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# Upstream/downstream food quality differences in a Caribbean Island River

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**Abstract** Caribbean rivers are inhabited by native macrofauna with a diadromous life cycle. The factors influencing the upstream migration of diadromous species are not well understood. Suggested primary factors include species density, habitat suitability and food availability. We hypothesized that food quality could be a key parameter in the upstream migration of macrocrustaceans. We sampled the main shrimp species and their potential food sources along an altitudinal gradient in the Grand Carbet River of Guadeloupe. Lipid analyses of the different food items reveal that biofilm and drifting organic matter are main sources of eicosapentaenoic acid (EPA). Biofilm is richer in EPA upstream, while drifting material is richer in EPA downstream. These opposed altitudinal gradients are reflected in shrimp lipids depending on whether they feed on biofilm or drifting organic matter. In addition, low EPA levels in shrimp suggest that dietary EPA could be a limiting factor in this system and that this differential altitudinal distribution of EPA could influence shrimp settlement.

**Keywords** Essential fatty acids · Tropical streams · Palaemonidae · Atyidae · West Indies

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## Introduction

Native freshwater macrofauna in small Caribbean islands mainly consists of the diadromous species (Keith 2003; Lejeune et al. 2014; Tabouret et al. 2015; Frotté et al. 2020a, b). A species with a diadromous-amphidromous life cycle hatches in freshwater systems, then drifts downstream and undergoes a marine larval dispersion. After a final metamorphosis in river mouths, juveniles migrate upstream to grow until they reach the adult reproductive stage (McDowall 2007). During their upstream migration, juveniles settle at different altitudes along the rivers. The reasons for this differential upstream migration across individuals of the diadromous species are not fully understood, although the effects of various factors such as species density, habitat suitability, food availability, and trophic resources are often mentioned (Keith 2003; Keith and Lord 2011).

Caribbean rivers are typically volcanic tropical island streams, characterized by a steep elevation, very turbulent and shallow waters, and marked dry and wet seasons. In these very oligotrophic environments, the autochthonous production of organic matter is restricted to the development of an epilithic biofilm on rock surfaces (Monti et al. 2018), while a significant amount of organic matter made of allochthonous material, including wood, leaves and fruit, is transferred from terrestrial riparian areas (Heartsill-Scalley and Aide 2003; Clark et al. 2017). Portions of this allochthonous production are subject to sedimentation (e.g., wood and leaf litter), while other portions flow downstream (e.g., drifting particulate organic matter), the fluxes of which are especially important in the lower reaches of these rivers (Moyer et al. 2013). The epilithic biofilm, leaf litter and drifting organic matter constitute major food sources for benthic macrofauna (Coat et al. 2009; Lefrançois et al. 2011).

Caribbean river macrofauna is dominated by crustaceans, represented by the Palaemonidae and Atyidae families, which present specific differences in terms of trophic ecology: Palaemonidae is detritus feeders and opportunistic predators, the epilithic biofilm also constitutes a significant component of their diet (Covich et al. 1999; Dudgeon 1999; Coat et al. 2009). Atyidae, on the other hand, is suspension feeders exploiting the drifting matter in fast stream flows, while also being able to become epilithic biofilm brushers in low-flow conditions (Pringle and Blake 1994; Covich et al. 1999; Freeman et al. 2003).

Given the paucity of food sources in terms of both quantity and diversity in Caribbean island rivers (Burns and Walker 2000; Brito et al. 2006), trophic interactions could be a significant driving force for species composition along rivers. In aquatic systems, food quality research has highlighted the role of polyunsaturated fatty acids (PUFA) as food quality markers. PUFA are involved in a wide variety of physiological processes but cannot be synthesized by most animals and therefore must be obtained from their diet. The high variability of dietary PUFA availability in aquatic ecosystems makes these essential compounds limiting factors in the growth and development of fish and invertebrates (Sargent et al. 1999; Wallis et al. 2002). Aquaculture studies have particularly emphasized the importance of eicosapentaenoic acid (EPA, 20:5ω3) in optimizing growth and survival of the tropical Palaemonid *Macrobrachium rosenbergii* species post larvae (De Man 1879) (D'Abramo and Sheen 1993; Tidwell et al. 1997; Cavalli et al. 1999; Das et al. 2007; Crab et al. 2010). Subsequently, EPA was shown to be of primary importance in the reproduction of crustaceans in lake environments (Müller-Navarra et al. 2000; Arts et al. 2009; Masclaux et al. 2014). In stream food webs, increasing attention is being paid to dietary PUFA limitation of invertebrates and most of these studies have highlighted the importance of dietary EPA in determining secondary production (Torrez-Ruiz et al. 2007, Guo et al. 2016, 2018, Torrez-Ruiz and Wehr 2019). This is particularly emphasized in forested headwater streams, where allochthonous detritus lacking EPA (Brett et al. 2017) constitute the main energy source for invertebrate consumers. Despite the fact that living primary producers contribute marginally to such ecosystem metabolism and energy flows, EPA-rich microalgae such diatoms are considered as a minor but high-quality food ensuring invertebrates growth (Crenier et al. 2017).

The objectives of this study were to assess the nutritional quality of various food sources along an altitudinal gradient in order to evaluate the extent to which nutritional quality could be a parameter influencing the altitudinal settlement of shrimp.

## Methods

### Study area

This study was conducted in the Grand Carbet River (on Guadeloupe Island), which is an island with volcanic geology, marked relief, and where precipitation is generally between 1,500 mm/year and 7,000 mm/year due to exposure to the trade winds, with a dense, permanent hydrographic network with high hydraulicity (30 to 200 l/s/km$^2$) (Wasson et al. 2004). This 12.9 km long river, taking its source at an altitude of 1,300 min the Soufrière volcano massif flows into the Atlantic Ocean on the East coast of the island of Guadeloupe and is characterized by a short river mouth followed by a rapidly increasing slope inducing highly hydrodynamic water flows surrounded by humid tropical vegetation (Fig. S1). Two stations were investigated along this river. The downstream station (star in Fig. S1, coord. 16.022847, -61.575497) was located in the first freshwater riffles at the river mouth, a zone which concentrates anthropogenic disturbances that reduce river flow and modify habitats. The upstream station (dot in Fig. S1, coord. 16.040454, -61.614322) was located in a pristine area in a mid-altitude habitat, with a preserved natural flow and a well-developed natural riparian forest.

### Sampling

The study focused on crustaceans, which represent an important relative abundance in the macrofauna and inhabit the entire continuum of the river. Individuals were collected by electrofishing (Deka 3000 electrofisher, Germany) during the dry season, between mid-March and early April 2017. We conducted fatty acid (FA) analyses on two ontogenetic stages (juveniles and adults) of three crustacean species: two Palaemonidae, *Macrobrachium faustinum* (de Saussure 1857), *Macrobrachium heterochirus* (Wiegmann 1836), and one Atyidae, *Atya innocous* (Herbst 1881). The juvenile stages were between 20 to 25 mm, sizes based on the determination of the fine age structure of the populations through cohort extraction analyses realized on the same samples (Frotté et al. 2020a, b). Five major food sources were sampled at each site: the epilithic biofilm was scraped from the surface of submerged rocks with a knife and a brush, according to standard NF T 90–354 in (i) slow and (ii) habitats with high velocity, (iii) fresh and (iv) decomposed leaf litter were handpicked and (v) drifting organic matter was trapped using a plankton net (64 µm mesh) placed in the river during 2 h. All samples were kept on dry ice while in the field, then frozen at -80 °C before preparation for fatty acid analysis.

### Fatty acid preparation and analyses

Protocols for fatty acid preparation and analyses are provided as supplemental information. Results are expressed in total FAs for each source and are differentiated by lipid class, i.e., neutral lipids (NL) and polar lipids (PL), found in the consumer.

### Statistics

Assumptions of normality and/or homogeneity of variance were systematically checked and the Van der Waerden's Normal test, a nonparametric test for comparing the means of more than two groups, was applied. This test converts the ranks from the nonparametric Kruskal–Wallis test to quantiles of the corresponding standard normal distribution. It provides the robustness of the Kruskal–Wallis test when the normality assumptions are not satisfied. When significant, it was followed by a post hoc test using the criterion Fisher's least significant difference (LSD) to determine which pairs of populations tend to differ, identified by letters.

## Results

EPA was only detected in the epilithic biofilm and drifting organic matter. EPA is the highly unsaturated fatty acid (HUFA) with the highest concentration observed in these food sources, sampled both in upstream and downstream sites (Table S1, Fig. 1). The EPA content of biofilm samples was significantly greater at the upstream site than the downstream site (Waerden test, $p < 0.05$), while the opposite was noted in the drifting organic matter samples (Waerden test, $p > 0.05$). The FA ratio of 20:5ω3 / (16:3ω3 + 16:4ω3 + 18:2ω6 + 18:3ω3) (Table S1, Fig. 1), presented significant differences, with the highest values noted upstream in both biofilm types (Waerden test, $p < 0.05$ for each).

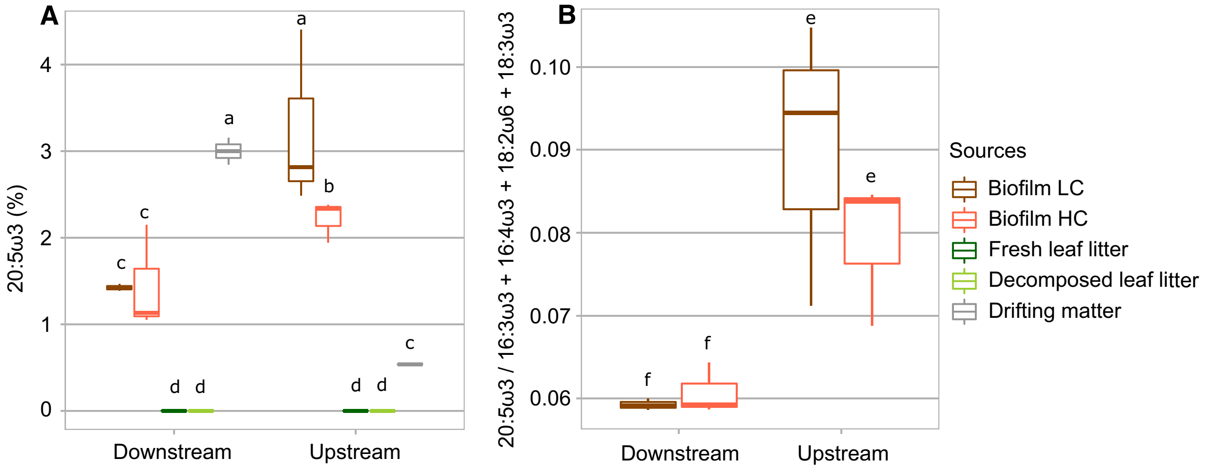
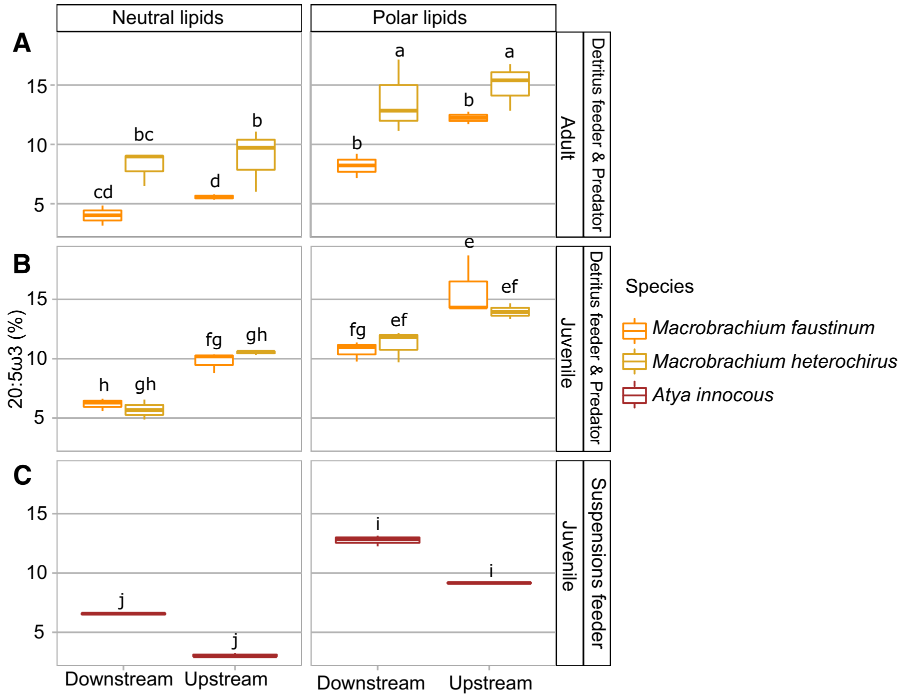


**Fig. 1** **A** Percent of 20:5ω3 and **B** ratio of 20:5ω3 / (16:3ω3 + 16:4ω3 + 18:2ω6 + 18:3ω3), considered to reflect the diatom/chlorophyceae-cyanobacteria abundance ratio in food sources sampled in downstream and upstream sites in the Grand Carbet River. Biofilm LC: biofilm sampled in a low current habitat; Biofilm HC: biofilm sampled in a high current habitat. Differences between samples were tested using Van der Waerden tests (panel **A**: Chisq = 24.90, df = 9, $p = 0.0031$, panel **B**: Chisq = 8.37, df = 3, $p = 0.039$). Letters *a* to *d* and *e* to f indicate sample groups (for panels **A** and **B,** respectively) according to Fisher's least significant difference (LSD) post hoc test with α = 0.05

In the case of the crustacean species, EPA was the most represented HUFA and was lower in neutral lipids (NL) than in polar lipids (PL) (Table S2, Fig. 2). The percentage of EPA was significantly greater at the upstream stations than at the downstream site in both lipid classes (NL and PL, Student t test and Van der Waerden test, $p < 0.05$ for all), in juveniles belonging to the deposit feeder species (Palaemonidae), while no significant difference between sites was found in adults (Student t-test and Van der Waerden test,

**Fig. 2** Percent of 20:5ω3 in both lipid classes obtained from detritus feeders, predators, and suspensions feeders, considering downstream and upstream sample sites in the Grand Carbet River. Differences between samples were tested using Van der Waerden test (panel **A**: Chisq = 18.71, df = 7, $p = 0.0091$, panel **B**: Chisq = 17.30, df = 7, $p = 0.016$, panel **C**: Chisq = 8.81, df = 3, $p = 0.032$). *Letters a* to *d*, *e* to *h* and *i* to *j* indicate sample groups (for panels **A**, **B** and **C,** respectively) according to Fisher's least significant difference (LSD) post hoc test with α = 0.05



$p > 0.05$). On the contrary, the percentage of EPA was significantly lower in upstream stations than in the downstream site in the case of the filter feeder (Atyidae), *A. innocous*.

## Discussion

EPA has been shown in natural environments to be essential to the growth and reproduction of crustaceans (Müller-Navarra et al. 2000; Arts et al. 2009; Masclaux et al. 2014). Studies conducted in aquaculture have shown that EPA also affects the survival of *Macrobrachium rosenbergii* shrimp juveniles (Tidwell et al. 1997; Cavalli et al. 1999; Das et al. 2007; Crab et al. 2010). Given that the ability to synthesize EPA from precursors such as linolenic acid (LNA) is extremely limited (D'Abramo and Sheen 1993; Cavalli et al. 2001) in shrimp, these essential fatty acids must come from their diet. In our study, only biofilms and drifting matter contained EPA. Shrimps thus rely on these food sources to fulfill their needs in essential fatty acids and especially in EPA.

Our results show a downstream-to-upstream enrichment of EPA in epilithic biofilms. The biofilms in these rivers are mainly composed of diatoms, chlorophyceae and cyanobacteria (Lefrançois et al. 2011). The $20{:}5\omega3 / (16{:}3\omega3 + 16{:}4\omega3 + 18{:}2\omega6 + 18{:}3\omega3)$ ratio may reflect the abundance of diatoms compared to chlorophyceae-cyanobacteria because diatoms are rich in EPA but do not contain 16C or 18C PUFA, unlike chlorophyceae-cyanobacteria (Dalsgaard et al. 2003; Koussoroplis et al. 2011). The FA ratio of $20{:}5\omega3$ was significantly higher upstream and these results are consistent with studies that have shown the prevalence of cyanobacteria downstream in Guadeloupe and Puerto Rico rivers (March and Pringle 2003; Lefrançois et al. 2011). Recent in vitro experiments conducted on the development of epilithic biofilm in Caribbean rivers have also shown that the diatoms/cyanobacteria ratio decreases in downstream-polluted conditions (Barbeyron et al. 2017). This altitudinal difference in biofilm fatty acid composition was also reflected in *Macrobrachium faustinum* and *M. heterochirus* lipids, which were richer in EPA upstream than downstream. The altitudinal difference reflected in the lipids found in *M. faustinum* and *M. heterochirus* supports the fact that biofilms are a major food source for these species, while dietary intakes of EPA in these river systems remain very limited. Indeed, EPA seems to be a limiting factor in this Caribbean river, as our results show that EPA concentrations, especially in neutral lipids found in *M. faustinum* and *M. heterochirus,* were very low compared to those observed for the same genera in aquaculture (Cavalli et al. 1999, 2001). It is therefore beneficial for biofilm-feeder species to live in upstream habitats in Caribbean rivers, and thus to migrate upstream to benefit from a biofilm richer in diatom EPA.

Conversely, we observed a downstream EPA enrichment in drifting matter. It should be noted that, in these turbulent and extremely fast rivers of few kilometers length, the transit time between upstream and downstream stations is short and is measured, at most, in hours. These hydrodynamic characteristics exclude the hypothesis that the drift from upstream to downstream allows for microbial colonization that could "change" the EPA concentration due to intense organic matter remodeling. Our results are discussed cautiously due to a very low sample size (2 samples downstream, and only one upstream). Nevertheless, this reversed altitudinal difference in drifting matter compared to biofilm was also reflected in *Atya innocous*—considered a suspension feeder—who can benefit from the EPA contained in drifting organic matter, as opposed to *Macrobrachium*. However, *A. innocous* is also known for plasticity in feeding behaviors, filtering drifting matter in high current habitats and brushing biofilm from rocks in low current habitats (Coat et al. 2009; Monti and Legendre 2009). This dietary plasticity allows them to optimize their intake of essential fatty acids when switching from one food source to another. In light of EPA enrichment, this capability could be interpreted as an ecological advantage that could contribute to the success of this species, the Atyidae representing the largest crustacean biomass in the rivers of Guadeloupe (Gillet 1983; Fièvet et al. 2001).

Our results reveal an upstream–downstream difference in EPA enrichment within the different food sources available in the river system, which is also reflected in the lipid composition of the species that feed on them. These altitudinal differences in food quality might be a crucial factor to take into account in the success of upstream migrations of diadromous species, because essential fatty acids such as EPA are involved in many physiological processes such as growth, reproduction and egg quality (Sargent et al. 1999; Wallis et al. 2002). These elements highlight both (i) the importance of maintaining the continuity of movement of the species along river systems to reach habitats with the highest food quality source accessible to them; and (ii) the need to maintain sufficient water flow to allow drifting of allochthonous organic matter downstream. In cases of a disruption or even a reduction in stream continuity, species will be differentially impacted, depending on their feeding strategies, with those having higher dietary plasticity being favored in environments subjected to strong environmental variations and/or anthropogenic impacts. Stream flow and its seasonal and daily fluctuations are known to play a major role in the downstream movement of the diadromous organisms in their descending part of their life cycle: the abundance of drifting larvae and larval survival depend on it (Teichert et al. 2014; Lagarde 2018), but our results underline the importance of preserving water continuity along the entire system and in both directions, as well as the upstream habitats in good ecological condition. The good accomplishment of the species displacements will maintain high food quality and maximize the success of upstream settlement and the growth of species. These results illustrate the importance of the principle of downstream/upstream subsidiarity, which means the imperative need to maintain sufficient flows and ecological aquatic continuity in the rivers of this region, generally in strong conflict around limited water resources.

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