CSIRO PUBLISHING

Marine and Freshwater Research, 2007, **58**, 596–607 www.publish.csiro.au/journals/mfr

Food web structure of a subtropical headwater stream

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Abstract. The food web structure of a headwater stream (Hapen Creek) in subtropical northern Taiwan, which is subject to regular typhoon disturbances, was characterised using stable isotope techniques. δ^{13}C and δ^{15}N signatures were used to examine (i) the relative contributions of allochthonous versus. autochthonous sources to the web, and (ii) the trophic organisation of the community including the predominant feeding guilds and the most prevalent feeding mode. This study presents food web attributes for one of the very few food webs studied to date in a subtropical region. Consumers utilised allochthonous and autochthonous carbon sources differently depending on their trophic positions. The majority of consumers exploited more autochthonous carbon sources. Consumers at higher trophic positions in the food web had more direct and greater association with benthic algae. Higher-order consumers also consumed allochthonous carbon in an indirect manner by assimilating lower-order insects. The results reveal the importance of invertebrate consumer snails and aquatic insects in the transfer of organic matter. Omnivores predominated in the food web; this may reflect an opportunistic foraging strategy that enables them to adapt to hydrological disturbances and a fluctuating food supply.

Additional keywords: allochthonous *v.* autochthonous flows, δ^{13}C, δ^{15}N, trophic interactions.

Introduction

The food webs of lotic ecosystems are influenced by interactions between top-down (consumption) and bottom-up (production) processes. These processes are influenced by the type of primary production, utilisation of primary production by consumers, feeding habits of consumers and organic matter flows through food chains within the web (e.g. Hill *et al.* 1995; Rosemond *et al.* 2001; March and Pringle 2003). In addition to the biological effects, the physical setting has also been demonstrated to be an important factor in characterising lotic food webs. For example, rivers in a warmer climate or with a more open riparian canopy facilitate autochthonous (algae) primary production in contrast to rivers in a cooler region and/or in a densely shaded condition where allochthonous (vascular plant litter) predominates (Vannote *et al.* 1980; Rosemond 1994; Finlay 2001). Contrary to expectations that forested headwater food webs in temperate areas are primarily reliant on allochthonous litter input (Vannote *et al.* 1980; Tavares-Cromar and Williams 1996), some studies also indicate consumers use substantial or at least partial amount of autochthonous sources in small streams (Rosenfeld and Roff 1992; Finlay 2001; England and Rosemond 2004). Recent research has found that omnivorous feeding modes are common in both temperate and tropical streams (Lewis *et al.* 2001; Mantel *et al.* 2004; Lancaster *et al.* 2005), especially where disturbance-induced fluctuations in the food supply may discourage predators from foraging solely on one trophic level.

Although many studies in temperate areas have revealed important stream food web issues, such as consumer carbon sources (Vannote *et al.* 1980; Finlay 2001), consumer trophic interactions (Tavares-Cromar and Williams 1996; Fisher *et al.* 2001; Kishi *et al.* 2005) and invasive predator influences (Nystrom and McIntosh 2003; Lancaster *et al.* 2005), our understanding of stream food webs in tropical and subtropical areas has been limited until recently, and was restricted to only a few areas such as Costa Rica, Puerto Rico, Brazil, Australia and Hong Kong. Tropical and subtropical areas differ from temperate areas in several aspects. For instance, the former receive longer and greater irradiation and have warmer water temperatures, which may facilitate algal production (Rosemond 1994; Kishi *et al.* 2005). Therefore, algae produced in-stream can serve as important food to consumers (Bunn *et al.* 1999; March and Pringle 2003; Mantel *et al.* 2004; Brito *et al.* 2006). Moreover, frequent natural disturbances (e.g. typhoons and hurricanes) and different species composition have been shown to affect the utilisation of primary production and food web structure in tropical and subtropical areas. Shredder insects, which are expected to be prevalent in small forest streams, are less prevalent in some tropical small streams (March and Pringle 2003; Brito *et al.* 2006), whereas shrimps may be functional shredders and trophic carnivores (March and Pringle 2003; Mantel and Dudgeon 2004). However, owing to a lack of data, it remains unclear whether strong reliance on autochthonous algae is a general pattern in small streams in subtropical areas.

Taiwan is located in both the subtropical and tropical zones of the West Pacific region where typhoons regularly occur from July to September and often produce major hydrologic disturbances. Records show that an average of 3.7 typhoons directly impact Taiwan each year (Wu and Kuo 1999). In addition, owing to Taiwan's steep topography, its rivers are characterised by short, rapid runs, thus causing the high level of rainfall associated with

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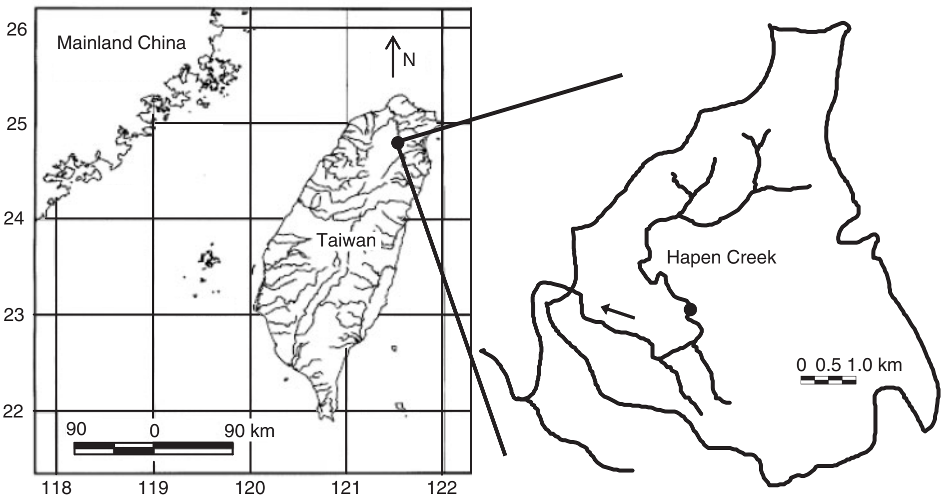

Fig. 1. Hapen Creek study area in the Fushan Long-Term Ecology Research Site, north-eastern Taiwan. The dot depicts the sampling station. An arrow indicates the downstream direction.

typhoons to create marked seasonal fluctuations in river flow. These fluctuations were observed to strongly affect fish populations (Tew *et al.* 2002; Chuang *et al.* 2004). Headwater regions of mountain streams in Taiwan also experience both monsoon storms (March–May) and desiccation in drought years. Moreover, Taiwan's riparian vegetation is generally evergreen rather than deciduous, but the forests can be severely defoliated during typhoons (Mabry *et al.* 1998). These extreme conditions cause severe changes in riverine flow patterns, nutrient input and food supply to consumers in the mountain streams.

Hapen Creek is located in a nature reserve in north-eastern Taiwan that experiences little human disturbance and is dominated by a fluctuating subtropical climate. Since little data is available from headwater streams in subtropical and tropical regions, Hapen Creek is an excellent system to study in order to improve our knowledge of food web attributes in this type of climate area.

Stable carbon and nitrogen isotope techniques have been extensively used to investigate food web structures of various ecosystems. The techniques can reveal the carbon sources and trophic positions of consumers because different types of primary producers have distinct stable isotope values and the fractionations of carbon and nitrogen isotopes between consumers and their food sources are predictable (Peterson and Fry 1987). Although temporal and spatial variation in δ^{13}C values of primary producers and consumers may occur (Boon and Bunn 1994; Huryn *et al.* 2001), cumulative data have shown no effects of such variations on distinguishing contributions of algae versus vascular plants in many stream ecosystems (Rosenfeld and Roff 1992; Finlay 2001). Food-web studies have repeatedly shown that δ^{13}C values are ~0–1‰ more enriched in consumers than in their diet along the food chain; as a result, δ^{13}C signatures are usually used to trace the carbon sources of the consumers. In contrast, δ^{15}N values show large increments but often within 3–4‰ changes in consumers as compared with that of their diet; therefore, δ^{15}N signature is usually used to estimate trophic positions of consumers (e.g. Peterson and Fry 1987; Vander Zanden and Rasmussen 2001; Post 2002). In addition, feeding experiments have also indicated that the turnover rates of carbon and nitrogen isotopes in response to assimilation of new food were consistent and the stable isotope compositions represented a long-term average in food consumption (e.g. in fish muscle, Hesslein *et al.* 1993). Consequently, the information that this method provides about food actually assimilated by consumers over a long time period is more informative than data based on gut content analyses, which provide only a snapshot of the diet (Pinnegar and Polunin 2000). In addition, a recently developed multiple-source mixing model allows estimation of the relative contribution of each possible organic matter source existing in natural, complicated food webs (Phillips and Gregg 2003; Mantel *et al.* 2004; Phillips *et al.* 2005).

Using stable carbon and nitrogen isotope measurements, we studied the characteristics of the Hapen Creek food web by examining (1) the relative contributions of allochthonous *v.* autochthonous sources to the organic matter flows through consumers, and (2) the trophic relationships between consumers. As part of our examinations of trophic relationships, we identified the predominant feeding guild, its role, and the main feeding mode.

Materials and methods

Study area

The Hapen Creek study site is a third-order mountain stream at ~534 m in elevation (24°46′N, 121°34′E) in Fushan Experimental Forest, northern Taiwan (Fig. 1). According to long-term data, large annual variation occurs in its morphometric and environmental characteristics, especially those correlated with hydrology (Table 1). Typhoons can cause defoliation of the riparian vegetation, erosion of the riverbed and filling in of pools (e.g. Typhoon Nari in September 2001: authors' pers. obs.). Sometimes an unusual drought results in 'no flow' conditions (e.g. July of 1997 and 1998: Chuang *et al.* 2004). Riparian vegetation consists mainly of broadleaf C3 plant trees including

Table 1. Environmental setting of Hapen Creek

Environmental characteristics	Mean	Annual range
Catchment area (ha)	525	
Elevation (m)	534	
Water temperature (°C)^A	18.7	16.5–22.3
Mean width (m)^B	5.8	1.7–10.5
Mean water depth (cm)^B	22.2	2–140
Mean water velocity (m s^{-1})^B	0.52	0–1.32
Percent shading (%)^B	49.8	38.6–57.6
Substrate	Gravel, cobbles	

^{A}Wang 2003; ^{B}Chuang *et al*. 2004.

Scheffera octophylla, *Machilus thunbergii*, *Litsea acuminata* and *Oreocnide pedunculata*. C4 plant grasses, such as *Miscanthus floridulus* and *Setaria viridis*, are also present along the stream bank, but only cover a small area.

Sample collection

Biological and sediment samples were collected from two riffles and two pools within a 500-m reach of Hapen Creek in April 2001. During this time, stream flow was stable and no flood or drought conditions occurred. Because fish swam back and forth between the riffles and pools owing to their close proximity, we combined riffle and pool samples.

Previous studies also indicate that δ^{13}C of algae from riffles and pools are not different in small unproductive streams (Finlay 2004). Litter fall and algal biomass peak during this season (Chang 1998; Wang 2003). We collected algae, particulate organic matter (POM), vascular plants and consumers (detailed compositions in Table 2). Fresh leaves from 17 species of C3 plants and two species of C4 plants were handpicked. In the stream, benthic algae (mainly diatoms) were brushed from rocks and filamentous red algae and green algae were picked by hand. A 1-mm mesh screen was deployed in the stream for 24 h to collect particulate organic matter larger than 1 mm, which was treated as coarse POM (CPOM). For fine POM samples (FPOM), ~10 L of stream water was collected and filtered. Particles larger than 53 μm and smaller than 1 mm were treated as FPOM. Sediment samples were taken from stream substrates and sieved. Retained sedimentary POM larger than 53 μm and smaller than 1 mm was treated as fine benthic particulate organic matter (FBOM). In total, consumers including macroinvertebrate and fish taxa that belonged to 20 'trophic species' (Table 2) (Cohen and Briand 1990) were collected.

Aquatic insects were collected using a 250-μm-mesh Surber sampler (Wildco, Buffalo, NY). Aquatic snails (*Semisulcospira libertine*) were sampled by hand. Crustaceans, including shrimp (*Macrobrachium asperulum*) and crab (*Geothelphusa* spp.), were collected using a seine. Aquatic insects and snails were kept for one day in clean water to allow for gut evacuation. Insects were identified to the lowest taxonomic level possible (Table 2). Terrestrial insects were also collected with a sweep-net. Fish were collected with a portable electroshocker (purchased at a Taiwan market).

All samples were kept on ice in the field and subsequently frozen until ready for stable isotopic analyses. For small insects, several individuals from the same taxa were pooled and treated as a single replicate and the entire body was used for measurement. For larger-sized consumers, specimens were treated individually as replicates and only the muscle was used.

Sample preparation and analysis

All samples were ground into powder, acidified with 1 M HCl to remove inorganic carbonates, rinsed with deionised water and then frozen at −70°C until measured. The combustion of samples and extraction and purification of the resultant CO_2 and N_2 followed the methods of Hsieh *et al.* (2000). The stable isotope ratios of samples were measured with a mass spectrometer (Finnigan Delta Plus, Thermo Fisher Electon Corporation, Boston, MA) and were reported in standard notation as: δX (‰) $= [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$ where X is ^{13}C or ^{15}N and $R = {}^{13}\text{C}/{}^{12}\text{C}$ or $^{15}\text{N}/{}^{14}\text{N}$ respectively. Standard reference materials included Pee Dee belemnite (PDB) for carbon and atmospheric nitrogen for nitrogen. Working standard materials, including NIST 8542 for carbon and IAEA-N2 and IAEA-N3 for nitrogen, were also used. The precision of the measurements was ±0.1‰ for δ^{13}C and ±0.2‰ for δ^{15}N.

Estimation of trophic positions

The δ^{15}N values of primary producers are highly variable, so the δ^{15}N values of primary consumers (aquatic insects and snails in this study) were used as a baseline to estimate the trophic positions of other consumers. The formula adheres to that of Cabana and Rasmussen (1996): trophic position of consumers = [(higher level consumers' δ^{15}N − primary consumers' δ^{15}N)/3.4] + 2, where 3.4 represents an increment in δ^{15}N per each increase in trophic position and +2 represents the trophic position of primary consumers that is one position higher than primary producers, a basal group counted as trophic position 1 (Vander Zanden and Rasmussen 2001; Post 2002). This estimation was used to construct organic matter flows in the Hapen Creek food web.

Mixing models analysis

Two mixing models were used in the present study. One was a two-source linear model using δ^{13}C single isotope signature (IsoError, version 1.04, available at http://www.epa.gov/wed/pages/models/stableIsotopes/isotopes/isoerror1_04.htm) following Phillips and Gregg (2001). It was used to estimate the relative contributions of allochthonous sources (terrestrial C3 plant detritus, CPOM herein) and autochthonous sources (benthic algae) to all consumers (see Table 2) and also was used to examine the relationships of these relative contributions along with the trophic positions of consumers in organic matter flows. The other was a multiple-source mixing model using both δ^{13}C and δ^{15}N isotope signatures. This model analysed three to six potential food sources for a given consumer and estimated their respective contributions to that consumer's diet (IsoSource, version 1.2, available at http://www.epa.gov/wed/pages/models/stableIsotopes/isosource/isosource.htm) (Phillips and Gregg 2003). In the present study, all possible

Table 2. The composition of trophic species, trophic positions, and algal contribution (%) to the food web of Hapen Creek

Trophic species (taxa or group)	No. of replicates	Trophic group	Trophic position	Percent algal contribution	
				Mean	s.e.
Primary sources					
Diatom and filamentous green algae (Benthic algae)	6		1		
Red alga (*Batrachospermum* sp.)	3		1		
Terrestrial C3 plants	17		1		
Terrestrial C4 plants	2		1		
Coarse particulate organic matter (CPOM)	4		1		
Fine particulate organic matter (FPOM)	4		2.1	12.4	8.3
Fine benthic organic matter (FBOM)	10		2.8	42.1	6.9
Primary consumers					
Aquatic snails (*Semisulcospira libertina*)	3	Scrapers	2	100.0	16.7
Crane flies (Diptera: Tipulidae, *Antocha* spp.)	2	Scrapers	2	75.7	10.4
Water pennies (Coleoptera: Psephenidae)	2	Scrapers	2	61.3	8.4
Mayflies (Ephemeroptera: Baetidae, Heptageniidae)	3	Collectors	2	46.0	6.3
Other small dipterans	1	Collectors	2	43.0	9.1
Caddisflies (Trichoptera: Stenopsychidae)	4	Collectors	2	13.4	15.5
Terrestrial insects	23	Herbivores	2	0.0	
Predatory insects					
Stoneflies (Plecoptera: Perlidae)	3	Omnivores	2.5	25.8	10.0
Damselflies (Odonata: Euphaeidae)	4	Omnivores	2.6	43.8	10.3
Dobsonflies (Megaloptera: Corydalidae)	2	Omnivores	2.6	60.7	5.7
Watersnipe flies (Diptera: Athericidae)	2	Omnivores	2.7	59.8	5.7
Crane flies (Diptera: Tipulidae, *Hexatoma* spp.)	2	Omnivores	2.9	78.3	9.9
Next-to-the-top consumers					
Crabs (*Geothelphusa* spp.)	4	Omnivores	3.2	58.1	10.0
Minnows (Pisces, Cyprinidae: *Varicorhinus barbatulus*)	3	Omnivores	3.3	84.9	6.7
River loaches (Pisces, Homalopteridae: *Crossostoma lacustre*)	3	Omnivores	3.3	64.1	8.9
Shrimps (*Macrobrachium asperulum*)	5	Omnivores	3.5	100.0	12.0
Top consumers					
Gobies (Pisces, Gobiidae: *Rhinogobius candidianus*)	3	Omnivores	3.7	36.0	15.0
Loaches (Pisces, Cobitididae: *Cobitis sinensis*)	3	Omnivores	3.7	78.2	8.2
Water scorpions (*Laccotrephes* sp.)	2	Omnivores	3.8	100.0	8.6
Chubs (Pisces, Cyprinidae: *Candidia barbata*)	8	Omnivores	3.9	58.1	6.5

combinations of contributions from each source were examined in 1% increments, with contribution rates ranging from 0% to 100%. Tolerance was initially set at 0.1‰, which was an indication of feasible solution (Phillips and Gregg 2003). It increased to greater values when the isotope values of consumers were out of bounds of polygons enclosing all possible food sources of target consumers. This was the case for loach and shrimp for which the tolerance was increased to 1.0‰ and 1.2‰ respectively. Whenever the isotope values of consumers could not be enclosed in a polygon and no possible solutions could be computed, the two-source linear model was used.

Although many studies reported an enrichment of 0–1‰ in δ^{13}C and 3–4‰ in δ^{15}N in consumers' tissue as compared with that of their food sources (Peterson and Fry 1987; Vander Zanden and Rasmussen 2001; Post 2002), some studies showed that these fractionations differed according to the type of consumer tissue being analysed (e.g. muscle, bone or whole body), the food type consumed (e.g. plant, invertebrates or vertebrates) and the type of linked trophic position (Kelly 2000). Thus, proper corrections in δ^{13}C and δ^{15}N fractionation values need to be made before estimating the contributions of food sources to consumers (McCutchan *et al.* 2003).

Based on literature records and our own observations, we applied different fractionation values for different trophic shifts in the Hapen food web. A +0.8‰ fractionation in δ^{13}C signature was used for crustaceans, fish and water scorpions owing to measures being made on their muscle tissue (Vander Zanden and Rasmussen 2001). However, −0.2‰ fractionation in δ^{13}C was used for most aquatic insect consumers because their whole bodies were acidified before analyses (McCutchan *et al.* 2003). To adjust δ^{15}N shifts, a +3.4‰ fractionation value was used for crustaceans, fish and water scorpions (Vander Zanden and Rasmussen 2001). However, fractionations have been shown to be lower for predatory insects than for primary consumer insects when they have vascular plant or algal diets; therefore, +1.4‰ fractionation was applied to the former and +2.2‰ to the latter (McCutchan *et al.* 2003).

In food web studies, lumping sources in the same trophic guild and/or taxon allows inferences to be made about the dietary importance of a logically defined aggregate of food sources (Phillips *et al.* 2005). In the present study, aquatic insects were divided into primary insects and predatory insects when analysing their contribution to the food sources of higher order consumers (i.e. crustaceans, fish and water scorpions).

Although red algae and C4 plants were sampled from Hapen Creek, they were not included in source model analyses for several reasons. First, neither was common at this study site. Second, previous studies showed C3 plants were the major allochthonous sources (Chang 1998). Third, we did not find red algae in fish gut analyses (Huang 2002). Although red algae (*Batrachospermum* sp.) may be incorporated into aquatic insects cases (e.g. larvae of caddisflies and chironomids), larvae were never observed to consume red algae in a controlled laboratory study (Keiper *et al.* 1998). In addition, feeding experiments with shredder insects showed a distinct preference for C3 over C4 species and stable isotope analysis also showed lack of assimilation of C4 carbon by these shredders (Clapcott and Bunn 2003). Fourth, owing to their great deviation from expectations in δ^{13}C fractionation for any Hapen Creek consumers, the multiple-source mixing model would produce no solution if we included red algae and C4 plants in the model. Together, these results suggested limited contribution of red algae and C4 carbon to aquatic food webs.

Autochthonous v. *allochthonous contributions to organic matter flows*

The contribution of autochthonous *v.* allochthonous organic matter was assessed by plotting each consumer's trophic position on the vertical axis against its location on a gradient of increasing autochthonous contributions to the given consumer's food on the horizontal axis. This gradient was expressed as a percentage (Table 2). The two-source linear model was used to estimate the consumers' locations on this gradient. Consumers were grouped into six assemblages based primarily on their trophic positions and carbon sources (see Fig. 3). In the flow pathways between assemblages, the contribution of a given food source assemblage to its consumer assemblage was expressed as an average of the mean percent contributions estimated by the multiple-source mixing model.

Statistical analysis

Differences in the values of primary producers and particulate organic matter were compared using one-way non-parametric ANOVAs. A Wilcoxon two-sample test using a normal approximation for two-sample comparisons and a Kruskal–Wallis test using a χ^2 approximation for more than two sample comparisons were performed (Zar 1984). All significant levels were set at $P = 0.05$.

Results

Stable isotopic compositions of primary producers

Primary producers, namely C3 and C4 plants, red algae and benthic algae, exhibited δ^{13}C values that were distinct from one another (Fig. 2) ($P < 0.001$). Among autochthonous sources, filamentous green algae (*Spirogyra* spp.) and diatoms (mainly *Gomphonema parvulum*, *Navicula decussis* and *Achnanthes lanceolata*) were ^{13}C enriched (−23.3‰ to −22.5‰), compared with red algae (*Batrachospermum* sp.), which was the most ^{13}C depleted (−37.4‰). Among vascular plants, C3 plants were depleted (−30.6‰) and C4 plants were highly ^{13}C enriched (−12.4‰). The δ^{15}N values of primary producers were indistinguishable from one another (−2.6‰ to −1.4‰, $P = 0.84$). Moreover, δ^{13}C values of filamentous green algae and diatoms were −23.3‰ and −22.5‰ and their δ^{15}N values were −2.6‰ and −1.4‰. Since both filamentous green algae and diatoms had similar δ^{13}C and δ^{15}N values, they were combined and treated as 'benthic algae' in the present study.

Stable isotopic compositions of particulate organic matter (POM)

Isotope values of CPOM averaged −30.3‰ in δ^{13}C and −3.7‰ in δ^{15}N and did not significantly differ from those of fresh leaves collected from riparian C3 plant species (for δ^{13}C, $P = 0.34$; for δ^{15}N, $P = 0.11$), thus indicating that the CPOM was mainly derived from terrestrial C3 plants. Isotope values of FPOM were −28.0‰ in δ^{13}C and −0.3‰ in δ^{15}N, significantly differing from those of C3 plants (for δ^{13}C, $P = 0.003$; for δ^{15}N, $P = 0.01$). However, FPOM isotope values were closer to those of C3 plants than to algae, indicating that C3 plants may have contributed more to FPOM than algae.

Compared with CPOM and FPOM, isotope ratios of benthic fine POM (FBOM) were significantly more enriched (for δ^{13}C, $P = 0.001$; for δ^{15}N, $P = 0.001$). These values were also greater than those of C3 plants (for δ^{13}C, $P < 0.0001$; for δ^{15}N, $P = 0.0001$) and fell approximately in the middle between those of benthic algae and FPOM. This suggests that the FBOM carbon sources were a mix of both allochthonous and autochthonous substances, whereas its nitrogen sources might have contained some δ^{15}N-enriched organisms such as bacteria and meiofauna.

Stable isotopic compositions of consumers and trophic positions

Macroinvertebrates exhibited δ^{13}C values ranging from a minimum of −29.5‰ for collectors' caddisflies to a high of −20.8‰ for prawns (Fig. 2). The primary consumers had δ^{15}N values averaging −0.6‰, with trophic positions numbered 2. These consumers were composed of snails and other aquatic insects (Fig. 2, Table 2). Predatory insects had δ^{15}N signatures that averaged 1.1‰, a value 1.7‰ greater than those of primary consumers. Their trophic positions numbered from 2.5 to 2.9.

Consumers such as minnows, river loaches, crabs and shrimps had δ^{15}N values that averaged 4.0‰ and their trophic positions ranged from 3.3 to 3.5 (Table 2). They were regarded as the next-to-the-top consumers. Top consumers, including gobies, loaches, water scorpions and chubs, had maximum δ^{15}N values that averaged 5.4‰ and their reported trophic positions ranged from 3.7 to 3.9 (Table 2). Chubs had the most enriched δ^{15}N signature and occupied the topmost position in the Hapen Creek food web.

With respect to terrestrial insects, the average of their δ^{13}C values was −25.8‰ and ranged from −31.6‰ in ladybugs and

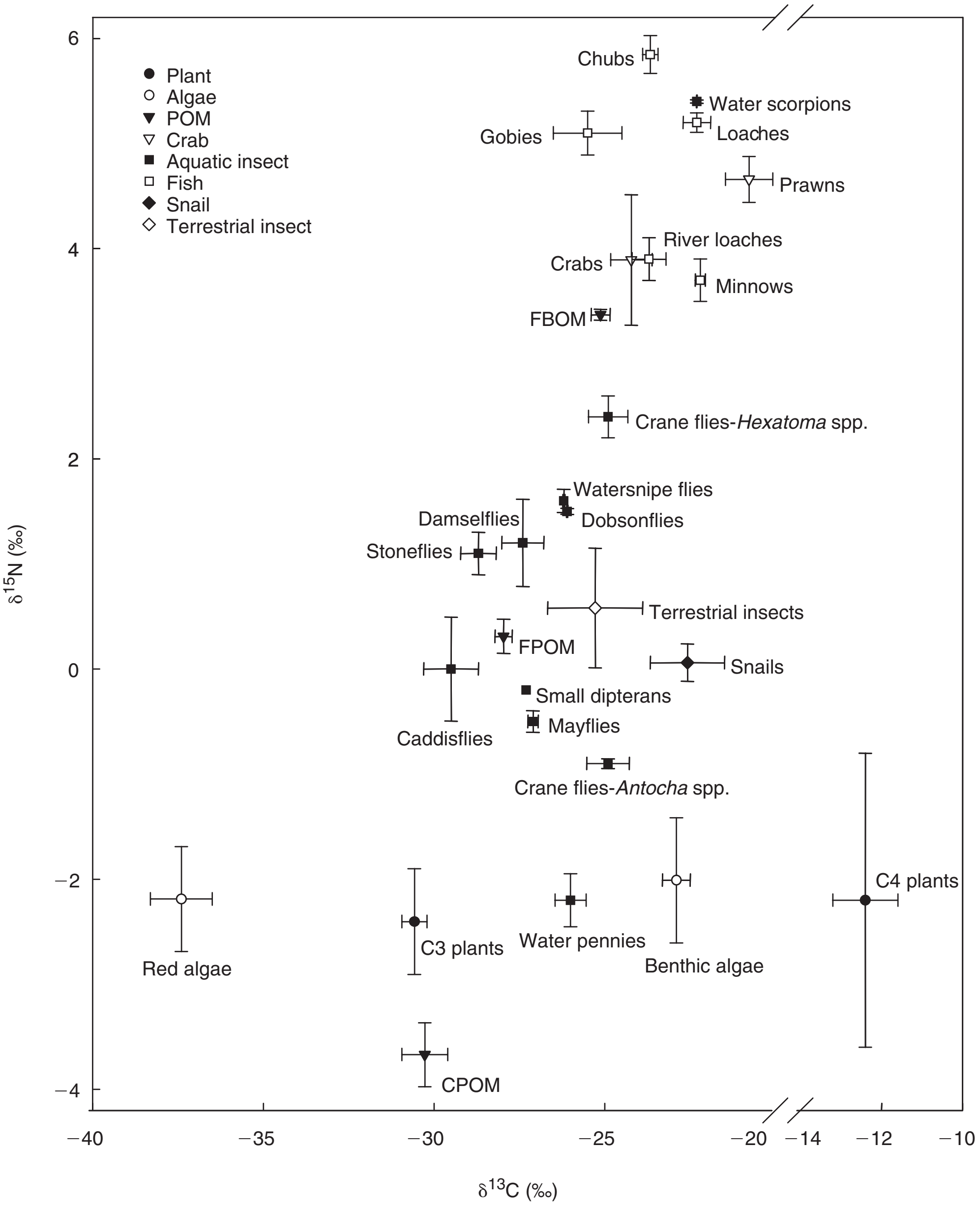

Fig. 2. Stable carbon and nitrogen isotope values of primary food sources and consumers in Hapen Creek.

caterpillars to −16.7‰ in scarabs, whereas their $\delta^{15}N$ values averaged 0.6‰, with ranges from −1.3‰ in grasshoppers to 3.5‰ in some unidentified dipterans (Fig. 2).

Potential food sources of consumers

The food–consumer relationships based on the mixing models are listed in Tables 3–5. The model suggests that CPOM and benthic algae were significant contributors to primary consumers, whereas FPOM was relatively minor. For example, caddisflies appeared to have obtained more carbon from CPOM than from benthic algae. Mayflies and other small dipterans appeared to assimilate both CPOM and benthic algae. In contrast, snails, crane flies (*Antocha* spp.) and water pennies appeared to take more carbon derived from benthic algae (Table 3).

Among predatory insects, stoneflies appeared to rely more on caddisflies. Damselflies were likely to feed on dipterans and a mix of caddisflies and mayflies. Dobsonflies and watersnipe flies had similar diets and consumed FPOM more frequently. Crane flies (*Hexatoma* sp.) ate snails with a mix of FBOM (Table 4). The predatory insects secured ~40% of food from the collector insects (Fig. 3).

Snails were the major contributor to the next-to-the-top consumers (Table 5). Crabs and minnows additionally assimilated a little FBOM, whereas river loaches were also supplemented by a mix of predatory insects (Table 5).

Table 3. Percent contributions (%) of basal food sources to primary consumers in Hapen Creek calculated by the multiple-source model (IsoSource) and expressed as mean with 1–99 percentile range in parentheses

FPOM and CPOM: fine and coarse particulate organic matter respectively

Consumers	Food source		
	CPOM	FPOM	Benthic algae
Aquatic snails[A]	0.0 (16.7)	–	100.0 (16.7)
Crane flies[A]	24.3 (10.4)	–	75.7 (10.4)
Water pennies[A]	38.7 (8.4)	–	61.3 (8.4)
Other dipterans	46.0 (45–47)	15.8 (15–17)	38.2 (38–39)
Mayflies	50.0 (50–50)	6.0 (6–6)	44.0 (44–44)
Caddisflies	61.8 (61–63)	35.8 (35–37)	2.4 (2–3)

[A] Calculated by the two-source linear model (IsoError) (mean with stand error in parentheses).

Among consumers at the top trophic position, loaches and gobies utilised FBOM; however, loaches' diet was mixed with rather abundant benthic algae, in contrast to that of gobies, which was mixed with primary and predatory insects. Water scorpions preferred snails and also consumed a mix of river loaches and minnows. The topmost predator, chubs, mainly utilised crabs and, to a lesser extent, a mix of predatory insects, terrestrial insects and snails (Table 5).

In addition to snails, diverse food sources were found in the diet of the next-to-the-top and the top consumer assemblages. FBOM contributed nearly one quarter (23.7%) of the diet for the top consumer group. Organic matter flows from terrestrial insects to the top consumer assemblage also occurred; however, the degree was low, at only 3.1% (Fig. 3).

Autochthonous v. *allochthonous contributions to organic matter flows*

According to their trophic positions and tendencies to use certain carbon sources (Table 2), consumers were differentiated into six assemblages and each served a different role in transferring organic matter in the food web (Fig. 3, Table 6). All consumer assemblages gained organic matter directly from benthic algae, although in various magnitudes (1.6–100%). By contrast, only two consumer assemblages, the scraper assemblage and the collector assemblage, gained organic matter directly from CPOM (31.5–52.6%), revealing a utilisation preference for autochthonous sources (Fig. 3).

Discussion

Characteristics of the food web of Hapen Creek

The results of the present study reveal the characteristics of a small headwater food web that contribute to our knowledge of food web structure in a subtropical region about which little is currently known. Dominant features of the Hapen Creek food web are as follows. Its carbon sources are derived from both autochthonous and allochthonous materials, with contributions varying according to the pathways. Among these pathways, autochthonous flows appear to be more prevalent. Snails play a major role in transferring autochthonous organic materials and aquatic insects transfer allochthonous C3 plant detritus. As for detrital organic matter, it is the finer portions, in particular FBOM, that are readily accessed by consumers at higher trophic positions such as crabs and gobies. In addition, terrestrial insects are another allochthonous source. Furthermore, the feeding mode is predominately omnivory.

Contributions of autochthonous and allochthonous carbon sources varying with pathways

In Hapen Creek's food web, discrepancies in the roles that autochthonous and allochthonous carbon sources play were identified. In general, autochthonous organic matter can flow through consumers at all different trophic positions. Consumers at high trophic positions accessed this source more easily and readily than might be expected, as seen in the assimilation of benthic algae directly by loaches or indirectly through snails to minnows and river loaches. By contrast, the allochthonous source must be processed first either by assimilation of collector and scraper insects or by transformation into finer particles such as FPOM and FBOM before it becomes available to consumers at higher trophic positions.

The importance of autochthonous benthic algae (diatom and filamentous green algae) seen in the Hapen Creek's organic matter flows differs from that of allochthonous C3 plant detritus predicted and reported for headwater streams with dense canopies in temperate regions (e.g. Vannote *et al.* 1980; Rosemond 1994; Finlay 2001). This discrepancy may be correlated with climatic conditions and the riparian coverage. Higher water temperature and more irradiation can accelerate algal production (Rosemond *et al.* 2001; Kishi *et al.* 2005) and a study in a subtropical stream has recorded that shading was an over-riding factor and had negative impact on periphyton biomass (Mosisch *et al.* 2001). In a relatively unshaded tropical stream, algae rather than allochthonous C3 plant detritus were the predominant carbon contributor to consumers (Brito *et al.* 2006). High discharge and severe defoliation caused by monsoon storms and typhoons may provide Hapen Creek with a wider and more open canopy (50%) than seen in temperate streams with similar watershed area (canopy cover >90%) (see review by Finlay 2001). Moreover, the water temperature ranges from 15°C to 22°C (Wang 2003), which provides warmth and allows penetration of sunlight, thus favouring algal growth and subsequently enhancing its role in this creek's food web. Use of benthic algae in Hapen Creek is consistent with what we would expect from a river subject to a warmer climate and greater sunlight exposure.

In tropical and subtropical areas, algae have been reported as a more important source than C3-plant-derived particulate organic matter even though the latter comprised the major portion of the available carbon pool (Venezuela: Lewis *et al.* 2001; Puerto Rico: March and Pringle 2003; Hong Kong: Mantel *et al.* 2004; Brazil: Brito *et al.* 2006; this study). Consumers may prefer algal materials to leaf litter owing to its higher nutritive value and digestibility. Food with lower carbon and higher nitrogen content provide higher quality for consumers (Elser *et al.* 2000). Nutritional analyses also revealed that algae possess higher levels of proteins and energy and lower levels of fibre than plant litter (Forsberg *et al.* 1993). Dietary protein and energy content were found to affect fish's ingestion and growth (Forsberg *et al.* 1993;

Table 4. Percent contributions (%) of potential food sources to predatory aquatic insect consumers in Hapen Creek
Values were expressed as mean with 1–99 percentile range in parentheses

Consumers	Food source							
	FPOM	FBOM	Benthic algae	Crane flies	Mayflies	Dipterans	Caddisflies	Snails
Stoneflies	0.2 (0–1)	–	3.5 (0–13)	7.5 (0–21)	19.8 (0–43)	–	68.9 (56–81)	–
Damselflies	13.4 (4–19)	–	7.8 (0–25)	11.2 (0–36)	20.8 (0–65)	25.8 (0–80)	21.1 (0–46)	–
Dobsonflies	36.1 (21–53)	–	11.4 (0–36)	10.8 (0–35)	10.6 (0–34)	13 (0–42)	–	18.1 (20–31)
Watersnipe flies	41.5 (28–57)	–	10 (0–32)	9.3 (0–30)	9.1 (0–29)	11.3 (0–37)	–	18.8 (4–30)
Crane flies (*Hexatoma*)	8 (0–26)	25.5 (17–33)	–	13.3 (0–43)	8 (0–26)	8 (0–26)	–	37.2 (18–49)

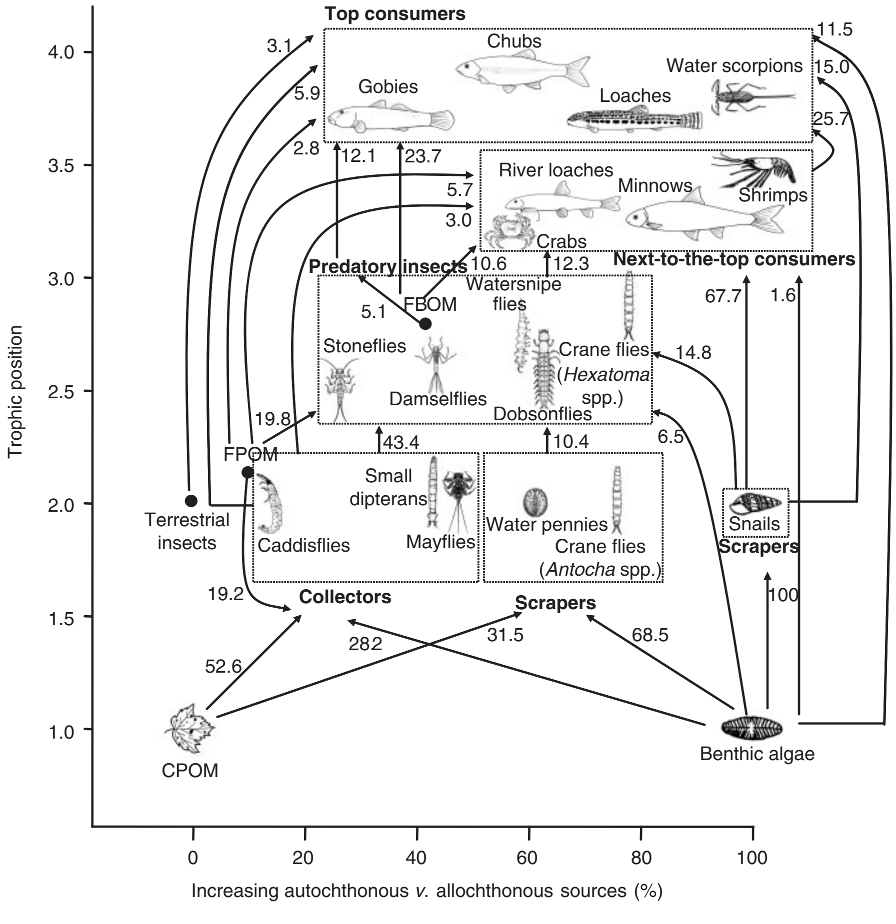

Fig. 3. Trophic interactions and organic matter flows in the food web of Hapen Creek. Each consumer assemblage in the food web is plotted by its trophic position against its position along a food source gradient that is expressed by the relative contributions (%) of allochthonous *v.* autochthonous origins. Arrows indicate a flow from a food source to a consumer assemblage. Values associated with the arrows depict the percent contribution of a given food source to a given consumer assemblage's diet and were calculated as the average of mean contribution to each consumer in that given consumer assemblage according to the estimations of multiple-sources mixing model. Standard deviations associated with means are listed in Table 6 (see also 'Materials and methods').

Bowen *et al.* 1995). Additionally, feeding experiments in crayfish exhibited greater assimilation efficiencies on filamentous algae (39%) than on detritus (14%) (Whitledge and Rabeni 1997). Detritivore insects (*Sericostoma personatum*) that ate algae had the greatest increases in fat, resulting in a higher growth rate than those that had to feed on macrophyte or litter (Friberg and Jacobsen 1999). Diatoms in Hapen Creek had a C:N ratio (6.55) similar to that found in fish (6.36) and aquatic insects (4.99), but

Table 5. Percentage contributions (%) of potential food sources to the next-to-the-top and the top consumers in Hapen Creek

Values are expressed as mean with 1–99 percentile range in parentheses

Consumers	Food source									
	Benthic algae	FPOM	FBOM	Primary insect	Predatory insect	Terrestrial insect	Snail	Crab	Minnow	River loach
Crabs	–	13.6 (0–37)	28.1 (12–41)	8.2 (0–23)	11.2 (0–30)	–	38.8 (33–48)	–	–	–
Minnows	6.2 (0–12)	–	11.5 (8–15)	2.5 (0–5)	–	–	79.8 (73–87)	–	–	–
River loaches	–	8.7 (2–16)	–	5.6 (0–11)	29.4 (26–32)	–	56.3 (55–58)	–	–	–
Shrimps	–	0.6 (0–3)	2.6 (0–7)	0.2 (0–2)	0.5 (0–3)	–	96 (93–100)	–	–	–
Gobies	–	11.3 (0–23)	41.2 (31–51)	23.7 (21–27)	23.7 (1–48)	–	–	–	–	–
Loaches	46 (46–47)	–	53.5 (53–54)	–	0.3 (0–1)	–	–	–	–	–
Water scorpions	–	–	–	–	8.6 (2–17)	–	42.9 (37–48)	–	24.6 (8–45)	23.8 (1–42)
Chubs	–	–	–	–	15.9 (4–24)	12.5 (1–29)	17.1 (10–22)	54.5 (53–57)	–	–

Table 6. Average contribution (%) of potential food sources to the functional feeding assemblages of consumers in Hapen Creek

Values are expressed as mean with standard deviation in parentheses. N showed the numbers of consumers in that assemblage

Consumer		Food source									
	N	CPOM	FPOM	FBOM	Benthic algae	Collectors	Scrapers (insects)	Scrapers (snail)	Predatory insects	Terrestrial insects	Next-to-the-top consumers
Collectors	3	52.6 (8.2)	19.2 (15.2)	–	28.2 (22.5)	–	–	–	–	–	–
Scrapers (insects)	2	31.5 (10.2)	–	–	68.5 (10.2)	–	–	–	–	–	–
Scrapers (snail)	1	0 (indefinite)	–	–	100.0 (indefinite)	–	–	–	–	–	–
Predator insects	5	–	19.8 (18.0)	5.1 (11.4)	6.5 (4.7)	43.5 (32.8)	10.4 (2.2)	14.8 (15.5)	–	–	–
Next-to-the-top consumers	4	–	5.7 (6.6)	10.6 (13.2)	1.6 (3.1)	3.0* (3.5)	–	67.7 (25.2)	12.3 (13.8)	–	–
Top consumers	4	–	2.8 (5.7)	23.7 (27.8)	11.5 (23.0)	5.9* (11.9)	–	15.0 (20.3)	12.1 (10.0)	3.1 (6.3)	25.7 (29.8)

Values with * indicated contributions from primary consumer insects including collectors and scrapers.

differed greatly from CPOM (38.0) (Huang 2002). These abovementioned data all reveal that algae have higher nutritive value than plant litter; as a result, this food source would benefit the majority of the consumers in Hapen Creek.

Utilisation of allochthonous detritus and terrestrial insects

In Hapen Creek, C3-plant-derived organic matter was utilised in the form of fine POM (e.g. by dobson flies and watersnipe flies) and fine benthic POM (e.g. by loaches and gobies). A similar phenomenon was also seen in the rivers in Tennessee (Mulholland *et al.* 2000) and Hong Kong (Mantel *et al.* 2004). The higher δ^{15}N values of FPOM and FBOM recorded in this study suggest that these detrital materials were colonised by some ^{15}N-enriched organisms such as bacteria and meiofauna. Studies in several headwater streams have shown that consumers at higher trophic positions were supported by bacteria-associated amorphous detrital particles (North Carolina: Hall and Meyer 1998), whereas larger predators benefited from meiofauna-associated food particles (south-east England: Schmid-Araya *et al.* 2002).

Allochthonous substances can also enter the Hapen Creek food web through other pathways (see Fig. 3) For instance, chubs can prey upon terrestrial insects (also confirmed by gut content analysis: Huang 2002) because of an upwardly opening mouth capable of catching terrestrial insects that accidentally fall into the stream. Experimental manipulation studies in forested headwater streams have also demonstrated that predatory fish gain important subsidies from riparian arthropods (e.g. Nakano *et al.* 1999).

Importance of aquatic insects and snails in transferring organic matter

Although the constituent species of the invertebrate group may vary from stream to stream, their profound effects on organic matter transfers, especially those from aquatic insects, have been extensively documented in temperate and some tropical stream food webs (e.g. Fisher *et al.* 2001; Mantel *et al.* 2004). In the Hapen Creek food web, the heaviest flows of organic matter occur not only through aquatic insects but also through snails. In addition, the pathways to transfer C3-plant-derived POM appear to be more divergent than those for transferring algae (see Fig. 3) because different sized POM were processed by different trophic guilds. For transferring coarse POM, collector mayflies, some small dipterans and caddisflies serve as major pathways, whereas scraper water pennies are less important in this respect. Mayflies and small dipterans are also the most diverse and most abundant taxa in this headwater stream (S. H. Shieh, pers. comm.). As a flow conductor for finer POM, predatory insects including dobsonflies, watersnipe flies and crane flies served as the main paths. Although fewer pathways present to transfer fine POM to higher trophic ordered consumers, flows to fish gobies and loaches were obvious (see also Tables 3–5). The significance of aquatic insects in transferring POM was also recorded in other studies. For example, in a tropical stream in Hong Kong, the Chironominae accounted for transferring finer POM, whereas several mayflies and chironomids worked together to pass on coarser POM in the food web (Mantel *et al.* 2004). In temperate streams, the shredder group served the same function (Finlay 2001).

With respect to the transfers of benthic algal organic matter to higher trophic ordered consumers in this study creek, the snail *Semisulcospira libertina* along with river loaches, minnows and shrimps provide rather prominent contributions (averaging 67.7%, see Fig. 3). Even in the top consumer assemblage, water scorpions and loaches also benefit from the snails' transfers (15.0%). Although snails have hard shells, several consumers can feed on them with specific structures. For example, minnows and chubs have pharyngeal teeth that can grind shells. The scorpion is a suctorial predator that has a pair of pincer-like legs and a stinging mouth apparatus for capturing and piercing prey; thus, it is capable of consuming hard-shelled snails and animals larger than itself. However, snails appear to be inedible for predatory insects, which lack competent feeding apparatus; therefore, their contribution to predatory insects probably is overestimated by the multiple mixing model.

The important role that snails and aquatic insects play in transferring algal organic matter has also been recorded in other studies. In a small tropical stream, the snail *Bortia* transported periphyton to top consumers such as shrimps and fishes, whereas the mayfly *Habrophlebiodes* transported filamentous algae to them. During the wet season, this snail constituted over 80% of the diet of shrimps (in Hong Kong: Mantel and Dudgeon 2004). Snails were also identified as an important energy source for crayfishes (in New Zealand: Parkyn *et al.* 2001).

Omnivorous feeding strategy in a fluctuating habitat

Multiple mixing model estimates showed that the predatory insects of Hapen Creek fed between two trophic levels. Similarly, consumers at higher trophic positions had diets from three different trophic levels. Our finding agrees with several recent studies in temperate and tropical food webs that showed omnivory as the predominant guild (Tavares-Cromar and Williams 1996; Evans-White *et al.* 2001; Mantel *et al.* 2004; Lancaster *et al.* 2005). The benefit of omnivory is supported by experimental evidence. For instance, less variation occurs in population sizes, as compared with those of non-omnivorous species (Morin and Lawler 2001). When considering the nutrients and energy that consumers can get, omnivory may be a compromise strategy that allows consumers to gain protein from scarce animal preys while also securing energy from abundant primary foods (Bowen *et al.* 1995). Omnivory has also been considered adaptive to a fluctuating food supply (Beaudoin *et al.* 2001). Hapen Creek is subject to natural disturbances such as typhoons, which increase the likelihood that certain food sources will become inaccessible and others become more available. Under these conditions, omnivory allows consumers have more trophic plasticity to utilise alternative food sources and avoid starvation.

Summary

As a small and partly shaded subtropical headwater, the Hapen Creek food web is fuelled by both autochthonous and allochthonous organic matter, with the former source being more readily available to consumers at higher trophic positions. The former was transferred in the food web mainly by the snail *Semisulcospira libertina* and the latter flowed through aquatic insects as well as fish groups according to POM size fractions. Coarse fractions were predominantly transferred by the collector insects such as mayflies and some small dipterans whereas fine fractions were mainly transferred by predatory insects including dobsonflies, watersnipe flies and crane flies. Fine fractions also flowed directly to gobies and loaches at the top trophic position. Omnivory appears to be a common feeding mode in the Hapen Creek food web, presumably a result of being a feeding strategy adaptive to a changing environment

Because we only sampled during one season, data collected from different seasons, including the typhoon season, would enhance our knowledge about the advantages and disadvantages of the omnivorous feeding strategy as well as about how climatic regime affects a subtropical stream food web. In addition, the inclusion in future studies of bacteria and meiofauna in food web analyses would deepen our understanding of organic matter flow in the food webs, particularly in flows related to C3 plant detritus.

Acknowledgements

The authors thank Ling-Chuan Chuang and Chi-Chang Liu for their assistance in field collections and Sen-Her Shieh and Chorng-Bin Hsu for aquatic insect collection and identification. We also thank Drs. Jacques C. Finlay and Shuh-Ji Kao and the abovementioned colleagues for valuable discussions on stream dynamics. We are grateful to two anonymous referees for valuable comments on the manuscript. This research was supported by a grant (NSC90–2621-B-002–007) from the National Science Council of Taiwan to YSL. The study complies with the current laws of the country in which it was performed.

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Manuscript received 18 July 2006, accepted 11 April 2007