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# Effects of dams on demographic structures of amphidromous fish and crustacean species in Caribbean rivers

by

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**Abstract.** – Caribbean island rivers are the home to migratory indigenous macro-fauna. Concurrently, they also serve as the main source of freshwater for human consumption. This production of drinking water involves the construction of a large number of structures across the riverbed, which can slow or even stop the migration of aquatic species. The resident river macro-fauna is composed of crustacean and fish species that all have a diadromous and mostly amphidromous life cycle, involving pro-larval drift downstream towards the sea, marine larval dispersal, followed by an upstream river migration to complete their growth and reproduction cycle. Our study compares, across three rivers on the island of Guadeloupe, the recruitment of five crustacean species and two fish species in the mouths of these rivers with species demographic distributions on either side of the major water withdrawal structure built along these rivers. Post-larval recruitment events were multispecific, discrete over time and their amplitude varied depending on the river. We show differential biological porosity of each obstacle according to species, revealing different specific crossing abilities. Our results also suggested that the impacts were not directly related to the height of the structure but that external, hydrological and environmental, conditions are involved. These achievements can be translated into operational measures such as the maintaining and monitoring of reserved minimal flows that are adapted to passways, as well as the setting up of protective measures for the natural environment.

## Key words

Sicydiinae  
Palaemonidae  
Atyidae  
Guadeloupe  
Upstream migration  
Freshwaters

## Résumé.

– Impacts des obstacles sur les amphidromes.

Les rivières caribéennes sont le lieu de vie d'une macrofaune indigène migratrice et aussi le principal lieu de prélèvement pour la production d'eau potable pour la population humaine. Cette production d'eau potable implique la construction d'un grand nombre d'ouvrages en travers du lit des rivières, qui peuvent ralentir ou stopper la migration des espèces. La macrofaune résidente est composée d'espèces de crustacés et de poissons qui ont toutes un cycle de vie diadrome et majoritairement amphidrome, impliquant une dévalaison larvaire vers la mer, une dispersion larvaire marine puis une montaison en rivière pour terminer leur croissance et se reproduire. Notre étude porte sur la comparaison du recrutement de cinq espèces de crustacés et deux espèces de poissons dans les embouchures de trois rivières proches, ainsi que sur la distribution démographique des différentes espèces de part et d'autre de l'ouvrage majeur de ces trois rivières. Les recrutements sont multispécifiques, discrets dans le temps et leur importance est variable selon l'embouchure. La porosité biologique de chaque obstacle est différente en fonction des espèces révélant différentes capacités de franchissement. Nos résultats suggèrent aussi que les impacts ne sont pas directement liés à la hauteur de l'ouvrage mais qu'interviennent des conditions externes à celui-ci, hydrologiques et environnementales. Ces acquis peuvent se décliner en mesures opérationnelles comme l'importance du maintien et de la surveillance de débits réservés adaptés et maîtrisés au niveau des passes, ainsi que la mise en place de mesures conservatoires de la ripisylve et de l'environnement naturel proche.

## INTRODUCTION

In the Caribbean islands, watersheds are occupied primarily by amphidromous species (Keith, 2003; Tabouret *et al.*, 2011, 2015; Lejeune *et al.*, 2014; Smith and Kwak, 2014; Frotté *et al.*, 2019). In these rivers, species diversity is low, 23 native species, of which only 14 are distributed across the entire river continuum, and includes both crustaceans and teleost fishes (Monti *et al.*, 2010). The most abundant species, belonging to the families Atyidae and Palaemonidae for

the crustaceans, and Gobiidae for the teleost fish, have anatomical features that allow them to colonize the river continuum, up to the head of the watersheds. For all these species, reproduction takes place in the river, then eggs hatch in freshwater and their pro-larvae move downstream to the sea (Keith, 2003; McDowall, 2010). After a period of larval marine dispersal and development, the post-larvae return to the lower reaches of the rivers to metamorphose and migrate upstream to complete their growth and reproduction cycle (McDowall, 2007). The particularities of this amphidro-

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mous type of life cycle enable these species to occupy island streams that are prone to frequent environmental perturbations, for example, high temporal hydrological variability, such as hurricanes and droughts, or anthropogenic pressures (Covich *et al.*, 2006; Hogan *et al.*, 2014; Smith and Kwak, 2015; Negishi *et al.*, 2019).

The volcanic Basse-Terre part Island of the Guadeloupe archipelago has small and steep watersheds with turbulent flows and the major part of the rivers have, in this island, the characteristics of mountain runoffs with steep terrains and channel gradients greater than a few percent. Such features are dominated by boulders and cobbles. Combined with extremely frequent and irregular tropical rainfall events, the characteristics of flow conditions in the channels are complex and vary greatly in time. Reliable measure of flows would be only possible through heavily equipped and automated stations (Zimmermann, 2013; Asano and Uchida, 2016) that are barely present and located in areas with human stakes. The concentrated human populations, and agricultural land, are distributed only on low-lying areas. Watersheds concentrate pesticides, sewage and other pollution in the downstream areas of rivers, which can limit the settlement of native species and benefit exotic species (Pringle, 1997). Moreover, the presence of numerous water withdrawal structures along all the watersheds reduces the water quantity and the flow variations downstream, which has an impact on the cues stimulating post-larvae recruitment and their upstream migration (Benstead *et al.*, 2000; Fièvet *et al.*, 2001). Currently, 117 flow-altering structures were listed in Guadeloupe in 2018 (Sandre and Eau France, 2019) and 73 of them were directly linked to water withdrawal, which represents an annual volume of 80 to 90 million m<sup>3</sup>. Reducing the amount of water reduces the heterogeneity of available habitats, which has a severe impact on native fauna (March *et al.*, 2003; Ramírez *et al.*, 2012; Crook *et al.*, 2015). Among the native species inhabiting the Caribbean rivers, some were shown having strong hydraulic preferences for high velocities such as *Macrobrachium heterochirus* (Wiegmann, 1836), *Atya innocous* (Herbst, 1792), *A. scabra* (Leach, 1816), *Sicydium plumieri* (Bloch, 1786) and *S. punctatum* Perugia, 1896. Others are much more ubiquitous such as the palaemonid *Macrobrachium faustinum* (de Saussure, 1857) and the atyid *Micratya poeyi* (Guérin-Méneville, 1855) (Monti and Legendre, 2009; Girard *et al.*, 2013). As a result, the reduction in natural flows could differentially affect the species residing in Caribbean freshwater rivers.

The presence of the numerous built-up structures along the water catchments, including low-head dams, also creates physical barriers that slow or impede upstream migration of aquatic species (Cooney and Kwak, 2013). Consequently, for species that cannot easily traverse these physical barriers, high densities of individuals accumulate below the dam acting as a bottleneck effect (March *et al.*, 2003). This high con-

centration of juveniles attracts predators such as fish-eating birds, palaemonid shrimps, or mountain mullet *Agonostomus monticola* (Bancroft, 1834), increasing the mortality of juvenile migrants (March *et al.*, 2003). Further, this concentration of individuals below the dam also increases both inter and intra-specific competition for habitat and food (Covich *et al.*, 2003). Crossing these physical obstacles is strongly influenced by the morphological traits of each species, determining their ability to move upstream (Fièvet, 2000; Keith, 2003; Kikkert *et al.*, 2009). Of the crustacean species, *Atya* spp. have the highest upstream movement/migration capacity, with their robust walking legs equipped with claws and a body profiled with an hydrodynamic shape, allowing them to move in highly dynamic flows (Fryer, 1977; Fièvet, 2000; Kikkert *et al.*, 2009). Likewise *Micratya poeyi*, which can be considered morphologically as a miniature *Atya* spp., and according to their small size can also penetrate into the gaps, exhibit very high upstream movement/migration capacity (Fryer, 1977; Fièvet, 2000). Conversely, the *Macrobrachium* spp. have large pincers that interfere with their walking movements and potentially contribute to reduce their capacity for upstream migration (Fièvet, 2000). The Gobiidae, *Sicydium* spp., have modified fused pelvic fins that form a pelvic sucker enabling them to station hold on rocks in dynamic flows and to climb waterfalls or dams, resulting in migration far upstream habitats (Keith, 2003). These species have wide distributions and high abundances across Guadeloupe, allowing for statistical inferences to be drawn from their demographic structuring.

Given the importance of the widespread water abstraction structures along the rivers of the Caribbean islands and the lack of knowledge about effective obstacle clearance capabilities of the indigenous macro-fauna species, the objectives of our study were to first describe the demography of seven amphidromous common species entering three proximate rivers on the islands of Guadeloupe. Each of these rivers has a dam, which varies in physical characteristics across the rivers. We then quantified the crossing ability and demographic structure of these seven fish and crustacean species between sites immediately below and above the dams.

## MATERIALS AND METHODS

### Study sites

The study was conducted in three rivers, Grand Carbet River, Pérou River and Moreau River (Basse-Terre, Guadeloupe), which are typical volcanic tropical island rivers with shallow waters and highly hydrodynamic characteristics, a reduced mouth, and a rapidly increasing slope (Fig. 1). They are located in the same hydrographic region and their mouths flow southeast-ward of the windward coast, which give them the same climate and the same influence of marine currents.



Figure 1. – Map of Guadeloupe with the three sampled rivers (bold lines) and study sites: downstream and upstream the water intakes (●) and the first riffle from the mouth of the rivers (★).

Table I. – Collection date, site location relative to dam (km) and species or species groups abundance for all sites sampled on Grand Carbet, Pérou and Moreau rivers.

	Grand Carbet			Pérou			Moreau		
	Downst. river	Downst. dam	Upst. dam	Downst. river	Downst. dam	Upst. dam	Downst. river	Downst. dam	Upst. dam
Collection date	03/17/17	03/16/17	04/04/17	02/15/17	02/17/17	02/24/17	06/02/17	05/04/17	05/18/17
Location relative to dam (km)	-6.56	-0.35	+0.01	-7.33	-0.15	+0.01	-5.69	-0.05	+0.01
Species or group abundance									
<i>Sicydium</i> spp.	397	160	151	61	305	424	177	163	22
<i>Macrobrachium faustinum</i>	365	11	11	342	24	14	388	8	7
<i>Macrobrachium heterochirus</i>	53	45	16	24	118	54	0	7	6
<i>Atya</i> spp.	169	439	210	81	425	456	14	21	41
<i>Micratelya poeyi</i>	1243	2124	1852	151	710	543	735	977	590

The mouths of the Grand Carbet and Pérou rivers are very similar, with shallow waters and a first riffle located 200 m to 500 m from the sea, corresponding to the downstream reaches studied. The mouth of the Moreau River is located in a swampy forest and consists of an extensive brackish water area, therefore the first sampled freshwater riffle was located at 1600 m from the sea (Fig. 1).

In the upstream part of these three rivers, major concrete structures were built for water abstraction across the entire width of the riverbeds. The structure built in the Grand Carbet River is the highest dam (5 m height) with a grid for water

extraction that occupies less than a third of its width. The Pérou dam has a medium height (4 m height) and also a grid that occupies less than a third of its width of its riverbed. The Moreau dam is the very low structure (0.1 m height) with a water extraction grid that occupies more than two thirds of its width (Fig. S1). The three dams are equipped with rustic multispecies passways, i.e. a simple breach in the obstacle. For each of the three rivers, the two other sampling reaches were positioned on reaches located directly downstream and upstream of each dam (Fig. 1, Tab. I).

### Sampling and data collection

Fish and crustaceans species were collected by electrofishing (Deka 3000 electrofisher, Deka-Gerätebau, Rudolf Mühlenbein, Germany) during the dry season from February to June 2017. The sampled reaches were 50 m long over the complete width of the riverbed, including all hydromorphological facies (Malavoi, 1989). Each reach was sampled only once during the sampling period. Within each sampled reach, the most abundant species were measured to the nearest millimetre: the two Gobiidae fish species, *Sicydium plumieri* and *S. punctatum*, the palaemonids *Macrobrachium faustinum* and *M. heterochirus* and the atyids *Atya innocous*, *A. scabra* and *Micratya poeyi*. For species whose juveniles could only be identified at the species level, the individuals were grouped by genus: *Sicydium* spp. and *Atya* spp. All reaches on the same river were sampled a few days apart between stations downstream and upstream of the dam and a few weeks apart between the station downstream of the river and those of the dam.

### Ethics

The capture of juvenile and the adult fishes and crustaceans was conducted directly in the field at each sampling reach, using nonchemical anaesthesia. The main advantages of electroanaesthesia over chemical anaesthetics include faster induction and recovery times (Ackerman *et al.*, 2005). Electroanaesthesia was done with direct current (DC) because it has been shown to be less harmful to fishes than the use of alternating current (Lamarque, 1990; Walker *et al.*, 1994). The electrofishing device was equipped with a 12-V DC shocking circular anode covered with a net, powered by a motorcycle battery. The shock was set on the minimum output voltage (250V) and a time of 15 to 30 seconds. The very low water conductivity of the rivers combined with the low voltage of the electric field and short duration of the shock caused only anodotaxis, a few second transient electroanarcosis, and no electrotetany. Immediately after electroanaesthesia, the animals were identified and counted and returned to the river directly downstream of the sampling-point with no withdrawal time.

### Data analysis

For the data collected at the downstream stations, the histograms of total lengths of each species (or group of species) were made on the total numbers of individuals. For identification of the age structure of/within each population, a cohort extraction analysis was performed using the mixdist package (Macdonald, 2018) through R environment (version R 3.5.1, R Development Core Team, 2008). This package fits a finite mixture distribution model to group data using maximum likelihood ratio and estimates the parameters of each age group, such as proportion, mean and variance, along with their standard deviations. A chi-square statistics

and its probability level assess the goodness-of-fit between the model and the data. Only the part of the histograms with sufficient data in class intervals ( $> 5$ ) was analysed.

At the dam level, the individuals collected at the two stations positioned at each side of the structure were grouped to same size intervals and then compared. A ratio was calculated with the number of individuals located upstream of the dam divided by the sum of the population upstream plus downstream of the dam, expressing the “biological porosity” (Monti *et al.*, 2018) of this barrier for each species. A porosity value of 0.5 indicates that there are as many individuals on either side of the dam, greater than 0.5 there are more individuals upstream than downstream of the dam, and less than 0.5 there are more individuals downstream than upstream of the dam. The average standard deviation of the data was also calculated.

## RESULTS

For each population sampled at the river mouth, the size structure varied across species and across rivers, despite close geographic proximity (histograms in Figs 2, 3, 4). The most variable recruitment occurred with in the gobiids *Sicydium* spp. with up to 212 individuals in the 25-30 mm size interval, and the little atyid *Micratya poeyi* with up to 301 individuals in the 7-8 mm size interval, both in the Grand Carbet River (Fig. 2). Even though the numbers of recruits varied widely for each size class, there is an apparent lack of recruitment for the smallest size of certain species, as *Sicydium* spp., *Atya* spp. and *M. poeyi*, particularly in the Moreau River. For all species, the modelled histograms (i.e. truncated on the right to keep only size classes containing more than 5 individuals) show multimodal structure, which is characteristic of discrete recruitment episodes over time (Figs 2, 3, 4).

At the mouth of the Grand Carbet River, in mid-March, sample sizes were sufficient to extrapolate the size structures of the gobiids *Sicydium* spp., the palaemonid *Macrobrachium faustinum* and the atyids *Atya* spp. and *Micratya poeyi*. However, for *M. heterochirus* the sample size was too small. The size mode of the smallest and just entering cohorts was 24 mm ( $\pm 0.3$ ), 16 mm ( $\pm 0.4$ ), 16 mm ( $\pm 0.6$ ) and 7 mm ( $\pm 0.1$ ), respectively, and these new age groups added to the populations represented 84%, 59% ( $\pm 0.04$ ), 61% ( $\pm 0.06$ ) and 67% ( $\pm 0.02$ ), respectively, which is a large fraction of these populations (Tab. II, Fig. 2). The data collected for the preceding age group, the mean sizes were 45 mm ( $\pm 0.9$ ), 26 mm ( $\pm 1.1$ ), 30 mm ( $\pm 0.9$ ) and 11 mm ( $\pm 0.1$ ) and representing 16%, 28% ( $\pm 0.04$ ), 39% ( $\pm 0.06$ ) and 26% ( $\pm 0.02$ ) of the populations, respectively.

Sampling the mouth of the Pérou River reveals a low intensity of colonization by species in mid-February. Only

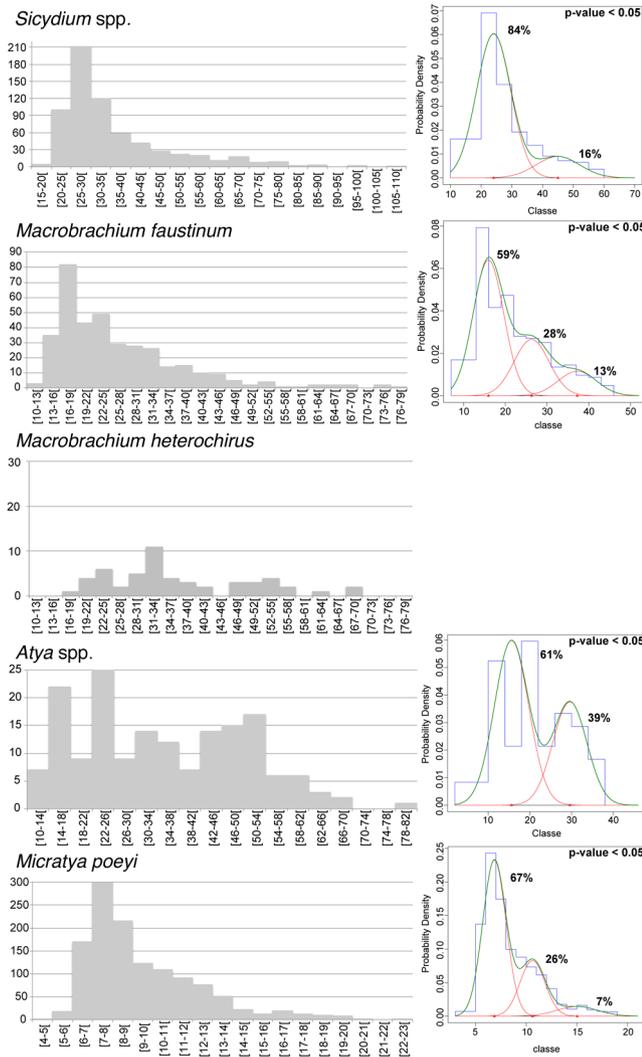


Figure 2. – Individual number histograms of each species broken down by size classes (mm) (left chart) and cohort extraction (right chart) downstream of the Grand Carbet River in March. Right chart: red curves are each cohort extracted by the model; green curve is the cumulative individual number in the modelled age groups.

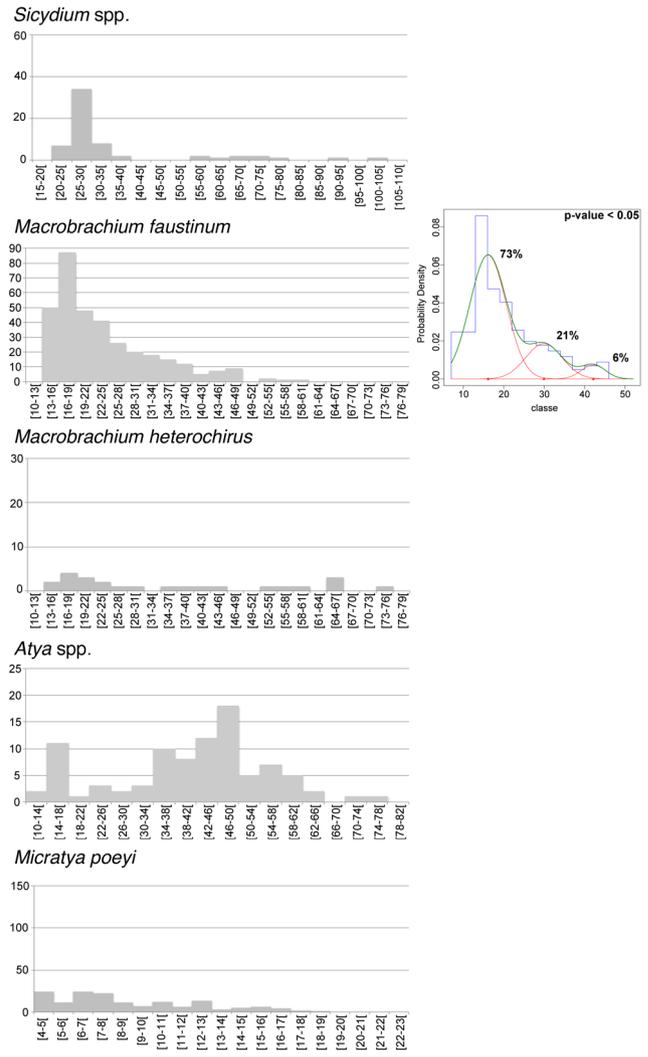


Figure 3. – Individual number histograms of each species broken down by size classes (mm) (left chart) and cohort extraction (right chart) downstream of the Pérou River in February. Right chart: red curves are each cohort extracted by the model; green curve is the cumulative individual number in the modelled age.

*M. faustum* had a strong enough recruitment and, consequently, was the only species that had a large enough sample size to be modelled. For the other species, their recruits were too low to be statistically modelled but with use of the histograms, we propose an approximate value for the mode of the very smallest cohort in the population. The mean sizes of the just entering age groups were estimated at 23 mm, 16 mm ( $\pm 0.4$ ), 15 mm and 5 mm, respectively for *Sicydium* spp., *M. faustum*, *Atya* spp. and *Micratya poeyi* and they represented 84% of the *Sicydium* spp. population, 73% ( $\pm 0.03$ ) of the *M. faustum* population, and 19% and 20% of the Atyids populations, respectively (Tab. II, Fig. 3). For *M. faustum*, the preceding entering age group represented 21% ( $\pm 0.03$ ) of the population.

Sampling in the mouth of the Moreau River in early June, revealed recruitment of *Sicydium* spp., *M. faustum*, and *Micratya poeyi* but *Atya* spp. did not recruit this season in this river. The size modes of the newest age groups were 35 mm ( $\pm 0.7$ ), 18 mm ( $\pm 0.6$ ), 11 mm ( $\pm 0.1$ ), respectively, and they represented 41% ( $\pm 0.06$ ), 29% and 57% ( $\pm 0.02$ ) of the populations (Tab. II, Fig. 4). When looking at the preceding age group, the mean sizes were 48 mm ( $\pm 1.9$ ), 28 mm ( $\pm 0.4$ ) and 16 mm ( $\pm 0.1$ ) representing 38% ( $\pm 0.06$ ), 64% and 43% ( $\pm 0.02$ ) of the population, respectively.

At the upstream sites, either below or above the dams, some of the study species were not present or too low in abundance to be mathematically modelled: *M. faustum* on the three rivers, and *M. heterochirus* on Moreau River.

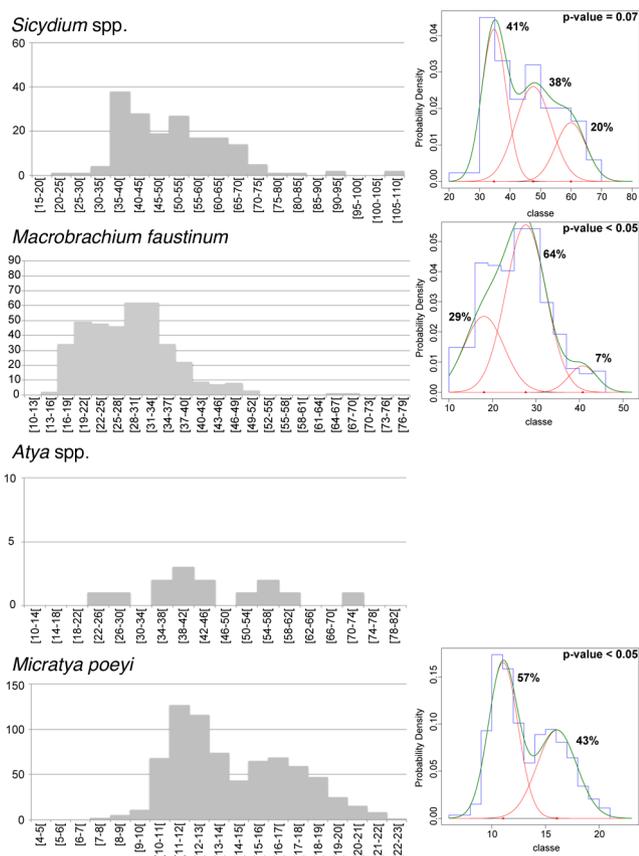


Figure 4. – Individual number histograms of each species broken down by size classes (mm) (left chart) and cohort extraction (right chart) downstream of the Moreau River in June. Right chart: red curves are each cohort extracted by the model; green curve is the cumulative individuals' number in the modelled age groups. No *Macrobrachium heterochirus* were caught.

Conversely, some other species or genera, *M. heterochirus*, *Sicydium* spp., *Atya* spp., *Micratya poeyi*, had a higher abundance upstream compared to the mouth sites (an exception for *Sicydium* spp. on Grand Carbet River). Species demographic structures were unequal on both sides of the dams, with species generally more abundant under the dams (Figs 5, 6, 7), and a size-dependent relation for the retention, marked by arrows positioned in figures 5 and 6.

The Grand Carbet dam was crossed by four species or genera, *Sicydium* spp., *M. heterochirus*, *Atya* spp. and *Micratya poeyi*, and they all had a crossing rate that increased with the body size. However, only *Sicydium* spp. and *Micratya poeyi* presented higher abundance above the dam with a maximum average crossing rate of 0.62 ( $\pm 0.11$ ) and 0.63 ( $\pm 0.04$ ), while *Atya* spp. and *M. heterochirus* were mainly trapped downstream of the dam with a maximum average crossing rate of 0.37 ( $\pm 0.08$ ) and 0.37 ( $\pm 0.11$ ), respectively (Fig. 5). The Moreau dam was crossed by three species or genera, *Atya* spp., *Sicydium* spp. and *Micratya poeyi*, and their crossing rates also increased with size. Only *Atya* spp.

presented abundance higher above the dam with an average crossing rate rising up to 0.90 ( $\pm 0.16$ ), *Sicydium* spp. and *Micratya poeyi* were trapped downstream of the dam with a maximum average crossing rate of 0.08 ( $\pm 0.08$ ) and 0.41 ( $\pm 0.05$ ), respectively (Fig. 7). *Macrobrachium heterochirus* was too scarce to analyse. The Pérou dam was crossed by four species or genera but their crossing patterns differed by size and species. *Sicydium* spp. had a maximum average crossing rate of 0.59 ( $\pm 0.06$ ) all sizes combined, *Micratya poeyi* had a maximum average crossing rate of 0.51 ( $\pm 0.06$ ) increasing with their body size, *Atya* spp. and *M. heterochirus* had a maximum average crossing rate of 0.55 ( $\pm 0.02$ ) and 0.38 ( $\pm 0.07$ ) decreasing with their body size, respectively (Fig. 6).

*Sicydium* spp. were best able to cross at a size of 35 mm on Grand Carbet dam and a size of 20 mm on the Pérou dam, but were mostly trapped downstream of the Moreau dam. *Atya* spp. were best able to cross at a size of 18 mm on the Pérou dam and 22 mm on the Moreau dam, whereas they were mostly trapped downstream of the Grand Carbet dam. *Micratya poeyi* was best able to cross at a size of 14 mm on Grand Carbet dam and 16 mm on the Pérou dam, whereas it was mostly trapped downstream of the Moreau dam. *Macrobrachium heterochirus* was mostly trapped downstream of the Grand Carbet and Pérou dams.

## DISCUSSION

### The variability of species recruitment

The comparison of the size structures obtained at the mouth of the three neighbouring rivers highlights that the recruitments of different species took place simultaneously in this ecoregion, but with important differences in amplitude. Other studies conducted in Caribbean island rivers have also revealed simultaneous multispecies recruitment in amphidromous species (Bell *et al.*, 1995; Benstead *et al.*, 2000; Engman *et al.*, 2017). However, the factors triggering the timing of post-larvae recruitment to the rivers are still unclear. During the sampling in mid-February on the Pérou River, *Macrobrachium faustinum* recruitment had started earlier and those of *Sicydium* spp., *Atya* spp. and *Micratya poeyi* were just beginning; in mid-March, the recruitment on the Grand Carbet River was simultaneous; and early June, only *M. faustinum* still recruited in Moreau River. The new age groups entering in Grand Carbet River, representing between 61% and 84% of these populations, are a large fraction of those populations indicating the existence of significant exchanges between the sea and the river. In the Moreau River, however, the newest age group represented a much lower proportion (between 29% and 57%) of their respective populations, suggesting either less favourable environments for settlement or reduced exchanges with the sea. Several

Table II. – Size (mm) mode, proportion and dispersion of the smallest and penultimate cohorts of each species that recruited at the downstream station of the three studied rivers. All models presented a chi-square < 0.05, except for *Sicydium* spp. from Moreau River with a chi-square = 0.07. For species with sufficient data, the standard deviation of the parameters were calculated using R-package Mixdist; for species with a small recruitment in Pérou River, the mode and proportion are estimated from the histograms; dash indicates that recruitment is absent or too low for a mode and a proportion to be estimated.

	Grand Carbet			Pérou			Moreau		
	Mode	Proportion	Dispersion	Mode	Proportion	Dispersion	Mode	Proportion	Dispersion
Last cohort									
Gobiidae, Sicydiinae									
<i>Sicydium</i> spp.	24.09 ± 0.29	0.84	5.56	23	0.84	–	34.74 ± 0.68	0.41 ± 0.06	3.96
Palaemonidae									
<i>Macrobrachium faustinum</i>	15.97 ± 0.39	0.59 ± 0.04	3.67	16.13 ± 0.37	0.73 ± 0.03	4.50	18.06 ± 0.58	0.29	4.60
<i>Macrobrachium heterochirus</i>	–	–	–	–	–	–	–	–	–
Atyidae									
<i>Atya</i> spp.	15.60 ± 0.65	0.61 ± 0.06	4.10	15	0.19	–	–	–	–
<i>Micratory poeyi</i>	6.86 ± 0.05	0.67 ± 0.02	1.15	5	0.20	–	11.06 ± 0.08	0.57 ± 0.02	1.37
Penultimate cohort									
Gobiidae, Sicydiinae									
<i>Sicydium</i> spp.	45.00 ± 0.86	0.16	7.12	–	–	–	47.59 ± 1.90	0.38 ± 0.06	5.89
Palaemonidae									
<i>Macrobrachium faustinum</i>	26.29 ± 1.10	0.28 ± 0.04	4.20	29.94 ± 0.95	0.21 ± 0.03	4.50	27.67 ± 0.42	0.64	4.60
<i>Macrobrachium heterochirus</i>	–	–	–	–	–	–	–	–	–
Atyidae									
<i>Atya</i> spp.	29.59 ± 0.91	0.39 ± 0.06	4.10	–	–	–	–	–	–
<i>Micratory poeyi</i>	10.62 ± 0.12	0.26 ± 0.02	1.23	–	–	–	16.06 ± 0.13	0.43 ± 0.02	1.84

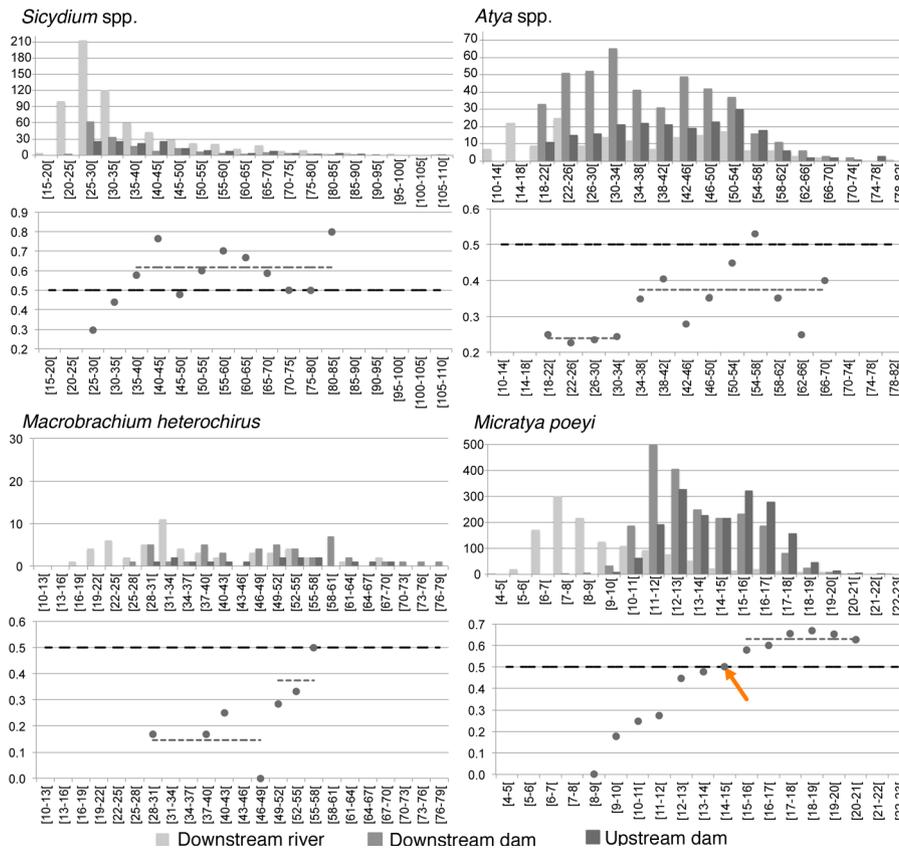


Figure 5. – Individual number histograms of each species broken down by size classes (mm) for the three stations (top chart) and porosity chart of the Grand Carbet River water intake (bottom chart). Bottom chart: arrow indicates the optimal size at crossing; dotted black line indicates 50% crossing; dotted grey lines indicate the mean crossing rate for these size classes. The size of the downstream and upstream population of *Macrobrachium faustinum* is too small and fragmented to be presented.

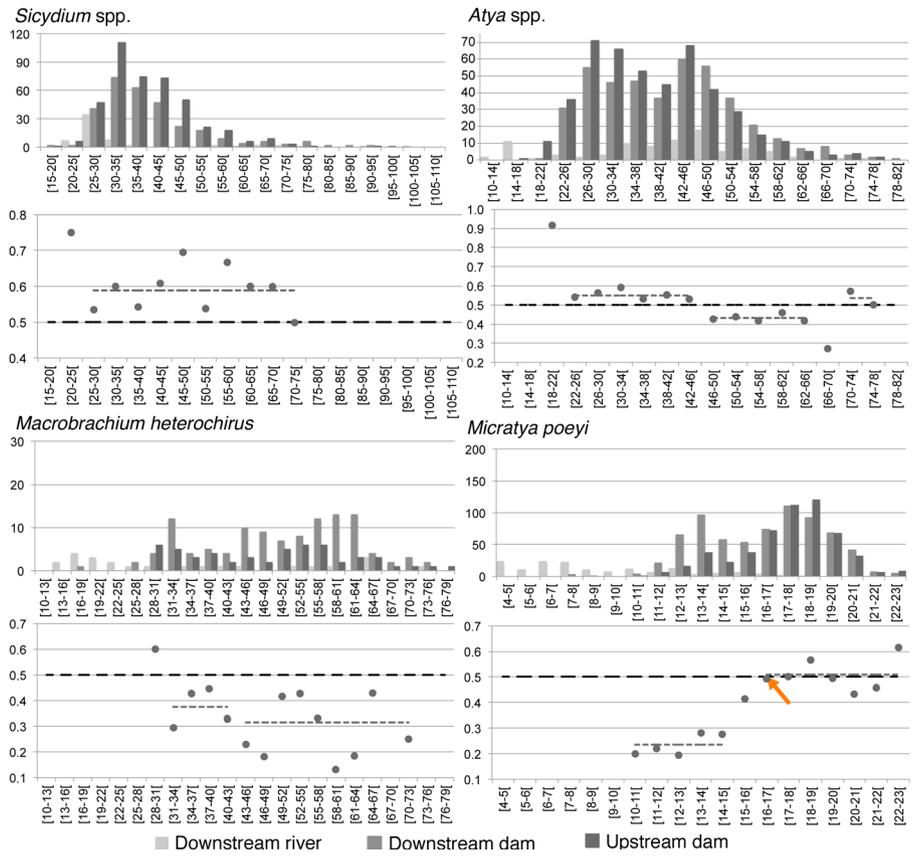


Figure 6. – Individual number histograms of each species broken down by size classes (mm) for the three stations (top chart) and porosity chart of the Pérou River water intake (bottom chart). Bottom chart: arrow indicates the optimal size at crossing; dotted black line indicates 50% crossing; dotted grey lines indicate the mean crossing rate for these size classes. The size of the downstream and upstream population of *Macrobrachium faustinum* is too small and fragmented to be presented.

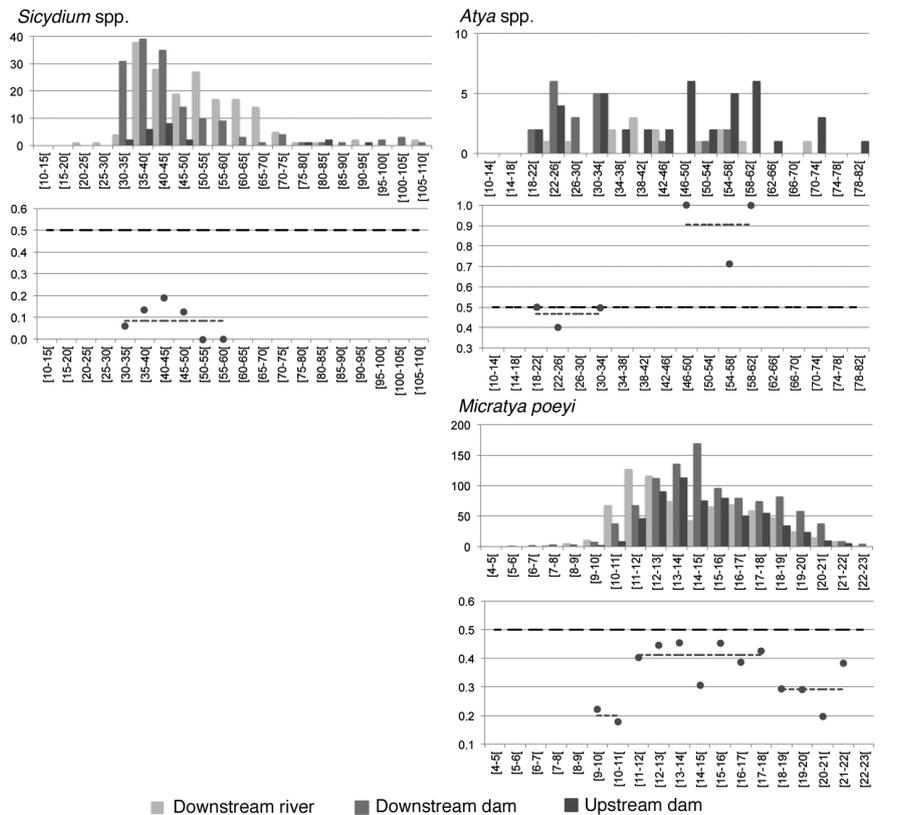


Figure 7. – Individual number histograms of each species broken down by size classes (mm) for the three stations (top chart) and porosity chart of the Moreau River water intake (bottom chart). Bottom chart: dotted black line indicates 50% crossing; dotted grey lines indicate the mean crossing rate for these size classes. The size of the downstream and upstream populations of *Macrobrachium faustinum* and *M. heterochirus* are too small and fragmented to be presented.

studies have concluded that, in tropical island streams with freshwater-marine connectivity, the heterogeneity of physical habitats (water velocity, substrate, depth, aquatic vegetation) is important for the settlement of native amphidromous fauna (Covich *et al.*, 1996; Fitzsimons *et al.*, 2002; Keith, 2003; Ramírez *et al.*, 2012; McRae *et al.*, 2013). The physical environment plays a key role through a combination of freshwater flows and moon phases that greatly influences the species recruitment in the rivermouths (Lespagnol, 2017).

In all species studied in Grand Carbet River and for *M. faustinum* in Pérou River, the high reduction of abundance between the smallest and the penultimate cohorts could be explained by significant mortality or migration, or strong heterogeneity in recruitment through time. In contrast, the lower reduction of abundance in Moreau River, compared to both other rivers, seems to indicate, despite having the lowest immigration rates from the sea, greater persistence of individuals (either survival or a lack of emigration) in the downstream part of this river. These results question the determinism of the species migration after entering the river. First, these differences could be related to the morphological traits of the species: among crustaceans, juveniles of migrating *Atya* spp. and *Micratya poeyi* are very well adapted to withstand high flows due to their morpho-anatomic adaptations (i.e. strong legs and hydrodynamic body shape) (Fryer, 1977; Fièvet, 2000; Kikkert *et al.*, 2009); while juveniles of migrating *Macrobrachium* spp. are relatively less adapted to withstand such high flows due to their heavy claws (Fièvet, 2000) but appreciate the calm waters of the downstream reaches; considering teleost fishes, *Sicydium* spp. are adapted to highly dynamic flows and waterfalls, equipped with their pelvic disc (Keith, 2003). Second, the upstream migration variations could be related to differential anthropogenic impacts in the three rivers. Pringle (1997) highlighted that anthropogenic impacts downstream of watersheds can trigger a cascade of upstream events, which can be magnified in the case of diadromous species. Hain *et al.* (2019) also suggested that amphidromous fishes were just as sensitive to conditions along migration pathways as those in the downstream part of watersheds

#### An unclear seasonality of recruitments

Grand Carbet River had generally the same size at recruitment with higher proportions of the largest cohorts than on the Pérou River (an exception was *M. faustinum* whose proportion of the largest cohort was lower). On the Moreau River, there was no recruitment of *Atya* spp. and the apparent absence of the *Micratya poeyi* cohort of recruits downstream in early June being probably consistent with their growth through time (no studies on the specific growth of *Micratya poeyi* in natural environment were found in literature). Conversely, we observed large proportions in the Moreau River for the two smallest cohorts of *M. faustinum*.

The second cohort of *M. faustinum* representing 64% with a 28 mm mode could correspond to the cohort that recruited between February and March as in the Grand Carbet and Pérou rivers, these results are consistent with previous studies on *M. faustinum* growth reporting growths of 12 mm in four months for the same size classes in Jamaica and Guadeloupe (Hunte and Mahon, 1983; Monti, 2005). The largest cohort representing a new recruitment of *M. faustinum*, three months after the previous one, occurred with a mode at 18 mm ( $\pm 0.6$ ). Several studies also observed such seasonal recruitments of amphidromous species mainly during wet season in Caribbean (Fièvet, 1999a; Kikkert *et al.*, 2009; Engman *et al.*, 2017) and Hawaii (Benbow *et al.*, 2004) but our data reveal discrete pulses of recruitment separated by only three months, not corresponding to seasons. No recruitment of *M. heterochirus* was observed in this dry season on the three rivers, although the species is found upstream. These results indicate that the entrance could have occurred during the preceding wet season or be submitted to more complex conditions for recruitment that could explain such low and highly variable abundances through time in the rivers of Guadeloupe (Monti *et al.*, 2018). Moreover, alternating high and low recruitment in the same river was reported by several authors for *Sicydium* spp., *Atya* spp. and *Macrobrachium* spp. in Puerto Rico and Dominica (Bell *et al.*, 1995; Benstead *et al.*, 2000; Engman *et al.*, 2017). All these results confirm that the attraction of the rivermouth is a crucial part of the river resilience, an “ecological performance” that varies greatly between proximate rivers and through time. In our study, Grand Carbet and Pérou rivers, with their high juveniles proportion, indicate a very good resilience at the time of sampling, while Moreau River had a lower ability to reconstruct of its populations.

#### Comparison of dams and a focus on *Sicydium* species

The Pérou River had the highest abundance of both fish and crustacean in its upstream reaches, except for *Micratya poeyi* which was more numerous on Grand Carbet River. The Pérou River dam had the best crossability for all species combined, except for *Macrobrachium* spp. that remained mainly trapped at the foot of the dam, while the Grand Carbet River dam showed lower crossability, and was crossable only by the *Sicydium* spp. and *Micratya poeyi*. Both structures were relatively similar, with a height of 5 m for Grand Carbet vs. 4 m for Pérou; a natural and well-preserved riparian forest; and a narrow grid width compared to the overall riverbed width. The main difference was the aspect of the fishway, it looks like a riffle on the Pérou River with andesitic blocks simply solidified by concrete, giving a wide range of speeds throughout the fishway which eases the passage upstream (Fig. S1); and a more modified attraction flow on Grand Carbet River may be unsuitable for upstream migrants. In contrast, the Moreau River dam was the most

species-impassable, only *Atya* spp. crossed it at more than 50%. This dam presented very different characteristics from the two previous ones, with a very low height (0.1 m); a very small riparian forest that created a wide open space above the river; a grid that occupied almost the entire width of the riverbed; a fishway that ended with a metal plate placed on the grid which probably strongly limits the possibilities of crossing, and an attraction flow embedded in the instream flow. As well as the crossability being influenced by environmental conditions, within this it is also highly species specific, as demonstrated in Kikkert *et al.* (2009) who described that the *Atya* spp. were the species the least impacted in their upstream migration by environmental conditions, unlike *Macrobrachium* spp. or fish species.

The new French national indice of ecological continuity (ICE) recently built for management purposes (Baudoin *et al.*, 2014) is based on measures of the physical conformation of the obstacles, and mainly their height. It allocates a score of species crossability for the majority of types of obstacles and species found in rivers from France considering exclusively continental Europe area but not tropical overseas territories. The results obtained in our study showed that, in the rivers of Guadeloupe, the crossability of a water intake or a low-head dam seems not directly related to its height or physical conformation but mainly to hydrological or environmental conditions, among which parameters: the amount of water withdrawn, the vegetation cover of its riverbanks and the accuracy of the orientation of the attraction flow on the multispecies passways, that all must be adapted to this very particular benthic fauna living therein. Our observations on the crossability of the obstacles have also been reported through other studies. In Puerto Rico, several studies concluded that ecological effects of dams and water abstraction depend on spatial context and temporal variability of flow (Benstead *et al.*, 1999; Kwak *et al.*, 2007; Crook *et al.*, 2009). It is essential that the management of the water withdrawn must take into account the very high seasonal variability of flow, especially at low flows, because the simple maintenance of a regular flow of water passing over the dam allows migrating species to move upstream (Greathouse *et al.*, 2006). The strong impact of the riparian forest removal on the distribution of amphidromous fauna has been reported, in particular by modifying the algal community of diatoms into filamentous algae and thus the quantity and quality of the available food resources (MacKenzie, 2008; Ramírez *et al.*, 2012; Holcomb *et al.*, 2016). Reducing undesirable rheotactic sources that attract fish away from the fishway is an effective management action that improves obstacle crossing (Fièvet, 1999b; Fièvet *et al.*, 2000; Lagarde *et al.*, 2015). Given these observations combined with our results and the known originalities of Caribbean freshwater species, the passways built for crossing the obstacles for fish and crustaceans in the rivers of Guadeloupe could be greatly

improved by focusing on technical optimizations of these additional aspects.

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**SUPPLEMENTARY MATERIAL**



Figure S1. – Pictures of the water intakes on the rivers Grand Carbet (A), Pérou (B) and Moreau (C). The direction of the arrow indicates the direction of the current.

