00 (0.00)

4. Discussion

4.1. Life Cycle

Mayflies show a remarkable variation in life history at species level. Temperature, food, habitat and photoperiod are major factors causing the observed variability.

The life cycles of many *Caenis* populations seem quite flexible. About half the *Caenis* life cycles were univoltine, mainly univoltine winter, while the other half were multivoltine, mainly bivoltine winter–summer (CLIFFORD, 1982). A typical case is *Caenis luctuosa*, displaying a considerable degree of life cycle flexibility throughout its distributional 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, for the first time we reported the life cycle of mayfly species in mainland of China and observed a bivoltine winter–summer cycle of *C. nigropunctata* and *E. sinensis*, 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 Wallace (2000). Heizhuchong stream runs among mountains (altitude >400 m). It probably bears similar inhabiting circumstances, such as water temperature (annual mean <16 °C), food quality, and photoperiod for the mayflies to develop, to the above mentioned streams in North America and Europe.

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 compared with the values ever reported for *Caenis* species (see Table 4). This is probably due to the relatively higher densities (average 4724 ind m^{-2} and 1569 ind m^{-2}) and bigger size of the two mayflies. Furthermore, in Heizhuchong stream we found richer food resources, more diverse microhabitats and less predators (only a species of *Sinopotamon teritisum* Dai *et al.* in moderate abundance), which imply that the mayflies occupy more food and spatial resources, and confront less predaceous pressure, which aids them to grow bigger in size and reproduce larger in population.

Annual P/B ratios of the mayfly species in Heizhuchong stream were moderate among the published data in Table 4. Annual P/B ratios of most studies were within the range of 4 to 16 (see Table 4), 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. 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 Wallace, 2000), and have also been found in hot and desert streams in the United States (Fisher and Gray, 1983; Gaines *et al.*, 1992). But 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 scope.

There is no report on the production of mayflies with respect to habitats, we for the first time attempt to explore relationship between habitats and secondary production of mayflies in riverine ecosystem. It seems that reaches with big round rocks are the best habitats for *E. sinensis* and *C. nigropunctata* to inhabit. This is probably due to that big rocks provide rich food resources and good shelters for these scrapers.

4.3. Food Consumed and Their Contribution to Production

Measuring the trophic basis of production is valuable because gut content analyses alone could be misleading since assimilation efficiencies vary by food types (Benke and Wallace, 1980, 1997; Benke *et al.*, 1984). Our results indicate that about 33.46% of *E. sinensis* production, and 70.79% of *C. nigropunctata* 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 *E. sinensis* production, and 18.77% of *C. nigropunctata* production, despite comprising only 32.44% of larval diet of *E. sinensis* and 7.56% of larval diet of *C. nigropunctata.* As a result of the low quality diet, a large portion of the total

Table 4. Comparison of secondary production and P/B ratio with other mayfly studies.

Species	P (mg DW/ m^2)	P/B	Habitat (Location)	Source
C. luctuosa	6349.81	15.98	Mediterranean semiarid stream (Murcia, Spain)	PERÁN *et al.*, 1999
C. amica	445.05	13.00	Experimental ponds (Virginia, USA)	CHRISTMAN and VOSHELL, 1992
C. amica	676	12.72	Experimental stream (Alabama, USA)	RODGERS, 1982
C. simulans	4200	4.20	Cold/mesic plains stream (Minessota, USA)	MACFARLANE and WATERS, 1982
Caenis spp.	82.10	59.1	The Ogeechee River (Georgia, USA)	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 *et al.*, 2001
C. luctuosa	93	7.1	Reach 9 (Northern Spain)	GONZÁLEZ *et al.*, 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
C. nigropunctata	1554	9.6	Heizhuchong Stream, Hubei, P.R. China	This study, 2004
H. limbata	4688	4.09	Blackwater Creek (central Florida,USA)	LOBINSKE *et al.*, 1996
H. limbata	3.123	4.59	Rock Springs Run (central Florida,USA)	LOBINSKE *et al.*, 1996
Hb. lauta	198.5	9.6	A Northern Spain stream	GONZÁLEZ *et al.*, 2003
Hd. confusa	412.6	5.7	A Northern Spain stream	GONZÁLEZ *et al.*, 2003
E. sinensis	9154	16.0	Heizhuchong Stream, Hubei, P.R. China	This study, 2004

amount of food consumed was egested as detritus, which will subsidize other taxa (VANNOTE *et al.*, 1980; FISHER and GRAY, 1983; WALLACE and WEBSTER, 1996; JOHNSON *et al.*, 2000; HALL *et al*, 2001).

So far, there no study on the trophic basis of production of *E. sinensis* and *C. nigropunctata* is known to which a direct comparison could be made, but compared with other reported mayfly species of the same functional feeding group in North America and Europe, our results are moderate. WALLACE *et al.* (1987) 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 to the largest proportion of their production. BENKE and JACOBI (1994) showed in Ogeechee River amorphous detritus contributed 69.7% of 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., 96.3% of *Isonychia*; diatoms were responsible the second most for to the production of *Baetis* spp. at 26.1%, *Stenonema* spp. at 23.4%, *Caenis* spp. at 11.5%, *Tricorythodes* sp. at 11.5%; fungi and vascular plant detritus contributed with a 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 led to 42.8% and 42.2% of the production of *Baetis,* 34.8% and 40.6% of *Epeorus*, 28.8% and 64.4% of *Eurylophella* in Bear Brook of Hubbard Brook Experimental Forest in the United States.

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