

Food Web Structure and Basal Resource Utilization along a Tropical Island Stream Continuum, Puerto Rico¹

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ABSTRACT

Tropical stream food webs are thought to be based primarily on terrestrial resources (leaf litter) in small forested headwater streams and algal resources in larger, wider streams. In tropical island streams, the dominant consumers are often omnivorous freshwater shrimps that consume algae, leaf litter, insects, and other shrimps. We used stable isotope analysis to examine (1) the relative importance of terrestrial and algal-based food resources to shrimps and other consumers and determine (2) if the relative importance of these food resources changed along the stream continuum. We examined $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of leaves, algae, macrophytes, biofilm, insects, snails, fishes, and shrimps at three sites (300, 90, and 10 m elev.) along the Río Espíritu Santo, which drains the Caribbean National Forest, Puerto Rico. Isotope signatures of basal resources were distinct at all sites. Results of two-source $\delta^{13}\text{C}$ mixing models suggest that shrimps relied more on algal-based carbon resources than terrestrially derived resources at all three sites along the continuum. This study supports other recent findings in tropical streams, demonstrating that algal-based resources are very important to stream consumers, even in small forested headwater streams. This study also demonstrates the importance of doing assimilation-based analysis (*i.e.*, stable isotope or trophic basis of production) when studying food webs.

Key words: Caribbean; Decapoda; Greater Antilles; lotic; prawn; Puerto Rico; rain forest; RCC; river; species interactions.

THE RIVER CONTINUUM CONCEPT suggests that as the physical structure of a river changes from headwaters to mouth, the relative importance of allochthonous versus autochthonous resources to consumers will also change (Vannote *et al.* 1980). For example, in forested headwater stream sites, allochthonous inputs such as leaves may form the base of the food web, while in wider low-elevation sites, autochthonous algal resources may be more important to consumers. Studies examining this pattern in temperate streams, characterized by fishes and insects, generally support this hypothesis (Winterbourn *et al.* 1984, Doucett *et al.* 1996); however, no published information exists about resource-use patterns along tropical island stream continua. Recent research in the tropics, in both small streams (Salas & Dudgeon 2001) and large river floodplains (Lewis *et al.* 2001), suggest a greater reliance of consumers on algal-based resources.

Freshwater shrimps are an important component of tropical streams worldwide. They are especially important in tropical island streams, where they are often very abundant along entire river con-

tinua (Hunte 1978, Marquet 1991, Fièvet *et al.* 2001, March *et al.* 2001) and play a major role in determining benthic community composition and the rate of organic matter processing (Pringle *et al.* 1999, Crowl *et al.* 2001, March *et al.* 2001). Initial studies in small headwater streams suggest that shrimp assemblages are highly dependent on terrestrial detritus as a food resource (Covich 1988 a, b; March *et al.* 2001). Research has also shown that shrimps can have strong negative effects on algal abundance (Pringle 1996, Pringle *et al.* 1999, March *et al.* 2002). While we know that shrimps are important in regulating standing stocks of both algae and leaves, we know little about the relative importance of these basal resources to shrimps, or if the relative importance varies along river continua.

Stable isotopes are a useful tool to identify basal resources utilized by consumers. Terrestrial and aquatic plants often differ in their ^{13}C signatures (Fry & Sherr 1989). Because ^{13}C signatures of consumers reflect those of the plants they eat, analysis of ^{13}C signatures have been used successfully to estimate the relative importance of different basal food resources in stream food webs (Winterbourn *et al.* 1984, Rounick & Hicks 1985, Hamilton *et al.* 1992, Doucett *et al.* 1996). Furthermore, analysis of ^{13}C signatures provides an advantage over gut content analysis because it measures the

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TABLE 1. *Physical parameters at each site.*

	High elevation	Mid elevation	Low elevation
Elevation (m)	300	90	10
Stream order	2	3	4
Channel width (m)	13	15	19
Mean daily discharge ^a (m ³ /sec)	0.19	1.11	2.56
% Canopy cover	69	33	21
Drainage area (km ²)	3	14	33

^a Calculated from USGS data (1 October 1995–30 September 1998).

amount of carbon assimilated from each food source as opposed to that ingested. This is important because food sources can differ greatly in quality. Assimilation efficiencies of leaves are typically low compared to algal resources (Benke & Wallace 1980, Whitley & Rabeni 1997). Stable isotopes are also useful in determining trophic level because the ¹⁵N signature is generally enriched by 2.5 to 3.5‰ with every trophic transfer (Peterson & Fry 1987, Hershey & Peterson 1996).

In this study, we used stable isotope analysis to describe the basic structure of the food web along a tropical island stream continuum in Puerto Rico. We addressed the following questions: (1) What is the relative importance of different basal food resources (*e.g.*, algae and leaves) to shrimps and other consumers? and (2) Does the relative importance of algal and leaf resources to consumers vary along the stream continuum?

METHODS

STUDY SITES AND NATURAL HISTORY.—We conducted this study along the Río Espíritu Santo in northeastern Puerto Rico. Three 100 m study sites were selected. The high-elevation site (300 m elev.) is in the second-order Quebrada Sonadora in the Caribbean National Forest, which is synonymous with the Luquillo Experimental Forest (LEF). Land use consists of tabonuco forest characterized by *Dacryodes excelsa* Vahl. Allochthonous inputs enter the river system throughout the year with two peaks, from March to May and September to October (Covich & McDowell 1996). The mid-elevation site (90 m elev.) is located *ca* 3.1 km downstream from the high-elevation site in a third-order portion of the Río Espíritu Santo. The low-elevation site (10 m elev.) is in a fourth-order segment of the Río Espíritu Santo, *ca* 4.2 river km downstream from the mid-elevation site. Land use is mostly residential and pasture at the mid- and low-elevation sites, but the riparian zone is predominantly for-

ested. Stream width widens and canopy cover decreases in a downstream direction (Table 1). The Espíritu Santo enters the ocean *ca* 6 km downstream of the low-elevation site.

Ten species of omnivorous freshwater shrimps inhabit rivers of the LEF, representing three families: Palaemonidae, Atyidae, and Xiphocarididae. The palaemonid shrimps *Macrobrachium carcinus* (L), *M. faustinum* (De Saussure), *M. crenulatum* Holthuis, *M. acanthurus* (Wiegmann), and *M. heterochirus* (Wiegmann) are thought to consume decomposing leaf litter, fine particulate organic matter, algae, macrophytes, insects, mollusks, small fish, and other shrimps (Covich & McDowell 1996). The atyid shrimps, represented by *Atya lanipes* Holthuis, *A. scabra* (Leach), *A. innocuus* (Herbst), and *Micratya poeyi* (Guérin-Méneville), consume fine particulate organic matter, leaf material, algae, and small sessile insects by brushing with their cheliped fans (Pringle *et al.* 1993). They use these same cheliped fans to filter feed when flow conditions are suitable (Covich 1988b). *Xiphocarid elongata* (Guérin-Méneville) consumes leaf matter, periphyton, fine particulate organic matter, insects, small flowers, and fruit using tiny pincers (Covich & McDowell 1996, Pringle 1996). Gut content information for these shrimp taxa is limited. Pringle *et al.* (1993) found mostly silt/detritus and “unidentified green material” in both *A. lanipes* and *X. elongata*. No gut content studies exist for *Macrobrachium* spp. from this river; however, in ponds in Jamaica, *M. carcinus* consumed mostly detritus but also algae, leaves, plant seeds, aquatic insects, fish, mollusks, and other crustacea (Lewis *et al.* 1966). In southern Australian streams, atyid and palaemonid shrimps were omnivorous; however, biofilm was a significant portion of their diet (Burns & Walker 2000). No information is available on food preference.

All of these shrimp species undergo extended larval development and are amphidromous (Covich & McDowell 1996, Johnson *et al.* 1998); adult

females release planktonic larvae that drift downstream to the estuary (March *et al.* 1998). Larvae spend 50–110 days in the estuary before migrating back upstream as metamorphosed postlarvae (Chace & Hobbs 1969, Hunte 1978, Benstead *et al.* 2000). Adult shrimps differ in their distribution along the elevation gradient; high-elevation sites are dominated by atyid shrimps (mostly *A. lanipes*) and *X. elongata*, while *Macrobrachium* spp. and *X. elongata* comprise the majority of the shrimp assemblage at lower-elevation sites (March *et al.* 2001, 2002).

The insect assemblage at all three sites is depauperate relative to continental tropical streams and is composed mostly of collector–gatherer insects such as baetid and leptophlebiid mayflies (Ephemeroptera) and chironomids (Diptera; Pringle *et al.* 1993, March *et al.* 2001).

Two genera of grazing freshwater snails, *Neritina* spp. and *Thiara* (*Tarebia*) *granifera* (Lamarck), inhabit mid- and low-elevation sites. They occur in high densities at the low-elevation site where they appear to reduce algal standing stocks (March *et al.* 2002).

SAMPLE COLLECTION.—We collected samples of leaves, biofilm, algae (mostly filamentous), macrophytes, insects, snails, shrimps, and fishes at three sites along the stream continuum during June 1999 (Table 2). Leaves and macrophytes were sampled from the stream, rinsed thoroughly to remove all fine particulate organic matter and insects, and placed in a plastic bag. To sample biofilm, we scrubbed rocks with a toothbrush over a dissecting pan and then removed live insects from the resulting slurry. The slurry was then filtered onto a pre-combusted glass fiber filter (0.7 μm). We sampled algae (mostly filamentous) by scraping substrata with a razor blade from areas in the stream where shrimps were unable to forage (*e.g.*, overhanging edges of boulders in fast flow). We carefully removed insects and detritus under a dissecting scope to obtain a more accurate algal signature. The most abundant insects at each site were collected with a small kick net from all major habitat types (cobble, bedrock, and leaf packs). Insects were later transported to the laboratory and stored in an aquarium in filtered water for several hours to void their guts. Snails were abundant only at the low-elevation site and were sampled by hand. Shrimps were sampled with unbaited minnow traps and an electroshocker. They were measured (carapace length) and identified to species when possible (small *Macrobrachium* shrimps were unidentifiable). Fishes were sampled

with an electroshocker and by angling. A single crab was collected by hand at the high-elevation site. Samples were stored frozen or dried until prepared for stable isotope analysis.

SAMPLE PREPARATION AND ANALYSIS.—All samples were re-dried at 60°C for at least 48 hours. Replicates of leaves and macrophytes were ground into powder with a ball mill. Insect samples were composites of multiple individuals. At both the mid- and low-elevation sites, leptophlebiid and baetid mayflies were combined to obtain sufficient mass for isotope analysis. Samples of muscle tissue were taken from snails, shrimps, and fishes. Individual snails, shrimp, and fish were analyzed separately. All samples were combusted to CO₂ and N₂ and analyzed in a Carlo Erba NA 1500 CHN analyzer connected to a Finnigan Delta C mass spectrometer. Stable isotope signatures were calculated as follows: $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (‰) = $[(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] \times 1000$, where R is (¹⁵N/¹⁴N) or (¹³C/¹²C). Standards were PDB carbonate for carbon and atmospheric N₂ for nitrogen.

We used a standard single isotope (¹³C), two-source (algae and leaves) linear model created by Phillips and Greg (2001) to estimate an index of trophic significance of algal and leaf material to consumers. We corrected for fractionation in consumers using a fractionation value of 0.4‰ $\delta^{13}\text{C}$ (but see McCutchan *et al.* in press) for each trophic level and assumed 1 trophic transfer for insects (all sampled were non-predatory), 2 for *Neritina* spp., *Thiara granifera*, *Sicydium plumieri*, *Epilobocera sinuatifrons*, and *Atya* and *Xiphocaris* shrimps, which consume insects and basal resources, and 2.5 for predatory fishes and *Macrobrachium* shrimps, which potentially consume shrimps, insects, and basal resources.

RESULTS

$\delta^{13}\text{C}$ OF FOOD RESOURCES AND CONSUMERS.—Basal food resources (algae and leaves) differed in their $\delta^{13}\text{C}$ signatures at each site (Fig. 1). At all sites, algal resources were considerably more enriched in $\delta^{13}\text{C}$ than leaves. Biofilm had a $\delta^{13}\text{C}$ signature intermediate to algae and leaves at each site. The macrophyte *Anacharis densa* was found only at the low-elevation site and had a distinctly depleted $\delta^{13}\text{C}$ signature. Insect $\delta^{13}\text{C}$ signatures at all sites were between leaf and algal signatures. Mixing models showed that insect shredders obtained more carbon from terrestrially derived detritus than algae (Table 2). This was consistent at both the mid- and

TABLE 2. Carbon and nitrogen isotope values and an index of algal reliance for consumers at each reach. The range of carapace length for shrimps is in parentheses.

Consumers/organic matter sources	N	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		Percent algal dependence	
		\bar{x}	SD	\bar{x}	SD	% Mean (linear model)	SE (%)
High-elevation Reach							
<i>Macrobrachium crenulatum</i> (28–37)	9	-22.23	0.61	6.97	1.19	58	3
<i>Macrobrachium</i> spp. small (14–18)	7	-19.67	0.90	6.81	0.24	79	5
<i>Atya lanipes</i> large (17–19)	6	-23.07	0.56	5.74	0.28	52	3
<i>A. lanipes</i> medium (11–13)	6	-21.52	2.02	5.29	0.49	65	8
<i>A. lanipes</i> small (6–10)	8	-22.19	0.87	5.41	0.54	60	4
<i>A. innocous</i> large (17–19)	3	-22.97	0.06	5.71	0.30	53	3
<i>A. innocous</i> medium (14–16)	3	-23.10	0.23	5.73	0.24	52	3
<i>A. scabra</i> (9–11)	2	-23.14	0.13	5.69	0.24	52	3
<i>Xiphocaris elongata</i> large (11–13)	5	-22.31	0.87	4.94	0.17	59	4
<i>X. elongata</i> medium (8–9)	4	-19.07	1.72	5.26	0.29	86	9
<i>X. elongata</i> small (6–7)	5	-17.56	1.19	6.64	0.33	99	7
<i>Sicydium plumieri</i>	3	-17.77	2.92	6.49	0.64	97	15
<i>Epilobocera sinuatifrons</i>	1	-23.78		4.91		46	9
Leptophlebiidae	3	-24.25	0.72	2.51	0.20	46	4
Stream Leaves	5	-30.01	0.14	0.13	0.68		
Algae	5	-18.24	1.32	1.40	0.63		
Biofilm	10	-22.96	1.51	5.12	1.34		
Mid-elevation Reach							
<i>Macrobrachium carcinus</i> (40–51)	2	-20.13	1.03	7.31	0.37	65	14
<i>M. crenulatum</i> (31)	1	-23.75		5.73		34	11
<i>Macrobrachium</i> spp. small (13–16)	5	-19.44	0.81	7.11	0.11	71	14
<i>Xiphocaris elongata</i> medium (9–10)	5	-15.43	0.53	6.06	0.31	106	21
<i>X. elongata</i> small (6)	5	-17.60	1.02	7.84	0.17	88	18
<i>Agonostomus monticola</i>	5	-18.92	0.88	8.93	0.56	75	15
<i>Anguilla rostrata</i>	1	-19.41		8.68		71	16
<i>Gobiomorus dormitor</i>	1	-17.56		8.02		87	19
<i>Sicydium plumieri</i>	4	-16.69	1.70	7.57	1.77	96	20
Leptophlebiidae, Baetidae	2	-22.11	0.69	4.35	0.57	53	11
<i>Phanocerus</i> sp.	2	-25.88	0.04	1.28	0.03	21	4
Stream Leaves	5	-28.79	0.40	0.62	0.12		
Algae	2	-17.03	3.25	2.16	0.30		
Biofilm	11	-20.15	0.19	3.38	0.43		
Low-elevation Reach							
<i>Macrobrachium acanthurus</i> (27)	1	-19.16		9.44		82	25
<i>M. heterochirus</i> (not measured)	1	-21.53		7.03		59	21
<i>Macrobrachium</i> spp. medium (10–11)	5	-20.99	3.16	9.88	2.35	71	17
<i>Macrobrachium</i> spp. small (3–6)	5	-20.27	1.30	9.34	0.65	64	20
<i>Xiphocaris elongata</i> medium (8–10)	5	-19.85	2.20	8.11	0.32	78	18
<i>X. elongata</i> small (5)	4	-19.80	0.90	7.42	0.12	78	20
<i>Eleotris pisonis</i>	1	-20.46		9.53		70	23
<i>Gobiomorus dormitor</i>	5	-19.28	0.42	9.03	0.84	81	18
<i>Sicydium plumieri</i>	1	-21.55		8.72		61	21
<i>Neritina</i> spp.	5	-21.48	2.94	8.55	0.35	62	19
<i>Thiara granifera</i>	5	-20.84	0.92	7.29	0.19	68	16
Leptophlebiidae, Baetidae	1	-23.30		6.13		48	20
<i>Chimarra albomaculata</i>	1	-21.78		6.42		63	22
<i>Phanocerus</i> sp.	1	-25.30		3.66		28	18
Stream Leaves	4	-28.55	0.29	1.47	0.75		
Algae	1	-18.36		5.96			
Biofilm	1	-24.11		6.42			
Macrophytes	4	-32.79	0.55	7.99	0.89		

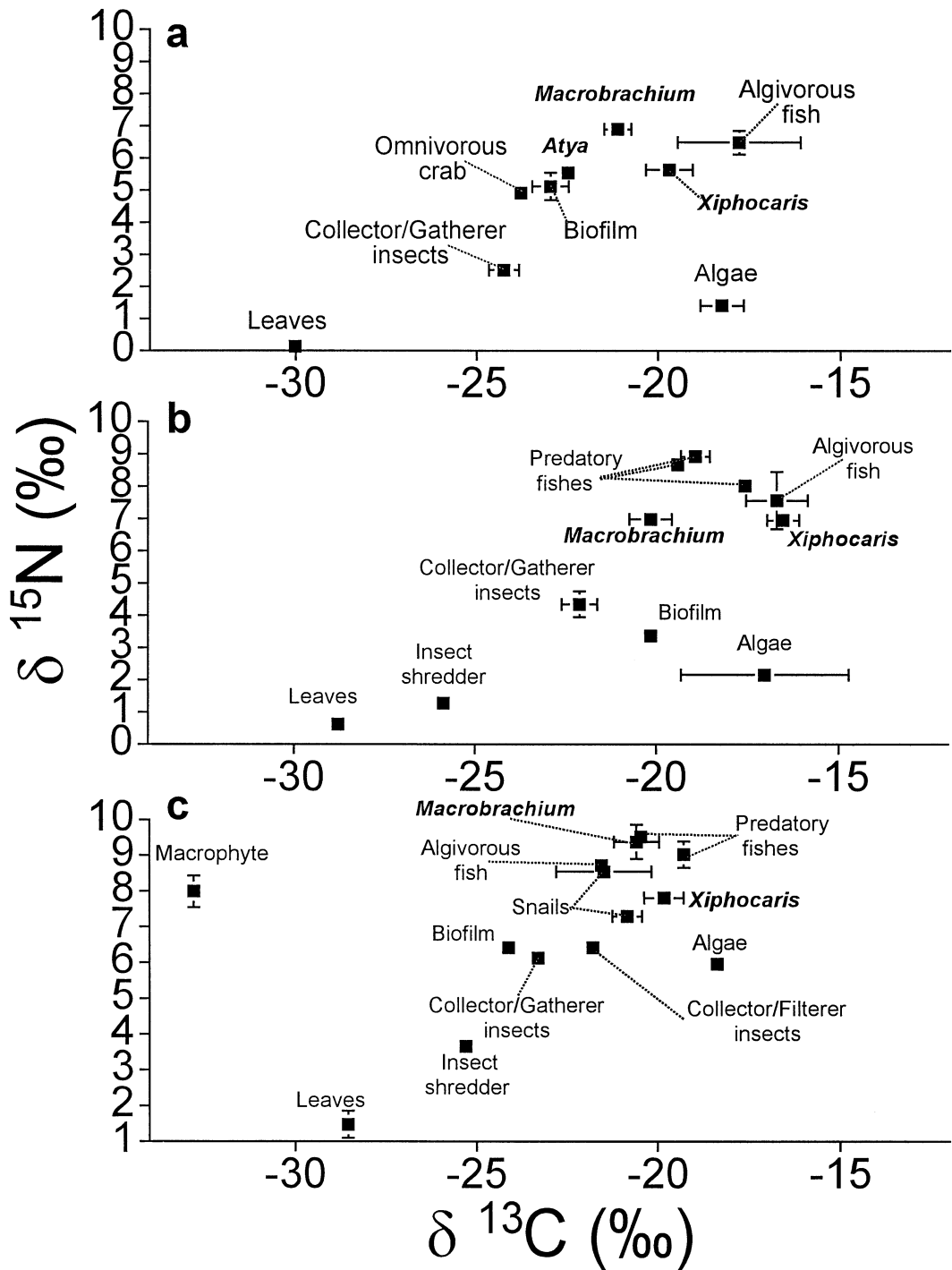


FIGURE 1. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) signatures of basal resources and consumers at the (a) high-, (b) mid-, and (c) low-elevation reaches. Points are means ± 1 SE. Points without error bars are a single sample. Shrimp samples are averaged for each genus.

low-elevation sites where insect shredders were found. Insect shredders were so rare at the high-elevation site that they were not sampled. Collector-gathering leptophlebiid and baetid mayflies relied almost equally on both algal and leaf-derived carbon at all three sites (Table 2). The collector-filtering caddisfly *Chimarra albomaculata* was only found at the low-elevation site and depended more on algal-based than leaf-based carbon.

In general, shrimps assimilated more algal- than terrestrial-based resources at all three study sites (Table 2); however, there was variation among taxa and among size classes within taxa. *Atya lanipes* relied slightly more on algal-based resources than *A. innocous* or *A. scabra*. Also, medium and small *A. lanipes* relied more heavily on algal-based resources than larger *A. lanipes*. *Xiphocaris* shrimps showed variation among size classes and among sites. At the high-elevation site, medium and small *Xiphocaris* relied more heavily on algal resources than large *Xiphocaris*. At the mid-elevation site, medium-sized *Xiphocaris* relied more on algae than small ones. There was no difference between *Xiphocaris* size classes at the low-elevation site. Smaller *Macrobrachium* shrimps also showed a greater reliance on algal-based resources than larger ones. One exception is a single *M. acanthurus* at the low-elevation site, which had a very high reliance on algal resources (82%). The only shrimp taxa that did not have a mean index of algal reliance greater than 50 percent was *M. crenulatum* at the mid-elevation site; however, we only sampled one individual at this site.

Snails (*Neritina* spp. and *T. granifera*) were only abundant at the low-elevation site and relied on 69 and 76 percent algal resources, respectively (Table 2). The omnivorous crab *Epilobocera sinuatifrons* was only found at the high-elevation site and relied on slightly more leaf-based than algal-based carbon.

Predatory fishes (*Agonostomus monticola*, *Anguilla rostrata*, *Gobiomorus dormitor*, and *Eleotris pisonis*) only occurred at mid- and low-elevation sites and relied on mostly algal-based resources. The green stream goby (*S. plumieri*) showed a very strong reliance on algal-based resources at the high- and mid-elevation sites and had a greater reliance on terrestrial-based resources at the low-elevation site compared to the upper two sites (Table 2).

$\delta^{15}\text{N}$ SIGNATURES.—Basal resources varied considerably in their $\delta^{15}\text{N}$ signatures. The mean signature of leaves at each site was less than 1.5‰. The mean $\delta^{15}\text{N}$ signature of algae was higher than leaves and varied among sites, increasing in the downstream

direction (Fig. 1). The mean signature of biofilm was higher than leaves at all three sites. The macrophyte *A. densa* at the low-elevation site had a very enriched $\delta^{15}\text{N}$ signature (Fig. 1). Mean insect $\delta^{15}\text{N}$ signatures generally were higher than algal or leaf resources but lower than biofilm. Insect shredders were 2.2‰ higher than leaves at the low-elevation site but only 0.7‰ higher than leaves at the mid-elevation site. Collector-gatherer and collector-filterer insects showed a mean $\delta^{15}\text{N}$ signature similar to biofilm at the low-elevation site, greater than biofilm at the mid-elevation site, and less than biofilm at the high-elevation site. Snails and the algivorous fish *S. plumieri* had $\delta^{15}\text{N}$ signatures between 0.9 and 2.3‰ higher than biofilm at the low-elevation site. At the mid-elevation site, *S. plumieri* had a $\delta^{15}\text{N}$ signature 4.2‰ higher than biofilm and 3.2‰ higher than insects. At the high-elevation site, *S. plumieri* had a $\delta^{15}\text{N}$ signature similar to that of biofilm. *Xiphocaris elongata* and *Atya* shrimps had mean $\delta^{15}\text{N}$ signatures similar to *S. plumieri*. There were no dramatic differences in $\delta^{15}\text{N}$ signatures among size classes of shrimps at any site. Predatory fishes and the predatory shrimp *Macrobrachium* spp. showed the highest $\delta^{15}\text{N}$ signatures at the low-elevation site. Their signatures were ca 3‰ greater than insects. At the mid-elevation site, predatory fishes were ca 4.6‰ higher than insects but only 1.7‰ higher than shrimps.

DISCUSSION

BASAL FOOD RESOURCES LEADING TO CONSUMERS.—Carbon and nitrogen isotope signatures of both algae and leaves were within the range of published values for each resource (Boon & Bunn 1994, France 1995). Biofilm (which is a mixture of algae, microbes, and both algal and leaf detritus) had a $\delta^{13}\text{C}$ signature intermediate to leaves and algae, which is consistent with other stable isotope studies in streams (Rosenfeld & Roff 1992). $\delta^{15}\text{N}$ signatures of biofilm were higher than algae and leaves, especially at the high-elevation site. Biofilm samples were potentially enriched due to microbial biomass and activity (Caraco *et al.* 1998). Although macroscopically visible insects were live-picked from biofilm samples, contamination with animal parts or microscopic fauna may have also contributed to the elevated biofilm $\delta^{15}\text{N}$ signatures.

Based on isotopic signatures, the macrophyte *A. densa* did not appear to be consumed by shrimps or other consumers. This supports the general finding that herbivory on macrophytes is minimal (Gregory 1983) and often restricted to specialized

taxa (Newman 1991). While previous studies have shown that crayfish consume macrophytes (Lodge 1991), our data suggest that this is not the case with shrimps.

Basal resource utilization varied among insect functional feeding groups. The shredder *Phanocerus* sp. mostly depended on leaf-based carbon while collector-gatherer leptophlebiid and baetid mayflies used algal- and leaf-based resources almost equally. Collector-gatherer insects likely consumed biofilm as well as leaf and algal resources directly. A recent ^{15}N addition in a nearby small stream found that leptophlebiid mayflies assimilated a highly labeled portion of the epilithon (biofilm; Merriam *et al.* 2002). The collector-filterer caddisfly *C. albomaculata* obtained slightly more of its carbon from algal resources. This finding is in agreement with results of a previous study on a congeneric species that found two-thirds of the material ingested was algae (Coffman *et al.* 1971).

Grazing snails relied more on algal- than leaf-based carbon; however, they assimilated up to 38 percent terrestrially derived organic matter. Fine particulate organic matter was the likely source of terrestrial carbon since snails were not important shredders at this site (March *et al.* 2001).

Variation in dependence on algal versus leaf based detritus among shrimp taxa can potentially be explained by feeding mode. *Atya* shrimps filter feed and sweep the substrate with their cheliped fans. These feeding modes likely result in greater consumption of fine particulate organic matter and biofilm, both of which likely contain terrestrial-based detritus, microbes, and algae. Accordingly, *Atya* had a $\delta^{13}\text{C}$ signature similar to biofilm. Based on its $\delta^{15}\text{N}$ signature (*ca* 3‰ above insects), *Atya* also appeared to assimilate insects. *Atya* have been observed to reduce insect abundance (*e.g.*, larval Chironomidae) in the field and insects have been found in their guts (Pringle *et al.* 1993). In contrast to *Atya*, which appear to indiscriminately feed with their cheliped fans, *Xiphocaris* and *Macrobrachium* shrimps have tiny pincers that may allow them to selectively ingest more algae.

Previous studies have shown that shrimp assemblages can have negative effects on sessile insects (March *et al.* 2001, 2002). Our $\delta^{15}\text{N}$ signatures support these findings and suggest that all three shrimp taxa feed on insects to some degree. *Macrobrachium* were more enriched in $\delta^{15}\text{N}$ than all other shrimp taxa, suggesting a greater reliance on insects and/or shrimps. This is supported by observations of their behavior, as well as gut content data from Jamaica showing that animal material

(insects, fish, mollusks, and other crustacea) was part of their diet (Lewis *et al.* 1966).

The greater reliance of the crab *E. sinuatifrons* on leaf-based detritus than shrimps is not surprising because *E. sinuatifrons* is semiterrestrial and associated with leaf packs when in the stream (Covich & McDowell 1996). The $\delta^{15}\text{N}$ signature of *E. sinuatifrons* suggests that it also consumes insects. In support of this, a recent feeding study found mayflies to be an important food resource for *E. sinuatifrons* (Henry *et al.* 2000).

All of the fishes relied more on algal- than terrestrial-based resources. Predatory fishes were more ^{13}C -enriched than insects, suggesting that they obtained their algal-based carbon via consumption of shrimps and/or directly from algae. *Agonostomus monticola* likely obtained its algal-based carbon from both sources since it has been observed consuming shrimps in these streams (J. G. March, pers. obs.) and algae has been found in guts of *A. monticola* in Jamaica (Aiken 1998). *Anguilla rostrata* likely obtained its algal signature primarily from shrimps, as it tends to eat the most abundant macroinvertebrate at a site (Tesch 1977). *Sicydium plumieri* is a grazer (Erdman 1986) and accordingly relied almost completely on algal-based resources at the high- and mid-elevation sites. The $\delta^{15}\text{N}$ signature also suggests some consumption of insects, which have also been found in their guts (J. G. March, pers. obs.).

RELATIVE IMPORTANCE OF BASAL FOOD RESOURCES ALONG THE CONTINUUM.—We expected to see a greater reliance of consumers and especially shrimps on leaf material at the high-elevation site than at the lower two sites for several reasons. First, initial observations at the high-elevation site revealed low standing stocks of algal biomass and continuous input of leaf litter. Second, a recent experiment showed that the shrimp assemblage significantly increased rates of leaf decay at this high-elevation site, but not at the lower two sites (March *et al.* 2001). Third, similar stable isotope studies along river continua in New Zealand (Winterbourn *et al.* 1984) and Canada (Doucett *et al.* 1996) found greater reliance on terrestrial-derived organic matter in headwater sites; however, we found that shrimps relied primarily on algal-based resources at all sites.

The lack of shift towards terrestrial resources at the high-elevation site may be due to the high relative availability of algae and high assimilation efficiency of algae by shrimps. While light levels in forested streams can often be limiting (Hill *et al.*

1995), a recent experiment at this site has suggested that low standing stocks of algae were due to shrimp grazing pressure (March *et al.* 2002). When shrimps were excluded for 35 days, algal biovolume increased 186-fold. This grazing study (March *et al.* 2002), in conjunction with a litter decay study (March *et al.* 2001), showed that shrimps were consuming both algae and leaves; however, algae are generally considered a higher quality resource than leaf detritus (Hall *et al.* 2001). Whitledge and Rabeni (1997) found that crayfish assimilated 39 percent of algae and only 14 percent of leaf detritus. A combination of high availability of algae and the higher quality of algal resources supports our finding that shrimps are assimilating mostly algal resources. Moreover, our results support Minshall's (1978) contention that algal-based resources can be a major energy source for consumers even in relatively small shaded streams. Similar findings were recently reported for forested streams in Hong Kong where insects appeared to rely more on algal than terrestrial-based resources (Salas & Dudgeon 2001). Another recent study in a rocky mountain stream found that algal carbon sources provided a major contribution to macroinvertebrate production (McCutchan & Lewis 2002).

Shrimps may rely more on terrestrially derived carbon in smaller headwater streams (*i.e.*, than those sampled in this study) with greater canopy cover. Isotopic signatures of shrimps have been obtained in a smaller headwater stream in this catchment, but isotopic signatures of autochthonous and terrestrial resources were not distinct (Kilham & Pringle 2000), precluding determination of their relative importance. In a small, heavily shaded headwater stream in an adjacent catchment as this study, Merriam *et al.* (2002) found very low standing stocks of algae and primary production was also very low; however, atyid shrimps assimilated a highly labeled portion of the epilithon, which may have been filamentous algae that was present during their study but not measured. Whether algal resources are more important than leaf detritus to shrimps in these heavily shaded streams is not yet known. But it is likely that algal resources are an

important component of shrimp diet, especially following defoliation disturbances such as tropical storms and hurricanes.

FUNCTIONAL TROPHIC ROLE OF FRESHWATER SHRIMPS. Recent studies have emphasized the importance of understanding both the functional and trophic role of stream consumers (Mihuc 1997, Whitledge & Rabeni 1997, Parkyn *et al.* 2001). For example, by combining experimental manipulations (Parkyn *et al.* 1997) with diet and stable isotope analysis (Parkyn *et al.* 2001), Parkyn and others were able to determine that the New Zealand freshwater crayfish (*Paranephrops planifrons*) was an important processor of organic matter (shredder), yet derived most of its carbon from aquatic insects (a higher quality food). Similarly, we have found that freshwater shrimps (mostly *X. elongata*) are the main shredders at the high-elevation site (March *et al.* 2001), yet derive most of their carbon from algal resources (this study). We encourage researchers to conduct both experimental manipulations and stable isotope or trophic basis of production studies (Hall *et al.* 2001) to understand species effects and the relative importance of different food resources to consumers.

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