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Foodweb structure in a tropical Asian forest stream

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Abstract. A food web based on the gut contents of consumers (invertebrates and fishes) in pools of Tai Po Kau Forest Stream (TPKFS), Hong Kong (southern China), indicated the importance of periphyton and fine organic particles; coarse particulate organic matter was a less important food source despite its higher relative abundance in this shaded hillstream. Stable isotope analysis of consumer tissues was undertaken to confirm this result. IsoSource software was used to model n -isotope and $>n + 1$ -sources, so that the relative contribution of the potential food sources could be determined. Results of an IsoSource mixed model of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures of primary consumers generally supported evidence from gut content analyses about the importance of autochthonous resources. Inconsistencies between the results of gut content analysis and isotope signatures of consumer tissues occurred in a few cases but could be explained either by small sample size or the wide range of feasible solutions provided by the isotopic mixed model. Both techniques were needed to resolve the trophic position of omnivores. For instance, the gut contents of balitorid loaches indicated that they were primarily herbivorous but their stable isotope signatures revealed a significant dependence on animal food.

Considerable overlap in the diets of predatory fishes and invertebrates (odonates, perlid stoneflies, palaemonid shrimps) was confirmed by both gut contents and stable isotope analyses. This finding, along with a lack of intraguild predation, resulted in a short mean and maximum foodchain length, high links per species, and high connectance for the TPKFS food web when compared with literature reports of other stream food webs. Periods of spate-induced disturbance during the wet season and limited algal productivity in TPKFS might also have contributed to the short food chains. Inconsistent levels of resolution for different taxonomic groups within the food web may have generated artefacts of low linkage complexity, high predator–prey ratio, and a small number of basal and intermediate species, a pattern that has been confirmed for stream food webs elsewhere. Our study is the first example of a food web based on complementary analyses of gut contents and stable isotope signatures for any tropical stream. This combined approach is recommended for future studies of food webs, especially in habitats where omnivores are an important component of the community.

Key words: Tai Po Kau Forest Stream, gut contents, stable isotope signatures, allochthonous, autochthonous, foodchain length, connectance, China.

Studies of food webs generate information on community structure, competition, nutrient dynamics, and cascading effects of predation (Winemiller and Polis 1996). Food webs are most often described on the basis of gut content analyses, which are labor intensive and dependent on the identification skills of the researcher. Bias can arise from variations in the gut clearance time of different prey, greater apparent incidence of prey with sclerotized parts, and difficulty in identifying soft-bodied or easily digested prey (Peckarsky 1996, Hershey and Peterson 1996). Furthermore, gut contents provide only a snapshot of the diet at a particular time and, more importantly, not everything present in the gut is equally assimilated (e.g., Whitedge and

Rabeni 1997, Parkyn et al. 2001, Hollows et al. 2002).

Investigation of the stable isotope signature of consumer tissue allows determination of the relative contribution of different types of food to accumulated biomass because the fractionation of C and N stable isotopes is fairly predictable (DeNiro and Epstein 1978, Minagawa and Wada 1984, Vander Zanden and Rasmussen 2001). The $\delta^{15}\text{N}$ signature of an animal indicates its trophic position because it is enriched by a value of 3 to 5 ‰ with each assimilation. The $\delta^{13}\text{C}$ signature indicates the nature of the food resource, with each assimilation resulting in enrichment by ~1 ‰. However, variation in fractionation values, in food resource signatures, and among individuals within a population can complicate interpretation of trophic interactions (DeNiro and Epstein 1978, Minagawa and Wada 1984, Lancaster and Waldron 2001).

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The alternative, but complementary, approaches of gut content analysis and determination of stable isotope signatures have explained patterns or corrected misconceptions arising from results of stable isotope analysis (Yoshioka et al. 1994, Hart and Lovvorn 2002) or gut contents alone (Evans-White et al. 2001, Parkyn et al. 2001). Although gut content data indicate that food webs of many forested streams are based on allochthonous foods (Yule 1996, Tavares-Cromar and Williams 1996, Hall et al. 2000), stable isotope studies have provided evidence of the importance of autochthonous resources in these habitats (Rosenfeld and Roff 1992, Finlay et al. 2002, March and Pringle 2003, but see Rounick et al. 1982, Hicks 1997). This finding contradicts a prediction of the river continuum concept (RCC) that metabolism of benthic communities in forested upland streams is heterotrophic and shredders that are primarily dependent on coarse particulate organic matter (CPOM) are relatively abundant (Vannote et al. 1980, Minshall et al. 1983). A specific example concerns CPOM in riffles of Tai Po Kau Forest Stream (TPKFS), Hong Kong. Standing stocks exceed periphyton by as much as 100 times (Dudgeon 1982). Nonetheless, Salas and Dudgeon (2001a, 2003) found that production by Ephemeroptera larvae was derived from autochthonous sources during the dry season. There was a slight increase in the allochthonous contribution during the wet season when periphyton biomass was reduced by spates, but the autochthonous contribution remained high. A more recent model, the riverine productivity model (Thorp and DeLong 2002), provides some alternative predictions to the RCC for larger streams (≥ 4 th-order), but it is not clear how this model applies to small (≤ 3 rd-order) forest streams in the tropics.

Food webs in aquatic environments generally have short food chains with 3 to 4 links, consistent predator-prey ratios, and scale-independent proportions of top, intermediate, and basal elements (Hall and Raffaelli 1993, but see Schmid-Araya et al. 2002a). Foodchain length in 2-dimensional environments, such as lake bottoms, streambeds, or the rocky intertidal is shorter than that in 3-dimensional habitats such as open-water pelagic systems (Briand and Cohen 1987, Bengtsson 1994). Food webs in small streams are, however, distinct from those in lakes and large rivers: they have higher connec-

tivity, a higher proportion of generalists, and are shorter and wider, i.e., have a greater proportion of herbivores and top species along with a higher number of top links (Briand 1985). Furthermore, higher levels of disturbance and lower algal productivity lead to reduced species number, lower numbers of links per species, and lower mean chain length in stream food webs (Jaarsma et al. 1998, Townsend et al. 1998, but see Post 2002). These web properties have no correlation with detrital standing stock (Townsend et al. 1998) but web properties vary with the taxonomic resolution of consumers (i.e., species, genus, or family), and higher connectance is characteristic of webs constructed at the family level (Lancaster and Robertson 1995, Thompson and Townsend 2000). In addition, discrepancies in the levels of taxonomic resolution among groups within the web (e.g., greater taxonomic resolution for macroinvertebrates and fishes than for basal food resources) lowers the value of foodweb parameters compared to food webs based on equally high resolution for all consumers and food resources (Thompson and Townsend 2000). These discrepancies confound comparison of food webs among studies, an exercise that is also affected by the tendency of foodweb properties to vary with season (Thompson and Townsend 1999, Schmid-Araya et al. 2002b).

Our study had 4 main objectives: 1) to quantify the level of basal resources (CPOM, fine particulate organic matter [FPOM], and periphyton) in TPKFS pools during the dry season when abiotic disturbance by spates is infrequent; 2) to determine the dry season foodweb structure of stream communities in pools by gut content analysis to assess the relative importance of autochthonous versus allochthonous food sources; 3) to verify results of gut content analysis and foodweb structure by investigation of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures of consumers, and to attempt to resolve any discrepancies between the results of the 2 techniques; and 4) to determine the structural properties of a dry season food web and compare them with published accounts of stream food webs.

Methods

Study site

Samples were collected from TPKFS, a forested stream in the Central New Territories, Hong

Kong SAR, China. TPKFS is a perennial stream situated in Tai Po Kau Nature Reserve, a managed forest on the southwest side of Tolo Harbour. It is an unpolluted stream originating ~400 m above sea level (asl) and draining secondary forest. The trees are a mixture of native and introduced species (Mantel 2003). The collection site is located at 200 m asl (UTM grid reference 50Q KK095822) and is a 3rd-order stream. Stream width is ~8 m during the dry season and 12 m at bankfull during the wet season. The substrate is poorly sorted, ranging from sand to large boulders. The waters are acid (pH 5.5–6.5), soft (conductivity 28–46 $\mu\text{S}/\text{cm}$), and well-oxygenated (83–95% saturation). The stream experiences a strongly seasonal discharge regime, as occurs in other streams and rivers in monsoonal Asia, and this dominant environmental factor influences benthic communities (Dudgeon 1995). Detailed information on TPKFS is given by Dudgeon (1992 and references therein) and Mantel (2003). All samples of food resources and consumers were collected from 3 pools in TPKFS over 2 dry seasons (1999 and 2001). The surface area of each pool was 30 to 50 m^2 .

Basal food resources

Samples of basal food resources for stable isotope analysis and biomass estimation included CPOM, FPOM, algae, cyanobacteria, and periphyton. CPOM was quantified from 4 to 5 sets of stratified samples in each of the 3 pools. Each set consisted of 3 samples, 2 from close to the banks and 1 from midstream, and each sample consisted of all litter enclosed by a Surber sampler (900- cm^2 base area, 1- mm^2 mesh), for a total of 12 to 15 samples per pool. Dry mass (DM) and ash-free dry mass (AFDM) of each litter sample was determined following Benfield (1996), and a single combined set of ground samples from each pool was analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopes.

FPOM biomass was quantified from a single set of stratified samples (2 samples close to the bank and 1 in midstream) of resuspended bottom sediment in each of the 3 study pools. Each sample contained 500 mL of stream water plus FPOM collected in a Nalgene bottle submerged in the middle of a sediment suspension produced by stirring a 25 cm \times 25 cm area of the pool bottom for 30 s. In the laboratory, inverte-

brates were removed from the settled material under a stereomicroscope at 20 \times magnification. The 3 FPOM samples from each pool were combined and filtered through Advantec GC50 glass fiber filters (0.5- μm pores), oven-dried at 60°C for 48 h, and weighed. Filters were then ashed following Benfield (1996). Three additional FPOM samples for stable isotope analysis were collected (1 sample of ~100 mg from each pool) following the same procedure. After filtration, the samples were oven-dried and ground with a pestle and mortar in preparation for analysis of stable isotope composition.

Periphyton biomass was estimated from 2 sets of stratified samples (as above) in each pool. Each sample consisted of the periphyton from 3 stones for a total of 18 stones in each pool (3 stones/sample \times 3 samples/set \times 2 sets/pool). The stones were gently washed in stream water to remove FPOM and any attached animals, and then scrubbed with a stiff brush and a small amount of water. The stone surface area was estimated from measurements of length (L), width (W), and height (H) (Mantel 2003). In the laboratory, samples were filtered, dried, and ashed as for FPOM. Additional periphyton samples, collected by scrubbing ~20 randomly collected stones per pool, were used for analysis of stable isotope signatures. A single combined sample from each pool was prepared for analysis following the same procedures as for FPOM.

Algal biomass was estimated by measuring chlorophyll *a* standing stocks on stones in 3 pools. Five small stones (8–18 cm length; mean surface area 70 cm^2) were randomly collected from each pool. The stones were stored individually in plastic bags and chlorophyll content was estimated in the laboratory using 90% ethanol extraction (Nagarkar and Williams 1997, Mantel 2003). Stone surface area was estimated as above. Chlorophyll *a* values were converted to algal AFDM by multiplying by 67 (APHA 1998).

Although filamentous algae was scarce in the study pools, 2 samples (mixtures including *Enteromorpha* and *Ulothrix*) were collected by hand, and transported in water to the laboratory. After drying, each sample (57–256 mg DM) was ground with a pestle and mortar prior to analysis of stable isotope signatures. Cyanobacteria were collected from emergent boulders by scraping black algal patches with a razor blade into plastic vials filled with stream water. *Phor-*

medium and *Calothrix* were the dominant components. Three replicate samples of cyanobacteria were prepared for stable isotope analysis as above.

Animal samples

Samples of fish, shrimps, and macroinvertebrates were collected from pools during the dry seasons of 1999 and 2001. Additional individuals of the shrimps *Macrobrachium hainanense* (Palaemonidae) and the prosobranch *Brotia hainanensis* (Pachychilidae) were collected from May to July 1999 for assessing ontogenetic differences in stable isotope signatures.

Macroinvertebrates were collected from the surface of >30 stones in each of the 3 pools (stone diameter 4–35 cm). With a hand net (triangular mesh 200 × 400 μm) or D-style drift net (300-μm mesh and 24-cm diameter) placed immediately downstream, each stone was lifted and the net moved forward and under the stone to enclose it. The macroinvertebrate samples were stored in 10% formalin. Stone surface areas were measured as above so that macroinvertebrate densities could be estimated.

Five fish species common in the pools were collected for gut content analysis and stable isotope determination: *Ctenogobius duospilus* (Gobiidae), *Liniparhomaloptera disparis* and *Pseudogastromyzon myersi* (Balitoridae:Balitorinae), *Schistura fasciolata* (Balitoridae:Neomacheilinae), and *Parazacco spilurus* (Cyprinidae). Fishes, snails, and shrimps collected for gut content analyses were preserved in 10% formalin in the field or frozen and preserved later. Collections of *P. spilurus* at night were used to supplement the daytime handnet collections.

Gut content analysis

Macroinvertebrate species collected from stones were identified mostly to species/genus, and Chironomidae larvae were identified to subfamily. Taxa with densities >4/m² were divided into 2, 3, or 4 size groups, and gut contents of all individuals in each size group were combined prior to analysis. Only the most numerous taxon of each family was analyzed (Table 1). The number of individual guts per size group for primary consumers varied from 6 to 58 (except for large *Brotia hainanensis* [*n* = 2], large *Sinopsephenus chinensis* [*n* = 2], and *Cari-*

dina cantonensis [*n* = 3]). All individuals of predatory macroinvertebrates and fishes collected were analyzed; the number of individuals per group varied from 2 to 14. Other studies of gut contents have typically used from 4 to 15 individuals per macroinvertebrate taxon (Tavares-Cromar and Williams 1996, Thompson and Townsend 2000, Rosi-Marshall and Wallace 2002, but see Lancaster and Robertson 1995). Using an ocular micrometer of a stereomicroscope, head width, head length, body length (without cerci), aperture width, or standard length (SL) for fishes were measured for use as an indicator of size, depending on the species. For species where size groups could not be defined, either a single size category was formed or, if large numbers of individuals were available, 3 to 4 replicates of the same size category were used to assess the extent of variation in gut content composites. All large macroinvertebrates (e.g., odonate larvae) and fishes were analyzed irrespective of their density. Preparation of filters for gut analysis followed Cummins (1973), with the addition of 0.3 mL of Lugol's solution for preserving the samples (APHA 1998). The slides were examined at 400× magnification under an Olympus BX50 microscope. At each crossing of the gridded filter, the 4 nearest food items were identified for a total ≤200 items. In some cases, only 100 items could be identified on the whole filter because some insect guts were empty. Gut contents of consumers were separated into 8 types of food items: filamentous algae, unicellular algae (except diatoms), diatoms, CPOM (≥1 mm, which was usually litter), FPOM (<1 mm, which was usually amorphous detritus), fungi, inorganics, and animal parts. Most prey were identified to family using voucher slides and drawings in Dudgeon (1999). The relative abundance of each category or prey type was calculated. The diet of fishes was determined following the procedure of Dudgeon (1987), and compared to data on 4 of these species collected from TPKFS riffles.

Stable isotope analyses

The isotopic signatures of fishes were determined from analysis of ≥100 mg DM of lateral muscle tissue, without bones or scales. Digestive tracts of the shrimps, *Macrobrachium hainanense* and *Caridina cantonensis* (Atyidae), were removed to avoid contamination by nonassimilat-

TABLE 1. Density of consumers mostly collected from stones from 3 pools in the Tai Po Kau Forest Stream. Abbreviations are those used for food webs in Figs. 2 and 3. – = animals that were not collected from stones. Taxa with numbers as abbreviations were either present in gut contents but not in benthic samples, or were in benthic samples but their densities could not be accurately estimated because they are nonbenthic taxa (e.g., Heteroptera). Densities of fishes were not estimated. Consumer species used in analyses of gut contents and stable isotope signatures (indicated by *) are shown in the last 2 columns. Numbers in parentheses indicate number of size groups. } = taxa combined in figures and for analyses.

Order/Family	Taxa	Abbreviations	Density range (no./m ²)	Guts	Isotopes
GASTROPODA					
Pachychilidae	<i>Brotia hainanensis</i> (Brot)	Bro	27–52	*(3)	*(3)
COPEPODA					
		3	–		
DECAPODA					
Atyidae	<i>Caridina cantonensis</i> Yu	A	0.0–0.3	*(1)	*(1)
Palaemonidae	<i>Macrobrachium hainanense</i> (Parisi, 1919)	Macrobrachium	–	*(2)	*(3)
HYDRACHNIDA					
		2	–		
EPHEMEROPTERA					
Baetidae		EPH			
		Bae			
	<i>Baetis</i> spp.		6–22	*(3)	*(1)
	<i>Chopralia</i> sp.		5–10		
	<i>Proclonon</i> sp.		16–44		
	<i>Afronurus</i> spp.	H	26–36	*(4)	*(4)
	<i>Compsoeuryia</i> sp.	Afr	13–14		
	Unidentified Heptageniidae		0.0–0.7		
	<i>Habrophlebiodes gilliesi</i> Peters	L	10	*(1)	*(1)
	<i>Choroterpes</i> spp.	Ha	2		
	<i>Isca purpurea</i> Gillies		0.0–0.3		
	<i>Torleya arenosa</i> Tong and Dudgeon	To	1–4	*(1)	*(1)
	<i>Serratella albostrigata</i> Tong and Dudgeon	S	0.3–1.2		
		OD			
ODONATA					
Amphipterygidae	<i>Philoganga retusta</i> Ris		0.0–0.7	*(3)	*(2)
Euphaeidae	<i>Euphaea decorata</i> (Selys)	Ed	0–2		
	Unidentified Odonata		0.3–0.6		

TABLE 1. Continued.

Order /Family	Taxa	Abbreviations	Density range (no./m ²)	Guts	Isotopes
PLECOPTERA					
HETEROPTERA	Perlidae	PL			
	Corixidae	Pr 1	2-3 0.0-0.3	*(3)	*(1)
TRICHOPTERA					
Glossomatidae	<i>Agapetus</i> spp.	TRI			
Ecnomidae	<i>Ecnomus</i> sp.	G E	0.0-0.3 0-1 1-4 1-2		
Hydroptilidae					
Xiphocentronidae	<i>Melanotrichia serica</i> Barnard and Dudgeon				
Polycentropodidae	<i>Pseudoneureclipsis</i> spp. <i>Polycentropus</i> sp. <i>Cheumatopsyche ventricosa</i> Li and Dudgeon 1988 <i>Cheumatopsyche spinosa</i> Schmid <i>Goerodes doligang</i> Malicky	Po Ps Hy C	2-4 0.0-0.7 1-4 1-2 0.0-0.6	*(1)	*(1)
Hydropsychidae	<i>Anisocentropus maculatus</i> Ulmer	An	1-4	*(3)	*(2)
Lepidostomatidae	Unidentified Calamoceratidae		1-2		
Calamoceratidae	<i>Helicopsyche</i> sp.	Hel	5	*(2)	*(1)
COLEOPTERA					
Hydrophilidae	<i>Berosus</i> sp.	CO	0.0-0.3		
Scirtidae	Scirtidae	7	-		
Psephenidae	<i>Eubrianax</i> sp. <i>Psephenoides</i> sp. <i>Sinopsephenus chinensis</i> Nakane Elmidae larvae	P Eu Si El	2-12 7-18 0-3 0-3	*(1) - *(1)	*(1) *(1) *(3)
Elmidae					
DIPTERA					
Nymphomyiidae	Nymphomyiidae	DI	-		
Dixidae	Dixidae	5	0.0-0.6		
Simuliidae	Simuliidae	4	-		
Ceratopogonidae	Ceratopogonidae		0-2		

TABLE 1. Continued.

Order/Family	Taxa	Abbreviations	Density range (no./m ²)	Guts	Isotopes
Chironomidae	Chironominae	Chn	4-7	*(2)	*(1)
	Orthocladiinae	Or	5	*(2)	*(1)
	Tanypodinae	Ta	3-4	*(2)	*(1)
Canacidae	Canacidae		0.0-0.6		
MEGALOPTERA	<i>Neochauliodes</i> sp.		0.0-0.3		
PISCES					
Ballitoridae	<i>Pseudogastromyzon myersi</i> Herre	Pseudo	-	*(2)	*(1)
	<i>Liniparhomaloptera disparis</i> (Lin)	Linipar	-	*(2)	*(1)
	<i>Schistura fasciolata</i> (Nichols and Pope)	Schistura	-	*(1)	*(1)
Gobiidae	<i>Ctenogobius duospilus</i> Herre	Ctenogobius	-	*(1)	*(1)
Cyprinidae	<i>Parazacco spilurus</i> (Günther)	Parazacco	-	*(3)	*(1)

TABLE 2. Standing stock biomass (mean \pm SE ash-free dry mass [AFDM]) of basal food resources in 3 pools in Tai Po Kau Forest Stream. Sample sizes are shown in parentheses. CPOM = coarse particulate organic matter, FPOM = fine particulate organic matter.

Pool	CPOM (g/m ²)	FPOM (g/L)	Periphyton (g/m ²)	Algae (g/m ²)
1	31.1 \pm 9.5 (15)	0.05 \pm 0.02 (3)	0.8 \pm 0.2 (6)	0.6 \pm 0.2 (5)
2	31.4 \pm 14.1 (12)	0.04 \pm 0.01 (3)	0.9 \pm 0.1 (6)	0.7 \pm 0.1 (5)
3	36.6 \pm 14.6 (12)	0.04 \pm 0.00 (3)	1.0 \pm 0.1 (6)	0.4 \pm 0.1 (5)
All pools	32.9 \pm 7.1	0.04 \pm 0.01	0.9 \pm 0.1	0.6 \pm 0.1

ed materials. Specimens of *Brotia hainanensis* were maintained in laboratory tanks for 2 d to allow gut clearance prior to killing by freezing. The snails and shrimps were decalcified with 1N HCl and rinsed in distilled water several times. Decalcification resulted in no effect on stable isotope signatures (Mantel 2003). All tissues were oven-dried at 60°C for 48 h, ground to a fine powder in a mortar, and stored in plastic vials for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope determination. Five individuals each of 3 size categories of *M. hainanense* and *B. hainanensis* were analyzed separately, and ontogenetic differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures compared using one-way ANOVA.

The guts were removed from macroinvertebrates of each size category in each taxon. Macroinvertebrates were then dried at 60°C for 48 h and ground in preparation for stable isotope analysis. Samples ranged from 2 to 10 mg DM, and size categories were combined if the mass of an individual size category was less than the 2 mg minimum required for analysis. Table 1 lists all species analyzed.

Samples of noninsect animals, cyanobacteria, and periphyton were sent to the Stable Isotope Research Facility for Environmental Research (SIRFER), Department of Biology, University of Utah, where they were analyzed for $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ with an analytical precision of $\pm 0.3\text{‰}$. The macroinvertebrate samples, and samples of FPOM, filamentous algae, and CPOM were analyzed by the Stable Isotope Facility, University of California, Davis (UC Davis; precision of $\pm 0.3\text{‰}$). Results (‰) are reported as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, i.e., the difference between the sample and an international standard (air for N and Pee Dee Belemnite for C; Peterson and Fry 1987). A positive value indicates enrichment of the heavy isotope relative to standard reference, whereas a negative value denotes depletion.

Fractionation values of +3.4‰ and +0.8‰

for $\Delta\delta^{15}\text{N}$ and $\Delta\delta^{13}\text{C}$, respectively, were used to account for enrichment in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from food or prey to consumer (Minagawa and Wada 1984, Vander Zanden and Rasmussen 2001). A 2-isotope, multiple-source mixed model that could delimit the range of possible contributions of >3 potential food resources (IsoSource, version 1.1) was used to determine the contribution of each food source to consumer diets (Phillips and Gregg 2003). The output of the program is a frequency distribution of feasible solutions for the food resources. This method is reliable only if a polygon, made by joining the fractionated resources with straight lines, encloses the value of the consumer on a $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ biplot (Phillips and Gregg 2003). When a polygon could not be drawn to enclose the value of the consumer, the 2-isotope, 3-source mixed model was calculated by means of IsoError software (version 1.04; Phillips and Gregg 2001). A 1-isotope, 2-source model was used (Phillips and Gregg 2001), if the 3-source mixed model provided negative resource variations because isotope mixtures fell outside the area constrained by the resource signatures. The values of the most likely food resources (i.e., fractionated resources in the gut with signatures closest to the animal) were chosen for inclusion in the mixed models. A SD of 0.5 for the signatures was applied in the IsoError program if samples of primary consumers were unreplicated.

“Tolerance” in the IsoSource program is an input that allows predicted resource combinations within the specified tolerance of the actual values to be included in the feasible solutions. Food resources may vary in their fractionation values (Adams and Sterner 2000, Hart and Lovvorn 2002) and may also vary in their isotopic signatures, so a tolerance of 1.0‰ was applied in the IsoSource model. The tolerance value used was conservative because greater tolerance results in an increased range of feasible solu-

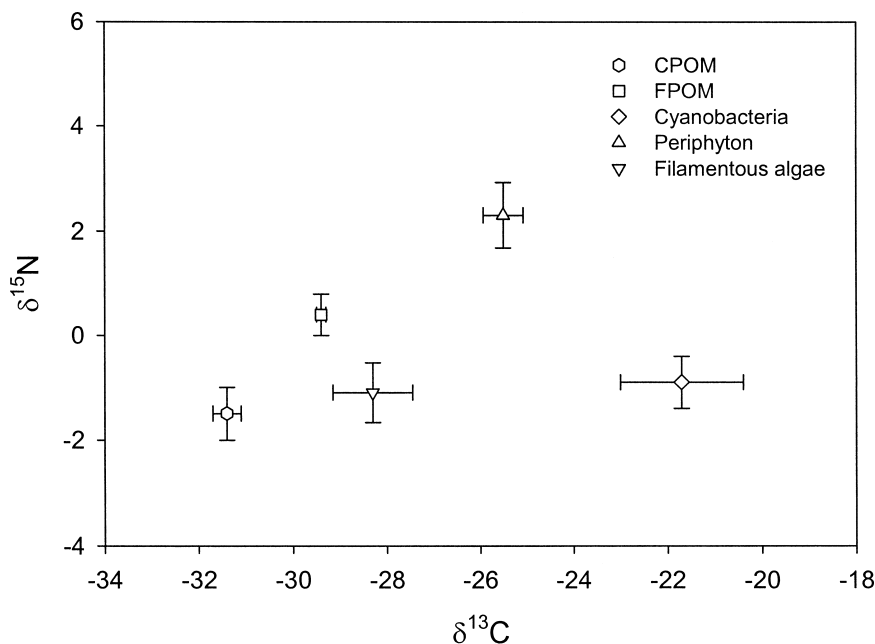


FIG. 1. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope biplot for basal food resources in pools of Tai Po Kau Forest Stream. Error bars represent SE. Sample size is 3 for all except filamentous algae, which had 2 replicates. CPOM = coarse particulate organic matter, FPOM = fine particulate organic matter.

tions, i.e., greater uncertainty. The tolerance of the IsoSource model was increased to 1.5‰ or 2.0‰ to enlarge the size of the polygon in the few cases where consumer signatures lay slightly outside the polygon on the biplot.

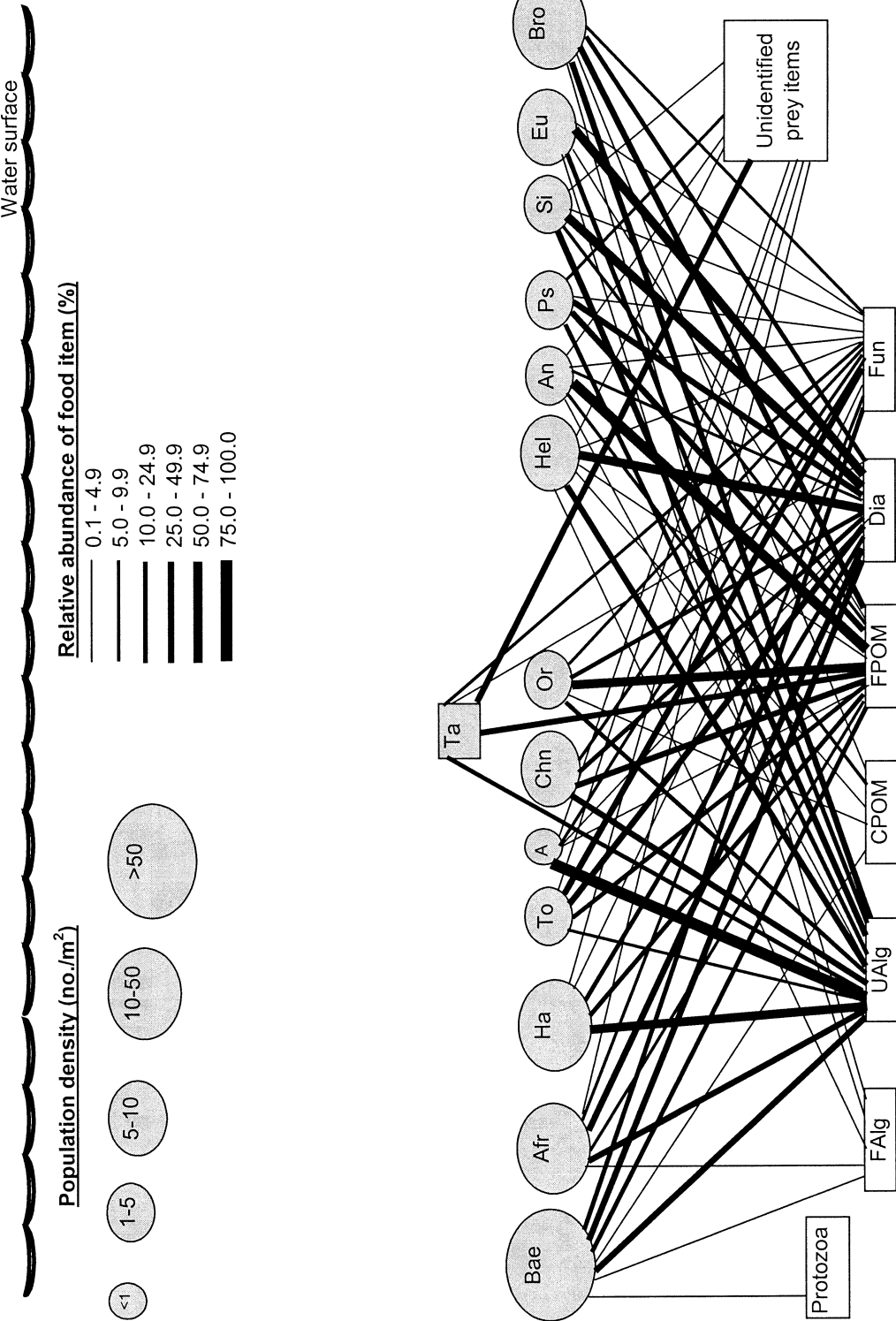
Properties of food webs generated from gut contents

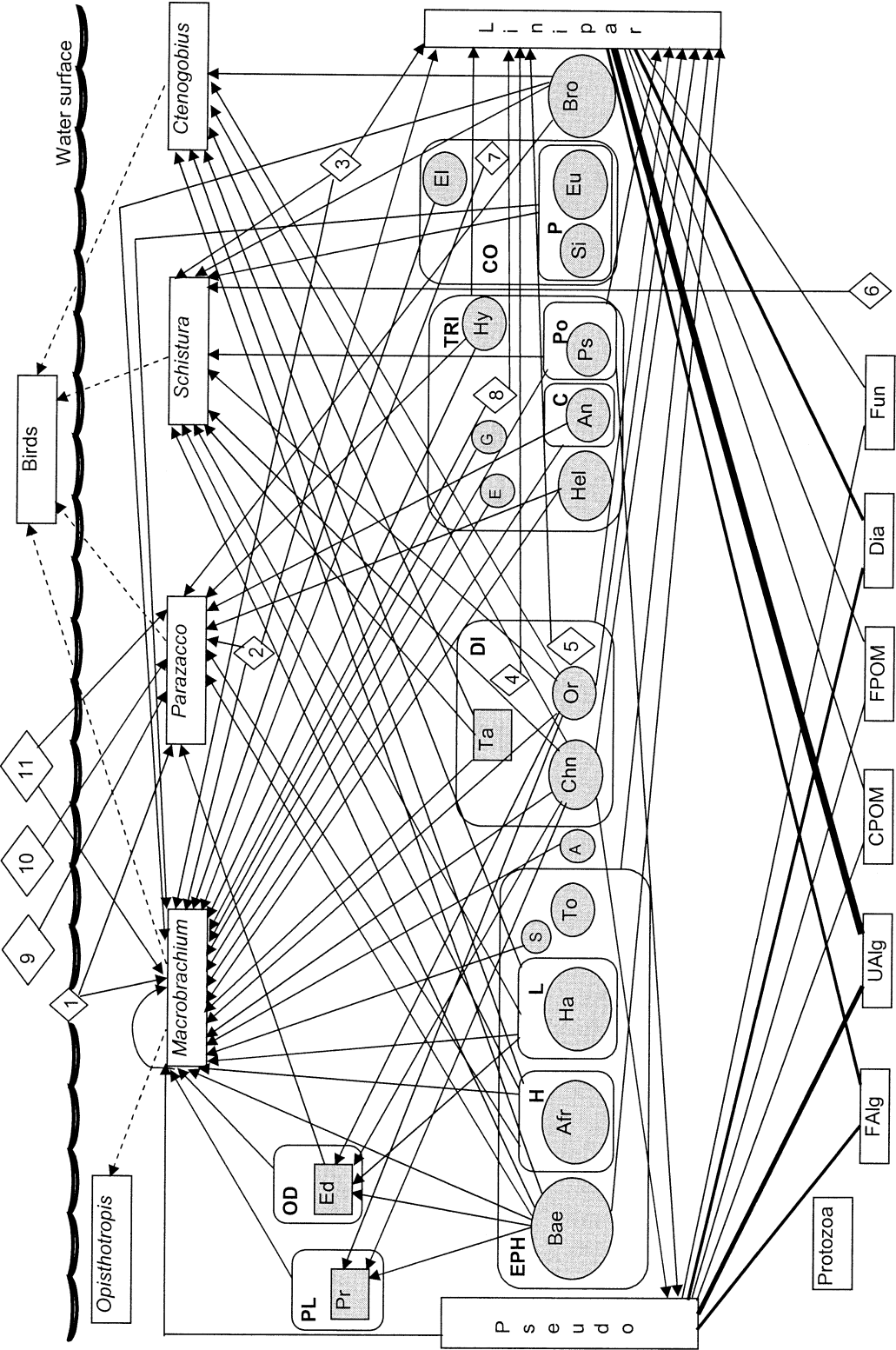
Gut content data were used to construct a food web for TPKFS pools. The following parameters were calculated for the food web: species richness (or web size, S); number of links (or number of ones in the foodweb matrix, L); mean and maximum length of all food chains; fraction of basal species (species with no prey, i.e., basal food resources); fraction of intermediate species (species that have predators and prey); fraction of top species (predatory species

that are not preyed upon); fraction of omnivores (animals feeding on >1 trophic level); predator-prey ratio (number of predators divided by number of prey); trophic connectance ($C_T = L / [S(S - 1)]$); realized connectance ($C_R = L / [S^2 - \{[(pp + ba)S] + (S - \{pp + ba\}) + (pr\{pp + ba\})\}]$; Jaarsma et al. 1998) (terms defined below); linkage complexity (product of species richness and realized connectance, or SC_R ; Briand 1985); and linkage density (total number of links in the web divided by the total number of species, L/S ; Pimm et al. 1991). The terms used in C_R are: pp—the number of primary producers (i.e., the categories of diatoms, and filamentous and unicellular algae in our study); ba—the number of nonalgal basal elements; and pr—the number of predators (Jaarsma et al. 1998). Thus, C_T is the number of links found in

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FIG. 2. Food web of basal food resources (white rectangles) in guts of benthic macroinvertebrate primary consumers (grey circles) and omnivorous/predatory secondary consumers (grey squares) in pools of Tai Po Kau Forest Stream. The size of grey circles/squares indicates population densities. The thickness of lines indicates relative abundance of food items in guts. Abbreviations for food items are FAlg = filamentous algae, UAlg = unicellular algae, CPOM = coarse particulate organic matter, FPOM = fine particulate organic matter, Dia = diatoms, Fun = fungi. Abbreviations for consumers are in Table 1.





the web divided by the potential number of interspecific interactions, whereas C_R is the number of links found in the web divided by the potential number of links in the web assuming all links were possible (i.e., S^2) minus the number of links to nonfeeding basal species and links from predatory species to basal food resources that might be incidental.

The predator-prey ratio was calculated using the definition of Jeffries and Lawton (1985) with 'prey' as primary consumers and 'predators' as any species that eat prey even if they are themselves preyed upon. All species collected from pools, not just those whose gut contents had been analyzed, were used for this calculation. Diets of species not examined were estimated from the gut contents of taxa in the same family or from the literature. In cases where several species may have been included in a taxon (e.g., chironomid subfamilies), it was assumed (following Jeffries and Lawton 1985) that the taxon consisted of ≥ 2 species. The prey-predator ratio was also calculated by dividing the sum of intermediate and basal species in the web by the sum of top and intermediate species (Cohen 1977).

Results

Basal food resources

CPOM was the dominant basal food resource (32.9 g AFDM/m²), and FPOM was the least prevalent (0.04 g AFDM/L) in TPKFS pools (Table 2). Algal biomass was 42 to 83% of periphyton biomass in the 3 pools. CPOM biomass exceeded fine particulate organic matter (FPOM) by 822 times and periphyton by 36 times. Stable isotope signatures of the basal food resources were widely separated and SEs did not overlap (Fig. 1). Cyanobacteria was the most $\delta^{13}\text{C}$ -enriched (-21.7‰) and CPOM was the least (-31.4‰); values of FPOM (-29.4‰), periphyton (-25.5‰), and filamentous algae (-28.3‰) were intermediate. The stable isotope value of FPOM was midway between CPOM

and periphyton on both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ axes, so FPOM was probably derived from both autochthonous and allochthonous sources (Fig. 1). Periphyton was the most $\delta^{15}\text{N}$ -enriched (2.3‰) and CPOM was the least (-1.5‰). The signatures of the 2 filamentous algae samples were close and have been averaged.

Gut contents

A total of 105 stones with a surface area of 4.55 m² was sampled from the 3 pools. Thirty-nine macroinvertebrate taxa (not including unidentified taxa, *Macrobrachium hainanense*, Scirtidae, Nymphomyiidae, and Simuliidae) were collected with a total density (mean \pm SE; $n = 2$) of $215.3 \pm 13.9/\text{m}^2$ (Table 1). The 19 macroinvertebrate taxa collected that were used in gut analysis represented 80% of the total macroinvertebrates collected. Details of the results of the gut content analyses are available at <http://www.hku.hk/ecology/staffhp/dd/GutContents.htm>.

The diet of *Brotia hainanensis* in pools changed with age: small snails fed on unicellular algae (46%) and diatoms (45%), medium individuals had guts filled with FPOM (63%) and unicellular algae (24%), and large individuals had FPOM as the dominant food item (82%) with small contributions from diatoms (9%), CPOM (5%), and unicellular algae (4%). Guts of *Caridina cantonensis* shrimps were dominated by unicellular algae (91%) with fungi and FPOM comprising a small proportion of the diet. Guts of Ephemeroptera were dominated by diatoms and other unicellular algae. The gut contents of small baetids and *Torleya arenosa* (Ephemerellidae) were comprised of ~26 to 36% hyphomycetes and fungal spores. The guts of large baetids contained small numbers of flagellate protozoans.

Among the caddisflies, *Pseudoneureclipsis* spp. had a mixed diet of FPOM (41%) and diatoms (38%), *Anisocentropus maculatus* was primarily a detritivore (77–94% FPOM) with no significant change in diet with size, and *Helicopsyche* sp. specialized on diatoms (54–80%) and unicellular

←

FIG. 3. Food web for predators/omnivores in pools of Tai Po Kau Forest Stream. Solid arrows indicate confirmed prey and dotted arrows indicate inferred predation. Opisthotropis–*Opisthotropis lateralis* (colubrid snake), 6–insect eggs, 8–*Psychomyia* sp., 9–adult Coleoptera, 10–adult Diptera, 11–Formicidae. Abbreviations for consumers are in Table 1.

algae (14–37%). Psephenid coleopterans (*Eubrianax* sp. and *Sinopsephenus chinensis*) fed on diatoms (52–73%) and unicellular algae (23–40%). Chironominae and Orthocladiinae guts were dominated by FPOM and unicellular algae (>67% of food items). Tanypodinae were omnivorous with a diet of 34 to 52% animal parts, probably other chironomids, as suggested by studies of the diet of Tanypodinae in riffles of the same stream (SKM, unpublished data).

Animal parts composed most of the gut contents (50–92%) of *Euphaea decorata* and perlid stoneflies. Baetidae, Chironominae, and Orthocladiinae made up most of the prey of both predators. *Macrobrachium hainanense* had 3 to 5 prey per gut, and consumed a wide array of prey with case-building Chironomidae (Orthocladiinae, Chironominae) and Baetidae dominant. Large individuals appeared to have a slightly wider diet, possibly because of the larger sample size ($n = 7$ to 14), compared to small individuals ($n = 2$ to 5).

The guts of the balitorine loaches *Pseudogastromyzon myersi* and *Liniparhomaloptera disparis* were dominated by nonanimal material: unicellular algae (44–55% of volume), diatoms (11–23%), and filamentous algae (5–25%). Animal material comprised <4% of the guts of *P. myersi* with 0.4 to 0.8 prey/gut, most of which could not be identified; no significant difference in gut contents was observable in small versus large individuals. In contrast, *L. disparis* guts contained 6 to 21% animal parts by volume with 3 to 10 prey in each gut; Chironominae and Orthocladiinae comprised 72 to 74% of all prey identified. The relative abundance of prey items (6% versus 21%) and the number of prey per gut (3 versus 10) was greater in large than small *L. disparis*.

Schistura fasciolata, a neomacheiline balitorid, was entirely predatory. It had >12 prey/gut; Baetidae comprised 44% of all prey identified. Chironomidae (Chironominae, Orthocladiinae, and Tanypodinae) were the 2nd-ranked prey (32% relative abundance), while *Brotia hainanensis*, copepods, and unidentified insect eggs were present in some guts. *Ctenogobius duospilus* (Go-biidae) had a similar diet to *S. fasciolata* with ~13 prey/gut. Chironominae and Orthocladiinae were the dominant prey (82% relative abundance), followed by Ephemeroptera (Baetidae 4.5%, Heptageniidae 1.5%, Leptophlebiidae 1.5%). Only a single *Brotia hainanensis* was

found in the 5 guts examined, and has not been previously reported as prey of *C. duospilus* and *S. fasciolata* (Dudgeon 1987).

The cyprinid *Parazacco spilurus* consumed mainly animals (57–80% relative abundance) with a small proportion of CPOM. A mean of 2 to 3 prey/gut was identified with terrestrial insects dominant (50–55%). Baetid and heptageniid larvae were also eaten.

The benthic food web of primary consumers in TPKFS pools is shown in Fig. 2. Inorganic material was ignored because it was present in low quantities in guts and was probably incidentally ingested. Diatoms (29%), unicellular algae (28%), FPOM (30%), and fungi (6.4%) were the most frequently encountered food items (<http://www.hku.hk/ecology/staffhp/dd/GutContents.htm>). CPOM (1%) was the next most encountered item, followed by filamentous algae (0.3%). The diet of secondary and tertiary consumers (predatory invertebrates and fishes) is shown in Fig. 3. Baetidae (9% of total links from prey to predators), Chironominae (9%), and Orthocladiinae (8%) were the most frequently encountered prey (Fig. 3). *Macrobrachium hainanense* had the highest number of links (27) versus predatory invertebrates (e.g., *Euphaea decorata* and Perlidae, ≤ 4 links) and fishes (e.g., *Ctenogobius duospilus*, *Parazacco spilurus*, ≤ 12 links).

Stable isotope signatures of primary and secondary consumers

$\delta^{13}\text{C}$ values of all primary consumers in pools were enriched relative to filamentous algae, CPOM, and FPOM (Fig. 4). *Anisocentropus maculatus* was an exception with a $\delta^{13}\text{C}$ signal enriched compared to CPOM alone. Baetidae, *Afronurus*, *Psephenoides*, *Helicopsyche*, and the omnivorous balitorid loaches (*Pseudogastromyzon myersi* and *Liniparhomaloptera disparis*) were enriched or similar in $\delta^{13}\text{C}$ signature relative to all basal food resources. The variation in the signatures of the primary consumers (SE of $\leq 1.3\text{‰}$ for $\delta^{13}\text{C}$ and $\leq 0.3\text{‰}$ for $\delta^{15}\text{N}$) was comparable to that of the basal food resources (SE of $\leq 1.3\text{‰}$ for $\delta^{13}\text{C}$ and $\leq 0.6\text{‰}$ for $\delta^{15}\text{N}$), and supported the use of a conservative tolerance of 1‰ in the IsoSource mixed model.

There was no difference ($\delta^{13}\text{C}$: $p = 0.86$, $\delta^{15}\text{N}$: $p = 0.47$) in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of small ($n = 5$, aperture width 6.8 ± 0.2 mm: $\delta^{13}\text{C}$

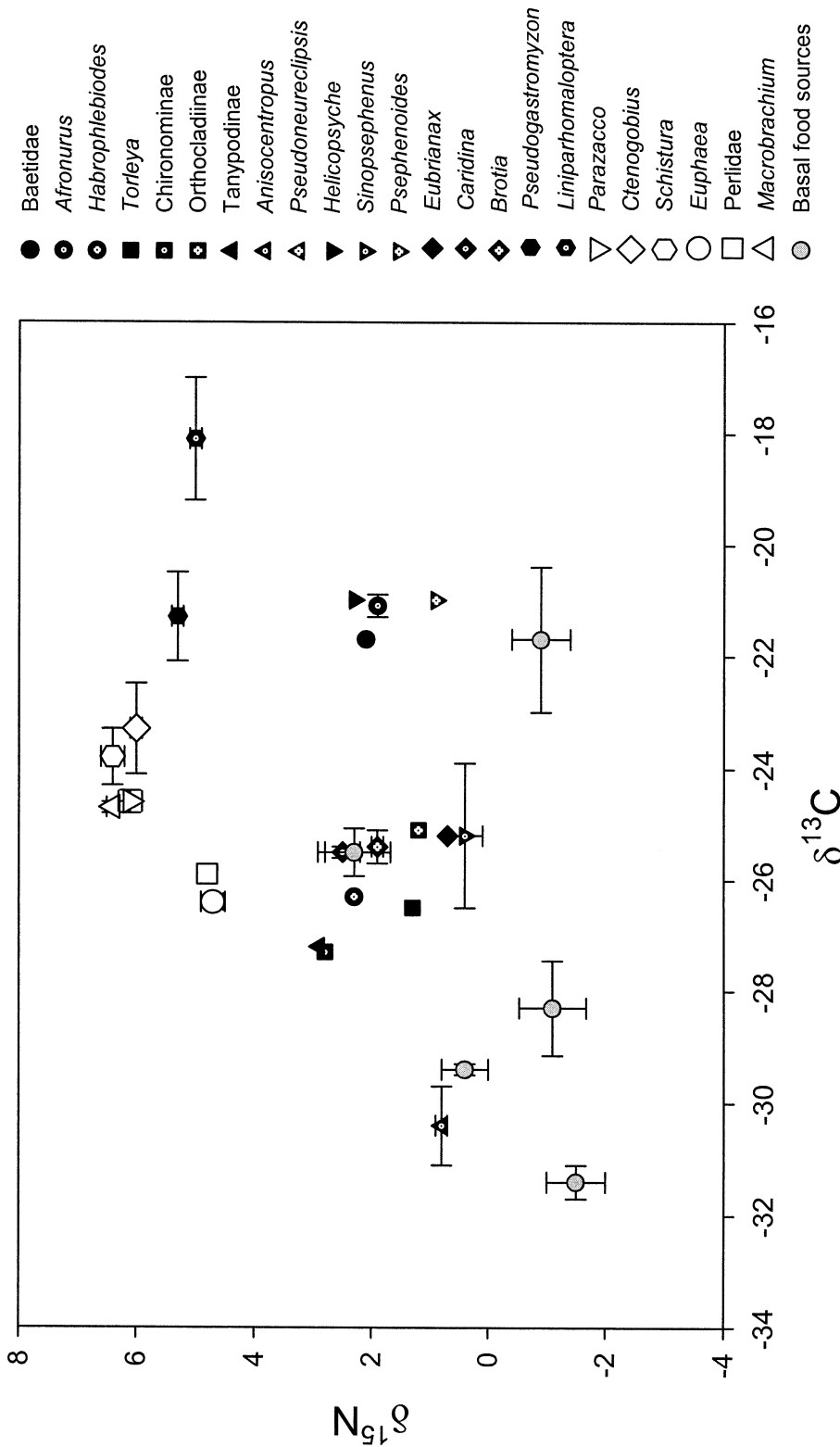


FIG. 4. Stable isotope biplot for primary and secondary consumers collected from Tai Po Kau Forest Stream pools. Basal food resources are shown as a single symbol (details in Fig. 1). Values are mean \pm SE. Note that *Pseudoneureclipsis* is hidden behind *Euphaea*.

TABLE 3. Percent contribution (mean with 1–99 percentile range in parentheses) of basal food resources to primary consumers in pools of Tai Po Kau Forest Stream calculated by the IsoSource model. – = food resources was not entered in model, FPOM = fine particulate organic matter, CPOM = coarse particulate organic matter. * = tolerance increased to 1.5‰; ** = tolerance increased to 2.0‰.

	Cyanobacteria	Periphyton	Filamentous	FPOM	CPOM
<i>Brotia</i>	15.6 (0–34)	67.4 (46–94)	–	10.9 (0–34)	6.0 (0–20)
<i>Caridina</i>	39.8 (24–58)	12.5 (0–34)	–	22.5 (0–62)	25.2 (0–50)
Baetidae	79.5 (68–96)	6.8 (0–18)	7.7 (0–22)	6.0 (0–20)	–
<i>Afronurus</i>	86.6 (78–98)	4.4 (0–12)	5.1 (0–16)	3.9 (0–12)	–
<i>Habrophlebiodes</i>	18.3 (0–38)	8.3 (0–24)	52.3 (8–88)	21.2 (0–58)	–
<i>Torleya</i>	33.2 (16–50)	0.7 (0–4)	16.3 (0–54)	2.1 (0–8)	47.7 (26–64)
<i>Helicopsyche</i>	86.2 (76–96)	6.1 (0–22)	3.2 (0–12)	2.6 (0–10)	1.9 (0–8)
<i>Eubrianax</i> *	41.7 (36–50)	0.0 (0–0)	5.2 (0–16)	0.4 (0–2)	52.8 (48–58)
<i>Psephenoides</i> **	77.7 (66–94)	4.6 (0–12)	7.4 (0–24)	5.3 (0–20)	4.9 (0–16)
<i>Sinopsephenus</i> **	38.2 (14–70)	1.1 (0–6)	21.2 (0–74)	2.9 (0–12)	36.6 (8–60)
Chironominae	17.7 (0–38)	16.0 (0–44)	–	30.7 (0–82)	35.6 (0–68)
Orthocladiinae	47.6 (46–50)	0.0 (0–0)	1.6 (0–4)	0.0 (0–0)	50.8 (50–52)

–25.6 ± 0.6‰, δ¹⁵N 2.0 ± 0.1‰), medium (*n* = 5, aperture width 8.8 ± 0.2 mm: δ¹³C –25.2 ± 0.8‰, δ¹⁵N 2.0 ± 0.2‰), and large (*n* = 5, aperture width 12.1 ± 0.3 mm: δ¹³C –25.5 ± 0.4‰, δ¹⁵N 1.7 ± 0.2‰) *Brotia hainanensis*. Similarly, δ¹³C and δ¹⁵N signatures of large (mean ± SE; δ¹³C, δ¹⁵N: –24.2 ± 0.3‰, 5.1 ± 0.1‰), medium (–24.5 ± 0.4‰, 4.7 ± 0.2‰), and small (–24.8 ± 0.3‰, 4.6 ± 0.1‰) *Macrobrachium hainanense* were similar (δ¹³C: *p* = 0.45, δ¹⁵N: *p* = 0.07).

Four to seven potential food resources were used in the IsoSource program for each consumer, although the program can accommodate a maximum of 10 resources. Including >7 resources resulted in excessive processing time (>4 h) and the results were less finely resolved than when <7 resources were included in the model. The number of possible resources in the diet of predators exceeded 7 in some cases, so sources with similar signatures were averaged (e.g., Baetidae and *Afronurus*). The results are summarized in Tables 3 to 5. Cyanobacteria were the major contributor (1–99 percentile: 66–98%; Table 3) to the biomass of Baetidae, *Afronurus* spp., *Helicopsyche* sp., and *Psephenoides* sp., whereas periphyton was a significant food for *Brotia hainanensis* (46–94%; Table 3). The contribution of other potential food resources to these consumers could not be uniquely quantified because they had overlapping ranges of feasible contributions that included 0, i.e., the possibility of no contribution. Cyanobacteria and CPOM were significant contributors to the biomass of

Caridina cantonensis, *Torleya arenosa*, *Eubrianax* sp., *Sinopsephenus chinensis*, Chironominae, and Orthocladiinae (Table 3). *Habrophlebiodes gilliesi* appeared to derive their biomass from filamentous algae (8–88%) and possibly FPOM (0–58%) (Table 3), whereas Tanypodinae depended mainly on FPOM (88–90%) and Orthocladiinae (10–12%; Table 4).

Pseudoneureclipsis spp. had an omnivorous diet but a tissue isotopic signature similar to predatory *Euphaea decorata* (*Pseudoneureclipsis* spp. is hidden behind *E. decorata* in Fig. 4). Accordingly, 2 analyses using the IsoSource mixed model were conducted: one using mixed resources (both basal food resources and prey items) and one using prey items only. The results for the mixed diet did not differentiate the relative contributions of the various foods (Table 4), and no particular prey species dominated the diet when the prey-only (Chironominae, Orthocladiinae, *Habrophlebiodes gilliesi*, and *Torleya arenosa*) analysis was undertaken (Table 4). This pattern of no prey species dominating the diet was seen in other predators (*Euphaea decorata*, Perlidae, *Macrobrachium hainanense*, *Schistura fasciolata*, *Ctenogobius duospilus*, *Parazacco spilurus*; Tables 4, 5).

The results of a 2-source model for C showed that the biomass of *Anisocentropus maculatus* was primarily derived from CPOM. The results were consistent whether CPOM and filamentous algae were included in the model (CPOM 93.5%, filamentous algae 6.5%) or CPOM and FPOM were included (CPOM 90.0%, FPOM 10.0%); CIs

for all these means were 0 to 100%. The balitorid *Pseudogastromyzon myersi* derived most of its biomass from Baetidae and Heptageniidae mayflies (mean of 74% or 78%; Table 6), although the gut contents were dominated by unicellular algae and diatoms (<http://www.hku.hk/ecology/staffhp/dd/GutContents.htm>). Similarly, the biomass of *Liniparhomaloptera disparis* was either derived from Baetidae and *Afromurus* (2-source model using a mixed diet of prey and cyanobacteria) or with equal contributions from Ephemeroptera (Baetidae and *Afromurus*) and Orthocladiinae (2-source model using prey species only) (Table 6).

Web properties

The web size was 28 (Fig. 3). If all species that were found in the guts of predators in pools were included (even those prey species not included in gut content analysis), the number of taxa was 43 (i.e., all basal food resources, primary and secondary consumers in Fig. 3, except eggs, birds, and the colubrid snake *Opisthotropis lateralis*). The fraction of basal species was 0.21 (= 6/28), the fraction of intermediate species was 0.57 (= 16/28, including Perlidae, *Euphaea decorata*, Baetidae, *Afromurus* spp., *Habrophlebiodes gilliesi*, *Torleya arenosa*, *Caridina cantonensis*, Chironominae, Orthocladiinae, Tanypodinae, Helicopsychidae, *Anisocentropus maculatus*, *Pseudoneureclipsis* spp., *Eubrianax* sp., *Sinopsephenus chinensis*, and *Brotia hainanensis*), and the fraction of top species was 0.21 (= 6/28; 5 fishes plus *Macrobrachium hainanense*). The number of links (L) was 157, and did not include basal links for primarily predatory species (*Euphaea decorata*, Perlidae, *Macrobrachium hainanense*, *Parazacco spilurus*, *Schistura fasciolata*, and *Ctenogobius duospilus*), although the basal food links for omnivores (*Pseudoneureclipsis* spp., Tanypodinae, *Liniparhomaloptera disparis*, and *Pseudogastromyzon myersi*) were included in the count. The maximum chain length was 3 and the mean chain length 2.04 (not including birds, snakes, and terrestrial insects). The trophic connectance (C_T) was 0.21 and the realized connectance (C_R) was 0.27. The linkage density (L/S), which is a measure of connectivity, was 5.57, and linkage complexity (SC_R) was 7.56. The predator-prey ratio sensu Jeffries and Lawton (1985) was 0.57 (Appendices 1 and 2 list the predator and prey spe-

cies), but following the definition of Cohen (1977) was 1.0.

Discussion

Comparison of gut content analyses and stable isotope signatures

The biomass of CPOM in TPKFS exceeded that of FPOM by >800 times and that of periphyton by 36 times. Similar results have been obtained in riffles of the same stream (Dudgeon 1982). Despite the predominance of CPOM, a food web based on gut contents revealed the importance of periphyton (unicellular algae and diatoms) and FPOM over CPOM. The sole exceptions to this pattern were large individuals of the shredder caddisfly *Anisocentropus maculatus* and small *Euphaea decorata*, which had 10 to 50% CPOM in their diet. Some diatoms may pass through the guts of consumers without being digested (Peterson 1987, but see Rounick et al. 1982), but their abundance in consumer diets suggested that they were important to the diet.

As was the case in TPKFS, algae dominated the gut contents of macroinvertebrates in a forested Sri Lankan stream, although some fishes and *Eubrianax* sp. ingested leaf litter (Costa and Fernando 1967). In contrast, allochthonous material (CPOM and FPOM) was the primary basal food resource in food webs of a tropical headwater stream on Bougainville Island, Papua New Guinea (Yule 1996), in a 3rd-order grassland stream in New Zealand (Jaarsma et al. 1998), and in forested 1st-order streams in the Appalachians, USA (Hall et al. 2000). In addition, FPOM alone was the major dietary component of consumers in Broadstone stream, a 2nd-order stream in the UK (Lancaster and Robertson 1995, Schmid-Araya et al. 2002b) and in a forested 3rd-order stream in Ontario (Tavares-Cromar and Williams 1996).

Stable isotope signatures of primary consumers in TPKFS suggested a high degree of dependence on cyanobacteria and/or periphyton, complementing the results of gut content analyses. Animal samples preserved in 10% formalin, as in our study, are $\delta^{13}\text{C}$ -depleted by $\sim 1.65\text{‰}$, while their $\delta^{15}\text{N}$ value remains unchanged (Kaehler and Pakhomov 2001, Sarakinos et al. 2002). This finding suggests that the trophic positions of consumers in our study are robust, although the $\delta^{13}\text{C}$ signatures would have

TABLE 4. Percent contribution (mean with 1–99 percentile range in parentheses) of basal food resources and primary consumers to omnivorous secondary consumers calculated by the IsoSource model. – = food resource not included in the model, FPOM = fine particulate organic matter. Baetidae + *Afronurus* signals were averaged.

	Periphyton	FPOM	Baetidae + <i>Afronurus</i>	Chironominae
Tanypodinae	0.0 (0–0)	89.0 (88–90)	–	0.0 (0–0)
<i>Pseudoneureclipsis</i> (mixed resources)	14.4 (0–52)	20.2 (0–58)	–	16.5 (0–54)
<i>Pseudoneureclipsis</i> (prey only)	–	–	–	24.4 (0–56)
<i>Euphaea</i>	–	–	1.8 (0–8)	28.1 (0–60)
Perlidae	–	–	4.3 (0–16)	19.1 (0–58)
<i>Macrobrachium</i>	–	–	18.1 (0–48)	11.8 (0–44)

shifted slightly to the left of their real positions (Fig. 4). Nonetheless, because the $\delta^{13}\text{C}$ signatures of the food sources collected from the pools were generally separated by $>2\text{‰}$ (with the exception of FPOM and filamentous algae, Fig. 1), this artefact would not dramatically change our results.

Other studies of stable isotope signatures have also shown the importance of autochthonous resources to Ephemeroptera in forested streams in Hong Kong (Salas and Dudgeon 2001a) and, more generally, to food webs in forested streams (Rosenfeld and Roff 1992, Finlay et al. 2002, March and Pringle 2003) and wetlands with abundant macrophytes (Hamilton et al. 1992, Lewis et al. 2001, but see Fisher et al. 2001 for temporal variability). This selection of algal resources might be based on higher food quality, in terms of energy and protein content (Bowen et al. 1995, Friberg and Jacobsen 1999), and easier assimilation of algae relative to macrophytes and leaf litter (Wallace et al. 1987, Whitlegde and Rabeni 1997).

The results of mixed models of stable isotopes suggested that CPOM was a major contributor to the biomass of certain taxa (*Caridina cantonensis*, *Torleya arenosa*, *Eubrianax* sp., *Sinopsephenus chinensis*, Chironominae, and Orthocladiinae). This finding contrasted with gut content anal-

yses, although studies of gut contents and ^{15}N tracer additions elsewhere have shown that CPOM is an important component of the diet of related taxa (Cummins 1973, Rosi-Marshall and Wallace 2002). The discrepancy might reflect seasonal variations in diet, which have been reported for lotic consumers elsewhere (Hildrew et al. 1985, Tavares-Cromar and Williams 1996, Thorp et al. 1998) because periphyton biomass in TPKFS is reduced during the wet season by spate-induced scouring (Dudgeon 1982). Some TPKFS consumers increase their dependence on CPOM at this time (Salas and Dudgeon 2001a), but the change is not great, and the scope for seasonal variation in diet in tropical Hong Kong is limited because many small species are multivoltine (Dudgeon 1995, Salas and Dudgeon 2001b). A more likely explanation is that taxa such as *Caridina cantonensis* collected food from the surface of leaf litter (as suggested by the presence of fungi or FPOM in their guts) and, thus, their tissues were close to the stable isotope signature of CPOM.

Discrepancies between gut contents and isotopic signatures were seen in the leptophlebiid *Habrophlebiodes gilliesi*: the signature indicated a high dependence on filamentous algae, which was not found in guts. In TPKFS, as in other fresh waters, filamentous algae are not a major

TABLE 4. Extended.

Orthocladiinae	<i>Habrophlebiodes</i>	<i>Torleya</i> or <i>Brotia</i>	<i>Eubrianax</i> or <i>Anisocentropus</i>	<i>Pseudoneureclipsis</i>
11.0 (10–12)	–	–	–	–
13.9 (0–48)	16.8 (0–62)	<i>Torleya</i> 18.3 (0–66)	–	–
15.1 (0–42)	24.7 (0–78)	<i>Torleya</i> 35.8 (0–86)	–	–
8.5 (0–32)	16.5 (0–64)	<i>Torleya</i> 28.8 (0–74)	<i>Eubrianax</i> 9.9 (0–34)	6.4 (0–24)
13.5 (0–48)	17.7 (0–64)	<i>Torleya</i> 21.5 (0–66)	<i>Eubrianax</i> 14.7 (0–50)	9.3 (0–30)
19.8 (0–64)	15.0 (0–58)	<i>Brotia</i> 17.8 (0–64)	<i>Anisocentropus</i> 9.8 (0–32)	7.6 (0–24)

food of primary consumers (Hicks 1997, Thorp et al. 1998, but see Costa and Fernando 1967). One possibility is that the isotopic signature of filamentous algae was coincidentally close to the actual food source of *H. gilliesi*. Indeed, one of the feasible solutions of the isotopic mixed model was a combination consisting primarily of cyanobacteria, FPOM, and periphyton (Table 3; Mantel 2003), and this solution was in agreement with the gut contents.

Unexpectedly, Tanypodinae had similar isotope signatures to Chironominae. The results of the isotopic mixed model suggested primary dependence on FPOM with a small (10–12%) contribution from Orthocladiinae prey. However, the gut contents contained 34 to 52% animal prey, and Tanypodinae are generally predatory (Cummins 1973, Warren 1989). *Pseudoneureclipsis* spp. (Polycentropodidae) guts contained only 8% animal parts, but isotopic signatures of their tissues implied a predatory lifestyle with $\delta^{15}\text{N}$ -enrichment of 2 to 4‰ relative to primary consumers. Many polycentropodid larvae are predatory (Cummins 1973, Dudgeon and Richardson 1988, Wiggins 1996). Most *Pseudoneureclipsis* spp. analyzed had empty guts, so the nonanimal material might have been *by-catch*, i.e., prey gut contents, and conclusions about diet based

on gut contents were likely distorted by the small sample size.

Macrobrachium hainanense had an isotopic signature higher than any other species of predatory invertebrates, such as the damselfly *Euphaea decorata*, and was 7.9‰ ^{15}N -enriched relative to detritus, matching results for *Macrobrachium* spp. in Puerto Rico with >6.5‰ ^{15}N -enrichment compared to leaf detritus (March and Pringle 2003). These animals are usually considered to be omnivores (Kilham and Pringle 2000, March and Pringle 2003). However, the isotopic mixed models denoted a broad range of prey, and recent gut content analyses have confirmed this result (Mantel and Dudgeon 2004).

Gut contents of the benthic fish *Ctenogobius duospilus* and *Schistura fasciolata* indicated that they were predators on benthic macroinvertebrates, whereas terrestrial insects dominated the guts of pelagic *Parazacco spilurus*, along with some nocturnally drifting Ephemeroptera (Dudgeon 1983a). Despite the importance of terrestrial insects in the diet of *P. spilurus*, its stable isotope signature was almost identical to the benthic predatory fishes. Information on the foraging range of the fishes in TPKFS is not available. However, juvenile cyprinids were found in shallow water and riffles in low-order streams

TABLE 5. Percent contribution (mean with 1–99 percentile range in parentheses) of primary consumers to predators calculated by the IsoSource model. Baetidae + *Afronurus* and *Eubrianax* + *Sinopsephenus* signals were averaged.

	Baetidae + <i>Afronurus</i>	<i>Habrophlebiodes</i>	Chironominae	Orthocladiinae	Tanypodinae
<i>Schistura</i>	20.3 (0–62)	13.6 (0–54)	15.1 (0–56)	9.3 (0–38)	13.2 (0–36)
<i>Ctenogobius</i>	18.5 (0–60)	14.2 (0–54)	14.5 (0–54)	11.6 (0–44)	12.6 (0–36)
<i>Parazacco</i>	15.4 (0–54)	15.1 (0–58)	15.4 (0–56)	12.9 (0–50)	9.3 (0–32)

in Taiwan, whereas larger individuals occupied pool areas during daytime (Han et al. 2000). In general, benthic fishes in streams appear to have limited foraging ranges (e.g., Petty and Grossman 2004, Sone et al. 2001) and balitorids, which were abundant in TPKFS, are rather sedentary (Martin-Smith 1998).

Pseudogastromyzon myersi and *Liniparhomaloptera disparis* fed primarily on a mixture of unicellular algae and diatoms, but a significant quantity of animal parts was found in some specimens (up to 21% by volume). Their $\delta^{15}\text{N}$ signatures were enriched by 5.9 and 6.2‰ compared to cyanobacteria, and were similar to that of *Macrobrachium hainanense* and to sympatric predatory fishes ($\leq \pm 1.4\text{‰}$). The habits of these pool-dwelling balitorid loaches contrasted to the strictly herbivorous diet of their conspecifics in TPKFS riffles (Dudgeon 1987). The sedentary habits of balitorids (Martin-Smith 1998) may explain part of the dietary variation of *P. myersi* and *L. disparis* in TPKFS.

The algivorous goby *Sicydium plumieri* in Puerto Rico (March and Pringle 2003) and the herbivorous North American cyprinid *Camposoma anomalum* (Evans-White et al. 2001) both had $\delta^{15}\text{N}$ signatures similar to predatory species, as did the pool-dwelling balitorids in TPKFS. These herbivorous fishes should be, therefore, classified as functional omnivores and trophic predators (sensu Parkyn et al. 2001), i.e., *you are what you assimilate*. Such omnivory may also account for the observation that all 5 species of TPKFS fishes had similar $\delta^{15}\text{N}$ signatures, and predatory fishes (*Ctenogobius duospilus* and *Schistura fasciolata*) were a maximum of only 1.4‰ $\delta^{15}\text{N}$ -enriched relative to omnivorous fishes.

Ontogenetic shifts in diet were observed in a

few species, such as *Euphaea decorata*, *Brotia hainanensis* and *Macrobrachium hainanense*, and have been observed in other predators and omnivores (Lancaster and Robertson 1995, Tavares-Cromar and Williams 1996, Lancaster and Waldron 2001, Woodward and Hildrew 2002). However, ontogenetic differences in isotope signatures were not discernable. Likewise, dietary differences between large and small parastacid crayfish also coincided with a consistency in stable isotope ratios (Parkyn et al. 2001, Hollows et al. 2002).

Foodweb properties

The foodweb properties of TPKFS were comparable to those of 9 lotic food webs summarized by Briand (1985), and to other webs constructed with a similar taxonomic resolution in basal species or food resources (Broadstone1, Duffin Creek, Lerderberg River; Table 7). Chironomidae and Ephemeroptera were the primary links between basal foods and secondary consumers, reflecting their high abundance (>60% of pool benthic fauna). Overall, the food-chain length in TPKFS pools was shorter than other lotic webs because most of the aquatic top predators fed on the same array of primary and secondary consumers without significant intra-guild predation or dietary segregation. High disturbance, low algal food resources (Jaarsma et al. 1998, Townsend et al. 1998) and/or small ecosystem size (Post 2002) might reduce food-chain length. The wet season in Hong Kong is characterized by heavy rainfall (Dudgeon and Corlett 1994, Mantel 2003), accompanied by spates that can alter the physical structure of the stream dramatically and affect the intensity of biotic interactions (Dudgeon 1993). One mea-

TABLE 5. Extended.

<i>Brotia</i>	<i>Pseudoneureclipsis</i>	<i>Eubrianax</i> + <i>Sinopsephenus</i>
12.6	11.2	4.7
(0–50)	(0–30)	(0–18)
13.9	8.2	6.4
(0–54)	(0–28)	(0–24)
14.7	9.1	8.1
(0–58)	(0–28)	(0–28)

surement of the primary production to community respiration (P/R) ratio in an unshaded pool of TPKFS was 1.02 (Dudgeon 1983b), which suggests that, even in a well-lit section of the stream, primary production was barely sufficient to meet the energy needs of consumers. Either or both spate-induced disturbance and limited algal food could account for the short foodchain length in TPKFS pools.

Taxonomic resolution of the food webs might contribute to some differences in foodweb properties observed among studies: food webs with high taxonomic resolution had higher linkage complexity than traditional webs, such as TPKFS and Lerderberg River, which had inconsistent levels of taxonomic resolution among basal, intermediate, and top species (Table 7; cf. Thompson and Townsend 2000). Food webs that included identification of meiofauna or algal species (Broadstone2, Healy Creek, Dempsters Creek; Table 7) had higher numbers of intermediate species (if meiofauna were identified) or basal species (if algae were identified) compared to TPKFS.

The overlapping diet of the top predators was reflected in the failure of isotopic mixed models to reveal any prey preference. This pattern of shared prey by the top predators may have caused the high connectance in the TPKFS food web compared to other lotic webs (Table 7). Links per species were high for TPKFS compared to most other lotic webs, except the New Zealand streams. The high degree of linkage could be an artefact if the dominant species in each family were generalist feeders because it was only these taxa, which comprised 80% of benthos abundance in pools, that were included in the gut content analyses. If any rare species that were not analyzed had highly specialized diets, their absence from the food web would have increased connectance and number of links per species. The high predator–prey ratio in TPKFS could have resulted from limited taxonomic resolution among basal species (Thompson and Townsend 2000). In addition, most dipteran and some coleopteran (particularly Elmidae) prey were identified only to family level (Appendix 1), thereby underestimating the number of prey species and, thus, further increasing the predator–prey ratio.

The diet of *Macrobrachium hainanense* appeared to be the most diverse with the largest number of links (27) among other predators (≤ 12) in TPKFS pools, but this finding was probably a bias introduced by the large sample size (146 *M. hainanense* guts examined versus ≤ 22 for other predators; see also Thompson et al. 2001). Likewise, there were fewer prey taxa in the guts of *Euphaea decorata* and perlid larvae in pools compared to their diet in riffles of the same stream (Dudgeon 1989, 2000), again probably showing the effect of sampling size.

TABLE 6. Percent contribution of food resources (mean with 95% CI in parentheses) for *Pseudogastromyzon myersi* using a dual isotope, 3-source model and for *Liniparhomaloptera disparis* using a N-isotope, 2-source model. – = food resources were not entered in model. Baetidae + *Afromurus* signals were averaged.

Taxon	Periphyton	Baetidae + <i>Afromurus</i>	Orthocladiinae or Cyanobacteria
<i>Pseudogastromyzon</i> (2 basal resources, 1 prey)	20.3 (0–81)	74.2 (6–100)	Cyanobacteria 5.5 (0–21)
<i>Pseudogastromyzon</i> (1 basal resource, 2 prey)	7.2 (0–51)	77.7 (15–100)	Orthocladiinae 15.2 (0–46)
<i>Liniparhomaloptera</i> (mixed diet)	–	86.2 (70–100)	Cyanobacteria 13.8 (0–30)
<i>Liniparhomaloptera</i> (prey species only)	–	50.0 (0–100)	Orthocladiinae 50.0 (0–100)

TABLE 7. Foodweb properties of streams. S = web size, L = number of links, C_R = realized connectance, C_L = lower connectance (2L/S[S - 1]), C_T = trophic connectance, C_D = directed connectance (L/S²), Pd-Pr (1) = predator-prey ratio (sensu Jeffries and Lawton 1985), Pr-Pd (2) = prey-predator ratio (sensu Cohen 1977). Broadstone1: Lancaster and Robertson (1995), Broadstone2: Schmid-Araya et al. (2002b), Healy Creek, Dempsters Creek: Jaarsma et al. (1998), Duffin Creek: Tavares-Cromar and Williams (1996), German Creek, Kye Burn, Little Kye Burn, Stony Creek: Thompson et al. (2001), Lerderberg River: Closs and Lake (1994). * = C_L used, # = connectance includes competitive links for predators.

Site	S	L	C _R	C _L	C _T	C _D
TPKFS, Hong Kong	28	156	0.27	0.41	0.21	0.20
Broadstone1, southern England	33	122		0.23		
Broadstone2, southern England	54-86	229-378				0.05-0.08
Briand (1985): USA, England, Finland, Japan	11-19					
Healy Creek, New Zealand	70-96	374-589	0.14-0.16			
Dempsters Creek, New Zealand	72-107	524-967	0.18-0.19			
Duffin Creek, Ontario, Canada	31-39	101-146		0.18-0.22	0.09-0.11	
German Creek, New Zealand	86		0.13			
Kye Burn, New Zealand	98		0.18			
Little Kye Burn, New Zealand	78		0.16			
Stony Creek, New Zealand	112					
Lerderberg River, Victoria, Australia	78					

Primary and secondary consumers in pools and riffles of a forested headwater stream in California fed primarily on food resources within their microhabitat (Finlay et al. 2002). This finding suggests that a food web constructed within a pool, as in our study, might be relatively compartmentalized and complete, although it could be improved by including tertiary consumers such as birds (Steinmetz et al. 2003) and by increasing the taxonomic resolution of basal food resources. A food web of riffles of TPKFS is presently being compiled and its results should provide a basis for comparison with the TPKFS pool food web. Web properties at TPKFS might vary with season, as suggested by results elsewhere (Thompson and Townsend 1999, Schmid-Araya et al. 2002b) and by variation in stable isotope signatures of Ephemeroptera in Hong Kong (Salas and Dudgeon 2001a). Drawing up a robust food web during the wet season would be difficult because regular disturbances caused by wet season spates in Hong Kong change community structure and interactions (Dudgeon 1993). The lack of inclusion of meiofauna and further resolution of algae, as in a few other studies (Jaarsma et al. 1998, Schmid-Araya et al. 2002b), also limits our ability to make comparisons. These limitations aside, our study is the first comprehensive food web based on analyses of both gut contents and stable iso-

tope signatures that has been constructed for an Asian stream. It provides a baseline for future research. For example, the broad overlap in diets of the top predators, reflected in the high connectance, suggests it is a robust food web where removal of a single ‘most connected’ species (i.e., any species that has the largest number of links in the web) might have little effect (Mantel 2003), whereas systematic removal of several of these species could lead to secondary extinctions (Dunne et al. 2002). Results of the gut content analyses agreed with those of stable isotopes for most of the strict primary consumers and predators. Elucidation of the food web avoided misleading conclusions arising from gut content or stable isotope analysis alone, particularly for omnivores, and this combined approach is recommended for future studies of food webs. Another important finding was the high dependence of the pool food web on autochthonous resources, providing further evidence of the inapplicability of some predictions of the river continuum concept to low-order tropical forest streams (e.g., Dudgeon 1994, Salas and Dudgeon 2001a, Dobson et al. 2002, March and Pringle 2003).

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Laboratory work on gut contents depended, in large part, on the patience and thoroughness

TABLE 7. Extended.

Max. chain	Mean chain	Basal	Inter-mediate	Top	Omnivores	L/S	SC _R	Pd-Pr (1)	Pr-Pd (2)
3	2.04	0.21	0.57	0.21	0.14	5.57	7.56	0.57	1.0
5	4.6					3.7		0.21	
	3.43–4.54	0.07–0.15	0.78–0.88	0.04–0.09		4.09–4.45	8.28–9.00*	0.27–0.38	
4	2.29	0.19	0.47	0.33			9.28#		
5	2.98–3.02	0.44–0.49	0.30–0.31	0.21–0.24	0.22–0.30	5.34–6.14	11.05–13.79		1.36–1.55
9–10	4.31–4.67	0.36–0.47	0.41–0.51	0.12–0.13	0.09–0.14	7.28–9.04	13.07–20.01		1.37–1.65
		0.15–0.19	0.03–0.46	0.36–0.78		3.14–3.74		0.0–0.07	
	2.40					4.10			2.00
	2.35					6.42			2.05
	2.39					4.81			1.78
	2.39					7.40			1.92
2–3	1.5–2.0	0.10–0.27	0.27–0.60	0.3–0.5		1–2	3–5	0.3–0.5	1.3–1.5

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APPENDIX 1. Diet of prey collected during the present study and used for calculating predator–prey ratio sensu Jeffries and Lawton (1985). FPOM = fine particulate organic matter, CPOM = coarse particulate organic matter.

Prey species	Diet/trophic status	No. of species	Reference
GASTROPODA			
<i>Brotia hainanensis</i>	FPOM, unicellular algae	1	Present study
COPEPODA			
	FPOM	2	Lancaster and Robertson (1995)
DECAPODA			
<i>Caridina cantonensis</i>	Unicellular algae primarily, some fungi, FPOM and animal parts	1	Present study
EPHEMEROPTERA			
<i>Baetis</i> spp.	Unicellular algae, diatoms	2	Baetidae: present study
<i>Chopralla</i> sp.	Unicellular algae, diatoms	1	Baetidae: present study
<i>Procloeon</i> sp.	Unicellular algae, diatoms	1	Baetidae: present study
<i>Afronurus</i> spp.	Unicellular algae, diatoms	2	Present study
<i>Compsoneturia</i> sp.	Unicellular algae, diatoms	1	Deduced from diet of <i>Afronurus</i>
<i>Choroterpes</i> spp.	Unicellular algae, FPOM, diatoms	2	Deduced from diet of <i>Habrophlebiodes</i>
<i>Habrophlebiodes gilliesi</i>	Unicellular algae, FPOM, diatoms	1	Present study
<i>Isca purpurea</i>	Unicellular algae, FPOM, diatoms	1	Deduced from diet of <i>Habrophlebiodes</i>
<i>Serretella albostrata</i>	CPOM, FPOM	1	Dudgeon (1992: 82): diet deduced from mouthparts
<i>Torleya arenosa</i>	Fungi, diatoms, FPOM	1	Present study
HETEROPTERA			
Corixidae	Piercers, herbivores, collector-gatherers	2	Polhemus (1996), Dudgeon (1999)
TRICHOPTERA			
<i>Agapetus</i> spp.	Diatoms, detritus	2	Wiggins (1996)
Hydroptilidae	Filamentous algae, diatoms	2	Keiper and Foote (2000)
<i>Melanotrichia serica</i>	FPOM, diatoms	1	Barnard and Dudgeon (1984)
<i>Goerodes doligug</i>	CPOM	1	Motomori et al. (2001), Wiggins (1996)
<i>Anisocentropus maculatus</i>	FPOM, CPOM, diatoms	1	Present study
<i>Helicopsyche</i> sp.	Diatoms, unicellular algae	1	Present study
COLEOPTERA			
Scirtidae	FPOM	2	CSIRO (1991), Dudgeon (1999)
<i>Eubrianax</i> sp.	Diatoms, unicellular algae	1	Present study
<i>Psephenoides</i> sp.	Diatoms, unicellular algae	1	Deduced from diet of <i>Eubrianax</i> and <i>Sinopsephenus</i>
<i>Sinopsephenus chinensis</i>	Diatoms, unicellular algae	1	Present study
Elmidae	Scrapers, collector-gatherers	2	CSIRO (1991), White and Brigham (1996)
DIPTERA			
Nymphomyiidae	Scrapers, collector-gatherers	2	Courtney et al. (1996)
Dixidae	Collector-gatherers	2	Courtney et al. (1996)
Simuliidae	Herbivores	2	Wallace et al. (1987)
Chironominae	Unicellular algae, FPOM	2	Present study
Orthocladiinae	FPOM, unicellular algae	2	Present study
Canacidae	Scrapers	2	Courtney et al. (1996)

APPENDIX 2. Diet of predatory taxa collected during the present study and used for calculating predator-prey ratio sensu Jeffries and Lawton (1985). FPOM = fine particulate organic matter.

Prey species	Diet/trophic status	No. of species	Reference
DECAPODA			
<i>Macrobrachium hainanense</i>	Predator	1	Present study
HYDRACHNIDA	Parasite, predator	2	Smith et al. (2001)
ODONATA			
<i>Philoganga vetusta</i>	Predator	1	Westfall and Tennessen (1996)
<i>Euphaea decorata</i>	Predator	1	Present study, Dudgeon (1989)
PLECOPTERA			
Perlidae	Predator	2	Present study, Dudgeon (2000)
HETEROPTERA			
<i>Enithares</i> spp.	Predator	2	Giller (1986)
TRICHOPTERA			
<i>Ecnomus</i> sp.	Predator	1	Barnard and Clark (1986)
<i>Polycentropus</i> sp.	Predator	1	Dudgeon and Richardson (1988)
<i>Pseudoneureclipsis</i> spp.	Predator	2	Present study
<i>Cheumatopsyche</i> spp.	Invertebrates, FPOM	2	Palmer et al. (1993)
COLEOPTERA			
<i>Berosus</i> sp.	Predator	1	White and Brigham (1996)
DIPTERA			
Ceratopogonidae	Generally predators	2	Courtney et al. (1996)
Tanypodinae	Animal parts, unicellular algae, FPOM	2	Present study
MEGALOPTERA			
<i>Neochauliodes</i> sp.	Predator	1	Dudgeon (1999)
PISCES			
<i>Liniparhomaloptera disparis</i>	Unicellular algae, filamentous algae, animal parts	1	Present study, Dudgeon (1987)
<i>Pseudogastromyzon myersi</i>	Unicellular algae, filamentation algae, animal parts	1	Present study, Dudgeon (1987)
<i>Schistura fasciolata</i>	Predator	1	Present study, Dudgeon (1987)
<i>Ctenogobius duospilus</i>	Predator	1	Present study, Dudgeon (1987)
<i>Parazacco spilurus</i>	Predator	1	Present study