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1 Hydraulic preferences of shrimps and fishes in tropical insular rivers

2

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25 ABSTRACT

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

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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

68 preference models represent how the abundance or occurrence of a taxon (e.g. guild of
69 species, species, life stage of a species) varies within the reach as a function of microhabitat
70 parameters (e.g. velocity, depth, substrate). The applicability of habitat models is generally
71 limited by their degree of transferability between rivers (Jowett, 2003; Lamouroux *et al.*,
72 2010; Lancaster and Downes, 2010). Indeed, habitat preferences can vary as a function of a
73 large number of biotic and abiotic factors such as competition, predation, and water chemistry
74 (Jackson *et al.*, 2001). In order to better quantify the generality of hydraulic preference
75 models, it is therefore interesting to study the hydraulic preferences of taxa using data
76 collected from different rivers at different times (seasons, years) (Leftwich *et al.*, 1997;
77 Lamouroux *et al.*, 1999a; Strakosh *et al.*, 2003; Vilizzi *et al.*, 2004; Dolédec *et al.*, 2007;
78 Méricoux *et al.*, 2009). The models developed at several sites have led to contrasting
79 conclusions, but have often highlighted the pertinence of models defined for a number of
80 rivers sharing the same hydromorphological characteristics (Lamouroux *et al.*, 1999b;
81 Lamouroux *et al. in press*).

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

93 In this study, we examine how the density of 15 taxa of the families of Atyidae,
94 Palaemonidae, Xiphocaridae, Gobiidae and Mugilidae vary as a function of the hydraulic
95 parameters of the microhabitat (velocity, depth, substrate). The datasets used come from two
96 regions: the French West Indies (Martinique, Guadeloupe) in the Caribbean and the island of
97 Reunion in the Indian Ocean. These are recent volcanic islands with comparable
98 hydromorphological characteristics (narrow valleys, abrupt reliefs, high waterfalls) (Falkland,
99 1992). Our main objectives were to (1) build hydraulic preference models for different
100 taxonomic groups in each of the two regions (Caribbean, Indian Ocean), (2) estimate the
101 transferability of models among datasets and groups of surveys, and (3) compare hydraulic
102 preferences among the species of the same family.

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METHODS

Reaches and sampling dates

106 We used five datasets (Table 1), three collected from the Caribbean and two from the Indian
107 Ocean (Figure 1). Abundance samples were taken in 121 reaches of 52 rivers during periods
108 of 1 to 12 years. The reaches were distributed over the entire island, in river sections with
109 persistent flows, and were sometimes located upstream or downstream of water intakes. The
110 length of the reaches varied from 0.05 to 2.75 km so that each reach encompassed a variety of
111 morphological units (e.g. riffles, rapids, pools, cascades). The reaches were located at an
112 altitude between 5 and 670 m, at a distance from the sea from 0.1 to 22.8 km and at a distance
113 of 1 to 34.5 km from the source. The surface area of the watersheds upstream of the reach was
114 on average (\pm standard deviation) 15 (\pm 15 km²) in the Caribbean and 70 (\pm 49 km²) in the
115 Indian Ocean. Most of the sampling was performed during the low flow period (when
116 hydraulic selection occurs), i.e. from December to May in the Caribbean (Chaperon *et al.*,
117 1983) and from November to April in the Indian Ocean (Robert, 1988). 20% of the surveys

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

120

121 *Sampling methods*

122 Sampling of fishes and shrimps was done by electrofishing using three methods (Table 1)
123 according to the objectives of previous studies (e.g. analysis of spatial patterns, Monti and
124 Legendre, 2009). The "points" method consisted in collecting 50 samples ($\sim 1 \text{ m}^2$) distributed
125 randomly in the reach by positioning a portable electrode (e.g. DEKA 3000 Lord; DEKA-
126 Gerätebau, Marsberg, Germany) without moving it (Fiévet *et al.*, 1996). The "habitat units"
127 method consisted in fishing about 20 samples from wider surface areas distributed in the
128 available morphological units. The surface area of the samples was 17 m^2 on average (± 8
129 m^2). The "quadrats" method consisted in fishing about 90 contiguous samples (squares of
130 surface area = 4 m^2) in the reaches. These different methods have been used by different
131 teams and were not intercalibrated in our reaches. However, point samples and habitat unit
132 samples have already been combined in habitat modelling. For example, Lamouroux *et al.*
133 (1999b) predicted fish density differences between reaches sampled by points from preference
134 models made in other reaches sampled by habitat units.

135

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

144 area was estimated visually using ordinal classes (Cailleux 1954; Malavoi and Souchon,
145 1989). The central value of the class of substrate was assigned to *d*.

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

153

154 *Taxa selected*

155 Of the 21 to 28 species sampled in each dataset (Table 1) only the taxa with a total abundance
156 > 200 individuals were chosen for the analysis. Therefore, we selected 11 taxa in the
157 Caribbean belonging to three families of shrimp (Atyidae, Xiphocariidae, Palaemonidae) and
158 two families of fish (Mugilidae, Gobiidae), and four taxa in the Indian Ocean belonging to
159 two families of shrimp (Atyidae, Palaemonidae) and one family of fish (Gobiidae) (Table 2).
160 In order to get round the problem of different surface areas of the samples used in the
161 analyses, the abundances of the samples were transformed to densities (\check{D} , number of each for
162 an equivalent surface of 10 m²). Taxa size classes were defined in order to infer the effect of
163 size preferences on hydraulic. The limits of classes were chosen to obtain comparable
164 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 M1: $\log(\check{D}) \sim a_{survey}$ (1)

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

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

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

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

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

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RESULTS

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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.

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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).

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Univariate models M1 – M4 by taxon

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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.

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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*),

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

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

256

257 *Univariate models M1 – M2 by size classes*

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

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

271

272 *Multivariate models M5 – M6*

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

277

278 DISCUSSION

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

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

288

289 Taxa showing the most marked hydraulic preferences are *A. scabra*, *M. heterochirus*, *X.*
290 *elongata*, *Sicydium sp.* in the Caribbean, and *C. acutipinnis* and *S. lagocephalus* in the Indian
291 Ocean. For example, the density of *A. scabra* and *X. elongata* can be multiplied by a factor of
292 ~ 5 for a change of velocity in the order of 0.5 m.s⁻¹.

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

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

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

314 Taxa showing weaker hydraulic preferences are *A. monticola*, *M. faustinum*, *M.*
315 *crenulatum*, *M. australe*, *A. innocous*, *M. poeyi* and the juvenile shrimps of the Caribbean.
316 These results are consistent with those of Monti and Legendre (2009) who reported weak
317 preferences for velocity for *M. faustinum* and *M. poeyi*. Concerning *M. crenulatum*, Monti
318 and Legendre identified strong preferences for low velocities for four sites under strong and
319 weak hydrological disturbance, suggesting that food predominates in influencing habitat
320 selection. Some of these species are also described with preference variables according to
321 diurnal phases (e.g. *A. innocous*) (Keith *et al.*, 1999; Lim *et al.*, 2002; Monti *et al.*, 2010). The
322 weak preferences of the species observed here can also be partly due to variations in fishing
323 efficiency or to our grouping of juveniles of some taxa (*A. scabra* and *A. innocous*; *M.*
324 *crenulatum*, *M. heterochirus* and *M. faustinum*). Regarding fishing efficiency, it is as poor as
325 the species are rare (*M. crenulatum*) and their mobility is high (*A. monticola*) (Fiévet *et al.*,
326 1999; King *et al.*, 2002). It is therefore possible that fishing efficiency explains the absence of
327 preference for velocity that we observed for the mobile *A. monticola*, whereas the taxon is
328 expected to prefer fast and well oxygenated water (Lim *et al.*, 2002). Fishing efficiency can
329 also explain that we observed weak preferences for *A. innocous*, which is an excellent
330 swimmer and very reactive in the presence of predators (Covich *et al.*, 2009; Hein and Crowl,
331 2010) or when disturbed by electrofishing (Fiévet *et al.*, 1999). Regarding the shrimp *M.*
332 *australe*, its weak regional preferences can be explained by its sheltering behaviour during the
333 day and variation due to its morphological plasticity (Zimmermann *et al.*, 2012). The
334 grouping of juveniles of different species of *Macrobrachium* is probably not very appropriate
335 since we observed that the adults of *M. faustinum* and *M. heterochirus* have different
336 preferences (forces and directions) regarding velocity and depth. This is less the case for the
337 juveniles of the family of Atyidae since the adults (*A. scabra*, *A. innocous* and *M. poeyi*) share

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

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

347

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

360

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

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

373

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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
<i>Caribbean</i>							
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
<i>Indian Ocean</i>							
Rp	Réunion	Points	17	1359	(13 - 85)	1999, 2001	25
Rh	Réunion	Habitat units	196	3284	(3 - 21)	2000-2011	28

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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 sp.</i> (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 sp.</i> (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 sp.</i> (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

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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	v	2.8	-	-	-	-	-	-	-
		h	1.2	0.5	0.4	-	-	-	-	-
		d	0.4	0.6	-	-	-	-	-	0.4
	AMO	v	-	-	-	-	-	-	-	-
		h	4.0	2.2	0.6	-	-	-	-	-
		d	-	-	-	-	-	-	-	-
	ASC	v	18.1	1.5	-	-	0.8	-	-	-
		h	5.4	0.9	2.2	1.1	2.0	1.2	1.2	1.2
		d	3.9	-	-	-	-	-	-	-
	ASP	v	1.9	-	-	-	-	-	0.5	-
		h	2.6	0.9	0.7	1.0	-	-	0.4	-
		d	-	1.2	-	-	-	-	0.5	-
	MCR	v	3.1	-	-	-	0.7	-	-	-
		h	0.5	-	-	-	-	-	-	-
		d	-	0.8	-	-	-	-	-	-
	MFA	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	v	7.1	0.7	-	-	-	-	-	-
		h	1.5	0.8	-	-	0.4	0.6	0.3	0.3
		d	1.0	0.4	-	0.2	0.3	-	-	0.3
	MPO	v	3.3	0.3	0.2	-	-	0.2	-	-
		h	2.9	1.1	-	-	-	-	0.2	-
		d	0.9	0.4	0.6	-	-	-	-	-
	MSP	v	1.1	0.9	-	0.5	-	-	-	-
		h	1.7	0.5	-	0.2	0.3	0.3	0.5	0.5
		d	0.5	-	-	-	-	-	-	0.3
SIC	v	3.8	0.5	0.1	-	0.2	0.3	0.1	0.1	
	h	2.8	0.8	0.2	0.3	-	0.3	-	-	
	d	0.3	-	-	-	-	-	0.1	-	
XEL	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	v	3.0	-	2.4	0.5	-	-	-	
		h	5.6	-	0.4	-	0.8	0.6	0.6	
		d	1.6	1.0	0.5	-	0.9	-	-	
	COA	v	9.3	1.5	1.4	-	2.1	0.2	0.2	
		h	5.3	1.5	1.3	-	-	-	-	
		d	1.1	-	-	0.5	-	0.0	0.0	
	MAA	v	5.4	-	-	0.3	1.9	2.4	2.4	
		h	1.4	1.5	-	0.4	-	1.7	1.7	
		d	3.0	0.9	-	1.3	-	0.0	0.0	
	SLA	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	-	-	

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186 Table 4: Supplementary deviance M2/M1 (% of the residual deviance of M1 explained by M2) for size classes.
 187 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

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190 Table 5: Explained deviance for M1 (% of the initial deviance) and supplementary deviance M_i/M_{i-1} (% of the
 191 residual deviance of M_{i-1} explained by M_i). Additional deviance is shown for significant cases only (P-value
 192 <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

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