

Trophic relationships in a tropical stream food web assessed by stable isotope analysis

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SUMMARY

1. Stable isotope analysis, coupled with dietary data from the literature, was used to investigate trophic patterns of freshwater fauna in a tropical stream food web (Guadeloupe, French West Indies).
2. Primary producers (biofilm, algae and plant detritus of terrestrial origin) showed distinct $\delta^{13}\text{C}$ signatures, which allowed for a powerful discrimination of carbon sources. Both autochthonous (^{13}C -enriched signatures) and allochthonous (^{13}C -depleted signatures) resources enter the food web. The migrating behaviour of fishes and shrimps between marine and freshwater during their life cycles can be followed by carbon isotopes. Here, shrimp $\delta^{13}\text{C}$ signatures were shown to shift from -16‰ (for juveniles under marine influence) to -24.7‰ (for adults in freshwater habitats). For resident species, $\delta^{13}\text{C}$ values partly reflected the species' habitat preferences along the river *continuum*: species living in river mouths were ^{13}C -enriched in comparison with those collected upstream.
3. Nitrogen isotopic ratios were also discriminating and defined three main trophic guilds among consumers. The $\delta^{15}\text{N}$ values of herbivores/detritivores were 5.0-8.4‰, omnivores 8.8-10.2‰ and carnivores 11-12.7‰.
4. Mixing model equations were employed to calculate the possible range of contribution made by respective food sources to the diet of each species. The results revealed the importance of omnivorous species and the dependence of riverine biota on terrestrial subsidies, such as leaf detritus and fruits. Finally, the abundance of shrimps and their feeding habits placed in relief their key role in tropical freshwater food webs. Isotopic analysis provides a useful tool for assessing animal feeding patterns.

Keywords: diadromous species ; food web ; freshwater fauna ; stable isotopes ; tropical stream

Introduction

Many tropical studies have described freshwater trophic webs as detritus-based systems, characterised by short food chains, with a high degree of omnivory (Mantel, Salas & Dudgeon, 2004; Motta & Uieda, 2005). In Caribbean island streams, animal communities are usually dominated by assemblages of fish and shrimp species whereas the abundance of aquatic insects is very small (Buzby, 1998; March & Pringle, 2003). The richness of macrofauna species is low compared with that of continental tropical streams or even temperate ones. Macrofauna composition mainly consists of species belonging to three decapod families (Palaemonidae, Atyidae and Xiphocarididae) and four fish families (Eleotridae, Gobiidae, Mugilidae and Anguillidae). Many of these species are diadromous (amphidromous or catadromous) during a short part of their life cycle (Pringle, 1997). The amphidromous species (e.g. palaemonid, atyid, xiphocaridid shrimps and gobiid fishes) spawn in freshwater habitats from which newly hatched larvae are passively transported towards the sea by river currents. Larvae go through a series of transformations in brackish or saline environments before migrating upstream into freshwater systems where they grow and mature. In catadromous species (e.g. Mugilidae, Anguillidae), individuals spend most of their life history in fresh water and undertake downstream migrations to breed in the sea. These migrations occur during short time periods synchronised by river flow and moon cycle as living pulses and they represent an important functional linkage between stream headwaters, downstream reaches and estuaries. Migrations determine the longitudinal variations in faunal abundance along the length of a river. Downstream reaches contain juveniles and most of the fish species, while adult shrimps are present along the entire stream

continuum (with some habitat preferences being displayed within species). These ecological characteristics, reinforced by frequent hydrological disturbances, influence the availability of food sources and bring high plasticity to freshwater food web structures. Plasticity is particularly expressed through the flexible macroconsumer diets that are reported in the literature. Dietary data highlight the importance of opportunistic diets and show differences in the diets of some species between distinct tropical areas. A synthesis of the references for these data is provided in Table 1. The literature provides us with useful data regarding the variability in the feeding behaviour of tropical freshwater species. However, it cannot provide an insight into the specific diets of species local to a particular area, such as our area of choice for this study, Guadeloupe. In our study, rather than rely solely on the data provided, we recognised the importance of investigating trophic patterns in the area in order to acquire more knowledge on the diets of the local species. The habitats and life cycles of the freshwater species of the French West Indies are today exposed to threats, such as water abstraction, land-use changes, nutrient enrichment and toxic contamination. A better knowledge of the trophic relationships between freshwater resident species is necessary to bring to light the fluxes of matter and pollutants in these insular ecosystems in order to manage and to conserve this vulnerable freshwater fauna. The main objectives of this study were to propose an accurate representation of the stream food webs in Guadeloupe island and to estimate the relative importance of the major food sources supporting them. The approach consisted of (i) inventorying all the local trophic links available in the river; (ii) determining their isotopic signatures and (iii) identifying the diets and trophic levels of the organisms using stable isotope techniques combined with dietary data from the literature. Because the isotopic signature of an animal reflects its assimilated diet (DeNiro & Epstein, 1978, 1981), stable isotope analysis has been chosen as a useful tool to estimate the trophic status of consumers in food webs and to quantify the proportion of different food sources in animal diets (Peterson & Fry, 1987). In order to fulfil these objectives, we chose to conduct extensive sampling over a single stream, which we judged to be characteristic of Guadeloupe island for three main reasons: first, the stream has an important species diversity, which accounted for nearly all the species that are identified in Guadeloupe freshwater ecosystems; secondly, it successively drains forests, agricultural lands and residential areas, the three main landscape patterns observable on the islands and thirdly, it is affected by anthropogenic pollution (particularly organo-chlorated insecticides), as are the majority of the island streams.

Table 1 Feeding habits of the studied species based on the literature

Taxa	Feeding guild	Diet	References
<i>Neritina punctulata</i>	Herbivorous grazer	Microscopic algae in biofilm	1, 2, 3
<i>Melanoides tuberculata</i>	Detritivore	Detritus, epiphytic algae	1, 4
	Carnivore	-	5
<i>Pomacea glauca</i>	Detritivore/herbivore	-	1
<i>Atya</i> sp.	Filter feeder	Drifting detrital particles	6, 7
	Detritivore/herbivore	FPOM, leaf material, algae, insects	8
<i>Xiphocaris elongata</i>	Detritivore/herbivore	Plant material, biofilm, FPOM, insects	9, 10
	Omnivore (hypothesis)	Plant material, insects	11
<i>Macrobrachium</i> sp.	Omnivore	Detrital, algal and animal resources	9, 12
<i>Sicydium</i> sp.	Herbivorous grazer	Epiphytic algae	13, 14
	Omnivore (hypothesis)	-	15
<i>Awaous banana</i>	Herbivore	Algae	16
	Omnivore	Peryphyton tendency	17
<i>Eleotris</i> sp.	Carnivore	Shrimps, fish, molluscs, (detritus)	18, 19, 20
	Omnivore	Plant material, small crustaceans, fish	21
<i>Anguilla rostrata</i>	Carnivore	Shrimps, fish, crab, (insects)	14
	Carnivore/detritivore	Shrimps, fish, organic debris	22
<i>Gobiomorus dormitor</i>	Carnivore	Shrimps, fish, (crab, insects)	14, 18, 21

- indicates no data about diets is provided.

References: 1. Pointier & Lamy, 1998; 2. Suty, 1990; 3. Pyron & Covich, 2003; 4. Madsen, 1992; 5. Songtham *et al.*, 2005; 6. Iwata *et al.*, 2003; 7. Covich, 1988; 8. Pringle *et al.*, 1993; 9. Covich & McDowell, 1996; 10. Pringle, 1996; 11. March *et al.*, 2001; 12. Dudgeon, 1999; 13. Erdman, 1986; 14. Gillet, 1983; 15. Mantel *et al.*, 2004; 16. Debrot, 2003; 17. Lim *et al.*, 2002; 18. Winemiller & Ponwith, 1998; 19. Hildebrand, 1938; 20. Teixeira, 1994; 21. Nordlie, 1981; 22. Pringle, 1997;.

Methods

Study site

The study was performed in the lower reach of the River Grande-Anse, in the south of the Island of Basse-Terre, Guadeloupe (16°00'N and 61°30'W). The River Grande-Anse is 8.7 km long with a 20 km catchment area, which successively drains forests, agricultural land and urbanised areas. Its source is located 1100 m above sea level. The sampled river bed, about 10 m wide and 2000 m long, extended from the river mouth to 50 m above sea level. It is characterised by small cascades, rapids, cobble-riffles, pools and large runs (according to the classification of Malavoi, 1989). This alternation of hydromorphological facies creates differences in stream velocity and a mosaic of habitats available for macrofauna. Ligneous riparian vegetation is abundant and is composed of both exotic [e.g. *Terminalia catappa* L., *Cocos nucifera* L., *Artocarpus altilis* (Park.) Fosb.] and native species [e.g. *Cecropia schreberiana* Miq., *Philodendron giganteum* Schott, *Dalbergia ecastaphyllum* (L.)] (Rousteau, pers. comm). The study area is subjected to a humid tropical climate and received 2412 mm of rainfall in 2006 (Météo France). The present study was conducted during the dry season (December-June) of 2006. Climatic disturbances are slight and population migrations limited during the dry season in comparison with the wet season.

Sample collection and preparation

Sample collection

Our aim was to take samples representing all the potential trophic links. Biofilm was scraped from the surfaces of submerged rocks with a knife and a brush. Filamentous green algae were collected in the river bed and rinsed to remove attached epibionts. Leaf and fruit detritus were collected from depositional areas where they accumulate naturally. Terrestrial litter was rinsed to remove silt and epibionts. Drifting particulate matter (DPM; composed of terrestrial plant fragments and other particulate organic matter) was collected with a 30- μ m meshed-net set up in the water column. Fishes and shrimps were captured using a backpack electro-fishing device (DEKA 3000 Gerätebau, Marsberg, Germany). Molluscs were picked up by hand and aquatic insects were collected using a Surber sampler. All the habitats were prospected to be sure to collect most of the species present in the entire food web. All plants and animals were sampled all along the study reach. Following this, they were frozen at -30 °C before being identified, enumerated and analysed for stable isotope signatures.

Tissue preparation for isotopic analysis

The total lengths of the fishes and the shrimps, and the main axis of the shell for the molluscs, were measured to the nearest millimetre. Samples were generally pooled to create a representative composite sample [e.g. about 30 individuals constituted one sample of *Macrobrachium faustinum* (De Saussure)]. Where possible, distinct pooled samples of each food web compartment (species or groups of producers) were analysed to obtain a representative isotopic signature. When sufficiently numerous, individuals were classified into different cohorts in order to compare the diets of both adults and juveniles. Muscle tissue was dissected from the lateral and caudal musculature of fishes and shrimps, respectively. Molluscs and small fishes and shrimps were analysed whole. Samples for isotopic measurements were oven dried for at least 48 h at 50 °C and ground to a homogenous powder using pestle and mortar. Samples that potentially contained carbonates (i.e. primary producers, molluscs extracted from their shells and organisms analysed whole) were acidified. Samples were placed for 24 h under a glass jar with fuming HCl (37%) (Merck, for analysis quality) in order to remove calcareous material. The $^{15}\text{N}/^{14}\text{N}$ ratios were measured before acidification due to known significant modifications of $^{15}\text{N}/^{14}\text{N}$ by acidification.

Stable isotope analysis

Measurements of carbon and nitrogen isotopic ratios were performed with a mass spectrometer (Optima; GV Instrument, Cambridge, U.K.) coupled to a C-N-S elemental analyser (Carlo Erba, Pisa, Italy) for combustion and automated analysis. Isotopic ratios were presented as δ values (‰) expressed relative to the Vienna PeeDee Belemnite (vPDB) standard and to atmospheric N_2 for carbon and nitrogen, respectively. Reference materials were IAEA-N1 ($\delta^{15}\text{N} = 0.4 \pm 0.2\text{‰}$) and IAEA CH-6 ($\delta^{13}\text{C} = -10.4 \pm 0.2\text{‰}$). Experimental precision (based on the standard deviation of replicates of an internal standard) was 0.3‰ and 0.4‰ for carbon and nitrogen respectively. Elemental results were expressed as a percentage of the considered element (C or N) relative to the total dry weight. The C : N ratios calculated from these values were proxies for animal lipid content (Kline, 1997) and were used to normalise $\delta^{13}\text{C}$ values for lipid content following the methods of McConnaughey &

McRoy (1979). A lipid normalization procedure, essential for lipid-rich tissues ($C : N > 4$) was used to remove the effects of lipid isotope (DeNiro & Epstein, 1977), enabling the identification of the source of carbon in samples based on the natural C gradient (Kline, 1997).

Data analysis and food source modelling

δC versus δN values were plotted to help in the determination of trophic linkages based on δN and to identify sources of nutrition using δC . The identified food sources were cross referenced with an extensive bibliography and were excluded if non-consistent with dietary data (mainly based on gut content analysis) and/or with species biology (habitat conditions, anatomical specificities, etc.). For each species, the potentially exploited diet items were then tested with a specific piece of software. The Microsoft Visual Basic program, called Isosource version 1.3 (Phillips & Gregg, 2003), was used to calculate the feasible ranges of the multiple potential food source contributions to consumer diets. This program has been designed for situations in which n isotopes (hereafter $\delta^{13}C$ and $\delta^{15}N$) are being used and more than $n + 1$ sources are likely to be contributing to the consumer signature (the mixture). The program was used here as a tool to estimate the proportion of food sources in an animal's diet, once these sources had been identified by the previous work described above. This program runs as follows. All possible combinations of source proportions (that sum to 100%) are iteratively created by some small increments. Secondly, the predicted isotope values of each mixture are computed using linear mixing equations that preserve mass balance. Isotope values of computed mixtures are then compared with the observed isotope values. The range of combinations that match within a specified tolerance value is then described (Phillips, 2001; Phillips & Gregg, 2003). In the present study, minor sources (i.e. contribution $<5\%$) were omitted, while major ones (i.e. contribution $>5\%$) were considered in the description of the animals' diet. Mantel *et al.* (2004) showed that including more than seven sources in the program resulted in excessive processing time and in less finely resolved results than when using fewer than seven sources. In the present study, when the number of potential resources in the diet of some consumers reached more than seven sources (eight sources for *Macrobrachium* species), calculations were performed with all of them and the source with the lowest contribution was removed. New calculations were then performed with the seven dominant sources. The mass balance tolerance was set as 0.4‰ to reflect source and mixture sample variability (Phillips & Gregg, 2003), and source increment was set as 1‰. A mean trophic fractionation of 1‰ was set for δC for all consumers (DeNiro & Epstein, 1978; Rau *et al.*, 1983), except for the strict carnivorous fish *Gobiomorus dormitor* (Lacepède, Eleotridae) (0.5‰). The literature reports that trophic fractionation for C should be smaller for carnivores that consume highly digested protein than for herbivores and omnivores that feed on vascular plants containing a high proportion of poorly digested complex carbohydrates (McCutchan *et al.*, 2003). Trophic fractionation of N is greater and increases with high-protein diets (McCutchan *et al.*, 2003). Fractionation values for N were assumed to be 2‰ for molluscs, 2.5‰ for detritivorous shrimps and algivorous fishes, 3‰ for omnivorous shrimps and fishes and 3.5‰ for strictly carnivorous fishes. These presumed feeding modes are based on dietary data in the literature coupled with the interpretation of the $\delta^{13}C$ versus $\delta^{15}N$ plot. A spreadsheet available on the web site of the U.S. Environmental Protection Agency (<http://www.epa.gov/wed/pages/models.htm>) was used to perform calculations for this model. Differences between the isotopic signatures of sources and consumers were tested using the Mann-Whitney or Kruskal-Wallis nonparametric tests (XLSTAT-Pro version 7-5-2; Addinsoft, Paris, France). Significant differences were accepted at a level of $P < 0.05$.

Results

Analysis of food web components

Drifting particulate matter, leaf and fruit detritus, biofilm and filamentous green algae were considered as basal resources. Their isotopic signatures (mean \pm SD) are presented in Table 2. Insect and planktonic biomasses were negligible in the study site. A total of 16 consumers were identified, including three mollusc, eight shrimp and five fish species. Their isotopic values are given in Table 3, with the total number of individuals of each species encountered during the sampling. These numbers are indicators of abundance, since the entire study site was explored. Populations of freshwater snails *Neritina punctulata* (Lamarck, Neritidae) and *Melanoides tuberculata* (Müller, Thiaridae) were dense, in contrast with *Pomacea glauca* (Linné, Ampullaridae), which was little represented in the lower part of the river. Among shrimps, Palaemonidae was found to be the most important family, with a dominance of *M. faustinum*, followed by *M. crenulatum* Holthuis, *M. acanthurus* (Wiegmann) and *M. heterochirus* (Wiegmann). The species *M. carcinus* (Linnaeus) was found to be rare in this ecosystem. Atyid shrimps [dominated by *Atya innocous* (Herbst)] and xiphocaridid shrimps [represented by the sole species *Xiphocaris elongata* (Guérin-Méneville)] were quite abundant. Among fish species, *Eleotris perniger* (Cope, Eleotridae) was highly dominant. *Awaous banana* (Valenciennes, Gobiidae) was frequent, while *G. dormitor*, *Anguilla rostrata* (Lesueur, Anguillidae) and *Sicydium punctatum* (Perugia, Gobiidae) were rare.

Table 2 Carbon and nitrogen isotopic signatures of the basal food sources (mean \pm SD)

Basal sources	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C : N
		Mean \pm SD	Mean \pm SD	
Drifting particulate matter	5	-28.6 \pm 0.3	4.3 \pm 1	14.1
Leaf detritus	5	-29.1 \pm 1.2	4.3 \pm 1.4	28.1
Fruit & seed detritus	1	-24.9	2.5	16.3
Biofilm	5	-21 \pm 0.2	3.3 \pm 0.3	12.3
Filamentous green algae	3	-22.7 \pm 0.7	7.7 \pm 0.7	10.3

n represents the number of composite samples analysed and C : N the atomic ratios (w : w).

Table 3 Mean (\pm SD) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) for consumers sampled in a Guadeloupe river

Species	A/J	Length (mm)	Ab.	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C : N
					Mean \pm SD	Mean \pm SD	
Mollusc							
<i>Neritina punctulata</i>	A	10-25	1033	6 (211)	-17.3 \pm 0.4	5.8 \pm 0.2	5.2
<i>Melanoides tuberculata</i>	A	10-25	1391	2 (348)	-17.5 \pm 0.5	7 \pm 0.1	5
<i>Pomacea glauca</i>	A	30-50	11	3 (3)	-24.3 \pm 1.7	5 \pm 0.1	4.6
Shrimp							
<i>Atya innocous</i>	A	25-60	625	16 (169)	-24.5 \pm 0.2	8.2 \pm 0.5	3.5
<i>Atya scabra</i>	A	30-60	195	7 (107)	-24.4 \pm 0.3	8.4 \pm 0.2	3.5
<i>Xiphocaris elongata</i>	J	10-15	>1000	3 (450)	-16 \pm 0.2	8.6 \pm 0.8	4.9
<i>Xiphocaris elongata</i>	A	40-60	621	3 (48)	-24.7 \pm 0.3	7.3 \pm 0.1	3.3
<i>Macrobrachium faustinum</i>	A	35-60	1337	6 (188)	-21.5 \pm 0.2	9 \pm 0.1	3.3
<i>Macrobrachium crenulatum</i>	A	45-65	125	6 (70)	-23.1 \pm 0.4	9.2 \pm 0.2	3.4
<i>Macrobrachium acanthurus</i>	J	25-55	108	1 (15)	-20.1	9.2	3.3
<i>Macrobrachium acanthurus</i>	A	105	11	1 (1)	-22.3	9.2	3.3
<i>Macrobrachium heterochirus</i>	A	25-60	80	5 (45)	-22.4 \pm 1.1	9.1 \pm 0.2	3.4
<i>Macrobrachium carcinus</i>	A	80	1	1 (1)	-19.2	10.2	3.3
Fish							
<i>Sicydium punctatum</i>	A	40-45	5	1 (5)	-20.8	8.9	3.2
<i>Awaous banana</i>	A	95-130	24	4 (4)	-19.3 \pm 0.3	10.1 \pm 0.9	3.4
<i>Eleotris perniger</i>	J	45-65	80	6 (41)	-18.2 \pm 0.1	8.8 \pm 0.4	3.4
<i>Eleotris perniger</i>	A	70-100	79	12 (47)	-18.7 \pm 0.8	9.8 \pm 0.9	3.3
<i>Anguilla rostrata</i>	A	600-700	2	2 (2)	-22.8 \pm 0.4	11 \pm 0.5	7.3
<i>Gobiomorus dormitor</i>	A	165-180	2	2 (2)	-22.2 \pm 0.7	12.7 \pm 0.8	3.1

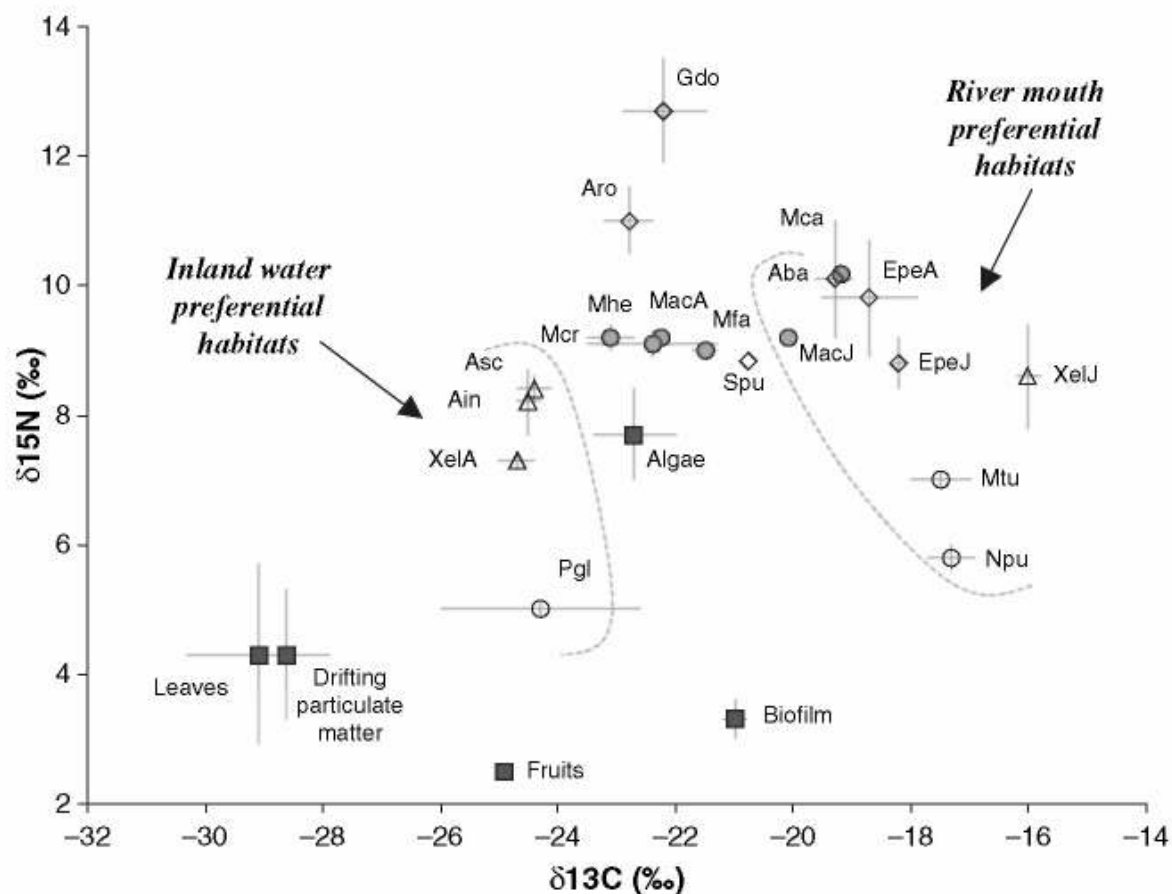
A, adult cohort; J, juvenile cohort; Ab., abundance (the total number of individuals encountered in the study site during the sampling); n, number of composite samples analysed followed by the total number of collected individuals (in brackets); C : N is the elemental ratio (w : w).

Carbon and nitrogen signatures in basal resources

Isotopic signatures of the dominant carbon sources were clearly distinguished, except for those of leaf detritus and DPM, which showed very similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Table 2, Fig. 1). The similarity between these two sources suggested that DPM is mainly composed of vegetation fragments. The low C/N ratio of DPM seems also to indicate the presence of fruit and seeds fragments. Therefore, we have aggregated them into a single basal source, which we have called 'plant detritus'. Thus, the four main sources of organic matter (plant detritus, fruits, biofilm and filamentous algae) were isotopically distinct. The Kruskal-Wallis test applied on plant detritus, biofilm and algae (the sources that numbered more than one sample) attested the significant differences between these three sources for $\delta^{13}\text{C}$ ($H = 12.618$, $P = 0.002$) and for $\delta^{15}\text{N}$ values ($H = 8.431$, $P = 0.015$). Results of the multiple comparison tests, with Bonferroni corrections, allowed us to distinguish plant detritus from biofilm $\delta^{15}\text{C}$ values and algae from biofilm $\delta^{15}\text{N}$ values. We observed depleted- ^{13}C mean signatures for terrestrial food

sources ($\delta^{13}\text{C}_{\text{plant detritus}} = -28.9\text{‰}$, $\delta^{13}\text{C}_{\text{fruit detritus}} = -24.9\text{‰}$) compared with aquatic signatures ($\delta^{13}\text{C}_{\text{algae}} = -22.7\text{‰}$; $\delta^{13}\text{C}_{\text{biofilm}} = -21\text{‰}$). This allowed a differentiation between allochthonous (terrestrial) and autochthonous (in-stream) pathways. The $\delta^{15}\text{N}$ values of the producers were low, and varied from 2.5‰ (fruit detritus) to 4.3‰ (plant detritus), except for filamentous green algae, which were N-enriched (7.7‰). The C : N ratios, presented in Table 2, were higher for terrestrial than for aquatic material. These values were used to compare the nutritional values of the food sources in terms of digestibility, with lower ratios indicating higher digestibility.

Fig. 1 Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($\pm\text{SD}$) of basal resources (black squares), molluscs (empty circles), *Atyidae* and *Xiphocarididae* shrimps (triangles), *Palaemonidae* shrimps (grey circles) and fish (diamonds) collected in River Grande-Anse. Species preferentially living close to the sea tend towards enriched- ^{13}C values while inland water living species tend towards depleted ones. Non-clustered species are less exacting in terms of habitat preferences (*Npu*, *Neritina punctulata*; *Mtu*, *Melanoides tuberculata*; *Pgl*, *Pomacea glauca*; *Xel* (*A* or *J*), *Xiphocaris elongata* adult or juvenile; *Ain*, *Atya innocous*; *Asc*, *Atya scabra*; *Mfa*, *Macrobrachium faustinum*; *Mcr*, *M. crenulatum*; *Mac* (*A* or *J*), *M. acanthurus* adult or juvenile; *Mhe*, *M. heterochirus*; *Mca*, *M. carinus*; *Spu*, *Sicydium punctatum*; *Epe* (*A* or *J*), *Eleotris perniger* adult or juvenile; *Aba*, *Awaous banana*; *Aro*, *Anguilla rostrata*; *Gdo*, *Gobiomorus dormitor*). 152 × 114 mm (600 × 600 DPI).



$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in consumers

Mean $\delta^{13}\text{C}$ values among species ranged from -16‰ for juveniles of *X. elongata* to -24.7‰ for adults of the same species. The distribution of $\delta^{13}\text{C}$ values for primary consumers showed that they depended substantially on one of the potential basal resources. The molluscs *N. punctulata* (-17.3‰) and *Melanoides tuberculata* (-17.5‰) were linked to biofilm. The difference in $\delta^{13}\text{C}$ values noted between molluscs and their resource is important and does not merely reflect the ^{13}C fractionation during the assimilation of their food. It is more likely that this indicates that animals mainly fed on one of the biofilm components, which would have an enriched carbon signature compared to the others. The mollusc *P. glauca* (-24.3‰) was found to depend on fruits and plant

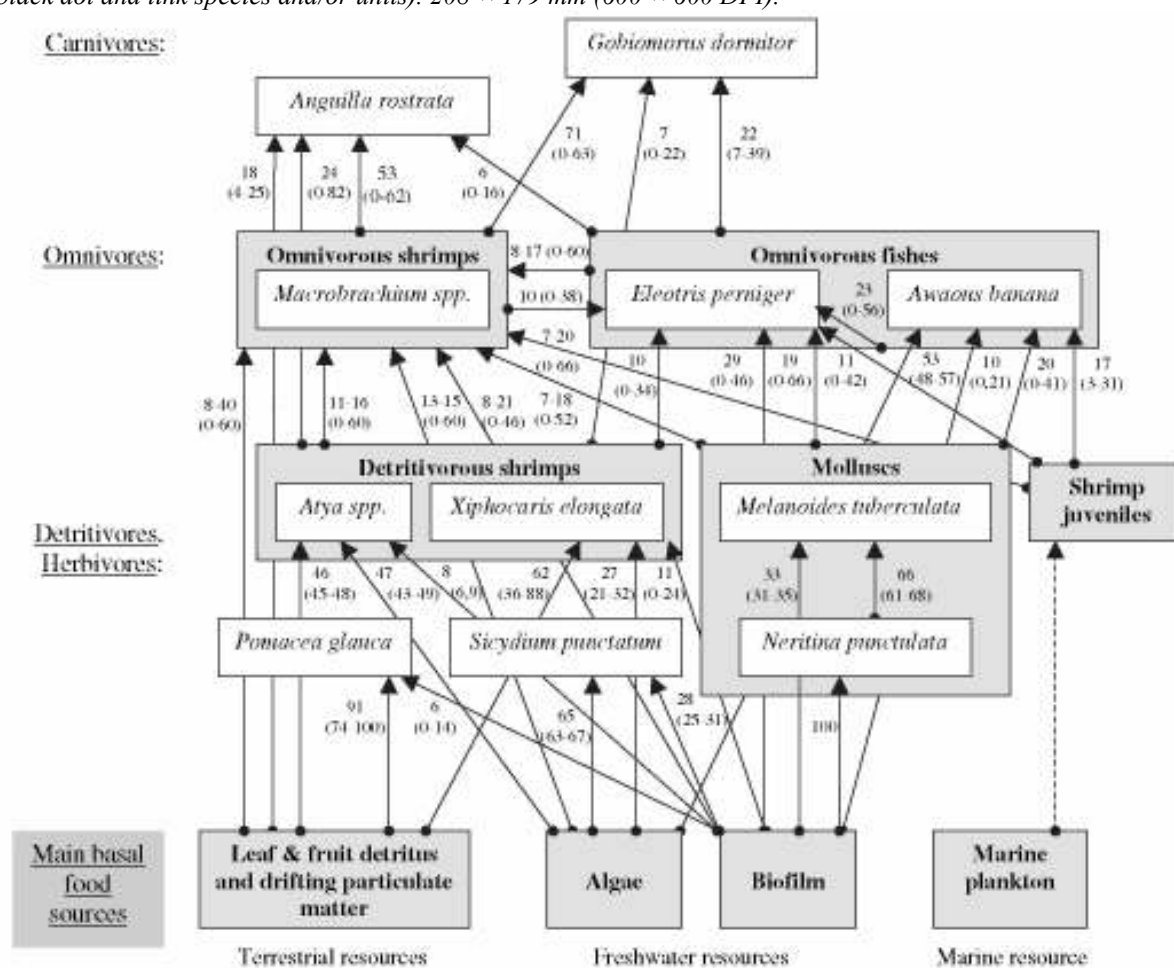
detritus and the fish *S. punctatum* (-20.8‰) was found to depend on algae. Atyidae and Xiphocarididae shrimps had a similar mean $\delta^{13}\text{C}$ (-24.4‰ to -24.7‰) situated between the plant detritus and algae carbon signatures, which suggested a contribution of these two primary sources. Secondary consumers, such as *Macrobrachium* species, exhibited a wide range of $\delta^{13}\text{C}$ values (-19.2‰ to -23.1‰) reflecting, in addition to interspecies variability, the contribution of diverse food sources in their diet. The C values of the fishes *A. banana* and *E. perniger* were enriched relative to those of shrimps and differed significantly from the $\delta^{13}\text{C}$ values of plant detritus. They were close to the $\delta^{13}\text{C}$ values of algae and biofilm but also to other consumer signatures, such as the molluscs *N. punctulata* and *M. tuberculata*. Carbon signatures of the biggest collected fishes, *A. rostrata* (-22.8‰) and *G. dormitor* (-22.2‰), were situated approximately at the median of the overall $\delta^{13}\text{C}$ distribution (-16‰ to -28.9‰). The ^{15}N values of consumers were enriched relative to the mean values of the dominant primary producers, with the exception of filamentous green algae, which exhibited high $\delta^{15}\text{N}$ signatures. Mean $\delta^{15}\text{N}$ values of the consumers varied from 5‰ for the bottom dweller mollusc *P. glauca* to 12.7‰ for the predator fish *G. dormitor*. Molluscs, xiphocaridid and atyid shrimps had the lowest $\delta^{15}\text{N}$ values of the consumers, ranging from 5‰ to 8.4‰. Palaemonid shrimps and the fishes *S. punctatum*, *E. perniger* and *A. banana* showed median $\delta^{15}\text{N}$ values ranging from 8.8‰ to 10.2‰. The highest $\delta^{15}\text{N}$ values were presented by *A. rostrata* (11‰) and *G. dormitor* (12.7‰). The $\delta^{15}\text{N}$ values of consumers were found to increase from a basal trophic position to the highest consumer ranks, generally in accordance with their presumed diet (based on literature data). Nevertheless, the juveniles of *X. elongata* presented a high $\delta^{15}\text{N}$ value (8.6‰) despite being considered to belong to a low trophic level. Moreover, the highest variability of $\delta^{15}\text{N}$ was recorded for the low trophic level (i.e. for herbivores and detritivores).

Relative contributions of the dominant food sources in the animals' diets

Among the different sources potentially available to consumers, only the most abundant were considered in the application of the mixing equations. Scarcely represented species (such as *P. glauca*, *S. punctatum* and *M. carcinus*, which showed an indicator of abundance level lower than 15, cf. Table 3) constituted anecdotic food components and were removed from the modelling. As included sources must differ isotopically (Phillips & Gregg, 2001), species from the same trophic guild with similar $\delta^{13}\text{C}$ values (according to Mann-Whitney test) were aggregated and an average $\delta^{13}\text{C}$ was used in the model. For example, the source 'molluscs' included *N. punctulata* and *M. tuberculata*. Each species analysed was then associated to the food sources it is likely to exploit, consistent with isotopic signatures, dietary data and biology. As an example, the fish *S. punctatum* was associated neither to animal prey (since no animal remains were ever found in its gut) nor to leaf detritus (since the fish lives in rapids where leaves do not accumulate). Instead *S. punctatum* was associated to algae and biofilm (which is consistent with isotopic signatures and which corresponds to the gut content analysis results and to the morphology of its dentition). Relative contributions of the potential food sources calculated using a mixing model are reported as ranges of food source proportions in the diet (Fig. 2). Means of possible solutions are also given for information but these are less reliable than ranges of possible solution. Minor sources (i.e. contribution <5%) were omitted in Fig. 2 for reasons of visibility. *Pomacea glauca* appeared to depend on fruit detritus (62-83%, mean = 73%) and plants (12-24%, mean = 18%), whereas autochthonous source consumption was rare (0-14%, mean = 6% of biofilm). Conversely, *N. punctulata* essentially fed on autochthonous resources (100% biofilm). *Melanoides tuberculata* showed a higher $\delta^{15}\text{N}$ value, which suggested that it had a more protein-enriched diet. Indeed, the mixing model proposed that molluscs contributed to between 61% and 68% (mean = 66%) of its diet. *Xiphocaris elongata* mainly depended on terrestrial resources: mixing model outcomes found a contribution of 36-55% (mean = 46%) of plant detritus, 0-33% (mean = 16%) of fruits, 21-32% (mean = 27%) of filamentous algae and 0-24% (mean = 11%) of biofilm. *Atya innocous* and *A. scabra* (Leach) had similar diets. They depended mainly on algae (respectively 43-44% and 48-49%) and plant detritus (47-48% and 45%). All the palaemonid species depended on the same food sources but showed varying resource contributions. *Macrobrachium carcinus* had a highly carnivorous diet: the cumulated means of consumer item proportions reached 66% (with 0-52% of molluscs, 0-66% of shrimp juveniles, 0-42% of detritivorous shrimps and 0-60% of omnivorous fishes), as against 34% of primary producers (with 0-32% of plant detritus, 0-36% of biofilm and 0-56% of algae). For other adult *Macrobrachium* species, the mixing model gave quite similar solutions, which were poorly constrained. For these omnivorous species, plant detritus formed the major component (ranging 0-60%, with means situated between 25% and 40% according to species), followed by biofilm (0-46%, with means situated between 8% and 21%), algae (0-62%, with means situated between 13% and 15%), detritivorous shrimps (0-60%, with means situated between 12% and 16%), molluscs (0-46%, with means situated between 7% and 13%), fishes (0-38%, with means situated between 8% and 9%) and shrimp juveniles (0-42%, with means situated between 7% and 9%). Fruits should also have been part of their diet (Larned, Chong & Punewai, 2001) but they did not appear here as a major food source (mean contribution <5%). *Sicydium punctatum* essentially fed on algae (63-67%, mean = 65%) and biofilm (25-31%, mean = 28%), while the other gobiid fish species, *A. banana*, exploited various food sources. This species appeared to eat both primary producers (algae:

48-57%, mean = 53%, biofilm: 0-21%, mean = 10%) and small consumers such as molluscs (0-41%, mean = 20%) and shrimp juveniles (3-31%, mean = 17%). The diet of adult specimens of *E. perniger* was dominated by shrimps (0-42%, mean = 31%), followed by biofilm (0-46%, mean = 29%), fishes (0-56%, mean = 23%) and molluscs (0-66%, mean = 19%). It differed from that of smaller specimens, which was mostly made up of biofilm (21-57%, mean = 40%), molluscs (0-64% = 32%) and shrimp juveniles (0-41%, mean = 15%). The food sources exploited by *A. rostrata* were dominated by shrimps (Palaemonidae: 0-75%, mean = 53%, Xiphocarididae and Atyidae: 0-82%, mean = 24%), followed by plant detritus (4-25%, mean = 18%) and fishes (0-16%, mean = 6%). In contrast, *G. dormitor* seemed to feed strictly on shrimps (0-81%, mean = 78%) and fishes (7-39%, mean = 22%).

Fig. 2 Food web of a Caribbean stream (Grande-Anse, Guadeloupe), based on stable isotope analysis (grey units show elements with similar carbon isotopic signatures and constitute the dominant potential food sources of this aquatic ecosystem during the dry season. Mean percent contributions of sources to adult consumers are indicated below the arrows when $\geq 5\%$. They are followed by the minimum and the maximum in parentheses (the presence of two means indicates a range of contributions for the different species of a genus). Arrows start with a black dot and link species and/or units). 208 × 179 mm (600 × 600 DPI).



Discussion

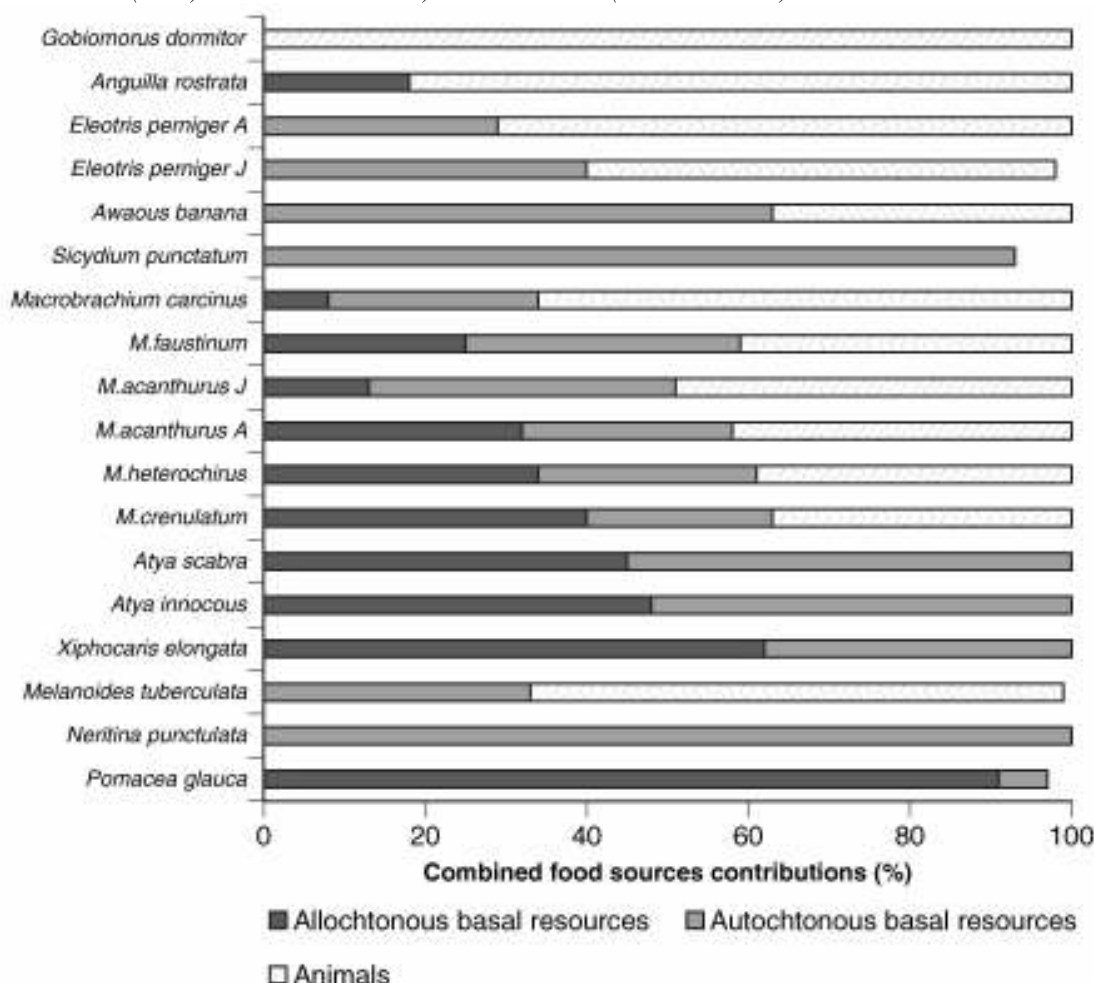
Overall $\delta^{13}\text{C}$ measurements ranged from between -28.9‰ for plant detritus and -16‰ for shrimp juveniles. These two ends of the scale characterise two contrasting environments: terrestrial and marine habitats, respectively. Indeed, shrimp juveniles are assumed to feed on marine zooplankton during their early life stages in coastal seawater (Kumlu, 1999) and partly conserve their marine signature in the river. Between the above two $\delta^{13}\text{C}$ measurements lie intermediate $\delta^{13}\text{C}$ values corresponding to freshwater autochthonous material. Isotopic distribution of food sources follows a longitudinal pattern along the study reach continuum: terrestrial food

sources are C-depleted compared to those in fresh water, which in turn are C-depleted compared to those in salt water (Fry & Sherr, 1984; Peterson & Fry, 1987). The low $\delta^{13}\text{C}$ values of plants found in the present study reflect the values found in the literature, which correspond to an average of -28‰ (Peterson & Fry, 1987; Loneragan, Bunn & Kellaway, 1997; Corbisier *et al.*, 2006). The carbon signature of filamentous green algae was also in the range previously reported for other tropical freshwaters, varying from -19‰ to -30‰ (Forsberg *et al.*, 1993; Parkyn, Collier & Hicks, 2001; Brito *et al.*, 2006). Biofilm $\delta^{13}\text{C}$ values (-21‰) were close to carbon measurements previously made in the Caribbean island of Puerto Rico: -22‰ to -27‰ (March & Pringle, 2003). As isotopic composition of consumers reflects their diet, species distribution follows the longitudinal pattern observed in basal resources. Indeed, species preferentially living close to the river mouth were found here to have enriched- ^{13}C values (e.g. *N. punctulata*, *M. tuberculata*, *M. acanthurus*, juveniles of *X. elongata*, *E. perniger* and *A. banana*), while others, which prefer inland water habitats, showed the most depleted values (*Atya* spp., adults of *X. elongata*, *P. glauca*). The carbon isotopic ratios of producers and consumers were found to decrease gradually with their distance from the sea and to reflect changes in habitat and food sources. In addition, isotopic carbon depletion was observed from young to adult cohorts of all the amphidromous species tested (*X. elongata*: -16‰ to -24.7‰, *E. perniger*: -18.2‰ to -18.7‰, *M. acanthurus*: -20.1‰ to -22.3‰). This not only reflects a diet shift between cohorts but also illustrates the transition from a marine to a freshwater diet occurring during upstream migration. Carbon isotopes constitute here a natural indicator of marine to freshwater migration. Mean $\delta^{15}\text{N}$ values, combined with calculated food source contributions, enabled the clustering of the river animals into three main trophic guilds (Fig. 2). The first one includes herbivorous and detritivorous organisms that essentially feed on basal resources. This group includes consumers with the lowest $\delta^{15}\text{N}$ values, i.e. molluscs, xiphocaridid and atyid shrimps. *Pomacea glauca* is classified as a detritivorous mollusc, while *N. punctulata* is considered as a herbivore. Mixing model outcomes suggested that this latter mollusc contributed to a large proportion of the *M. tuberculata* diet. As animal remains are rarely found in *M. tuberculata* gut content (Madsen, 1992), this mollusc may act as a detritivore, which consumes, in addition to biofilm, dead individuals or faecal pellets from other organisms living in the same habitat (i.e. *N. punctulata*). Indeed, no detrital source from dead organisms was entered into the model and we considered that each animal food source represented both live and dead organisms. The shrimp *X. elongata* is clearly dependent on terrestrial carbon resources. As this species inhabits calm habitats close to the river banks where leaf detritus is abundant, its diet is likely to be detritivorous and dominated by dead leaves. This hypothesis is consistent with several studies that have reported that *X. elongata* exhibits a feeding reliance on leaves (March *et al.*, 2001; March & Pringle, 2003). By contrast, atyid shrimps live in waterfalls where high water velocity precludes depositional areas. The plant detritus on which they partly feed is assumed to be composed of DPM rather than leaves. It can be concluded that *A. innocous* and *A. scabra* filter DPM in addition to feeding on algal material. Organisms of this first guild have relatively distant $\delta^{15}\text{N}$ signatures (e.g. *P. glauca* and *Atya scabra*), since one of their resources (algae) has a higher $\delta^{15}\text{N}$ value than the other three. This high signature level of algae reflects the high nitrogen content measured in water samples from the lower part of the River Grande-Anse (nitrate levels in the study site are twice as high as the mean value measured in the lower parts of the Guadeloupean rivers (S.I.E.E., 1999; DIREN: Direction Régionale de l'Environnement, unpubl. data). As mentioned in other isotopic studies (Costanzo *et al.*, 2001; Corbisier *et al.*, 2006), this nutrient enrichment, due to the input of nitrogenous fertilisers and sewage waste in the river catchment area, is considered to be the cause of the N-enrichment of algae. The evaluation of the trophic level of *S. punctatum* is considered to be biased since this fish shows a strong reliance on algae. Its high nitrogen signature is probably due to the ^{15}N -enrichment of algae rather than to an omnivorous diet. Indeed, gut content analyses made by Gillet (1983) in Guadeloupe detected the presence of diatoms, while no animal remains were ever found.

Moreover, the specific dentition morphology of *S. punctatum*, examined by Watson (2000), fits the dietary requirements associated with the consumption of algae. Considering the proximity between the position of *S. punctatum* and algae, this fish has been included in the first guild, as an algae feeder. The second trophic guild brings together omnivorous consumers with median $\delta^{15}\text{N}$ values (palaemonid shrimps and the fishes *E. perniger* and *A. banana*). *Macrobrachium* species are both predators and detritivores. Taking into account their abundance and diet, freshwater shrimps appear to play a significant trophic role in the food web. They exert a predation pressure on both the adjacent and lower levels (palaemonid shrimps) and appear as important processors of organic matter (mostly atyid and xiphocaridid shrimps) (March *et al.*, 2001; Parkyn *et al.*, 2001). The fishes *A. banana* and *E. perniger* are both omnivores but the first of these has a herbivorous tendency, while the second has a more carnivorous diet. As reported by Winemiller & Ponwith (1998), our mixing model results showed a shift in the diet of *E. perniger*, which was found to feed on more fishes and shrimps as its size increased. The last guild includes the carnivorous organisms with the highest $\delta^{15}\text{N}$ values. *Anguilla rostrata*, which at first seems to be omnivorous, since it ingests an important amount of plant detritus (Pringle, 1997; Fiévet, Dolédec & Lim, 2001), is classified among the carnivorous fishes because of its diet focused on shrimps. *Gobiomorus dormitor* feeds heavily on animal prey and does not depend on primary producers: it is considered as strictly carnivorous.

These last two predator species finally integrate both allochthonous and autochthonous carbon signatures via the assimilation of consumers, which themselves feed on basal resources. Initial carbon resources become combined in the upper trophic levels. Shrimp juveniles, with a high $\delta^{15}\text{N}$ signature that is imputed to the influence of the marine environment in which they had just been living, are considered to be zooplankton feeders. As reported for other tropical stream food webs (Schmid-Araya *et al.*, 2002), a dominance of omnivorous species was observed here, compared to a lower diversity of herbivorous and carnivorous organisms. This is responsible for the presence in the studied river of several short food chains to the detriment of long top-down trophic cascades (Fig. 2). The feeding habits of the consumers deduced from the isotopic analysis were compared to the quantitative dietary data available in the literature. The present results are in agreement with those concerning the diets of the well-studied species, such as *Macrobrachium* spp. or *A. rostrata*. This allowed us to extrapolate the results to the feeding behaviour of the less-studied species (e.g. *A. banana* and *M. tuberculata*). The studied food web depends on three main basal food sources: filamentous green algae, biofilm and terrestrial detritus. Allochthonous resources (leaf, fruit and seed detritus) seem to be largely exploited, especially by the abundant shrimp community. Contrary to temperate aquatic ecosystems, fruit detritus is an important food resource in tropical streams where riparian fruit input is high and continues all year (Lamed *et al.*, 2001). Exported fruits encountered in River Grande-Anse were dominated by breadfruit, almonds, guavas and mangos. They have a higher nutritional value (C : N = 16.3, in Table 2) than the other forms of detritus (C : N = 28.1). Algal-based material (filamentous green algae and biofilm) remains an important exploited food source since it is consumed by a large number of species (all but carnivorous fishes). The importance of these autochthonous sources may be attributed to their higher nutritional value, in term of proteins, as judged from their lower C : N ratios (12.3 for biofilm and 10.3 for algae). Other neotropical studies have mentioned the high digestibility and nutritional value of algae and biofilm compared to vascular plants or plant detritus (Forsberg *et al.*, 1993; Lamberti, 1996; Kieckbusch *et al.*, 2004; Mantel *et al.*, 2004). Finally, the food web studied here depends on both allochthonous and autochthonous primary production, as summarised in Fig. 3. This graph highlights the importance of terrestrial subsidies, which contribute on average to 40% of the basal resources exploited by adult consumers. Autochthonous resources contribute to the other 60%. Among animal resources, snails represent an important source of energy, as mentioned for other tropical streams (Parkyn *et al.*, 2001; Pyron & Covich, 2003). Shrimp juveniles form a non-negligible food source for the omnivorous guild and indirectly represent the supply of matter from the marine environment. By contrast, the poor biomass of aquatic insects does not constitute any consistent food source, neither does the planktonic biomass, which is quasi absent in such turbulent rivers. As fishes and shrimps partially feed on the same resources, there are potentially in competition. The present results show that (i) detritivorous shrimps exhibit similar food choices; (ii) omnivorous shrimps have almost identical feeding niches and (iii) they share a common trophic position with the omnivorous fishes. The distinct habitat preferences between species in tropical running water play an important role in the species' coexistence (Tokeshi, 1999), reducing the likelihood of their encounter and resulting in a partition of territory and food sources (Hansen, Hart & Merz, 1991). Even so, predation exists between some competitors, as shown in the results: omnivorous shrimps and fishes prey upon each other, with the larger individuals feeding on the smaller ones. It is possible that shrimps developed their nocturnal activity as a response to avoid intra-guild predation by diurnal active fishes (Pringle & Hamazaki, 1998). In conclusion, the food web of this Caribbean river shares many common characteristics with other freshwater tropical stream food webs (the importance of detrital resources, a high degree of omnivory and short food chains). In addition, it reveals the dependence of riverine biota on terrestrial inputs, with an average contribution of allochthonous resources estimated to 40% of the total basal resource contribution to the diet of adult animals. Moreover, the supply of marine resources, made through the consumption of shrimp juveniles, represents the oceanic influence and highlights the ecotonal functional position of the studied freshwater system. The food web in the river mouths of Caribbean rivers collects and exploits the energy sources from both adjacent environments. The isotopic approach undertaken here to investigate dietary patterns provided a good understanding of the fluxes of matter transferring through the food web and will be used in future studies to investigate fluxes in pollution.

Fig. 3 Relative contributions of combined dominant food sources to consumer diets: exploited food sources are divided into allochthonous resources (plant and fruit detritus), autochthonous resources (filamentous green algae and biofilm) and animals (molluscs, shrimps and fishes). Sums may not reach 100% since small contributions (<5%) were not considered). 146 × 136 mm (600 × 600 DPI).



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