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Are autochthonous foods more important than allochthonous resources to benthic consumers in tropical headwater streams?

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Abstract. Increasing evidence suggests that autochthonous foods are the principal basis of consumer production in tropical forest streams, despite the predominance of terrestrial detritus inputs. The relative importance of autochthonous and allochthonous energy for the dominant benthic consumers was investigated in 3 tropical headwater streams with different shading conditions in Hong Kong with a combination of assimilation-based analyses: stoichiometry, C and N stable isotopes, and fatty acid (FA) profiling. The snail *Brotia hainanensis* (Pachychilidae), shrimps *Caridina cantonensis* (Atyidae) and *Macrobrachium hainanense* (Palaemonidae), and their potential basal food sources (leaf litter, fine particulate organic matter [FPOM], periphyton, cyanobacteria, and filamentous algae) were collected in Tai Po Kau Forest Stream (shaded 1), Shing Mun Stream (shaded 2), and Pak Ngau Shek Stream (open) during the 2004 dry season (January and February). All samples were analyzed for C:N ratios, $\delta^{13}C$, and $\delta^{15}N$ values. Total FAs were extracted from each sample, and concentrations of 35 important FAs were analyzed by gas chromatography–mass spectrometry (GC–MS). C:N ratios of algal foods were markedly lower than those of terrestrial detritus and similar to those of the test animals at all 3 sites, a result that suggested that autochthonous sources were relatively more nutritious than were allochthonous sources. Autochthonous foods were more ^{13}C and ^{15}N enriched than were allochthonous foods at all sites. The algal sources contributed to 29 to 98% of consumer biomass, generally more than was attributed to the terrestrial sources (2–71%). Consumers also showed distinctive FA profiles indicating consumption of autochthonous foods, especially periphytic diatoms and cyanobacteria, as revealed by the elevated concentrations of FA biomarkers such as palmitoleic (16:1[*cis*-9]) and eicosapentaenoic acids (20:5[all *cis*-5,8,11,14,17]) in the consumers, periphyton, and cyanobacteria. Our results suggest that autochthonous resources are possibly more important than allochthonous foods to secondary production in tropical headwater streams.

Key words: energy flow, fatty acids, food web, stable isotopes, stoichiometry, trophic level.

Consumers in tropical and temperate headwater streams might derive energy from contrasting basal food sources. Forested headwaters usually have a considerable supply of leaf litter coupled with dense riparian cover. Thus, they are expected to have limited autochthonous production because of extensive shading. The river continuum concept (RCC) suggests that allochthonous detritus is the major energy source in shaded headwaters, whereas the importance of autochthonous foods and fine particulate organic matter increases in wider downstream sites along the river continuum (Vannote et al. 1980). Studies on temperate

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lotic food webs generally support this hypothesis (e.g., Winterbourn et al. 1984, Hicks 1997, Hall et al. 2001, but see Thorp and Delong 1994). However, recent research demonstrates that the RCC does not fully reflect the relative importance of the basal resources in tropical lotic ecosystems. Autochthonous foods, especially periphytic microalgae and cyanobacteria, are disproportionately important to consumers in small shaded streams in northeastern Puerto Rico (March and Pringle 2003), southeastern Brazil (Moulton et al. 2004, Brito et al. 2006), and tropical Asia (Salas and Dudgeon 2001, Mantel et al. 2004, Yam and Dudgeon 2005).

Functional feeding group classification (sensu Cummins 1973), upon which some tenets of the RCC are based, might not provide a reliable indication of basal energy source of consumers (Mihuc 1997). Consumption and processing of food materials do not directly imply assimilation of all the components into consumer tissues and, thus, might misrepresent the energy flow in lotic food webs. Recent research suggests that, although the xiphocarid shrimp, *Xiphocaris elongata,* is an effective detritus processor that ingests a significant amount of coarse particulate organic matter (March et al. 2001), most of its energy is derived from autochthonous C sources (March and Pringle 2003). Parkyn et al. (2001) and Hollows et al. (2002) found that parastacid crayfishes (*Paranephrops* spp.) appear to function as omnivores by consuming both leaf litter and other invertebrates but are actually predators that obtain most of their energy from invertebrate prey.

Understanding the trophic roles of consumers is essential for improving our knowledge of stream energy flow and nutrient cycling (Mihuc 1997, Parkyn et al. 2001, Vanni et al. 2002). Assimilation-based analyses, such as stoichiometry, stable isotopes, and fatty acids, have been increasingly applied in aquatic ecology because they allow detailed examination of consumer–resource relationships (e.g., Peterson and Fry 1987, Peterson 1999, Müller-Navarra et al. 2000, Frost et al. 2002, Sterner and Elser 2002, Sushchik et al. 2003). Elemental compositions (e.g., C and N) of consumers and their foods control the rates and ratios of nutrient recycling in ecosystems and reflect the degree of nutrient constraints imposed upon consumers by their resources (Vanni et al. 2002, Dodds et al. 2004). Resource C-to-nutrient ratios are indicators of food quality and might underlie consumer food choices. In particular, foods with low C:N are preferred by consumers (Frost et al. 2002, Sterner and Elser 2002).

Stable isotopes and fatty acids (FAs) can be used to discriminate among basal resources assimilated by consumers in lotic ecosystems because allochthonous and autochthonous foods usually contain distinct ^{13}C:^{12}C ratios (Peterson and Fry 1987) and essential FA (EFA) biomarkers (Napolitano 1999, Müller-Navarra et al. 2000). ^{13}C:^{12}C ratios are only slightly fractionated, and EFAs are conservative (especially those in structural and storage lipids, e.g., phospholipids and triacylglycerols) along food chains (Peterson and Fry 1987, Napolitano 1999). Thus, ^{13}C:^{12}C ratios and FA profiles of consumers can reflect the diets they have assimilated. Researchers have applied stable isotopes and EFAs successfully to elucidate the trophic basis of food webs in various aquatic habitats (e.g., Müller-Navarra et al. 2000, Hall et al. 2001, Sushchik et al. 2003). Stable isotopes are also useful for estimating the trophic positions of consumers because ^{15}N:^{14}N ratios are progressively enriched by 3 to 4‰ with every trophic transfer (Vander Zanden and Rasmussen 2001, Phillips et al. 2005). A recent study emphasized the use of stable isotopes and EFAs in tandem because their combined application yields important insights into pathways of energy transfer (Perga et al. 2006).

In our study, which was undertaken in Hong Kong within the Asian tropics, the relative importance of autochthonous and allochthonous resources in 3 streams with different riparian shading was determined with 3 assimilation-based techniques: stoichiometry, stable isotopes, and FA profiling. Atyid and palaemonid shrimps and pachychilid snails were selected as the study animals because they are abundant and widespread in streams in Hong Kong and elsewhere in Asia (Dudgeon 1999) and contribute significantly to benthic biomass and secondary production (Mantel and Dudgeon 2004b, Yam and Dudgeon 2006, Li and Dudgeon 2009). For instance, pachychilids constitute almost 30% of macroinvertebrate biomass in shaded Hong Kong streams (Li and Dudgeon 2009). All 3 study species have mixed diets (Mantel et al. 2004, Yam and Dudgeon 2005, Li and Dudgeon 2008) and are appropriate models for investigating the trophic basis of stream food webs in Hong Kong. We hypothesized that diet of aquatic consumers would change with riparian shading, such that allochthonous sources would be the trophic basis of consumer production in the shaded sites, whereas autochthonous foods would be more important at the unshaded site.

Methods

Study sites

Three 3rd-order streams with different degrees of riparian shading, situated in the central New Territories of Hong Kong Special Administrative Region (China), were selected for our study: Tai Po Kau Forest Stream (shaded 1), Shing Mun Stream (shaded 2), and

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Pak Ngau Shek Stream (open). Tai Po Kau Forest Stream (lat 22°25′17″N, long 114°10′37″E) is a perennial shaded stream that flows through secondary forest at ~200 m asl inside Tai Po Kau Nature Reserve. Shing Mun Stream (lat 22°23′51″N, long 114°8′47″E) flows inside Shing Mun Country Park adjacent to and at the same altitude as Tai Po Kau Nature Reserve and also drains secondary forest. More than 70% of the channels of shaded 1 and shaded 2 is shaded by riparian trees. Pak Ngau Shek Stream (lat 22°26′24″N, long 114°7′22″E) is at slightly lower elevation (~100 m asl) and drains a mixture of secondary forest, shrubland, and abandoned agricultural land. More than 80% of the channel is unshaded.

A 150-m long section of each stream was selected as the study site and the source of animals used in our study. The sites were generally unpolluted and had low PO_4^{3-} and NO_3^- levels. PO_4^{3-} concentrations in shaded 1 (dry season monthly mean = 0.3 mg/L) and shaded 2 (0.3 mg/L) were slightly higher than were NO_3^- concentrations (0.1 mg/L in both streams), whereas the opposite was observed at the open site (0.5 and 1.2 mg/L for PO_4^{3-} and NO_3^-, respectively) (Salas 1998). Further descriptions of the 3 streams are given by Dudgeon and Wu (1999) and Salas and Dudgeon (2001).

Sample collection

Between January and February 2004 (dry season), the snail *Brotia hainanensis* (Brot 1872) (Gastropoda: Pachychilidae), shrimps *Caridina cantonensis* (Yu 1938) (Decapoda:Atyidae) and *Macrobrachium hainanense* (Parisi 1919) (Decapoda:Palaemonidae), and their potential food sources at each study site were collected. *Brotia hainanensis* and *C. cantonensis* have mixed feeding modes and consume both allochthonous and autochthonous foods (Mantel et al. 2004, Yam and Dudgeon 2005), whereas *M. hainanense* is a predator that consumes a wide range of benthic macroinvertebrates (Mantel et al. 2004).

Density and biomass data are as follows: *B. hainanensis*, ~60 individuals (ind)/m^2 and ~1150 mg shell-free dry mass/m^2 (Li and Dudgeon 2009); *C. cantonensis*, ~100 ind/m^2 and ~800 mg ash-free dry mass (AFDM)/m^2 (Yam and Dudgeon 2006); *M. hainanense*, 3 to 5 ind/m^2 and ~500 mg AFDM/m^2 (Mantel and Dudgeon 2004b). For each animal species, 5 replicate samples each consisting of 5 to 15 individuals of similar sizes were used. Shell aperture widths of *B. hainanensis* were 18.4 ± 0.3 mm (mean ± 1 SE), whereas carapace lengths of *C. cantonensis* and *M. hainanense* were 7.4 ± 0.1 mm and 17.4 ± 0.5 mm, respectively. Shell aperture width was used as an indicator of snail size because decollation of the shell apex hindered the use of shell length (Dudgeon 1982b). Snails were hand picked from the stream bed, and shrimps were collected with a hand net (mesh size: 250 μm). Animals were acclimated under laboratory conditions without food for 3 d to allow gut clearance and were then stored at −20°C.

Five replicate samples of leaf litter (~500 g each) of mixed species were collected from the stream bed by hand. Water samples containing suspended fine particulate organic matter (FPOM) were collected with Nalgene bottles (5 replicates of 2 L each) after kicking the surface of the stream bed for 30 s. Nalgene bottle openings were covered by a hand net (mesh size = 250 μm) to avoid collection of coarse particulate organic matter during this process. Periphyton and cyanobacteria were scraped from submerged stones coated with green and black patches of algae, respectively (3 replicates, each consisting of algal patches from 25 to 30 stones). Filamentous algae (*Cladophora* spp.), which were present (in small amounts) only at shaded 2, were hand picked (7 samples of ~1 g each). Samples of basal foods were stored at −20°C before processing.

Laboratory procedures for stoichiometry, stable isotope, and FA analyses

Carbonate shells of animals were removed before analysis because shell ^{13}C:^{12}C ratio differs from that of body tissue (Hershey and Peterson 1996). Animals were freeze dried (VF3 +SL; VirTis, New York), whereas leaf litter and filamentous algae were oven dried to constant mass at 60°C. Periphyton and cyanobacteria were centrifuged at 5000 rpm into pellets (Universal 30 RF; Hettich Zentrifugen, Tuttlingen, Germany). FPOM was collected by filtering the water samples. Algal pellets and FPOM were oven dried. All samples were homogenized with a mortar and pestle or a small coffee mill (for leaf litter).

Stable isotope analysis was conducted at the University of California Davis Stable Isotope Facility to determine the sample bulk tissue ^{13}C:^{12}C and ^{15}N:^{14}N ratios with an isotope ratio mass spectrometer (Europa Hydra 20/20; Europa Scientific, Cambridge, UK). The ratios were reported as $\delta^{13}C$ and $\delta^{15}N$ values (in ‰) and were defined as the ‰ deviation from an international standard (Peedee Belemnite for C and air for N): $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$, where $R = {}^{13}C:{}^{12}C$ or $^{15}N:{}^{14}N$ (Peterson and Fry 1987). A 2-isotope, multiple-source mixed model (IsoSource, version 1.3.1; http://www.epa.gov/wed/pages/models/stableIsotopes/isosource/isosource.htm) was used to calculate the percentage contribution of each food to consumers (Phillips et al. 2005), with $\delta^{13}C$ and

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$\delta^{15}N$ fractionations per trophic transfer (1 trophic transfer for *B. hainanensis* and *C. cantonensis*, and 2 for *M. hainanense*) set at 0.5‰ and 2.2‰, respectively, as recommended by McCutchan et al. (2003). Molar C:N ratios of samples also were measured with the isotope ratio mass spectrometer.

Total FAs were extracted by the method of Bligh and Dyer (1959) and were methylated to FA methyl esters with 14% BF_3–methanol solution. Detailed description of FA extraction procedures is given in Lau et al. (2008). Sample FA concentrations were analyzed by an Agilent 6890N gas chromatography coupled with an Agilent 5973 mass spectrometer (GC–MS; Agilent Technologies, Santa Clara, California). The 37 Component FA Methyl Ester Mix (Supelco, Bellefonte, Pennsylvania) was used as a FA standard, and nonadecanoic acid (C19:0) methyl esters (Sigma, St. Louis, Missouri) were used as the internal standard. A DB-225 capillary column (30.0-m length, 0.25-mm internal diameter, 0.25-μm film thickness; Agilent Technologies) was used with a splitless injection mode. Oven temperatures were programmed as follows: 60°C for 3 min, increasing by 40°C/min to the final temperature of 200°C, which was kept for 33 min. Carrier gas was He with a column flow rate of 1.1 mL/min (constant flow). A 1-μL sample was injected into the GC–MS for each analysis.

Data analysis

C:N ratios, $\delta^{13}C$, and $\delta^{15}N$ signatures of the food sources and consumers from each study site were compared by 1-way analyses of variance (ANOVA) followed by Tukey multiple comparisons in SPSS (release 14.0.0, SPSS, Chicago, Illinois). Log(x) transformed data were used when variances of the groups in comparison were heterogeneous. Nonmetric multidimensional scaling (nMDS) was used to ordinate sample FA profiles (FA concentrations were log[$x + 1$] transformed) based on group-average clustering of Bray–Curtis similarities. Ranks of similarities between sample FA profiles in the underlying nMDS similarity matrix were also compared using analysis of similarities (ANOSIM). nMDS and ANOSIM were done with Primer (version 6, Primer-E, Plymouth, UK). Statistical significance was set at $\alpha = 0.05$.

Results

C:N ratios of autochthonous foods (periphyton, cyanobacteria, and filamentous algae) were consistently lower than those of allochthonous sources (leaf litter and FPOM) and appeared more similar to those of the consumers at all 3 sites (1-way ANOVA, all $p < 0.001$; Table 1). Mean C:N ratio differences between leaf litter and periphyton ranged from 31.1 (shaded 1) to 56.0 (open) and were similar to those between leaf litter and cyanobacteria, which ranged from 31.6 (shaded 1) to 54.3 (open). Mean C:N ratio differences between FPOM and periphyton and between FPOM and cyanobacteria ranged from 8.4 (open) to 17.3 (shaded 2) and 6.7 (open) to 17.3 (shaded 2), respectively. *Brotia hainanensis* had higher C:N ratios than did shrimps in the shaded sites, but no significant difference was found among the consumer C:N ratios in the open site (Table 1).

Allochthonous sources were generally more ^{13}C and ^{15}N depleted than were the autochthonous foods and the consumers at all 3 sites (1-way ANOVA, all $p < 0.001$; Table 1, Fig. 1A–C). $\delta^{13}C$ values of leaf litter were 5.4‰ (shaded 2) to 9.0‰ (open) lower than those of periphyton, and 4.4‰ (shaded 2) to 6.7‰ (shaded 1) lower than those of cyanobacteria. FPOM was 3.6‰ (shaded 2) to 8.3‰ (shaded 1) and 1.7‰ (open) to 2.6‰ (shaded 1) more ^{13}C depleted than were periphyton or cyanobacteria. $\delta^{13}C$ signatures of consumers were distinct from those of leaf litter but similar to those of periphyton and cyanobacteria, especially at the open site and at shaded 2 (Table 1, Fig. 1A–C).

Leaf litter had the lowest $\delta^{15}N$ at all 3 sites (Table 1, Fig. 1A–C). It was 2.3‰ (shaded 1) to 6.7‰ (open) and 2.6‰ (shaded 1) to 4.2‰ (open) more ^{15}N depleted than were periphyton and cyanobacteria, respectively. In contrast, FPOM generally had $\delta^{15}N$ signatures similar to those of periphyton and cyanobacteria. All food sources in the shaded sites had lower $\delta^{15}N$ values than those of the consumers, but periphyton and *B. hainanensis* in the open site were exceptionally ^{15}N enriched and had mean $\delta^{15}N$ values 1.21‰ and 0.62‰ higher than those of *M. hainanense*, which includes other invertebrates in its diet (Mantel and Dudgeon 2004a, Mantel et al. 2004).

Based on the calculations using the IsoSource model (Table 2), leaf litter was a relatively minor energy source for consumers (0.8–17.1% contribution) in most cases, except for *B. hainanensis* in shaded 1 (28.7%) and *C. cantonensis* at the open site (41.9%), whereas FPOM accounted for 18.5 to 32.2% of the biomass of primary consumers in these 2 sites. *Brotia hainanensis* and *C. cantonensis* in shaded 2 showed significant dependence on autochthonous foods (80.3% and 97.8%, respectively), especially periphyton. The percentage contributions of autochthonous resources to *C. cantonensis* biomass in shaded 1 and shaded 2 were, respectively, 2× and 3× those in the open site (Table 2). Leaf litter was not an important basal resource for *M. hainanense* at any study site, particularly the shaded streams, and autochthonous primary production supported 52.4 to 95.7% of *M. hainanense* biomass (Table 2). Across all

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TABLE 1. Mean (SE) molar C:N ratios and $\delta^{13}C$ and $\delta^{15}N$ signatures of foods and consumers collected from Tai Po Kau Forest Stream (shaded 1), Shing Mun Stream (shaded 2), and Pak Ngau Shek Stream (open) during the dry season (January and February) of 2004. LL = leaf litter, FPOM = fine particulate organic matter, PP = periphyton, CY = cyanobacteria, FAl = filamentous algae, BH = *Brotia hainanensis*, CC = *Caridina cantonensis*, MH = *Macrobrachium hainanense*, n = number of replicate samples. In each row, mean values with the same superscript are not significantly different (Tukey test, $p > 0.05$).

Site	LL	FPOM	PP	CY	FAl	BH	CC	MH
n								
Shaded 1	5	5	3	3	—	5	4	5
Shaded 2	5	5	3	3	7	5	3	5
Open	5	5	3	3	—	5	4	5
Molar C:N								
Shaded 1[a]	40.08^{E}	25.57^{D}	8.98^{C}	8.49^{C}	—	5.60^{B}	4.26^{A}	4.17^{A}
	(1.10)	(0.84)	(0.11)	(0.22)	—	(0.09)	(0.03)	(0.09)
Shaded 2[a]	58.05^{E}	26.07^{D}	8.75^{B}	8.76^{B}	13.36^{C}	6.36^{B}	4.14^{A}	4.44^{A}
	(3.76)	(2.32)	(0.36)	(0.18)	(1.03)	(0.25)	(0.01)	(0.09)
Open[a]	65.23^{D}	17.63^{C}	9.20^{B}	10.96^{B}	—	4.87^{A}	3.96^{A}	4.07^{A}
	(8.82)	(0.40)	(0.52)	(1.43)	—	(0.09)	(0.03)	(0.05)
$\delta^{13}C$								
Shaded 1[b]	-29.88^{A}	-29.24^{B}	-20.94^{E}	-23.20^{D}	—	-26.05^{C}	-24.65^{CD}	-24.73^{CD}
	(0.17)	(0.10)	(0.91)	(0.79)	—	(0.21)	(0.04)	(0.10)
Shaded 2	-30.79^{A}	-29.02^{B}	-25.37^{CD}	-26.39^{C}	-28.24^{B}	-25.69^{C}	-24.16^{DE}	-23.88^{E}
	(0.20)	(0.21)	(0.64)	(0.23)	(0.35)	(0.11)	(0.15)	(0.17)
Open	-29.81^{A}	-26.40^{B}	-20.85^{D}	-24.69^{BC}	—	-22.77^{CD}	-24.77^{BC}	-21.49^{D}
	(0.70)	(0.15)	(0.43)	(0.94)	—	(0.25)	(0.13)	(0.21)
$\delta^{15}N$								
Shaded 1	-3.27^{A}	-0.70^{B}	-0.97^{B}	-0.70^{B}	—	0.51^{C}	2.06^{D}	4.41^{E}
	(0.22)	(0.23)	(0.27)	(0.08)	—	(0.05)	(0.10)	(0.08)
Shaded 2[c]	-3.89^{A}	-0.45^{B}	-0.54^{B}	-0.91^{B}	1.80^{C}	0.62^{BC}	2.11^{CD}	4.55^{D}
	(0.14)	(0.35)	(0.55)	(0.24)	(0.59)	(0.10)	(0.17)	(0.08)
Open[c]	1.59^{A}	4.26^{B}	8.26^{D}	5.82^{BCD}	—	7.67^{D}	4.34^{BC}	7.05^{CD}
	(0.55)	(0.22)	(0.79)	(1.57)	—	(0.15)	(0.27)	(0.30)

[a] $\log(x)$ transformed
[b] $\log(x + 33)$ transformed
[c] $\log(x + 6)$ transformed

sites, algal foods contributed to 29 to 98% of the consumer biomass, and such contributions were generally higher than those attributed to allochthonous sources (2–71%).

In total, 35 FAs were identified among the samples (Appendix). Consumers contained higher FA concentrations than did the basal food sources at all sites (Appendix). Distinct site groupings were not apparent in the nMDS plot (Fig. 2A), but results from ANOSIM indicated significant differences in the FA profiles of food sources and consumers among the 3 sites (global $R = 0.43$, $p = 0.001$). Sample FA profiles at shaded 1 were more dissimilar to those at shaded 2 ($R = 0.42$, $p = 0.001$) than to those at the open site ($R = 0.28$, $p = 0.015$), whereas highest dissimilarity was found between the shaded 2 and the open sites ($R = 0.58$, $p = 0.001$). nMDS ordinations showed distinct groupings among basal food sources and consumers (Fig. 2B), but in general, all consumers were closer to the autochthonous food sources than to the allochthonous food sources. This finding was further supported by ANOSIM results (global $R = 0.79$, $p = 0.001$). Subsequent pairwise tests of similarities indicated that R values were lower for test pairs between autochthonous foods and consumers (R range, 0.57–0.96, $p < 0.05$) than for test pairs between allochthonous foods and consumers (all $R = 1$, $p = 0.001$). Periphyton, cyanobacteria, filamentous algae, and consumers were characterized by FAs 14:0, 16:0, 16:1(*cis*-9), 18:1(*trans*-9), 20:4(all *cis*-5,8,11,14), and 20:5(all *cis*-5,8,11,14,17), whereas leaf litter was higher in FAs 18:2(all *cis*-9,12), 18:3(all *cis*-9,12,15), 23:0, and 24:0 than were the autochthonous sources (Appendix).

Discussion

The stoichiometric analysis indicated that autochthonous foods have lower C:N ratios and are more valuable foods than are allochthonous foods (Sterner and Elser 2002). C and N stable isotope signatures of the autochthonous and allochthonous foods were well differentiated and were comparable to published values (e.g., Peterson and Fry 1987, Bunn et al. 1997). In-stream primary production was consistently more

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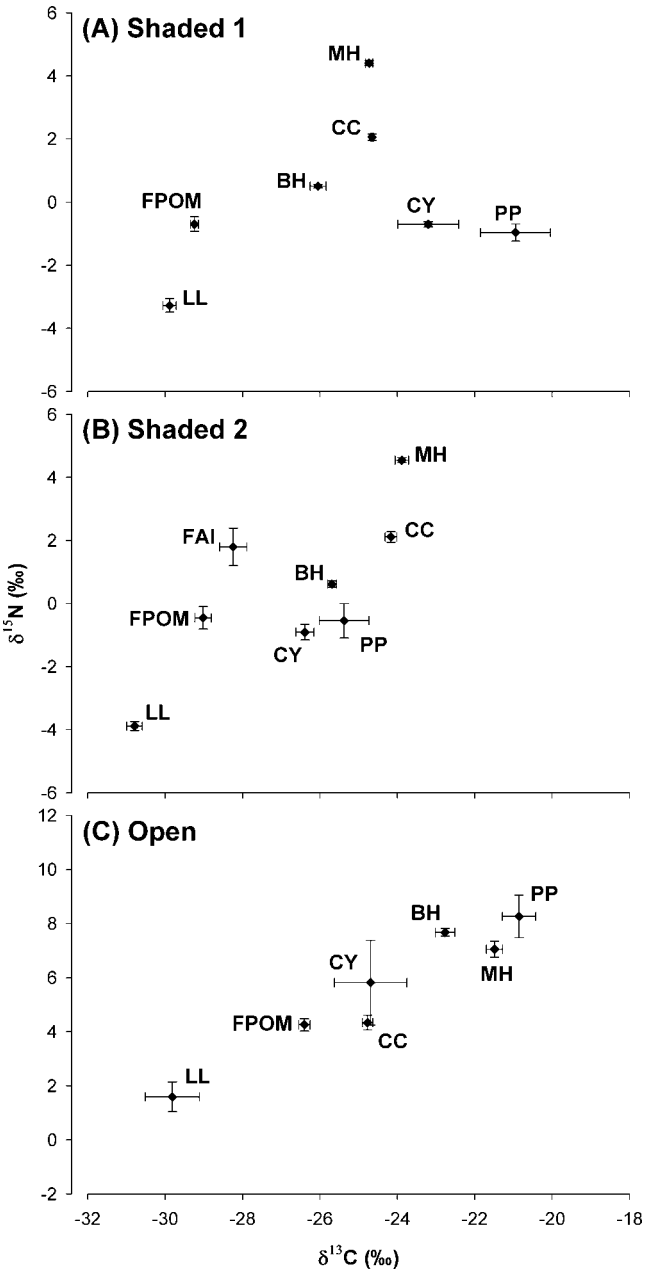


FIG. 1. Biplot of $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ±1 SE) of food and animal samples collected from (A) Tai Po Kau Forest Stream (shaded 1), (B) Shing Mun Stream (shaded 2), and (C) Pak Ngau Shek Stream (open) during the dry season (January and February) of 2004. See Table 1 for abbreviations.

^{13}C and ^{15}N enriched than was terrestrial detritus (March and Pringle 2003, Brito et al. 2006), whereas C signatures of FPOM were between those of periphytic algae and leaf litter, as noted in other studies of Hong Kong streams (Salas and Dudgeon 2001, Mantel et al. 2004).

Our stable isotope analyses suggested that food chains in the 3 study streams tended to be algal based, particularly in shaded 2 and the open site. In most cases, FPOM was a more important energy source than was leaf litter for consumers (except for *C. cantonensis* at the open site), probably because of its lower C:N ratio and higher palatability (Bretschko and Moser 1993, Burns and Walker 2000). Periphyton and cyanobacteria contributed to >60% of *C. cantonensis* biomass in the shaded sites and ~30% in the open site, a result that provides evidence that availability of microalgae for consumers was not limited by shading. Previous studies also reported that periphyton can support >60% and 35 to 60% of *Caridina* spp. biomass in unshaded and shaded streams in Hong Kong (Mantel et al. 2004, Yam and Dudgeon 2005). Likewise, algae are important to atyid shrimps (*Atya* spp.) in the shaded streams in Puerto Rico and account for 52 to 65% of their biomass (March and Pringle 2003).

Resource elemental ratios might influence food use by *B. hainanensis*. This snail was particularly dependent on algae (≥70%) in shaded 2 and the open site, but it assimilated more allochthonous than autochthonous foods in shaded 1. The mean difference in leaf litter C:N ratios between shaded 1 and the other 2 sites was surprisingly high (−21.56 ± 3.59, mean ±1 SE) and might account for the increased dependence of *B. hainanensis* upon allochthonous sources at shaded 1. *Brotia hainanensis* has alternative feeding modes and can function as a shredder or a grazer (Dudgeon 1982a, 1999). Our present results are generally consistent with the stable isotope analysis results from a study on pools in Tai Po Kau Forest Stream (where shaded 1 was situated), which indicated that this snail derived energy mainly from periphytic algae and cyanobacteria, which contributed to 67% and 16% of its biomass, respectively (Mantel et al. 2004). The diets of *C. cantonensis* and *B. hainanensis* varied among the 3 sites, but *M. hainanense* tended to depend mainly on autochthonous basal foods, with relatively higher reliance on cyanobacteria than on periphyton in shaded 1 and the open site. This result provides further evidence that food chains in the study streams were characterized by high levels of autochthony.

Brotia hainanensis had higher $\delta^{15}N$ values at the open site than at shaded 1 and 2 because of its apparent reliance on ^{15}N-enriched periphyton and cyanobacteria at this site. Intersite variations in $\delta^{15}N$ among *M. hainanense* were lower than for the other 2 consumers, a result that reflected the relatively stable trophic positions of these predators across the study streams. Other *Macrobrachium* species also showed limited variations in $\delta^{15}N$ (<1‰) among tropical fresh waters in Brazil (Brito et al. 2006). *Macrobrachium hainanense* had relatively lower $\delta^{15}N$ values than *B. hainanensis* because this predatory shrimp would have assimilated

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TABLE 2. Mean percentage contributions (1–99 percentile range) of basal foods to consumers from Tai Po Kau Forest Stream (shaded 1), Shing Mun Stream (shaded 2), and Pak Ngau Shek Stream (open) during the dry season (January and February) of 2004. FPOM = fine particulate organic matter.

	Brotia hainanensis			*Caridina cantonensis*			*Macrobrachium hainanense*		
Foods	Shaded 1	Shaded 2	Open	Shaded 1	Shaded 2	Open	Shaded 1	Shaded 2	Open
Allochthonous									
Leaf litter	28.7 (0–65)	9.8 (0–25)	11.5 (0–32)	7.1 (0–16)	0.8 (0–4)	41.9 (14–65)	4.5 (0–11)	1.6 (0–7)	17.1 (0–44)
FPOM	30.0 (0–70)	9.9 (0–34)	18.5 (0–51)	32.2 (6–56)	1.4 (0–6)	29.0 (0–81)	43.1 (20–64)	2.7 (0–10)	26.9 (0–71)
Total	58.7	19.7	30.0	39.3	2.2	70.9	47.6	4.3	44.0
Autochthonous									
Periphyton	18.3 (0–43)	39.8 (1–81)	44.7 (19–67)	23.6 (0–56)	89.4 (76–98)	11.7 (0–32)	19.8 (0–49)	81.5 (60–95)	25.5 (1–53)
Cyanobacteria	23.0 (0–57)	34.6 (0–84)	25.3 (0–75)	37.1 (0–79)	6.4 (0–23)	17.5 (0–51)	32.6 (0–70)	10.7 (0–38)	30.5 (0–83)
Filamentous algae	— —	5.9 (0–19)	— —	— —	2.0 (0–8)	— —	— —	3.5 (0–13)	— —
Total	41.3	80.3	70.0	60.7	97.8	29.2	52.4	95.7	56.0

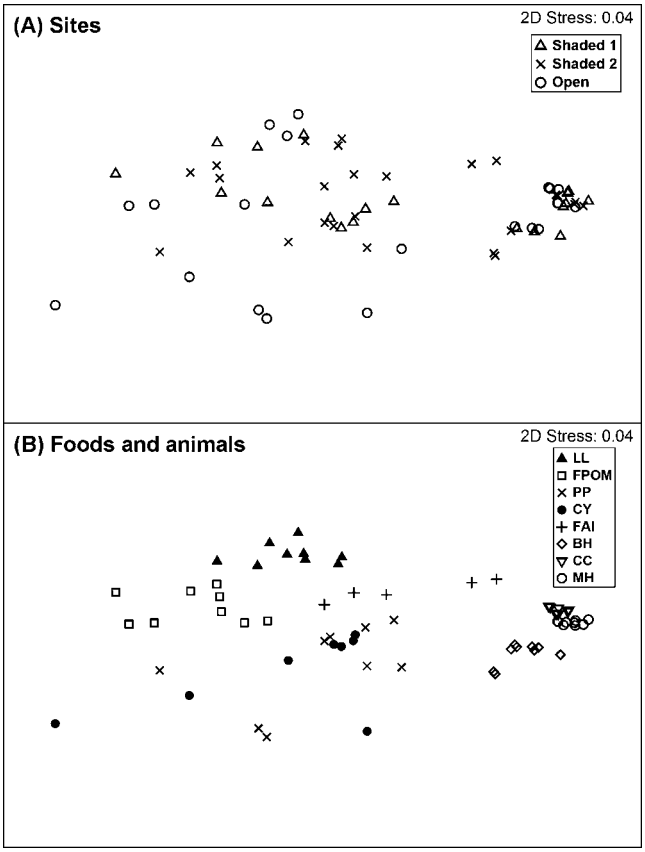


FIG. 2. Nonmetric multidimensional scaling (nMDS) configuration (2-dimensional) of fatty acid profiles of food and animal samples collected from Tai Po Kau Forest Stream (shaded 1), Shing Mun Stream (shaded 2), and Pak Ngau Shek Stream (open) during the dry season (January and February) of 2004. Data were ordinated by (A) site and by (B) food and animal categories. See Table 1 for abbreviations.

macroinvertebrates, such as chironomids and calamoceratid caddisflies (Mantel and Dudgeon 2004a, Mantel et al. 2004), which can be >5‰ more ^{15}N depleted than *B. hainanensis* in some Hong Kong streams (Lau et al. 2009).

FA profiling yielded complementary results to stable isotope analysis but provided some additional insights into consumer diets. Cyanobacteria and periphyton contained high concentrations of palmitoleic acid (i.e., monosaturated FA 16:1[*cis*-9]) and were characterized by the presence of the polyunsaturated eicosapentaenoic acid (FA 20:5[all *cis*-5,8,11,14,17]), which was virtually absent from other food sources included in our study (except the scarce filamentous algae). These 2 FAs are typical biomarkers for cyanobacteria and diatoms in freshwater habitats and were dominant in lipids of a range of primary consumers, such as Ephemeroptera, Trichoptera, and zooplankton, in temperate rivers and lakes (Napolitano et al. 1994, Goedkoop et al. 1998, Müller-Navarra et al. 2000, Sushchik et al. 2003). Palmitoleic and eicosapentaenoic acids were abundant in all consumers in our study, but their concentrations were lower in the tissues of both species of shrimps from the open site than from shrimps in the shaded sites. This result supports our stable isotope analysis results and indicates significant dependence on autochthonous foods in the study streams.

Caridina cantonensis FA profiles were distinctive in that they contained docosahexaenoic acid (DHA; i.e., the polyunsaturated FA 22:6[all *cis*-4,7,10,13,16,19]) at all sites. Biosynthesis of this essential FA by animals is unlikely (Olsen 1999), but, surprisingly, DHA was not

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present in any of the potential food sources sampled. DHA is a typical biomarker for dinoflagellates (Fredrickson et al. 1986, Napolitano 1999), which might be associated with the periphyton matrix (Azim and Asaeda 2005). The DHA concentrations of the periphyton samples in our study might have been below the detection limit of the GC–MS and were accumulated gradually during the life span of the shrimp. Bacterial food sources are important for consumers in some freshwater ecosystems (e.g., Perga et al. 2006), but dependence on bacteria was not evident in our study because consumers contained only trace amounts of FAs, such as 15:0, 15:1(*cis*-10), 17:0, and 17:1(*cis*-10), that are regarded as bacterial biomarkers (Sun et al. 2000, Kainz and Mazumder 2005).

In contrast to the autochthonous foods, allochthonous resources usually are characterized by relatively high amounts of long C-chain FAs (Napolitano 1999). Samples of allochthonous leaf litter in our study contained relatively higher concentrations of such FAs (e.g., 23:0 tricosanoic acid and 24:0 tetracosanoic acid) than did periphyton and cyanobacteria samples. However, consumers showed only limited or no accumulation of these 2 FAs, a result that indicated little assimilation of allochthonous sources during their feeding history.

Saturated FAs, such as 16:0 hexadecanoic acid and 18:0 octadecanoic acid, were abundant in consumers from all 3 sites. These FAs are used for energy storage and are crucial for biosyntheses of other FAs through C-chain elongation and desaturation (Gurr 1974, Vagelos 1974). Our results showed a general increase in hexadecanoic acid and octadecanoic acid concentrations from *B. hainanensis* and *C. cantonensis* to *M. hainanense*, a pattern that suggests that higher trophic levels tend to have higher concentrations of these 2 saturated FAs. However, our study involved animals of only 2 trophic levels. A wider array of animals at different trophic levels would have to be sampled to verify the feasibility of applying hexadecanoic and octadecanoic acids as indicators of trophic level.

As was the case for the stoichiometry results, stable isotope analysis and FA profiling indicated that foods of terrestrial origin were not the principal basal energy source in the 3 streams in our study, most probably because the high C:N ratio of allochthonous litter presented significant nutrient constraints for consumers (Sterner and Elser 2002). Our study was confined to the dry season and included only 3 species (albeit important ones). Therefore, our ability to generalize about the food base in Hong Kong streams is limited. Nonetheless, our findings support results of previous studies showing that autochthonous foods are the major energy source for aquatic consumers in tropical headwaters, even at shaded sites containing abundant terrestrial detritus (Salas and Dudgeon 2001, March and Pringle 2003, Mantel et al. 2004, Yam and Dudgeon 2005, Brito et al. 2006, Lau et al. 2008). In addition, seasonal changes in the degree of autochthony in Hong Kong streams are fairly minor. *Brotia hainanensis* shows no seasonal change in isotopic signature, although shifts in the signatures of some consumers (e.g., leptophlebiid mayflies) indicate a slightly greater use of allochthonous resources in the wet season (Lau et al. 2009).

Net primary production in streams is related to water temperature, light intensity, and day length (DeNicola 1996, Hill 1996). Because these attributes increase with decreasing latitude, they might account for the greater importance of autochthonous production to consumers in tropical than in temperate streams. However, alternative explanations also might be possible. For instance, leaves of many tropical trees are relatively unpalatable to detritivores or are recalcitrant and are not used directly as a food source by invertebrates in tropical streams (Stout 1989, Coley and Aide 1991, Irons et al. 1994, Coley and Barone 1996). Specialist shredders are particularly scarce in Hong Kong streams where they are represented by only 6 species (plus 2 facultative shredders), mainly calamoceratid caddisflies and eulichadid beetle larvae (Li and Dudgeon 2008, 2009). These 6 species account for an average of only 1% of benthic macroinvertebrate abundance in Hong Kong streams. Their contribution to biomass is higher but fluctuates greatly depending on the presence of occasional large eulichadid larvae and is considerably less than the biomass of grazers or collector-gatherers (Li and Dudgeon 2009).

Application of assimilation-based analyses, as described herein, allows detailed investigation of trophic basis of consumers (e.g., Peterson and Fry 1987, Peterson 1999, Müller-Navarra et al. 2000, Sushchik et al. 2003). Stable isotope analysis and FA profiling gave complementary results in our foodweb study. Stable isotope analysis clearly indicated the major energy source for consumers (i.e., autochthonous foods) and indicated the relative trophic positions of the study consumers, whereas FA profiling demonstrated that periphytic diatoms and cyanobacteria were the primary C source. The combined use of stable isotope analysis and FAs is effective for accurate elucidation of food sources of consumers and is potentially useful for solving ambiguities in consumer–resource relationships. Application of assimilation-based analyses in freshwater foodweb studies might yield further insight into the relative importance of allochthonous and autochthonous food sources and

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the utility of the RCC as a model of stream ecosystem functioning.

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APPENDIX. Mean (SE) concentrations (×10 μg/g) of 35 fatty acids of food and animal samples collected from Tai Po Kau Forest Stream (shaded 1), Shing Mun Stream (shaded 2), and Pak Ngau Shek Stream (open) during the dry season (January and February) of 2004. Names are formatted *A*:*B*(*cis*/*trans*-*C*) where *A* = total number of C atoms, *B* = number of double bonds, *C* = position of double bond counted from the methyl end of the molecule.

	Leaf litter						Fine particulate organic matter					
	Shaded 1		Shaded 2		Open		Shaded 1		Shaded 2		Open	
Fatty acid	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
C10:0	—	—	0.08	(0.05)	—	—	—	—	—	—	—	—
C11:0	<0.01	(<0.01)	0.12	(0.07)	—	—	—	—	—	—	—	—
C12:0	0.1	(0.06)	0.49	(0.2)	0.4	(0.26)	—	—	—	—	—	—
C13:0	<0.01	(<0.01)	0.04	(0.03)	—	—	—	—	—	—	—	—
C14:0	0.93	(0.29)	2.22	(0.41)	1.24	(0.46)	0.41	(0.25)	0.36	(0.12)	0.09	(0.09)
C14:1(*cis*-9)	0.15	(0.09)	0.01	(<0.01)	0.04	(0.04)	—	—	—	—	—	—
C15:0	0.1	(0.05)	0.21	(0.07)	0.09	(0.04)	—	—	—	—	—	—
C15:1(*cis*-10)	0.13	(0.09)	0.35	(0.09)	0.06	(0.02)	—	—	—	—	—	—
C16:0	5.72	(1.34)	11.92	(2)	6.1	(0.47)	6.8	(2.29)	4.93	(0.36)	3.51	(0.58)
C16:1(*cis*-9)	0.34	(0.1)	0.61	(0.14)	0.35	(0.1)	0.88	(0.41)	0.44	(0.02)	0.91	(0.33)
C17:0	0.29	(0.13)	0.6	(0.12)	0.24	(0.02)	—	—	—	—	—	—
C17:1(*cis*-10)	0.04	(0.03)	0.14	(0.04)	0.03	(0.02)	—	—	0.11	(0.11)	0.13	(0.13)
C18:0	1.3	(0.35)	1.97	(0.05)	1.05	(0.27)	1.78	(0.74)	1.04	(0.13)	1.08	(0.23)
C18:1(*trans*-9)	2.6	(0.73)	4.31	(0.86)	1.7	(0.23)	1.32	(0.67)	2.21	(0.26)	1.25	(0.83)
C18:1(*cis*-9)	0.11	(0.09)	0.35	(0.18)	0.06	(0.04)	—	—	—	—	—	—
C18:1(*cis*-11)	<0.01	(<0.01)	—	—	<0.01	(<0.01)	0.02	(0.01)	0.01	(<0.01)	0.02	(<0.01)
C18:2(all *cis*-9,12)	1.85	(0.42)	5.1	(0.18)	3.12	(0.54)	0.51	(0.09)	0.54	(0.11)	0.18	(0.11)
C18:3(all *cis*-6,9,12)	—	—	—	—	—	—	—	—	—	—	—	—
C18:3(all *cis*-9,12,15)	1	(0.33)	6.03	(0.11)	6.83	(0.47)	0.13	(0.13)	—	—	0.24	(0.18)
C20:0	0.21	(0.09)	0.24	(0.04)	0.13	(0.05)	—	—	0.02	(0.02)	—	—
C20:1(*cis*-11)	0.01	(0.01)	0.01	(<0.01)	<0.01	(<0.01)	—	—	—	—	—	—
C20:2(all *cis*-11,14)	—	—	<0.01	(<0.01)	—	—	—	—	—	—	—	—
C20:3(all *cis*-8,11,14)	—	—	—	—	—	—	—	—	—	—	—	—
C20:4(all *cis*-5,8,11,14)	0.01	(0.01)	0.07	(0.01)	0.02	(<0.01)	0.14	(0.05)	0.08	(0.01)	0.13	(0.05)
C21:0	0.15	(0.09)	0.2	(0.05)	0.07	(0.01)	—	—	—	—	—	—
C20:3(all *cis*-11,14,17)	—	—	<0.01	(<0.01)	<0.01	(<0.01)	—	—	—	—	—	—
C20:5(all *cis*-5,8,11,14,17)	0.04	(0.02)	0.11	(0.03)	0.03	(0.01)	0.08	(0.07)	—	—	0.12	(0.07)
C22:0	1.26	(0.74)	1.09	(0.22)	0.41	(0.08)	0.89	(0.28)	1.14	(0.14)	0.46	(0.07)
C22:1(*cis*-13)	0.06	(0.02)	0.05	(0.02)	0.01	(<0.01)	—	—	—	—	—	—
C22:2(all *cis*-13,16)	—	—	—	—	—	—	—	—	—	—	—	—
C22:4(all *cis*-7,10,13,16)	—	—	—	—	—	—	—	—	—	—	—	—
C23:0	0.34	(0.17)	0.48	(0.11)	0.15	(0.03)	0.02	(0.02)	0.11	(0.04)	—	—
C22:6(all *cis*-4,7,10,13,16,19)	—	—	—	—	—	—	—	—	—	—	—	—
C24:0	0.67	(0.31)	0.74	(0.18)	0.38	(0.09)	1.19	(0.5)	1.21	(0.16)	0.45	(0.1)
C24:1(*cis*-15)	—	—	—	—	—	—	—	—	—	—	—	—

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Appendix. Extended.

	Periphyton						Cyanobacteria						Filamentous algae	
	Shaded 1		Shaded 2		Open		Shaded 1		Shaded 2		Open		Shaded 2	
Fatty acid	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
C10:0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C11:0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C12:0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C13:0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C14:0	6.49	(1.54)	1.66	(0.88)	2.95	(0.29)	3.79	(<0.01)	3.15	(0.05)	0.16	(0.02)	3.52	(1.78)
C14:1(*cis*-9)	0.4	(0.1)	0.04	(0.04)	0.13	(0.01)	0.03	(0.03)	0.05	(<0.01)	0.16	(0.02)	2.35	(1.27)
C15:0	0.19	(0.1)	0.06	(0.03)	—	—	0.17	(0.02)	0.23	(0.01)	0.05	(0.01)	0.05	(0.04)
C15:1(*cis*-10)	0.01	(0.01)	0.16	(0.16)	7.9	(0.79)	—	—	—	—	0.74	(0.07)	—	—
C16:0	41.31	(8.89)	16.71	(6.46)	34.48	(1.65)	30.19	(4.68)	22.91	(0.33)	3.97	(0.16)	207.52	(100.86)
C16:1(*cis*-9)	21.3	(7.19)	7.49	(3.35)	8.26	(0.41)	12.37	(1.86)	8.98	(0.09)	3.1	(0.27)	21.5	(11.62)
C17:0	0.04	(0.03)	0.02	(0.01)	—	—	—	—	0.05	(<0.01)	0.04	(<0.01)	1.48	(0.62)
C17:1(*cis*-10)	0.1	(0.05)	1.11	(1.09)	0.46	(0.05)	0.31	(0.06)	0.17	(<0.01)	3.69	(0.34)	0.02	(0.02)
C18:0	2.86	(0.54)	1.68	(0.57)	7.39	(0.28)	2.48	(0.37)	1.65	(0.01)	1.41	(0.09)	12.32	(5.93)
C18:1(*trans*-9)	6.09	(1.86)	6.56	(3.54)	3.49	(0.35)	5.9	(0.19)	4.4	(0.07)	7.29	(0.63)	10.03	(3.54)
C18:1(*cis*-9)	0.85	(0.85)	0.18	(0.12)	—	—	0.03	(0.03)	0.2	(0.01)	0.12	(0.01)	14.43	(9.43)
C18:1(*cis*-11)	0.01	(0.01)	<0.01	(<0.01)	0.01	(<0.01)	0.02	(<0.01)	0.01	(<0.01)	0.04	(<0.01)	0.07	(0.03)
C18:2(all *cis*-9,12)	2.92	(0.66)	1.03	(0.51)	0.86	(0.09)	1.79	(0.17)	1.87	(0.04)	0.22	(0.02)	25.38	(12.87)
C18:3(all *cis*-6,9,12)	<0.01	(<0.01)	—	—	—	—	—	—	—	—	—	—	0.48	(0.3)
C18:3(all *cis*-9,12,15)	2.45	(0.69)	0.62	(0.33)	1.37	(0.13)	1.41	(0.5)	0.97	(0.02)	0.06	(<0.01)	73.9	(37.04)
C20:0	—	—	—	—	—	—	—	—	—	—	—	—	0.07	(0.06)
C20:1(*cis*-11)	—	—	1.46	(1.44)	—	—	0.87	(0.07)	0.44	(<0.01)	0.43	(0.03)	0.58	(0.26)
C20:2(all *cis*-11,14)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C20:3(all *cis*-8,11,14)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C20:4(all *cis*-5,8,11,14)	0.18	(0.03)	0.21	(0.07)	0.6	(0.03)	0.31	(0.04)	0.23	(<0.01)	0.13	(0.01)	0.53	(0.2)
C21:0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C20:3(all *cis*-11,14,17)	—	—	—	—	—	—	—	—	—	—	0.03	(<0.01)	0.07	(0.07)
C20:5(all *cis*-5,8,11,14,17)	1.08	(0.41)	0.48	(0.17)	0.47	(0.04)	0.65	(0.07)	0.57	(<0.01)	0.14	(0.01)	2.95	(1.55)
C22:0	0.71	(0.37)	0.23	(0.16)	0.12	(<0.01)	0.42	(0.04)	0.19	(<0.01)	0.02	(<0.01)	4.54	(2.37)
C22:1(*cis*-13)	—	—	—	—	—	—	—	—	0.04	(<0.01)	—	—	0.3	(0.23)
C22:2(all *cis*-13,16)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C22:4(all *cis*-7,10,13,16)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C23:0	—	—	—	—	—	—	—	—	—	—	—	—	0.01	(0.01)
C22:6(all *cis*-4,7,10,13,16,19)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C24:0	0.41	(0.36)	0.08	(0.06)	—	—	0.08	(0.01)	0.07	(<0.01)	—	—	4.22	(2.17)
C24:1(*cis*-15)	—	—	—	—	—	—	—	—	—	—	0.27	(0.03)	—	—

APPENDIX. Extended.

	Brotia hainanensis						*Caridina cantonensis*						*Macrobrachium hainanense*					
	Shaded 1		Shaded 2		Open		Shaded 1		Shaded 2		Open		Shaded 1		Shaded 2		Open	
Fatty acid	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
C10:0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C11:0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C12:0	—	—	—	—	—	—	—	—	—	—	—	—	9.55	(9.55)	4.92	(2.84)	—	—
C13:0	—	—	—	—	—	—	—	—	—	—	—	—	1.55	(1.55)	—	—	—	—
C14:0	89.84	(19.84)	63.85	(8.26)	56.95	(5.78)	64.29	(2.91)	42.9	(1.47)	10.99	(3.1)	39.02	(14.08)	50.47	(2.46)	20.97	(5.9)
C14:1(*cis*-9)	29.92	(9.78)	14.04	(1.77)	15.71	(1.92)	—	—	—	—	—	—	—	—	—	—	—	—
C15:0	6.06	(1.33)	4.45	(0.35)	6.54	(0.98)	31.69	(1.68)	17.43	(0.67)	15.64	(2.17)	9.69	(3.2)	6.16	(1.88)	7.43	(2.49)
C15:1(*cis*-10)	0.07	(0.07)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C16:0	211.33	(44.21)	176.56	(1.58)	142.92	(14.13)	413.3	(9.45)	329.39	(11.42)	236.67	(17.2)	321.95	(48.8)	393.77	(14.21)	389.42	(85.23)
C16:1(*cis*-9)	88.38	(25.91)	48.9	(0.74)	61.95	(6.7)	385.5	(9.6)	339.33	(8.64)	140.79	(21.34)	141.17	(37.79)	190.49	(9.48)	71.86	(17.87)
C17:0	25.76	(4.49)	17.39	(0.28)	21.13	(2.22)	20.02	(0.61)	13.35	(0.07)	14.53	(1.37)	13.82	(2.47)	15.6	(2.17)	12.95	(3.5)
C17:1(*cis*-10)	2.4	(1.17)	0.28	(0.17)	2.36	(0.45)	27.84	(0.78)	14.01	(0.49)	6.94	(1.33)	11.48	(2.96)	9.32	(1.61)	3.41	(1.55)
C18:0	70.7	(13.76)	64.58	(3.58)	50.43	(5.64)	75.68	(1.87)	64.61	(3.27	61.21	(5.59)	99.01	(17.47)	135.17	(8.44)	122.78	(22.32)
C18:1(*trans*-9)	107.5	(27.21)	85.53	(22.54)	72.25	(8.69)	273.82	(11.35)	216.06	(1.32)	119.8	(19.34)	620.36	(178.66)	576.46	(68.09)	612.06	(163.81)
C18:1(*cis*-9)	17.08	(9.33)	2.2	(1.94)	13.29	(3.75)	186.05	(4.3)	137.8	(3.93)	117.78	(11.53)	136.97	(16.19)	204.07	(24.87)	107.79	(28.28)
C18:1(*cis*-11)	0.23	(0.04)	0.15	(0.01)	0.27	(0.03)	0.92	(0.07)	0.63	(0.01)	0.51	(0.05)	0.6	(0.09)	0.57	(0.07)	0.43	(0.09)
C18:2(all *cis*-9,12)	49.68	(13.98)	15.29	(5.1)	35.27	(5.6)	152.16	(6.27)	135.6	(0.66)	123.42	(15.44)	229.97	(18.64)	316.76	(41.66)	594.05	(53.27)
C18:3(all *cis*-6,9,12)	—	—	—	—	—	—	2.15	(0.25)	0.02	(0.02)	—	—	0.16	(0.13)	0.02	(0.02)	—	—
C18:3(all *cis*-9,12,15)	16.41	(6.97)	0.96	(0.91)	12.47	(2.31)	92.52	(5.5)	63.97	(1.55)	96.7	(13.59)	82.7	(21.32)	121.68	(8.23)	116.93	(17.98)
C20:0	1.89	(0.9)	0.96	(0.18)	0.59	(0.33)	—	—	—	—	—	—	0.93	(0.89)	1.05	(0.36)	0.24	(0.24)
C20:1(*cis*-11)	20.13	(5.32)	9.61	(1.28)	6.45	(0.76)	3.25	(0.35)	1.83	(0.21)	—	—	6.3	(2.17)	5.67	(0.88)	4.76	(1.87)
C20:2(all *cis*-11,14)	16.86	(5.06)	3.45	(1.33)	11.02	(1.99)	3.27	(0.27)	1.55	(0.31)	1.31	(0.44)	13.77	(2.31)	15.85	(1.99)	21.44	(2.69)
C20:3(all *cis*-8,11,14)	1.05	(0.76)	—	—	0.27	(0.26)	—	—	—	—	—	—	0.67	(0.52)	—	—	—	—
C20:4(all *cis*-5,8,11,14)	58.43	(15.7)	19.01	(6.2)	71.78	(15.01)	110.31	(3.58)	92.95	(5.5)	107.37	(2.78)	163.57	(5.51)	105.25	(4.44)	177.88	(21.61)
C21:0	0.67	(0.48)	0.12	(0.09)	0.34	(0.16)	—	—	—	—	—	—	0.18	(0.18)	0.24	(0.24)	0.06	(0.06)
C20:3(all *cis*-11,14,17)	—	—	—	—	—	—	1.52	(0.3)	0.56	(0.14)	1.03	(0.21)	6.97	(1.59)	14.23	(2.19)	5.19	(1.53)
C20:5(all *cis*-5,8,11,14,17)	12.56	(4.82)	2.28	(0.9)	5.53	(1.35)	199.01	(1.38)	176.58	(7.56)	106.39	(4.47)	184.6	(17.26)	233.13	(25.75)	187.25	(17.78)
C22:0	0.72	(0.27)	0.68	(0.12)	0.59	(0.12)	2.09	(0.19)	0.68	(0.13)	0.14	(0.07)	3.54	(1.76)	5.38	(0.41)	2.65	(0.51)
C22:1(*cis*-13)	—	—	—	—	—	—	—	—	—	—	—	—	1.38	(0.16)	1.45	(0.06)	—	—
C22:2(all *cis*-13,16)	0.08	(0.08)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C22:4(all *cis*-7,10,13,16)	5.93	(2.97)	0.27	(0.27)	14.22	(4.57)	—	—	—	—	—	—	—	—	—	—	—	—
C23:0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C22:6(all *cis*-4,7,10,13,16,19)	2.15	(0.39)	—	—	3.23	(1.12)	100.2	(3.11)	66.06	(0.44)	97.22	(6)	37.84	(5.46)	29.12	(2.71)	54.43	(4.91)
C24:0	—	—	—	—	—	—	0.06	(0.06)	—	—	—	—	0.13	(0.13)	—	—	—	—
C24:1(*cis*-15)	—	—	—	—	—	—	—	—	—	—	—	—	2.86	(0.53)	2.84	(0.17)	—	—

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