Hydraulic preferences of shrimps and fishes in tropical insular rivers

Virginie Grandgirard, Dominique Monti, P. Valade, Nicolas Lamouroux, J.P. Mallet, H. Grondin

► To cite this version:

Virginie Grandgirard, Dominique Monti, P. Valade, Nicolas Lamouroux, J.P. Mallet, et al.. Hydraulic preferences of shrimps and fishes in tropical insular rivers. *River Research and Applications*, 2014, 30 (6), p. 766 - p. 779. 10.1002/rra.2675 . hal-01072479

HAL Id: hal-01072479

<https://hal.science/hal-01072479>

Submitted on 8 Oct 2014

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Hydraulic preferences of shrimps and fishes in tropical insular rivers

Virginie Girard^{1,2}, Dominique Monti³, Pierre Valade⁴, Nicolas Lamouroux¹, Jean-Paul Mallet², Henri Grondin⁵.

Short title: Hydraulic preferences of diadromous species

Key words: micro-habitat preferences; generalized additive models; transferability; Caribbean; Indian Ocean

¹ IRSTEA Lyon, UR MALY, 5 rue de la Doua CS70077 69626 VILLEURBANNE Cedex, France, virginie.girard@irstea.fr, nicolas.lamouroux@irstea.fr

² ASCONIT Consultants, Espace Scientifique Tony Garnier, 6-8 Espace Henry Vallée, 69 366 LYON Cedex 07, jp.mallet@asconit.com

³ EA926 DYNECAR, Université des Antilles et de la Guyane, Fouillole, BP 250, 97157 Pointe-à-Pitre, dominique.monti@univ-ag.fr

⁴ O.C.E.A. Consult', Organisme Consultant en Environnement Aquatique, BP 22, Centre Régional d'Application Aquacole 97 427 Etang Salé, pierre.valade@oceare

⁵ A.R.D.A., B.P. 16, Z.I. Les Sables, 97427 Etang Salé, grondin.arda@wanadoo.fr

Correspondence to: V. Girard, IRSTEA Lyon, UR MALY, 5 rue de la Doua CS70077 69626 Villeurbanne Cedex, France; Phone: (+33)4 72 20 89 18; Fax: (+33)4 78 47 78 75; Email: virginie.girard@irstea.fr

ABSTRACT

Hydraulic habitat models based on the preferences of species for the hydraulic characteristics of their microhabitats are frequently used to evaluate the impact on the habitat of a change in river flow regime. Their application in a tropical insular environment is still limited as little is known about the hydraulic preferences of species. Hydraulic preferences models have been developed for 15 taxa (diadromous shrimps and fishes) sampled in 52 rivers in the Caribbean (the French West Indies) and the Indian Ocean (the Reunion island). Five datasets were used and group 8353 samples collected by electrofishing during 320 surveys (reach×date) performed between 1999 and 2011. Generalised additive models were used to link variations of taxa density within surveys to the hydraulic characteristics of the microhabitat (velocity, depth, substrate). Hydraulic preferences within each region (Caribbean and Indian Ocean) are significant for most of the taxa and vary little between rivers and surveys. The hydraulic variables explain up to 18.1% (univariate models) and 30.0% (multivariate models) of the deviance of densities within survey. Of the taxa selected, *Atya scabra*, *Macrobrachium heterochirus*, *Xiphocaris elongata* and the Sicydiinae are the most demanding.

INTRODUCTION

Tropical insular rivers are characterised by extreme and unpredictable hydrological events (typhoons, cyclones, Tew *et al.*, 2002) that alternate with sometimes severe periods of low flow (Covich, 2006) that are decisive for aquatic communities (Poff and Ward, 1989). The communities of these rivers are characterised by low density and are mainly composed of three families of shrimp (Atyidae, Palaemonidae, Xiphocaridae) and four families of fish (Eleotridae, Gobiidae, Mugilidae and Anguillidae) (Covich and McDowell, 1996), all of which are diadromous (McDowall, 2004). The catadromous species (Mugilidae, Anguillidae) spend their lives in rivers and reach the sea and/or river outlets to reproduce. Amphidromous species (Atyidae, Palaemonidae, Xiphocaridae, Gobiidae) spawn and grow in freshwater except during larval stages which require a saline environment. The complex lifecycle of these species makes them especially vulnerable to increasing demographic pressure (Mittermeier *et al.*, 2005; Smith *et al.*, 2008), such as dams that modify flow regimes and river habitats, and impede their migrations (March *et al.*, 2003; Milton, 2009). Many aspects of the flow regime may affect the habitats and the life cycle of tropical species (e.g. Welcomme and Halls, 2004). For example, the timing and the amplitude of floods may trigger fauna migration and reproduction (e.g. Way *et al.*, 1998; Blanco and Scatena, 2005; Kikkert *et al.*, 2009). However, little is known about the ecological impact of changes in low to moderate flows (Pringle *et al.*, 2000; Monti and Legendre, 2009).

Hydraulic habitat models have been used widely around the world to facilitate the management of low to medium discharges (Tharme 2003; Conallin *et al.*, 2010). This method uses models that predict the amount of favourable habitat at the reach scale ($\sim 10^2$ - 10^3 m²) as a function of discharge rate (Bovee, 1982; Ginot, 1995). Habitat models combine the hydraulic model of a stream reach with models of hydraulic preferences. Classically, hydraulic

preference models represent how the abundance or occurrence of a taxon (e.g. guild of species, species, life stage of a species) varies within the reach as a function of microhabitat parameters (e.g. velocity, depth, substrate). The applicability of habitat models is generally limited by their degree of transferability between rivers (Jowett, 2003; Lamouroux *et al.*, 2010; Lancaster and Downes, 2010). Indeed, habitat preferences can vary as a function of a large number of biotic and abiotic factors such as competition, predation, and water chemistry (Jackson *et al.*, 2001). In order to better quantify the generality of hydraulic preference models, it is therefore interesting to study the hydraulic preferences of taxa using data collected from different rivers at different times (seasons, years) (Leftwich *et al.*, 1997; Lamouroux *et al.*, 1999a; Strakosh *et al.*, 2003; Vilizzi *et al.*, 2004; Dolédec *et al.*, 2007; Méricoux *et al.*, 2009). The models developed at several sites have led to contrasting conclusions, but have often highlighted the pertinence of models defined for a number of rivers sharing the same hydromorphological characteristics (Lamouroux *et al.*, 1999b; Lamouroux *et al. in press*).

Not much is known about the hydraulic preferences of tropical river species (Pringle *et al.*, 2000; Scatena, 2004; Boulton *et al.*, 2008). Research into these species has mainly focused on (1) the altitudinal distribution of species and the importance of maintaining upstream/downstream connectivity (Holmquist *et al.*, 1998), (2) trophic links and the role of macro-consumers (Crowl *et al.*, 2006; Coat *et al.*, 2009), (3) the effects of extreme events on population structures (e.g. the harmful effect of low water levels on the abundance of *Macrobrachium sp.*, Covich *et al.*, 2006) and (4) the mechanisms and role of dispersion in population renewal (Keith *et al.* 2008; Crook *et al.*, 2009). However, few works have focused on the role of hydraulic constraints (e.g. shift of driving force under natural disturbance, Monti and Legendre, 2009) and the habitat selection mechanisms at the reach scale (e.g. habitat selection for Sicydiinae, Teichert *et al. in press*).

In this study, we examine how the density of 15 taxa of the families of Atyidae, Palaemonidae, Xiphocaridae, Gobiidae and Mugilidae vary as a function of the hydraulic parameters of the microhabitat (velocity, depth, substrate). The datasets used come from two regions: the French West Indies (Martinique, Guadeloupe) in the Caribbean and the island of Reunion in the Indian Ocean. These are recent volcanic islands with comparable hydromorphological characteristics (narrow valleys, abrupt reliefs, high waterfalls) (Falkland, 1992). Our main objectives were to (1) build hydraulic preference models for different taxonomic groups in each of the two regions (Caribbean, Indian Ocean), (2) estimate the transferability of models among datasets and groups of surveys, and (3) compare hydraulic preferences among the species of the same family.

METHODS

Reaches and sampling dates

We used five datasets (Table 1), three collected from the Caribbean and two from the Indian Ocean (Figure 1). Abundance samples were taken in 121 reaches of 52 rivers during periods of 1 to 12 years. The reaches were distributed over the entire island, in river sections with persistent flows, and were sometimes located upstream or downstream of water intakes. The length of the reaches varied from 0.05 to 2.75 km so that each reach encompassed a variety of morphological units (e.g. riffles, rapids, pools, cascades). The reaches were located at an altitude between 5 and 670 m, at a distance from the sea from 0.1 to 22.8 km and at a distance of 1 to 34.5 km from the source. The surface area of the watersheds upstream of the reach was on average ($\pm$ standard deviation) $15 (\pm 15 \text{ km}^2)$ in the Caribbean and $70 (\pm 49 \text{ km}^2)$ in the Indian Ocean. Most of the sampling was performed during the low flow period (when hydraulic selection occurs), i.e. from December to May in the Caribbean (Chaperon *et al.*, 1983) and from November to April in the Indian Ocean (Robert, 1988). 20% of the surveys

(reach×date) in the Caribbean were carried out during the high flow period but when discharge rate was relatively low.

Sampling methods

Sampling of fishes and shrimps was done by electrofishing using three methods (Table 1) according to the objectives of previous studies (e.g. analysis of spatial patterns, Monti and Legendre, 2009). The "points" method consisted in collecting 50 samples ($\sim 1 \text{ m}^2$) distributed randomly in the reach by positioning a portable electrode (e.g. DEKA 3000 Lord; DEKA-Gerätebau, Marsberg, Germany) without moving it (Fiévet *et al.*, 1996). The "habitat units" method consisted in fishing about 20 samples from wider surface areas distributed in the available morphological units. The surface area of the samples was 17 m^2 on average ($\pm 8 \text{ m}^2$). The "quadrats" method consisted in fishing about 90 contiguous samples (squares of surface area = 4 m^2) in the reaches. These different methods have been used by different teams and were not intercalibrated in our reaches. However, point samples and habitat unit samples have already been combined in habitat modelling. For example, Lamouroux *et al.* (1999b) predicted fish density differences between reaches sampled by points from preference models made in other reaches sampled by habitat units.

Each sample was characterised by three microhabitat variables: average velocity (v), average water depth (h) and the size of the substrate (d). v , h and d were estimated on the basis of measurements along one vertical (44% of cases) or several verticals distributed in the sampling area (56% of cases). On each vertical, point velocities were measured using a current meter (a propeller for dataset Gq; an electromagnetic current meter for the other datasets) at $0.2h$, $0.4h$ and $0.8h$ at the bottom of the bed when $h > 0.20 \text{ m}$, otherwise at $0.4h$. However, 5.4% of the velocities were estimated at the water surface as a function of the distance travelled by a float over a given time. The dominant substrate size d of the sample

area was estimated visually using ordinal classes (Cailleux 1954; Malavoi and Souchon, 1989). The central value of the class of substrate was assigned to *d*.

Each individual fish was measured and identified at species level (Keith *et al.*, 1999, Lim *et al.*, 2002, Monti *et al.*, 2010), except for three taxa in the Caribbean (Table 1): *Sicydium sp.* groups two species of fish, *Sicydium punctatum* and *Sicydium plumeri*, of the Gobiidae family (subfamily Sicydiinae); *Atya sp.* groups the juvenile shrimps of *Atya scabra* et *Atya innocous*; and *Macrobrachium sp.* groups the juvenile shrimps of the family of Palaemonidae (subfamily *Macrobrachium*). However, the individuals of dataset Gq (Table 1) were not measured.

Taxa selected

Of the 21 to 28 species sampled in each dataset (Table 1) only the taxa with a total abundance > 200 individuals were chosen for the analysis. Therefore, we selected 11 taxa in the Caribbean belonging to three families of shrimp (Atyidae, Xiphocariidae, Palaemonidae) and two families of fish (Mugilidae, Gobiidae), and four taxa in the Indian Ocean belonging to two families of shrimp (Atyidae, Palaemonidae) and one family of fish (Gobiidae) (Table 2). In order to get round the problem of different surface areas of the samples used in the analyses, the abundances of the samples were transformed to densities ($\check{D}$, number of each for an equivalent surface of 10 m²). Taxa size classes were defined in order to infer the effect of size preferences on hydraulic. The limits of classes were chosen to obtain comparable numbers.

165

166 *Statistical modelling*

167 For each taxon of each region, we modelled the $\check{D}$ as a function of microhabitat variables with
168 a series of generalised additive models (GAMs). GAMs permit considering nonlinear
169 relations, that are frequent when studying hydraulic preferences (e.g., Lamouroux *et al.*,
170 1999a; Jowett *et al.*, 2008). They have a flexible structure that does not require prior
171 determination of the form of the relation (Guisan and Zimmerman, 2000, Guisan *et al.*, 2002).
172 Six models (Eqs. 1-6) were defined with a log link function. The reference model M1 (Eq. 1)
173 assumes that the density is constant by survey, so that there is no hydraulic preference. Model
174 M2 (Eq. 2) defines the regional model where the abundance varies similarly in each survey as
175 a function of a microhabitat variable. By comparing M2 in relation to M1, we quantify the
176 strength of hydraulic preference independently of the other biotic and abiotic factors acting at
177 the scale of the reach on a given date. In model M3 (Eq. 3), the hydraulic preferences can vary
178 as a function of the dataset, i.e. the island or the sampling method. In model M4 (Eq. 4), the
179 hydraulic preferences can vary as a function of the dataset and groups of surveys. The latter
180 two models permit appreciating the transferability of the results between rivers. Different
181 criteria were used to define two groups of surveys in M4 (with comparable numbers): the
182 season of low and high flow in the Caribbean; the years $<$ and $\geq$ 2009 in the Caribbean and
183 the years $<$ and $\geq$ 2005 in the Indian Ocean; the altitude ($\leq$ or $>$ 165 m in the Caribbean; $<$
184 and $\geq$ 80 m in the Indian Ocean); the wind coast exposure (exposed or not); the size of the
185 watershed ($\leq$ or $>$ 10 km² in the Caribbean; $\leq$ or $>$ 50 km² in the Indian Ocean); the situation
186 in relation to water intakes (upstream of an intake or not; only in the Caribbean). Lastly,
187 models M5 and M6 (Eqs. 5-6) define multivariate models for a taxon with or without a term
188 of interaction between microhabitat variables. Concerning the preference models of taxa size
189 classes, we fitted M1 and M2 only. Our series of models is:

$$190 \quad M1: \quad \log(\check{D}) \sim a_{survey} \quad (1)$$

$$191 \quad M2: \quad \log(\check{D}) \sim a_{survey} + s(p) \quad (2)$$

$$192 \quad M3: \quad \log(\check{D}) \sim a_{survey} + s(p) + s(p:p_{dataset}) \quad (3)$$

$$193 \quad M4: \quad \log(\check{D}) \sim a_{survey} + s(p) + s(p:p_{dataset}) + s(p:p_{survey}) \quad (4)$$

$$194 \quad M5: \quad \log(\check{D}) \sim a_{survey} + s(v) + s(h) + s(d) \quad (5)$$

$$195 \quad M6: \quad \log(\check{D}) \sim a_{survey} + s(v) + s(h) + s(d) + s(v, h, d) \quad (6)$$

196 where p corresponds either to v , h or d ; $s()$ is a smoothing function (of cubic spline type); p :
197 $p_{dataset}$ is the term of interaction between the hydraulic variable and the *dataset* variable;
198 $p:p_{survey}$ is the term of interaction between the hydraulic variable and a group of surveys. The
199 parameter a_{survey} permits ignoring differences in density between surveys which do not reflect
200 the microhabitat hydraulic preferences.

201 For all the models, we chose a negative binomial (NB) type error distribution, which
202 can account for the over-dispersion of abundance data, as suggested by Gray *et al.* (2005,
203 freshwater macro-invertebrates) and Vaudor *et al.* (2009, freshwater fishes) for data of the
204 same type. We set the dispersion parameter (θ) of the NB distribution for each taxon when
205 fitting model M1. We also set the degree of freedom of the smoothing function of the GAMs
206 at three to avoid any over-parameterisation (Jowett *et al.*, 2008). Lastly, for each taxon we
207 eliminated the surveys where the number of individuals was less than three. The models were
208 fitted using the functions available in the *mgcv* package (Wood, 2006) of the R software (R
209 Development Core Team, 2010).

210 We described the quality of our two series of nested models (M1-M4 and M1, M5-
211 M6) using the additional deviance explained in comparison to the previous model. In
212 addition, we used a likelihood ratio test to compare a given model with the previous one.

213

214

RESULTS

215

216

217

218

A total of 8353 samples were collected from 320 surveys, making it possible to establish and study the preferences of 11 taxa and 16 size classes in the Caribbean, four taxa and eight size classes in the Indian Ocean (Table 2). The velocities of the samples varied from 0 to 2.80 m.s⁻¹, the depths from 0.02 to 1.90 m and the substrate from 0 to 1.024 m.

219

220

221

222

223

224

The dispersion parameter θ varied from 0.06 (*A. scabra*) to 0.46 (*M. poeyi*) for the taxa of the Caribbean, and from 0.32 (*A. serrata*) and 1.10 (*S. lagocephalus*) for the taxa of the Indian Ocean (Table 2, standard error on $\theta \leq 0.03$ for all species). The low values of θ , which indicate over-dispersion of densities, were obtained for rare species (*M. crenulatum*, *A. monticola*) and those known to be gregarious (*A. scabra*; Lim *et al.*, 2002; Monti *et al.*, 2010).

225

226

Univariate models M1 – M4 by taxon

227

228

229

230

231

232

The deviance explained by the survey in reference model M1 varied from 20.3 to 56.0% (on average 36%, Table 3). The addition of microhabitat variables in M2 explained from 0 to 18.1% (average 4.3%) of the residual deviance of M1. The model of velocity preferences was generally more efficient than that of preferences of depths and substrates (on average 6.9, 4.4 and 1.6% of explained deviance, respectively). Examples of fits of M2 models to the data observed are given in Figure 2.

233

234

235

236

237

Hydraulic preferences were significant for most of the species, except *A. monticola* (v and d), *M. crenulatum*, *Atya sp.* and *X. elongata* (d) (Table 3). The strongest preferences, relative to velocity and depth, concerned *A. Scabra*, *M. heterochirus*, *X. elongata* and *Sicydium sp.* in the Caribbean and *S. lagocephalus* and *C. acutipinnis* in the Indian Ocean. The taxa had preferences for low (*X. elongata*, *M. crenulatum*, *M. faustinum*, *M. australe*),

intermediate (*A. innocous*, *M. poeyi*) or high (*A. Scabra*, *M. heterochirus*, *A. serrata* and Sicydiinae) velocities, whereas most taxa preferred shallow depths, except *X. elongata*, *M. crenulatum* and *M. australe* (Figures 3 and 4). *A. scabra*, *M. heterochirus*, *A. serrata*, *C. acutipinnis* and *S. lagocephalus* preferred coarse substrates whereas *M. australe* preferred fine substrates (Figures 3 and 4).

The preferences for velocities and depths, and to a lesser extent substrates (Table 3), differed between datasets. However, the additional deviance explained by M3 in comparison to M2 remained low: it was < 2.2% in the Caribbean and < 1.5% in the Indian Ocean (Table 3). The main differences observed in the Caribbean are the variations of preferences in the range of high velocities ($> 0.5 \text{ m.s}^{-1}$) (cf. *A. scabra* in Figure 3) and preferences for shallower or deeper water depths (cf. *A. monticola* in Figure 3). In the Indian Ocean, we observed preferences for lower velocities and an absence of preferences for depths in the dataset sampled by "points" in comparison to "habitat units" for *C. acutipinnis* (v , h) (Figure 4). Regarding variations between groups of surveys, the comparison of M4 and M3 indicated that the localisation parameters of reaches and the sampling period generally had little influence on hydraulic preferences (explained relative deviance < 2.4%, Table 3). The highest values observed concerned *A. scabra* in the Caribbean, and *A. serrata*, *M. australe* and *C. acutipinnis* in the Indian Ocean.

Univariate models M1 – M2 by size classes

The hydraulic preferences according to size classes were mostly significant except for the preferences of *X. elongata* (h), *A. monticola* (h) and *A. serrata* (d) of small sizes and the preferences of adults of *Sicydium* sp. (d) and *A. monticola* (v) (Table 4, Figure 5). The deviance explained by the models by size classes was close to that of the model by taxon. The deviance explained was nonetheless higher for size classes concerning the preferences for

substrate. The preferences of larger individuals for velocities were weaker than those of smaller individuals for the species *A. scabra* and *X. elongata*; on the contrary, the preferences of larger individuals for velocities were stronger than those of smaller individuals for the species *Sicydium sp.*. Size classes generally preferred similar depth ranges except for the taxa *X. elongata*, where larger individuals tended to prefer deeper habitats (Figure 5). The preferences of larger individuals for substrate are weaker than those of smaller individuals for *M. australe* and *M. heterochirus*; conversely, larger individuals of *A. scabra*, *A. serrata* and *S. lagocephalus* have stronger preferences for substrate.

Multivariate models M5 – M6

The multivariate models without interactions (M5) explained from 2.8 to 24.4% of the residual deviance of M1 (Table 5). The addition of an interaction term (M6) improved the explained deviance between 3.7 and 9.4% for some taxa: *Sicydium sp.*, *X. elongata*, *C. acutipinnis* and *S. lagocephalus* (Table 5).

DISCUSSION

The within-survey deviance explained by microhabitat variables varies between 0 and 18.1% (univariate regional models) and from 4.1 to 30.0% (multivariate regional models). The poor performances achieved by the models built are partly due to the small size of the scale of observation ($\sim 1 \text{ m}^2$) and likely result from the particular life cycle of the taxa (diadromous and opportunistic species). Similarly, the within-survey deviance of models of hydraulic preferences of the white shrimp *Paranephrops planifrons*, a diadromous species of the rivers of the north island of New Zealand, varies from 7 and 11% (Jowett *et al.*, 2008). By way of

comparison, Dolédec *et al.* (2007) showed that models of European regional preferences for macro-invertebrates explained on average 25% of within-survey variance.

Taxa showing the most marked hydraulic preferences are *A. scabra*, *M. heterochirus*, *X. elongata*, *Sicydium sp.* in the Caribbean, and *C. acutipinnis* and *S. lagocephalus* in the Indian Ocean. For example, the density of *A. scabra* and *X. elongata* can be multiplied by a factor of ~ 5 for a change of velocity in the order of 0.5 m.s⁻¹.

The preferences of shrimps for high (*A. scabra*, *M. heterochirus*) or low (*X. elongata*) velocities are probably linked to their capacity to resist currents or not and their foraging strategy. Indeed, *A. scabra* and *M. heterochirus* are larger in comparison to the other species of the same family (*M. poeyi*, *M. faustinum*) and have larger morphological attributes (pincers, legs, spines on pincers) (Lim *et al.*, 2002) that allow them to move in rapids where densities of drifting benthos, particles and/or individuals are higher (Orth and Maughan, 1983; Brooks *et al.*, 2005). Furthermore, the feeding mode of *A. scabra* is probably more specialised than for *A. innocous*, likewise with *M. heterochirus* in comparison to *M. crenulatum*. On the contrary, *X. elongata* has a strong preference for low velocities and deeper water since it lives essentially in the water column (Lim *et al.*, 2002). In addition, our results corroborate those of Monti and Legendre (2009) who showed that *M. heterochirus* and *X. elongata* have notable preferences for velocities in environments with strong hydrological disturbances.

The fish of the subfamily of Sicydiinae in the two regions (*Sicydium sp.*, *C. acutipinnis* and *S. lagocephalus*) prefer fast-flowing and shallow habitats. Their hydraulic preferences are probably linked to the presence of periphytic biofilm whose quality and development are conditioned by bed shear stress and light, respectively (Julius *et al.*, 2005; Lefrançois *et al.*, 2011; Tabouret *et al.*, 2011). The hydraulic preferences of *S. lagocephalus* and *C. acutipinnis* are comparable to those given by the logistic models built by Teichert *et al.* (*in press*), except that the authors showed that *C. acutipinnis* has stronger preferences for

depths than velocities. This difference in preference strength can be due to the longer sampling period covered by our dataset.

Taxa showing weaker hydraulic preferences are *A. monticola*, *M. faustinum*, *M. crenulatum*, *M. australe*, *A. innocous*, *M. poeyi* and the juvenile shrimps of the Caribbean. These results are consistent with those of Monti and Legendre (2009) who reported weak preferences for velocity for *M. faustinum* and *M. poeyi*. Concerning *M. crenulatum*, Monti and Legendre identified strong preferences for low velocities for four sites under strong and weak hydrological disturbance, suggesting that food predominates in influencing habitat selection. Some of these species are also described with preference variables according to diurnal phases (e.g. *A. innocous*) (Keith *et al.*, 1999; Lim *et al.*, 2002; Monti *et al.*, 2010). The weak preferences of the species observed here can also be partly due to variations in fishing efficiency or to our grouping of juveniles of some taxa (*A. scabra* and *A. innocous*; *M. crenulatum*, *M. heterochirus* and *M. faustinum*). Regarding fishing efficiency, it is as poor as the species are rare (*M. crenulatum*) and their mobility is high (*A. monticola*) (Fiévet *et al.*, 1999; King *et al.*, 2002). It is therefore possible that fishing efficiency explains the absence of preference for velocity that we observed for the mobile *A. monticola*, whereas the taxon is expected to prefer fast and well oxygenated water (Lim *et al.*, 2002). Fishing efficiency can also explain that we observed weak preferences for *A. innocous*, which is an excellent swimmer and very reactive in the presence of predators (Covich *et al.*, 2009; Hein and Crowl, 2010) or when disturbed by electrofishing (Fiévet *et al.*, 1999). Regarding the shrimp *M. australe*, its weak regional preferences can be explained by its sheltering behaviour during the day and variation due to its morphological plasticity (Zimmermann *et al.*, 2012). The grouping of juveniles of different species of *Macrobrachium* is probably not very appropriate since we observed that the adults of *M. faustinum* and *M. heterochirus* have different preferences (forces and directions) regarding velocity and depth. This is less the case for the juveniles of the family of Atyidae since the adults (*A. scabra*, *A. innocous* and *M. poeyi*) share

relatively similar preferences. Lastly, the more flexible mode of feeding (filtering and scraping) of *M. poeyi* and *A. innocous* in comparison to *A. scabra* (mainly filtering) can also explain less selective use of microhabitats.

The comparison of inter-species hydraulic preferences suggests that food strategies (filtering and/or scraping) and morphological adaptations (size, apical spine) effectively influence habitat selection. This result supports that aquatic taxa have developed strategies shaped by the flow regime (Poff and Ward, 1989; Poff, 1997). The use of life history traits is therefore encouraged for overcoming problems of identification and/or lack of data on a particular species (Blanck *et al.*, 2007).

The low additional deviance explained by datasets or groups of surveys suggests that regional models are pertinent for expressing taxa preferences. Likewise, the performance of models regarding size class does not suggest a notable improvement. These results should nonetheless be seen relatively. For example, it is possible that our definitions of groups are not very appropriate for expressing different competition conditions. These effects can exist for certain species (*S. lagocephalus* and *C. acutipinnis*, Lord *et al.*, 2011) and might partially explain the variations observed between groups in our results (*C. acutipinnis*). Likewise, taking the hydrological regime (Monti and Legendre, 2009) into account in more detail would undoubtedly lead to more thorough models. Lastly, a breakdown of taxa by life stage rather than by size class could be more pertinent to reflect the physiological needs of species (Bielsa *et al.*, 2003, for *S. lagocephalus*) and their behaviours regarding different predators (e.g. longer rostrum in *X. elongata* in the presence of predatory fish, Covich *et al.*, 2009).

To sum up, the hydraulic preferences of insular tropical taxa are generally weaker than in temperate regions. This observation, as well as the complexity of the life cycle of these taxa, tends to emphasise that the hydraulic preferences of taxa should only be taken into account

within an approach that provides a more general description of their habitat during their life cycle. This approach would imply in particular taking into account the ecological effect of various flow regime attributes (e.g., timing and duration of floods, flashiness; Bunn and Arthington, 2002), the longitudinal connectivity (e.g., Greathouse *et al.*, 2006) and the potential threat of introduced species (Donlan and Wilcox, 2008). Nonetheless, our results show that the hydraulic preferences of certain taxa are significant (e.g., *A. scabra*, *M. heterochirus*) and consistent with the knowledge available on these taxa. Our regional models can contribute to describe the hydraulic preferences of these taxa and model how the management of low to average discharges modifies their available habitat.

ACKNOWLEDGMENTS

We thank the staff from "Association Réunionnaise de Développement de l'Aquaculture" and from Asconit Consultants for their collaboration in this project and for collecting part of the data. We also thank Sylvie Méricoux, Jean-Michel Olivier, Philippe Keith and Thierry Oberdorff for helpful discussions. The "Direction Régionale de l'Environnement, de l'Aménagement et du Logement" of Guadeloupe, the "Office de l'eau" of Martinique and "Office de l'eau" of Reunion provided financial support.

REFERENCES

- Bielsa S, Francisco P, Mastrotillo S, Parent JP. 2003. Seasonal changes of periphytic nutritive quality for *Sicyopterus lagocephalus* (Pallas, 1770) (gobiidae) in three streams of Reunion Island. *Annales De Limnologie-International Journal of Limnology* **39**:115–127.
- Blanck A, Tedesco PA, Lamouroux N. 2007. Relationships between life-history strategies of European freshwater fish species and their habitat preferences. *Freshwater Biology* **52**:843–859.
- Boulton AJ, Boyero L, Covich AP, Dobson M, Lake S, Pearson R. 2008. Are tropical streams ecologically different from temperate streams? In *Tropical Stream Ecology*, Dudgeon D (ed.). Academic Press (Aquatic Ecology Series): London; 257–284.
- Bovee KD, 1982. A guide to stream habitat analysis using the instream flow incremental methodology. instream flow information. In *Western energy and land use team*, U.S. Fish and wildlife Service (ed.): Fort Collins, Colorado.
- Brooks AJ, Haeusler T, Reinfelds I, Williams S. 2005. Hydraulic microhabitats and the distribution of macroinvertebrate assemblages in riffles. *Freshwater Biology* **50**:331–344.
- Bunn SE. & Arthington AA. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, **30**: 492-507.
- Cailleux A. 1954. Limites dimensionnelles des noms des fractions granulométriques. *Bulletin de la Société géologique de France* **4**: 643–646.
- Chaperon P, L'Hôte Y, Vuillaume G. 1983. Les ressources en eaux de surface de la Guadeloupe. *Cahier ORSTOM, Série Hydrologie* **20**:149–178.
- Coat S, Monti D, Bouchon C, Lepoint G. 2009. Trophic relationships in a tropical stream food web assessed by stable isotope analysis. *Freshwater Biology* **54**:1028-1041.
- Conallin J, Boegh E, Jensen JK. 2010. Instream physical habitat modelling types: An analysis as stream hydromorphological modelling tools for EU water resource managers.

- 26 *International Journal of River Basin Management* **8**:93-107.
- 27 Covich AP. 2006. Dispersal - Limited biodiversity of tropical insular streams. *Polish Journal*
- 28 *of Ecology* **54**:523-547.
- 29 Covich AP, Mcdowell WH. 1996. The stream community. *The Food Web of a Tropical Rain*
- 30 *Forest* 433–459.
- 31 Covich AP, Crowl TA, Heartsill-Scalley T. 2006. Effects of drought and hurricane
- 32 disturbances on headwater distributions of palaemonid river shrimp (*Macrobrachium*
- 33 *spp.*) in the Luquillo Mountains, Puerto Rico, *Journal of the North American*
- 34 *Benthological Society* **25**:99–107.
- 35 Covich AP, Crowl TA, Hein CL, Townsend MJ, Mcdowell WH. 2009. Predator-prey
- 36 interactions in river networks: comparing shrimp spatial refugia in two drainage basins.
- 37 *Freshwater Biology* **54**:450–465.
- 38 Crook KE, Pringle CM, Freeman MC. 2009. A method to assess longitudinal riverine
- 39 connectivity in tropical streams dominated by migratory biota. *Aquatic Conservation:*
- 40 *Marine and Freshwater Ecosystems* **19**:714–723.
- 41 Crowl TA, Welsh V, Heartsill-Scalley T, Covich AP. 2006. Effects of different types of
- 42 conditioning on rates of leaf-litter shredding by *Xiphocaris elongata*, a Neotropical
- 43 freshwater shrimp. *Journal of the North American Benthological Society* **25**:198–208.
- 44 Dolédec S, Lamouroux N, Fuchs U, Mérioux S. 2007. Modelling the hydraulic preferences
- 45 of benthic macroinvertebrates in small European streams. *Freshwater Biology* **52**:145–
- 46 164.
- 47 Falkland AC. 1992. Small tropical islands: water resources of paradise lost. *IHP Humid*
- 48 *Tropics Programme Series 2*. UNESCO: Paris.
- 49 Fiévet E, De Morais LT, De Morais AT. 1996. Quantitative sampling of freshwater shrimps:
- 50 Comparison of two electrofishing procedures in a Caribbean stream. *Archiv für*

- Hydrobiologie* **138**:273–287.
- Fiévet E, Bonnet-Arnaud P, Mallet JP. 1999. Efficiency and sampling bias of electrofishing for freshwater shrimp and fish in two Caribbean streams, Guadeloupe Island. *Fisheries Research* **44**:149–166.
- Ginot V. 1995. EVHA, a Windows software for fish habitat assessment in streams. *Bulletin Francais de la Pêche et de la Pisciculture* 303–308.
- Gray BR. 2005. Selecting a distributional assumption for modelling relative densities of benthic macroinvertebrates. *Ecological Modelling* **185**:1–12.
- Guisan A, Zimmermann NE. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* **135**:147–186.
- Guisan A, Edwards jr TC, Hastie T. 2002. Generalized linear and generalized additive models in studies of species distributions: Setting the scene. *Ecological Modelling* **157**:89–100.
- Hein CL, Crowl TA. 2010. Running the predator gauntlet: do freshwater shrimp (*Atya lanipes*) migrate above waterfalls to avoid fish predation? *Journal of the North American Benthological Society* **29**:431–443.
- Holmquist JG, Schmidt-Gengenbach JM, Yoshioka BB. 1998. High dams and marine-freshwater linkages: Effects on native and introduced fauna in the Caribbean. *Conservation Biology* **12**:621–630.
- Jackson DA, Peres-Neto PR, Olden JD. 2001. What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:157–170.
- Jowett IG. 2003. Hydraulic constraints on habitat suitability for benthic invertebrates in gravel-bed rivers. *River Research and Applications* **19**:495–507.
- Jowett IG, Parkyn SM, Richardson J. 2008. Habitat characteristics of crayfish (*Paranephrops planifrons*) in New Zealand streams using generalised additive models (GAMs).

- 76 *Hydrobiologia* **596**:353–365.
- 77 Julius M, Blob R, Schoenfuss H. 2005. The survival of *Sicyopterus stimpsoni*, an endemic
78 amphidromous Hawaiian gobiid fish, relies on the hydrological cycles of streams:
79 evidence from changes in algal composition of diet through growth stages fish. *Aquatic*
80 *Ecology* **39**:473–484.
- 81 Keith P, Vigneux E, Bosc P. 1999. *Atlas des poissons et crustacés d’eau douce de la Réunion*.
82 Muséum national d'Histoire naturelle **39**: Paris.
- 83 Keith P, Hoareau TB, Lord C, Ah-yane O, Gimonneau G, Robinet T, Valade P. 2008.
84 Characterisation of post-larval to juvenile stages, metamorphosis and recruitment of an
85 amphidromous goby, *Sicyopterus lagocephalus* (Pallas) (Teleostei: Gobiidae: Sicydiinae).
86 *Marine and Freshwater Research* **59**:876–889.
- 87 King AJ, Crook DA. 2002. Evaluation of a sweep net electrofishing method for the collection
88 of small fish and shrimp in lotic freshwater environments. *Hydrobiologia* **472**:223–233.
- 89 Lamouroux N, Capra H, Pouilly M, Souchon Y. 1999a. Fish habitat preferences in large
90 streams of southern France. *Freshwater Biology* **42**:673–687.
- 91 Lamouroux N, Olivier JM, Persat H, Pouilly M, Souchon Y, Statzner B. 1999b. Predicting
92 community characteristics from habitat conditions: fluvial fish and hydraulics. *Freshwater*
93 *Biology* **42**:275–299.
- 94 Lamouroux N, Mérigoux S, Capra H, Dolédec S, Jowett IG, Statzner B. 2010. The generality
95 of abundance-environment relationships in microhabitats: A comment on Lancaster and
96 Downes (2009). *River Research and Applications* **26**:915–920.
- 97 Lamouroux N, Mérigoux S, Dolédec S, Snelder TH. 2012. Transferability of hydraulic
98 preference models for aquatic macroinvertebrates. *River Research and Applications* DOI:
99 10.1002/rra.
- 100 Lancaster J, Downes BJ. 2010. Linking the hydraulic world of individual organisms to

- 101 ecological processes: putting ecology into ecohydraulics. *River Research and Applications*
102 **26**:385–403.
- 103 Lefrancois E, Coat S, Lepoint G, Vachieri N, Gros O, Monti D. 2011. Epilithic biofilm as a
104 key factor for small-scale river fisheries on Caribbean islands. *Fisheries Management and*
105 *Ecology* **18**:211–220.
- 106 Leftwich KN, Angermeier PL, Dolloff CA. 1997. Factors influencing behavior and
107 transferability of habitat models for a benthic stream fish. *Transactions of the American*
108 *Fisheries Society* **126**:725–734.
- 109 Lim P, Meunier FJ, Keith P, Noël PY. 2002. *Atlas des poissons et crustacés d'eau douce de la*
110 *Martinique*. Muséum national d'Histoire naturelle **51**: Paris.
- 111 Lord C, Tabouret H, Claverie F, Pecheyran C, Keith P. 2011. Femtosecond laser ablation
112 ICP-MS measurement of otolith Sr:Ca and Ba:Ca composition reveal differential use of
113 freshwater habitats for three amphidromous Sicyopterus (Teleostei: Gobioidae:
114 Sicydiinae) species. *Journal of Fish Biology* **79**:1304–1321.
- 115 Malavoi JR, Souchon Y. 1989. Méthodologie de description et quantification des variables
116 morphodynamiques d'un cours d'eau à fond caillouteux. Exemple d'une station sur la
117 Filière (Haute Savoie). *Revue de Géographie de Lyon* **64**:252–259.
- 118 March JG, Benstead JP, Pringle CM, Scatena FN. 2003. Damming tropical island streams:
119 Problems, solutions, and alternatives. *Bioscience* **53**:1069–1078.
- 120 McDowall RM. 2004. Ancestry and amphidromy in island freshwater fish faunas. *Fish and*
121 *Fisheries* **5**:75–85.
- 122 Méricoux S, Lamouroux N, Olivier JM, Dolédec S. 2009. Invertebrate hydraulic preferences
123 and predicted impacts of changes in discharge in a large river. *Freshwater Biology*
124 **54**:1343–1356.

- 125 Milton DA. 2009. Living in Two Worlds: Diadromous Fishes, and Factors Affecting
126 Population Connectivity Between Tropical Rivers and Coasts. In *Ecological Connectivity*
127 *among Tropical Coastal Ecosystems*, Nagelkerken I (ed.). Springer: Netherlands; 325–
128 355.
- 129 Mittermeier RA, Gil PR, Hoffman M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, Da
130 Fonseca GAB. 2005. *Hotspots revisited: Earth's biologically richest and most endangered*
131 *terrestrial ecoregions*. Conservation International: Washington, DC.
- 132 Monti D, Keith P, Vigneux E. 2010. *Atlas des poissons et des crustacés d'eau douce de la*
133 *Guadeloupe*. Muséum national d'Histoire naturelle **69**: Paris.
- 134 Monti D, Legendre P. 2009. Shifts between biotic and physical driving forces of species
135 organization under natural disturbance regimes. *Canadian Journal of Fisheries and*
136 *Aquatic Sciences* **66**:1282–1293.
- 137 Orth DJ, Maughan OE. 1983. Microhabitat Preferences Of Benthic Fauna In A Woodland
138 Stream. *Hydrobiologia* **106**:157–168.
- 139 Poff NL, Ward JV. 1989. Implications of streamflow variability and predictability for lotic
140 community structure - a regional-analysis of streamflow patterns. *Canadian Journal of*
141 *Fisheries and Aquatic Sciences* **46**:1805–1818.
- 142 Pringle CM, Freeman MC, Freeman BJ. 2000. Regional effects of hydrologic alterations on
143 riverine macrobiota in the New World: tropical-temperate comparisons. *BioScience*
144 **50**:807–823.
- 145 R Development Core Team. 2010. *R: A language and environment for statistical computing*.
146 R Foundation for Statistical Computing: Vienna, Austria. ISBN 3-900051-07-0, URL
147 <http://www.R-project.org/>.
- 148 Robert R. 1988. Géographie de l'eau à l'île de La Réunion: Essai de distribution régionale de
149 l'alimentation et de l'écoulement. *Annales de Géographie* **539**:112–116.

- Scatena FN. 2004. A survey of methods for setting minimum instream flow standards in the Caribbean Basin. *River Research and Applications* **20**:127–135.
- Smith KL, Flores IC, Pringle CM. 2008. A comparison of current and historical fish assemblages in a Caribbean island estuary: conservation value of historical data. *Aquatic Conservation-Marine and Freshwater Ecosystems* **18**:993–1004.
- Strakosh TR, Neumann RM, Jacobson RA. 2003. Development and assessment of habitat suitability criteria for adult brown trout in southern New England rivers. *Ecology of Freshwater Fish* **12**:265–274.
- Tabouret H, Lord C, Bareille G, Pecheyran C, Monti D, Keith P. 2011. Otolith microchemistry in *Sicydium punctatum*: indices of environmental condition changes after recruitment. *Aquatic Living Resources* **24**:369–378.
- Tew KS, Han CC, Chou WR, Fang LS. 2002. Habitat and fish fauna structure in a subtropical mountain stream in Taiwan before and after a catastrophic typhoon. *Environmental Biology of Fishes* **65**:457–462.
- Tharme RE. 2003. A global perspective on environmental flow assessment: emerging trends in the development and application of environmental flow methodologies for rivers. *River Research and Applications* **19**:397–441.
- Vaudor L, Lamouroux N, Olivier JM. 2011. Comparing distribution models for small samples of overdispersed counts of freshwater fish. *Acta Oecologica-International Journal of Ecology* **37**:170–178.
- Vilizzi L, Copp GH, Roussel JM. 2004. Assessing variation in suitability curves and electivity profiles in temporal studies of fish habitat use. *River Research and Applications* **20**:605–618.
- Wood SN. 2006. *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC: Boca Raton, FL.

176 Table 1: Datasets characteristics

Dataset code	Island	Sampling method	Number of surveys	Number of samples (min-max per station)		Sampling Years	Number of taxa sampled
Caribbean							
Gp	Guadeloupe	Points	32	1455	(10 - 52)	2005, 2008, 2009	23
Gq	Guadeloupe	Quadrats	27	1811	(79 - 99)	2005	22
Mp	Martinique	Points	21	946	(31 - 50)	2008, 2010	21
Indian Ocean							
Rp	Réunion	Points	17	1359	(13 - 85)	1999, 2001	25
Rh	Réunion	Habitat units	196	3284	(3 - 21)	2000-2011	28

177

Table 2: Selected taxa and their main ecological characteristics. Habitat use and feeding groups are summarized from information detailed in Coat *et al.* (2009, 2011), Keith *et al.* (1999), Lim *et al.* (2002) and Monti *et al.* (2010). Abbreviations for feeding guilds are: F for filter feeding, H for Herbivore, D for Detritivore, O for Omnivore. θ (σ_θ) is the dispersion coefficient (and its standard error) fitted for the taxa.

Taxa Code	Taxa	Family	Habitat use	Feeding group	Number of occurrence in sample	Number of individuals	θ	σ_θ	Mean size (mm)
<i>Caribbean</i>									
AIN	<i>Atya innocous</i> (Herbst, 1972)	Atyidae	Rapid	F, D/H	1139	8873	0.22	0.01	47
ASC	<i>Atya scabra</i> (Leach, 1815)	Atyidae	Rapid	F, D/H	391	1556	0.06	0.00	51
ASP	<i>Atya</i> sp. (juvenile)	Atyidae			560	2135	0.09	0.00	
MPO	<i>Micratya poeyi</i> (Guérin-Méneville, 1885)	Atyidae	Vegetation	F, D/H	2407	25759	0.46	0.01	18
XEL	<i>Xiphocaris elongata</i> (Guérin-Méneville, 1855)	Xiphocariidae	Pool, river banks	D/H	956	5513	0.11	0.00	44
MCR	<i>Macrobrachium crenulatum</i> (Holthuis, 1950)	Palaemonidae	Rapid, deep run	O	345	565	0.06	0.00	57
MFA	<i>Macrobrachium faustinum</i> (de Saussure, 1857)	Palaemonidae	Pool, shelter	O	1814	5657	0.34	0.01	42
MHE	<i>Macrobrachium heterochirus</i> (Wiegmann, 1836)	Palaemonidae	Rapid	O	1010	1793	0.14	0.01	48
MSP	<i>Macrobrachium</i> sp. (juvenile)	Palaemonidae			1147	2984	0.17	0.01	
AMO	<i>Agonostomus monticola</i> (Bancroft, 1834)	Mugilidae	Rapid	D/H	307	617	0.06	0.00	124
SIC	<i>Sicydium</i> sp. (Perugia, 1986; Bloch, 1786)	Gobiidae	Rapid	H	2208	11658	0.32	0.01	50
<i>Indian Ocean</i>									
ATY	<i>Atyoida serrata</i> (Bate, 1888)	Atyidae	Rapid, vegetation	F, D/H	532	2974	0.32	0.01	18
MAA	<i>Macrobrachium australe</i> (Guérin-Méneville, 1838)	Palaemonidae	Pool	O	476	1444	0.51	0.02	42
COA	<i>Cotylopus acutipinnis</i> (Guichenot, 1863)	Gobiidae	Rapid	H	1033	2719	0.92	0.03	44
SLA	<i>Sicyopterus lagocephalus</i> (Pallas, 1770)	Gobiidae	Rapid	H	2423	11512	1.10	0.03	60

Table 3: Explained deviance for M1 (% of the initial deviance) and supplementary deviance M_i/M_{i-1} (% of the residual deviance of M_{i-1} explained by M_i). Additional deviance is shown for significant cases only (P-value <0.05).

	Taxon	M1	Hydraulic parameter	M2/M1	M3/M2	M4/M3				
						Altitude	With-drawals	Coast exposure	Basin surface area	years
<i>Caribbean</i>	AIN	52.4	v	2.8	-	-	-	-	-	-
			h	1.2	0.5	0.4	-	-	-	-
			d	0.4	0.6	-	-	-	-	0.4
	AMO	20.3	v	-	-	-	-	-	-	-
			h	4.0	2.2	0.6	-	-	-	-
			d	-	-	-	-	-	-	-
	ASC	30.7	v	18.1	1.5	-	-	0.8	-	-
			h	5.4	0.9	2.2	1.1	2.0	1.2	1.2
			d	3.9	-	-	-	-	-	-
	ASP	20.9	v	1.9	-	-	-	-	0.5	-
			h	2.6	0.9	0.7	1.0	-	0.4	-
			d	-	1.2	-	-	-	0.5	-
	MCR	32.3	v	3.1	-	-	-	0.7	-	-
			h	0.5	-	-	-	-	-	-
			d	-	0.8	-	-	-	-	-
	MFA	30.9	v	1.6	0.3	-	0.6	0.1	0.5	-
			h	0.9	-	0.4	0.2	-	0.4	-
			d	0.5	-	-	-	-	0.2	-
	MHE	24.3	v	7.1	0.7	-	-	-	-	-
			h	1.5	0.8	-	-	0.4	0.6	0.3
			d	1.0	0.4	-	0.2	0.3	-	0.3
	MPO	45.0	v	3.3	0.3	0.2	-	-	0.2	-
			h	2.9	1.1	-	-	-	-	0.2
			d	0.9	0.4	0.6	-	-	-	-
	MSP	28.1	v	1.1	0.9	-	0.5	-	-	-
			h	1.7	0.5	-	0.2	0.3	0.3	0.5
			d	0.5	-	-	-	-	-	0.3
	SIC	33.2	v	3.8	0.5	0.1	-	0.2	0.3	0.1
			h	2.8	0.8	0.2	0.3	-	0.3	-
			d	0.3	-	-	-	-	0.1	-
	XEL	29.7	v	8.1	-	1.0	0.4	-	0.8	-
			h	2.4	0.7	0.4	-	0.4	-	-
			d	-	0.7	-	-	-	-	-
<i>Indian Ocean</i>	ATY	48.7	v	3.0	-	2.4	-	0.5	-	-
			h	5.6	-	0.4	-	-	0.8	0.6
			d	1.6	1.0	0.5	-	-	0.9	-
	COA	56.0	v	9.3	1.5	1.4	-	-	2.1	0.2
			h	5.3	1.5	1.3	-	-	-	-
			d	1.1	-	-	-	0.5	-	0.0
	MAA	44.4	v	5.4	-	-	-	0.3	1.9	2.4
			h	1.4	1.5	-	-	0.4	-	1.7
			d	3.0	0.9	-	-	1.3	-	0.0
	SLA	39.7	v	16.9	0.3	1.3	-	0.3	0.8	-
			h	13.5	0.9	1.6	-	0.5	1.1	-
			d	2.7	-	0.3	-	-	0.6	-

Table 4: Supplementary deviance M2/M1 (% of the residual deviance of M1 explained by M2) for size classes. Additional deviance is shown for significant cases only (P-value <0.05).

Region	Taxon	Size class (mm)		M2/M1		
				v	h	d
<i>Caribbean</i>	AIN	≤ 45		2.7	2.5	-
		> 45		2.4	1.2	-
	AMO	≤ 115		1.8	-	1.1
		> 115		-	7.7	1.3
	ASC	≤ 50		20.9	10.1	3.1
		> 50		16.9	3.2	5.2
	MCR	≤ 55		1.3	2.5	-
		> 55		2.8	1.7	-
	MFA	≤ 40		2.1	0.5	0.5
		> 40		3.0	1.6	0.6
	MHE	≤ 45		7.4	3.3	2.0
		> 45		6.0	1.4	0.9
	MPO	≤ 15		2.1	4.3	0.5
		> 15		3.2	4.5	0.8
	SIC	≤ 45		2.6	5.4	-
		> 45		5.5	2.5	0.5
	XEL	≤ 40		11.0	-	-
		> 40		8.8	2.5	-
<i>Indian Ocean</i>	ATY	≤ 20		3.1	6.0	-
		> 20		3.7	5.2	4.3
	COA	≤ 35		8.2	9.4	0.5
		> 35		8.5	4.1	1.3
	MAA	≤ 40		7.4	2.1	3.6
		> 40		3.8	1.4	1.2
	SLA	≤ 55		11.6	13.6	1.0
		> 55		16.2	9.7	3.7

Table 5: Explained deviance for M1 (% of the initial deviance) and supplementary deviance M_i/M_{i-1} (% of the residual deviance of M_{i-1} explained by M_i). Additional deviance is shown for significant cases only (P-value <0.05).

Region	Taxon	M1	M5/M1	M6/M5
<i>Caribbean</i>	AIN	52.4	3.8	1.4
	AMO	20.3	4.6	2.8
	ASC	30.7	23.7	0.9
	ASP	20.9	4.1	2.8
	MCR	32.3	3.3	1.5
	MFA	30.9	2.8	1.3
	MHE	24.3	8.3	1.0
	MPO	45.0	6.5	1.2
	MSP	28.1	3.3	2.7
	SIC	33.2	6.4	3.7
	XEL	29.7	10.1	5.3
<i>Indian Ocean</i>	ATY	48.7	9.2	1.7
	COA	56.0	11.0	9.4
	MAA	44.4	3.6	2.5
	SLA	39.7	24.4	5.7