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Food Web Structure of Benthic MacroInvertebrates in a Second Order Stream of the Hanjiang River Basin in Middle China

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ABSTRACT

Because few detailed invertebrate food webs on riverine ecosystems have been reported in Asia, we undertook a dietary study on Heizhuchong Stream, a second order stream in Hubei Province, China. Dietary information was obtained from foregut content analysis of the dominant benthic macroinvertebrates from June 2003 to June 2004. Allochthonous inputs were the most important food sources for the macroinvertebrate community; amorphous detritus comprised 38.3-98.8% of their diets.

INTRODUCTION

The major goal of food web theory is to learn the operational patterns of natural communities (Pimm et al. 1991). Early analyses of collections of the reported food webs from various habitats suggested that food webs show consistent structural patterns (Briand and Cohen 1984, Cohen et al. 1990, Pimm et al. 1991). However, these patterns were widely debated among the later researchers (Polis 1994, Dunne 2005). The main debates were focused on limitations of data employed for these analyses, such as the poor quality of many food web data, the small subsets of trophic species analyzed, differences in the methodologies used, the definition of a linkage by ignoring the linkage strength, the level and standardization of taxonomic resolution, and mathematical artifacts (Lawton 1989, Winemiller 1990, Hall and Raffaelli 1991, Martinez 1991 and 1993, Closs et al. 1993, Thompson and Townsend 2000). In recent years food webs constructed with a higher taxonomic resolution (Hall and Raffaelli 1991, Martinez 1991, Tavares-Cromar and Williams 1996, Schmid-Araya et al. 2002a) invalidated some earlier generalizations (e.g., constant L/S, where L is the number of linkages between species of a community, S is the total number of species) and showed that features such as short food chain and omnivory are common in riverine food web structure (Motta and Uieda 2005).

In the 1980s, Benke et al. (1984) recognized the flaws in qualitative methods, and developed detailed quantitative food webs for assemblages of caddisflies, mayflies, and chironomids in streams by combining measures of energy flow (secondary production) with gut content analysis. Later on, other ecologists followed their approach or a variation of their approach to conduct studies on functioning analysis of various ecosystems (Cohen et al. 1993, Tavares-Cromar and Williams 1996, Benke and Wallace 1997, Johnson et al. 2000, Benke et al. 2001, Hall et al. 2001). Thus far, much progress has been made in quantitative description of food webs in aquatic ecosystems (Schmid-Araya et al. 2002b, Zanda and Fetzer 2007). However, most work has been done on the aquatic communities in the USA and European countries (Benke and Wallace 1997, Benke et al. 2001, Tavares-Cromar and Williams 1996, Zanda and Fetzer 2007). As known, food web structure varies spatially and temporally and markedly varies in riverine landscapes of different land use modes (Woodward and Hildrew 2002). Asia is a typical agricultural continent. There land use modes differ greatly from those of the

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western developed countries, but until now, little research was conducted on food webs of the aquatic community (Mantel and Dudgeon 2004, Zanden and Fetzer, 2007), which seriously restricts the sustainable development of the riverine landscapes in most of the Asian countries (Dudgeon et al. 2000).

The objective of this work was to construct a quantitative food web of the macroinvertebrate community in a second order stream of the Hanjiang River basin in middle China on a species level of taxonomic resolution.

MATERIALS AND METHODS

Heizhuchong Stream drains a small catchment (52 km^2) located in subtropical, Hubei Province (31°70'N, 111°81'E). Between the upper and lower reaches of the stream, we established six sampling sites, representing the typical habitats present—boulders, cobble, gravel-sand, macrophytes, snags, and bedrock. Since the relative proportions of the selected habitats were roughly equal within the sampled sections, we assumed that such habitats play equal roles in the stream. Although each sampling site was separated by about 1,000 m, the water quality was really similar (Table 1). The most downstream site was subject to intermittent municipal waste.

Quantitative benthic samples were collected monthly from June 2003 to June 2004. At each site, three 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, organisms were sorted and identified to the lowest possible taxonomic level. The head width and body length of each specimen were measured to the nearest 50 μm using a micrometer.

We used diet analysis to estimate consumption of various food items by following the methods of Benke and Wallace (1997) and Salas and Dudgeon (2003) and analyzed gut contents of the dominant species for each month (except for January and February when the most animals were in intermittent diapause because temperature dropped below 5°C). Each time, we dissected guts of 15 individual animals of different sizes. We suspended the contents in distilled water and then filtered the contents onto a membrane filter. Material was placed onto a microscope slide and cleared with immersion oil. We quantified gut contents by measuring the relative areas of six food categories (amorphous detritus, fungi, filamentous algae, vascular plant detritus, diatoms,

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

Parameter	Value
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 - 8.0)
Conductivity (μS/cm)	228 (191 - 293)
Oxygen (mg/L)	11.6 (9.7 - 14.8)
Oxygen saturation (%)	108 (100 - 126)
Periphyton (g/m^2)	24.3 (3.4 - 92.1)
CPOM[a] (g dry wt/m^2)	20.4 (10.3 - 56.7)

[a] Course particulate organic matter

and animal materials) on each filter (Cummins 1973) using a compound microscope equipped with a video image analyzer. We estimated monthly ingestion and relative contribution of each food type to monthly production using assimilation efficiencies—10% for amorphous detritus, 10% for vascular plant detritus, 30% for diatoms and filamentous algae, 50% for fungi, and 70% for animal material (Benke and Wallace 1997)—and a net production efficiency (production/assimilation) of 40% (Wallace et al. 1987). These calculations resulted in an estimate of the amount of food consumed (g m^{-2} a^{-1}) necessary to support the observed secondary production of each consumer examined. The trophic basis of production was estimated for each taxon annually. To estimate consumption by the entire macroinvertebrate community, we calculated the sum of the food type consumed by the portion of the community analyzed and then divided this by the proportion of secondary production they comprised.

A two-way analysis of variance (ANOVA) was performed to compare differences between intra- and inter-food categories. Bonferroni multiple comparison tests were used in post-hoc comparisons if ANOVA detected significant differences (Benke and Wallace 1997, Salas and Dudgeon 2003).

RESULTS AND DISCUSSION

Eighty-four invertebrate consumers were identified in the Heizhuchong Stream. Aquatic insects were the most diverse group representing 83.5% of the total taxon richness, followed by oligochaetes (4.7%), molluscs (4.7%), and crustaceans (3.5%). Aquatic insects presented the highest density values. Based on the density and occurrence, *Sinopotamon teritisum*, *Pentaneura* sp., *Polypedilum* sp., *Tvetenia discoloripes*, *Eukieferiella potthasti*, *Microtendipes* sp., *Chaetocladius* sp., *Pagastia* sp., *Hydropsyche* sp., *Epeorus sinensis*, *Caenis nigropunctata*, *Leptophlebia* sp., *Ephemera* sp., and *Corbicula fluminea* were the dominant species, comprising 73.8-94.3% of the community abundance and 89.4-95.7% of its biomass.

Nearly all species In Heizhuchong Stream, depended heavily on the allochthonous inputs. Amorphous detritus occupied 38.3% of the diet (*Hydropsyche* sp.) to 98.81% (*Polypedilum* sp.). Diatoms and fungi were the second most important food types, consisting of 0-33.2% and 0-3.1% of the diets of the dominant species, respectively. Animal material was only found to be one of the main food types of *S. teritisum*, *Pentaneura* sp., and *Hydropsyche* sp., occupying 52.2%, 14.7%, and 40.5 % of their diets, respectively. Vascular plant detritus and filamentous algae occurred rarely in a few species for a period of time (Fig. 1). Patterns of the six food types for each species varied significantly ($p<0.01$ or 0.05).

The annually quantitative food web of Heizhuchong Stream (Fig. 2) showed a relatively high degree of trophic complexity. The diagram had five basal resources. All other organisms sampled including a crab *S. teritisum* fed on them directly or indirectly. *S. teritisum* played an important role in connections between different species, consuming most items present in the stream. The total organic matter flow was at 5191.9 g dry mass/m^2.yr^{-1}.

Like other reported aquatic food webs (Warren 1989, Closs and Lake 1994, Tavares-Cromar and Williams 1996, Thompson and Townsend 2003), our results suggest that the key basal food resource of macroinvertebrate community in headwater (orders 1-3) streams is detritus, and most organisms sampled are detritivores. Detritus plays an important role in the food web as the key source of energy and nutrients for macroinvertebrates, and it nearly all originates from allochthonous drainage, which means external subsidies from terrestrial systems can produce a range of direct and indirect food web effects (Kawaguchi and Nakano 2001, Nakano et al. 1999). Additionally, detritus often serves as shelter for animals and can modify the physical and chemical characters of the microhabitat (Moore et al. 2004).

Previously reported detritus-based food webs showed that a majority of trophic interactions were weak, and these webs were donor controlled (Pimm 1982). This also exists in Heizhuchong Stream. Like other stream food webs (Benke and Wallace 1997,

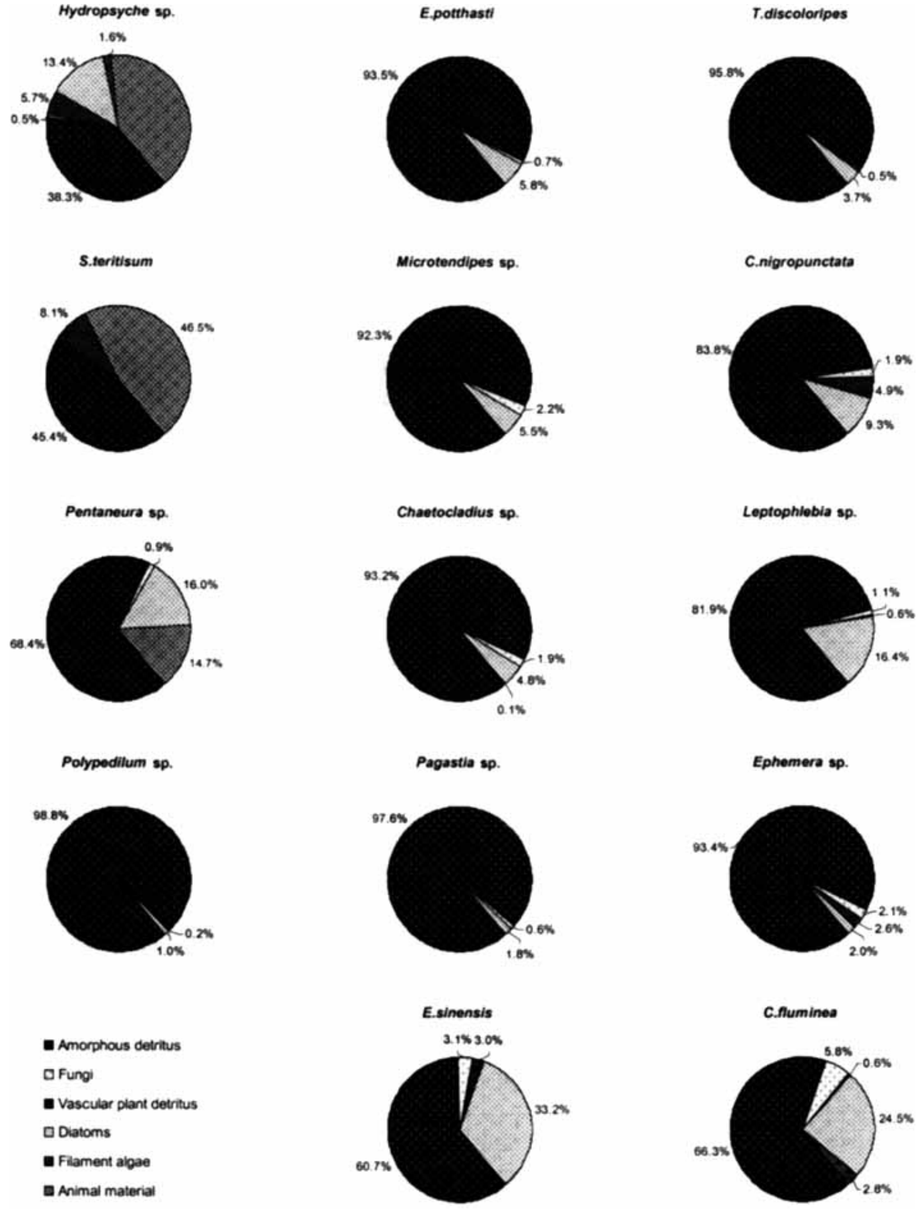

Figure 1. Annual ingestion proportions of each food type in the dominant macroinvertebrate species in Heizhuchong Stream.

Benke et al. 2001, Motta and Uieda 2005), our analysis showed that most energy flow was concentrated in a few pathways, and the amount of energy flow through the rest was less than 5% of the total value, which would have little effect on the abundant food supply in the stream.

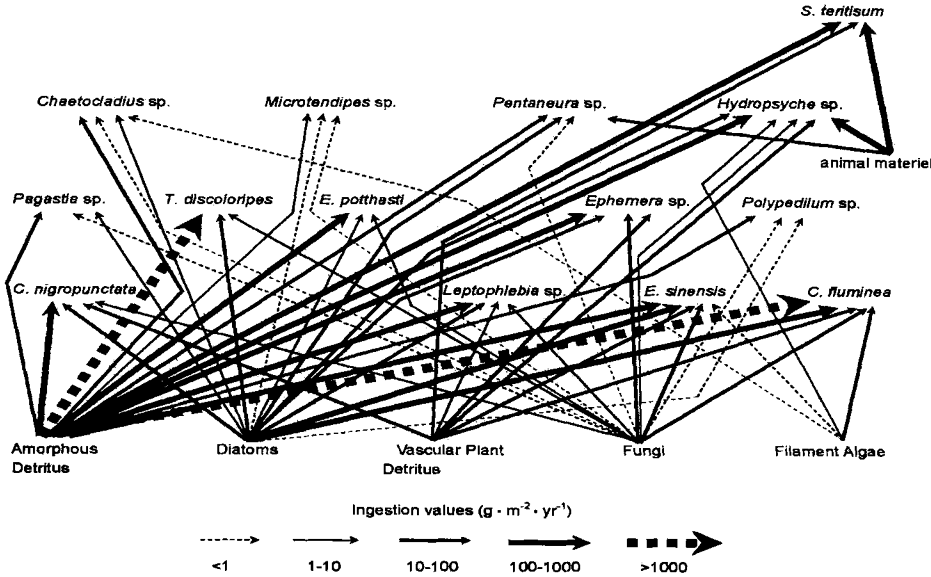

Figure 2. Annual quantitative food web for the macroinvertebrate community in Heizhuchong Stream. The web illustrates the rate of consumption (g m^{-2} yr^{-1}) of each trophic interaction. The width of the arrows indicates the rate of flow.

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