
Spatio-temporal dynamics of larval fish in a tropical estuarine mangrove: example of the Mahury river estuary (French Guiana)

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Abstract :

The present study focuses on the structure and dynamics of the ichthyoplankton community of the Mahury Estuary (French Guiana) and the factors that influence them. Data were collected on three mangrove sites located in the inner, middle, and outer areas of the estuary. More than 45 000 larvae were collected, representing 31 families and 67 taxa. The community was numerically dominated by few species: Engraulidae was the most abundant family, followed by Gobiidae, Eleotridae, and Sciaenidae. As expected, the most abundant larval taxa were estuarine and mangrove species, with the addition of freshwater species in the inner area of the estuary and taxa with marine affinities in the outer area. The densities of most species were influenced by site more than by season. Temporal variations in the dominant species were influenced largely by their life history strategy, with a majority of the fish species spending their entire life history in mangroves and estuaries.

Résumé

La structure et la dynamique spatio-temporelle de l'ichtyoplancton de l'estuaire du Mahury (Guyane française) ont été étudiées ainsi que les paramètres environnementaux pouvant les influencer. Trois sites constitués de mangroves, répartis d'amont en aval, ont été échantillonnés. Plus de 45 000 larves ont été collectées appartenant à 31 familles et 67 taxa. Le peuplement est dominé en nombre par peu d'espèces : les Engraulidae constituent la famille la plus abondante, suivie par les Gobiidae, Eleotridae et Sciaenidae. Comme pressenti, les taxa les plus abondants sont des espèces estuariennes et vivant dans les mangroves, avec des espèces plutôt associées à des conditions d'eau douce dans la partie supérieure de l'estuaire et des espèces avec une affinité pour les eaux marines dans la partie inférieure. Les densités de la plupart des espèces sont plus influencées par le site que par la saison. Les variations temporelles des espèces dominantes sont en lien avec leur cycle biologique, avec une majorité des espèces de poissons ayant un cycle de vie se déroulant entièrement dans les mangroves et estuaires.

INTRODUCTION

23 Mangroves are known to play an important role in fish nurseries throughout the world (Beck
24 et al. 2001; Dahlgren et al. 2006; Nagelkerken 2009; Sheaves et al. 2013; Abu El-Regal and Ibrahim
25 2014; Lee et al. 2014). In French Guiana, the coast is influenced by the Amazon River, the source of
26 large deposits of nutrients and morphosedimentary dynamics that are unique in the world (Gardel
27 and Gratiot 2005; Proisy et al. 2009; Anthony et al. 2010) and favour the development of mangroves
28 (Artigas et al. 2003; Baltzer et al. 2004; Fromard and Proisy 2010). Mangroves occupy around 80% of
29 the French Guiana coast, covering 700 km². There are two types of mangroves that can be
30 distinguished according to their location; a highly fluctuating seafront mangrove (Walcker et al. 2015)
31 and an estuary mangrove.

32 Although on a worldwide scale mangroves are highly threatened by numerous pressures and
33 are considered endangered by the IUCN (Spalding et al. 2010; Polidoro et al. 2014), the mangroves in
34 French Guiana are relatively well preserved. They are, however, subject to some pressures, mainly in
35 relation to human activity and demographic growth such as urbanisation, hydraulic modifications,
36 agricultural development, pollution and embankment work, although this is still fairly limited. Small-
37 scale fishing activities take place in this ecosystem (Blanchard et al. 2011), and two thirds of the
38 species captured by this type of fishing are estuarine or coastal (Cissé and Blanchard 2010). With the
39 high abundance of food and refuge from predation, mangroves are a suitable habitat for many fish
40 species that spend all or part of their life-cycle there (Nagelkerken 2009; Saint-Paul and Schneider
41 2010; Igulu et al. 2014). The role of estuaries as a nursery habitat for fishes has been well established
42 (Beck et al. 2001; McLusky and Elliott 2004; Dantas et al. 2012; Potter et al. 2015).

43 In estuaries, fish species exhibit a diversity of life history (Elliott et al. 2007; Potter et al.
44 2015): Estuarine dependant species spend their entire life cycle in the ecosystem (e.g. resident
45 species) while others spend only a portion of their life in estuaries or make only brief incursions
46 (anadromous, catadromous, marine migrants, marine stragglers; Able 2005). The percentage of these

47 different categories of estuarine fish varies globally (Whitfield 1999). For example, the estuarine
48 obligate species represent 21% of the total species in South African estuaries (Whitfield 1999) and
49 45% in southern New Jersey, USA (Able 2005). Thus the structure of estuarine larval fish communities
50 also likely mirrors this diversity: Species-specific reproduction occurs inside or outside of the estuary.
51 The connectivity between spawning areas and nurseries fluctuates with species and modes of
52 reproduction. Many species of fish have pelagic eggs and larvae which are carried by tidal currents
53 via passive and/or selective transport to immigrate to and remain in the estuary (Fortier and Leggett
54 1982; Boehlert and Mundy 1988; Sanvicente-Añorve et al. 2011). During the free-living egg and larval
55 stages, environmental conditions within the estuary influence development and survival (Miller and
56 Kendall 2009a). Temperature, photoperiod, tides, latitude, water depth, substrate type, salinity, and
57 exposure are among the most important ecological factors influencing spawning (Miller and Kendall
58 2009a). Temperature, salinity, and food supply are also the most important factors controlling the
59 growth rate of larvae (Miller and Kendall 2009b).

60 Very few studies have been conducted on fish larvae in the mangroves between the Amazon
61 and the Orinoco Delta which are the two largest rivers in South America. Only one study has been
62 carried out in French Guiana (Tito de Morais and Tito de Morais 1994). The geographically closest
63 studies have been undertaken in North Brazil, on the other side of the Amazon and consequently in
64 different environmental conditions (Barletta-Bergan et al. 2002a; b; Bonecker et al. 2007; Sarpedonti
65 et al. 2008; Barletta and Barletta-Bergan 2009; Sarpedonti et al. 2013).

66 Given the limited knowledge of fish larvae in French Guiana and the importance of fishing
67 resources for the growing Guianese population, it is essential to improve our knowledge of the
68 structure and dynamics of larval fish communities in this geographical area. Therefore, the objectives
69 of this study were: (1) to describe the spatio-temporal structure of larval fish communities in an
70 estuarine mangrove over a year, and (2) to identify the environmental factors that are associated
71 with the spatio-temporal dynamics of these communities.

MATERIAL AND METHODS

Study Site

72 The Mahury River Estuary, situated east of Cayenne, was chosen to study the structure of
73 coastal larval fish communities (Figure 1). The banks of this tidal estuary are colonised by a vast area
74 of mangrove essentially constituted of trees of the genus *Rhizophora*. The long prop roots of these
75 trees provide protection for numerous fish species for part or all of their life cycle (e.g., Vance et al.
76 1996; Sheaves and Molony 2000; Lugendo et al. 2007b).

77 Situated between 3 and 5°N latitude, French Guiana benefits from an equatorial climate. The
78 temperature is relatively constant throughout the year (mean ~27°C) and annual rainfall of
79 approximately 3000 l m⁻² per year. Three main seasons are: rainy from January to June, a less rainy
80 (minor rainy) in March-April, and dry from July to December. The mean flows of the Mahury River
81 thus follow this seasonality and range between 10-15 m³s⁻¹ during the low-water period (September
82 to November) and 230-550 m³s⁻¹ during the high-water period (April to June; Lasserre and Collinet
83 2003). The semi-diurnal tide ranges (0.90 - 2.50 m) influence river flow and the sediment re-
84 suspension (Orseau 2016), which fluctuates between 80 and >400 mg l⁻¹ (Froidefond et al. 2002). In
85 addition, the Mahury estuary and the whole coast of French Guiana are influenced by the discharge
86 of the Amazon River during the rainy season via the North Brazil current (Muller-Karger et al. 1988).
87 This current transports low salinity waters that are rich in suspended matter (100-150 Mt) and
88 nutrients to the entire coast of French Guiana (Eisma et al. 1991; Gensac 2012). Thus the entire coast
89 of French Guiana is often considered as an open estuarine system.

Sampling and sample processing

90 Every month for 13 months (Feb 2014-2015) we sampled three sites along the estuary, in an
91 upstream gradient (site A, B and C, respectively; Figure 1). Fish larvae were sampled by adapting a
92 method used by Barletta-Bergan et al. (2002b). A plankton net (500 µm mesh, Ø 0.4 m, 2 m long;
93 with a flowmeter) was deployed and towed horizontally under the surface for 10 min in the daytime

94 during the ebb tide. Each site was sampled in triplicate for 3 consecutive days at the time of the new
95 moon. The choice of the new moon was made following Barletta and Barletta-Bergan (2009) who
96 showed that this period presented the greatest species diversity and the highest densities in a
97 relatively similar, geographically proximate habitat. In total, we collected 117 samples from each site
98 for a total of 351 samples.

99 All samples were fixed in a 4% formalin solution mixed with sea water for 3 days and then
100 preserved in 70% ethanol until they were processed in the laboratory. Identification of specimens to
101 the most precise taxonomic group possible was carried out using determination keys, guides or
102 scientific publications on larvae (Richards 2006; Fahay 2007) or adult fish from the region (Le Bail et
103 al. 1984a; b; Rojas-Beltran 1984; Planquette et al. 1996; Le Bail et al. 2000; Léopold 2004). The
104 number of individuals per taxon was enumerated for each sample and normalised to a fixed volume
105 of filtered water (i.e. 100 m³). Based on the above adult fish literature, we assigned each taxon an
106 ecological guild based upon its preferred habitat (where they spend a majority of their life-cycle):
107 marine, estuarine–marine, estuarine, mangrove, estuarine–freshwater, and freshwater.

108 Concurrent with larval sampling, environmental parameters such as water temperature,
109 conductivity, turbidity, dissolved oxygen, and pH were measured *in situ* using a multiparameter
110 probe before and after each collection. All environmental variables were measured at the surface
111 and near the bottom.

Statistical analyses

112 As the data were rarely normal, only non-parametric tests were used. Comparison between
113 different factors (sites and seasons) was carried out using PERMANOVA (Permutational multivariate
114 analysis of variance) undertaken on similarity matrices of biotic as well as abiotic data. In order to
115 reduce heteroscedasticity data were first log transformed ($\log(X+1)$). Because each variable
116 measured near the bottom was significantly correlated with the surface variable (Pearson
117 correlation; $p < 0.0001$; $r > 0.94$) with the exception of turbidity which was not significant at all of the

118 sites (site A; Pearson correlation; $p>0.05$), analyses only used the surface measurements of the
119 variables, and with addition of bottom turbidity.

120 The analysis of the general structure of the data was carried out using different exploratory
121 analyses such as PCA (Principal Component Analysis) and CCA (Canonical Correspondence Analysis).
122 PCA on the environmental data enables the identification of correlations between variables and site
123 structure; CCA enables two datasets to be simultaneously analysed by combining the concepts of
124 ordination and regression. For CCA, one dataset contained the community descriptions of the larval
125 fish (dependant variables) while the other contained site-specific of environmental factors
126 (independent variables). For these analyses we used similarity matrices either from the Bray-Curtis
127 index to compare quantitative abundance data (Legendre and Legendre 1998), or from the
128 normalised Euclidean distance to examine the environmental data. To improve the clarity of the
129 visual presentation of the data, environmental data of each site were clustered and delimited by a
130 polygon whose vertices stand for the outermost data for each site. Observations were then
131 confirmed using PERMANOVAs.

RESULTS

Larval fish communities

132 Over the 13 months sampling period, a total of 45 148 fish larvae and post-larvae were
133 collected, belonging to 13 orders, 31 families, and 67 taxa (Table 1). Five families were predominant
134 in the community and represented almost 90% of the total abundance (Table 1). The Engraulidae
135 family alone (8 species) represented approximately one third of the community. Gobiidae (6 species)
136 and Eleotridae (4 species) each comprised 20% of the total amount. Sciaenidae (8 species)
137 represented 10% of the total abundance, and Clupeidae (2 species) made up 5%. The remaining 26
138 families represented around 11% of the total catch.

139 The majority of larvae surveyed were estuarine/marine species (29 species), mangrove
140 species (10 species), or marine species (9 species) (Table 1). The remaining species were freshwater
141 species (7), estuarine species (3), estuarine/freshwater species (6), or undetermined (3). More than
142 half of the sampled taxa (36) were present at all three sites (Table 1), most of them estuarine/marine
143 and mangrove species, and only one freshwater taxon. The other taxa tended to be marine species.
144 From downstream to upstream, we observed a variation (Figure 2) in the relative abundance of each
145 ecological guild whose spatial distribution showed that marine (M) and estuarine/marine (EM)
146 species were more abundant in the mouth of estuary (site A) than upstream (sites B and C),
147 representing nearly 50% of the assemblage. Then estuarine species increased from 5% downstream
148 (site A) to 27% upstream (site C). Mangrove species were numerous in the three sites but the
149 maximum relative abundance was found in the middle of the estuary (site B) with 60%.

150 Among all sampled taxa, sixteen represented around 90% of the total abundance (Table 1).
151 The principal taxa encountered were the *Eleotris sp1* amphidromous species, the anchovy
152 *Anchoviella lepidentostole*, the goby *Ctenogobius stigmaticus* and the anchovy *Anchoviella*
153 *guianensis*. These 4 species combined comprised more than 50% of the total catch.

Spatial and temporal variability of communities

154 An average of 14 ± 5 taxa (\pm Standard Deviation) was collected during each sampling effort,
155 but the spatial distribution of these taxa was not uniform. The total number of taxa collected at each
156 site varied from site A with 60 taxa to site B with 48 and C with 46 taxa (Table 1). The average
157 number of taxa varied significantly across sites and season (PERMANOVA, $p < 0.05$; Figure 3 & Table
158 2). The average number of taxa at all sites was significantly lower during the early dry season (12 ± 3)
159 than for the other seasons (> 13), which were not significantly different. The average number of taxa
160 at site A (18 ± 3) was significantly higher than at sites B (13 ± 5) and C (10 ± 5), with the latter two sites
161 not significantly different. Species richness varied across sites (Figure 3), with more distinct and
162 significant fluctuations at sites B and C compared to site A (PERMANOVA; $p < 0.05$). Indeed, the

163 species richness was not influenced by the season at site A contrary to site B where a significant
164 decrease was observed during the early dry season (PERMANOVA; $P<0.05$), and to site C where a
165 diminution was noted between the wet season and the dry season (PERMANOVA; $P<0.05$).

166 The overall average abundance of 129 ± 163 individuals per 100 m^3 was highly variable (Table
167 2), with abundance at site A ($180\pm 169\text{ ind.}100\text{m}^{-3}$) significantly greater than that of site B (102 ± 149
168 $\text{ind.}100\text{m}^{-3}$) and site C ($104\pm 162\text{ ind.}100\text{m}^{-3}$; the latter two not significantly differing from each
169 other). Although there were month to month fluctuations (e.g. January 2015), there was no
170 significant difference in total larval fish abundance among seasons (PERMANOVA; $p>0.05$). However,
171 a few significant interactions “season x site” appeared regarding the site level. For site A, the early
172 dry season induced an increase of the total abundance (PERMANOVA; $p<0.05$), while the trend is
173 opposite for site B and site C (PERMANOVA; $p<0.05$).

Study of environmental conditions

174 PCA of the environmental data from the three sites over the year enabled the analysis of
175 global variations in environmental conditions (Figure 4). The first two axes explain 73% of the data
176 variability. Axis 1 (45%) was strongly negatively related to temperature, conductivity, and dissolved
177 oxygen, all of which increase during the dry season and decrease with the heavy rainfall during the
178 rainy season. The study sites are thus characterised by strong seasonality: data corresponding to the
179 dry season are on the left of the figure and those for the rainy season are on the right. Between the
180 two main seasons, intermediate values correspond to the minor rainy season and the start of the dry
181 season. Axis 2 explains 28% of the variation and follows a turbidity gradient (near the bottom) and,
182 to a lesser extent, conductivity (Figure 4). Along this axis, sites are ordered according to an
183 upstream/downstream gradient with the most downstream site (site A) on the top left of the figure.
184 Across both PCA axes, data from site A are substantially more variable.

185 PERMANOVA tests confirm these observations of significant differences among sites
186 (PERMANOVA; $F=57.0$; $p<0.001$) and seasons (PERMANOVA; $F=120.9$; $p<0.001$), and for the

187 interaction of sites and seasons (PERMANOVA; $F=3.6$; $p<0.001$ – Table 2). The principal variables
 188 responsible for these differences are temperature, conductivity, and turbidity. Correlation tests on
 189 monthly rainfall data (data from Météo-France) and temperature, conductivity, and dissolved oxygen
 190 show high seasonality among these three parameters (Figure 5), with average maximal temperature
 191 ($30.4\pm 0.1^{\circ}\text{C}$), conductivity ($29290\pm 6737 \mu\text{S cm}^{-1}$) and dissolved oxygen values ($93.3\pm 2.9\%$) are
 192 attained in October during the dry season (Figure 5) and minimal values ($25.1\pm 0.1^{\circ}\text{C}$, $106\pm 60 \mu\text{S cm}^{-1}$
 193 and $66.8\pm 1.3\%$) in January-February, during the minor rainy season. Turbidity is influenced more by
 194 upstream – downstream position than by season (Figure 5).

Relationship between environmental factors and community structure

195 The CCA enabled environmental and species data to be combined in a single ordination
 196 (Figure 6). Sites were primarily organised among an upstream/downstream gradient (in accordance
 197 with the preceding PCA). Superimposing the species abundance data enabled the identification of
 198 the species with the most affinity to some environmental conditions and sites. Thus, for this CCA and
 199 despite the low explained data variability of this analysis (23%), species were more closely structured
 200 according to site than according to season (Figure 6-A): species with a greater affinity to highly turbid
 201 conditions (site A) are at the top right and species with a greater affinity for low turbidity conditions
 202 (site C) are at the bottom left. Among the species that were explained by $>50\%$ of environmental
 203 data (7 species, Figure 6-B), *Gobionellus oceanicus*, *Anchoviella lepidentostole*, *Colomesus psittacus*,
 204 and Sciaenidae spp. were abundant at site A, the most downstream site. Conversely, Clupeidae spp.
 205 was characteristic of more upstream sites (sites B and C). *Anchoviella surinamensis* and *Anchoviella*
 206 *guianensis* are intermediate species that were present at all three sites.

DISCUSSION

207 Environmental conditions of the Mahury estuary fluctuated across seasons and sites. Among
 208 the variables measured, temperature, conductivity, dissolved oxygen and, turbidity explained most
 209 of the environmental change, similar to other estuarine systems in the world (Blaber 2000; Bianchi

210 2007; Wolanski and Elliott 2016). The upstream/downstream classification of our sites tracked
211 changes in turbidity and conductivity which was independent of the season. An increasing
212 heterogeneity of data was also noted towards the river mouth, probably due to the marine influence
213 (swell and tide – Day et al. 2012). Otherwise, season (via rainfall) effects on temperature,
214 conductivity, and dissolved oxygen content followed similar patterns to those observed by Barletta et
215 al. (2003; 2005) in North Brazil or in other tropical or subtropical estuaries (Pichler et al. 2015; Blaber
216 and Barletta 2016; Pichler et al. 2017; Possatto et al. 2017).

217 Amongst the world’s mangroves, those of the Indo-Pacific are considered to have the
218 greatest fish diversity with over a hundred taxa (Robertson and Blaber 1992; Thollot 1996; Wei-dong
219 et al. 2003). Although only based on larvae, the 67 taxa that make up our community are a good
220 reflection of diversity encountered in Atlantic mangroves. Moreover, the number of taxa is
221 comparable, if not even slightly higher, to that of similar studies previously carried out in French
222 Guianese mangroves (59; Tito de Morais and Tito de Morais 1994) and in North Brazil (54-63;
223 Barletta-Bergan et al. 2002a; b). Nevertheless, the diversity encountered is well below the 150 fish
224 species surveyed during studies on French Guiana’s adult coastal communities (Puyo 1949; Le Bail et
225 al. 1984a; b; Rojas-Beltran 1984; 1986). In effect, certain species are absent from our samples as
226 their larvae do not have a planktonic phase (e.g., Ariidae which incubate their eggs and young in their
227 mouths until an advanced stage of development; Carpenter 2002).

228 The primary families in the Mahury Estuary (Engraulidae, Gobiidae, Sciaenidae and
229 Eleotridae) are similar to those observed in nearby mangroves but not necessarily in the same order
230 of abundance or in the same proportions. As in numerous other studies (e.g., Tito de Morais and Tito
231 de Morais 1994; Bonecker et al. 2007; Sarpedonti et al. 2008; Bonecker et al. 2009; Costa et al. 2011),
232 Engraulidae dominate our community in contrast to Clupeidae which are minimally represented.
233 With some exceptions, Clupeidae tend to be less abundant at low latitudes (e.g. in Iberian Peninsula:
234 Garrido et al. 2009; Ramos et al. 2017) where they are replaced by Engraulidae (Haedrich 1983; Costa

235 et al. 2011; Sarpedonti et al. 2013). Gobiidae also represent a large part of our larval fish
236 communities like in most tropical estuaries (Costa et al. 2011; Jiang et al. 2016; Mérigot et al. 2017).

237 A small number of species defines the Mahury larval community and fluctuates along the
238 estuary in relation to conductivity (salinity) and turbidity. As observed in other estuaries in the world
239 (Neira et al. 1992; Tzeng and Wang 1992; Pichler et al. 2017; Ramos et al. 2017), an increase in
240 number of species from upstream to downstream is apparent. This pattern, which is also valid for
241 adult fish community (Jaureguizar et al. 2004; Barletta et al. 2005; 2008), showed that the salinity
242 largely influences the fish assemblages and spatial distribution in estuaries. Seasonal fluctuations of
243 key environmental factors, such as salinity (conductivity), temperature and dissolved oxygen, also
244 highly influenced the species richness in our study. Indeed, although the number of species, closer to
245 the river mouth (site A), was quite stable throughout the year despite the greater heterogeneity of
246 habitat conditions, the season had a greater influence upstream. The lower rainfall and flows during
247 the early dry season led to an increase of salinity and therefore the estuary became inappropriate for
248 freshwater estuarine opportunists (Barletta et al. 2003; 2005), explaining the lowest number of
249 species of this season of transition. Salinity plays a major role in the fish species composition, as
250 many studies have also shown in South America estuaries (Barletta et al. 2005; Blaber and Barletta
251 2016; Pichler et al. 2017). The majority of species found in this study were estuarine/marine and
252 mangrove residents which are associated with highly turbid conditions and complete their entire life
253 cycle within this habitat (Cyrus and Blaber 1987a; b; Neira et al. 1992; Mai et al. 2014). Unlike in
254 subtropical estuaries, ichthyofauna that complete their entire life cycle within tropical estuaries
255 constitute most of total assemblages (Blaber 2000), and thus larvae of these species must be more
256 tolerant to seasonal variations in environment. In addition, the high turbid waters closer to the
257 mouth of the river (site A) probably provide protection through reduced visual cues to predators and
258 are attractive for many larvae of resident or transient species which remain there until they reach a
259 size that reduces their susceptibility to predation (Blaber 2000; Pichler et al. 2015).

260 The total abundance of Mahury larval fish communities is amongst the highest found in the
261 literature for the North of South America. In effect, with 129 ind. 100m⁻³, the annual average
262 abundance for all sites is more than 10 times higher than in an estuary of North Brazil (9 ind. 100m⁻³)
263 where the salinity conditions are similar to those of our estuary (Barletta-Bergan et al. 2002b), and
264 comparable to that obtained in less saline water (oligohaline: 132 ind. 100m⁻³; Sarpedonti et al.
265 2013). These differences between studies are likely due to different sampling methods, conditions,
266 productivity, habitats, and years. Similarly to species richness, total abundance followed an
267 upstream/downstream gradient with higher abundances at the river mouth where salinity and
268 turbidity were more important. These high abundances in the lower estuary were due to the
269 presence of several dominant species and by a high number of species. Species are mostly
270 estuarine/marine residents and reproduce in the most saline part of the estuary, similar to findings
271 elsewhere (Cyrus and Blaber 1987c; Tito de Morais and Tito de Morais 1994; Whitfield 1994;
272 Barletta-Bergan et al. 2002b; a). Unlike many studies conducted worldwide on adult or larval fish
273 communities (Barletta et al. 2005; Blaber and Barletta 2016; Pichler et al. 2017), no strong seasonal
274 fluctuations of total larval fish abundance were observed at the Mahury estuary scale. Only few
275 variations appeared at the site level between the early dry season and the other seasons. When
276 rainfall decreased during the early dry season, salinity increased in the three sites, triggering an
277 increase of total abundance close to the river mouth (site A) and a decrease upstream (sites B and C).
278 The result obtained at the river mouth is similar to those of many studies in tropical estuaries
279 (Barletta-Bergan et al. 2002b; a; Lugendo et al. 2007a; Huang et al. 2016). The lowest abundance of
280 larvae during the wet season can be linked to the increase of rainfall and freshwater discharge, which
281 was recognized to increase seaward drift of larvae (Barletta-Bergan et al. 2002b). The fact that there
282 was no significant seasonal variation in total larval fish abundance (although there were month to
283 month fluctuations) could derive from highly abundant species which differed according to site. Two
284 species of Gobiidae, *Ctenogobius stigmaticus* and *Gobionellus oceanicus*, were responsible for this
285 high abundance in January 2015 at site A (downstream), although *Eleotris sp1* and *Anchoviella*

286 *guianensis* were responsible at site C (upstream; Figure 7). Site B, situated between the two sites,
287 presented an intermediate case with the presence of these two species but with less abundance.
288 Consequently there is inter-site variability between species, diversity and abundance. Furthermore,
289 we can notice that the dominant species do not have necessarily a peak of abundance at the same
290 time (Figure 7). Some species seem to reproduce throughout most of the year such as *Anchoviella*
291 *lepidentostole*, which presents a peak of larval abundance at the beginning of the dry season
292 (July/August). Conversely, other species reproduce at more specific time of the year. For example, *C.*
293 *stigmaticus* and *Eleotris sp1* have a short period of reproduction with a maximum abundance of
294 larvae in January/February, while the spawning period of *G. oceanicus* and *A. guianensis* lasted from
295 November to February.

296 The larval fish community of the Mahury estuary was numerically dominated by few species,
297 as typically observed for adult fish communities in other estuaries worldwide (Maes et al. 2005;
298 Elliott et al. 2007; Mériçot et al. 2017). Differences in composition and structure of larval fish among
299 the three sites are mainly related to the presence and abundance of dominant species. In the lower
300 estuary, the community was essentially characterised by the presence and/or abundance of
301 *Gobionellus oceanicus*, *Anchoviella lepidentostole*, *Colomesus psittacus*, and Sciaenidae spp. The
302 species *G. oceanicus* is an amphidromous Goby with adults that are highly abundant in the
303 mangroves and intertidal mudflats of French Guiana (Rojas-Beltran 1986; Le Bail et al. 2012). Farther
304 upstream, *Eleotris sp1* is another highly abundant amphidromous species that belongs to the
305 Eleotridae family. Larvae of amphidromous species comprise a significant portion of the Mahury
306 larval fish community, in greater abundance than observed elsewhere (Tito de Morais and Tito de
307 Morais 1994; Barletta-Bergan et al. 2002a; b; Bonecker et al. 2007; Sarpedonti et al. 2008; Bonecker
308 et al. 2009; Costa et al. 2011). Engraulidae larvae are also highly abundant in estuaries in northern
309 South America (Bonecker et al. 2007; Sarpedonti et al. 2008; Bonecker et al. 2009; Costa et al. 2011).
310 As in previous studies (Tito de Morais and Tito de Morais 1994; Bonecker et al. 2007), *A.*
311 *lepidentostole* is the dominant Engraulidae species in Mahury Estuary. This coastal species is

312 common in tropical estuaries (Froese and Pauly 2016) and migrates within the estuaries to spawn
313 (Cervigón 1985). *C. psittacus* is a euryhaline pufferfish (Tetraodontidae) that is typical of the turbid
314 and brackish coastal and river waters (Cervigón et al. 1993; Léopold 2004). Sciaenidae larvae are
315 often observed in large numbers in the estuaries of northern South America (e.g., Tito de Morais and
316 Tito de Morais 1994; Barletta-Bergan et al. 2002b; Bonecker et al. 2009; Sarpedonti et al. 2013) and
317 other neotropical estuaries (Camargo and Isaac 2005). These species can tolerate large variations in
318 salinity which allow them to live in estuaries that are strongly influenced by freshwater inputs (Saint-
319 Paul and Schneider 2010). These results on the spatial variability in the specific composition of larval
320 fish communities in the Mahury estuary should nevertheless be approached with caution, due to the
321 low explained data variability of the CCA (Figure 6). Indeed, the analysis did not highlight the
322 importance of some species that were less abundant (marines and freshwater species) though
323 characteristic of the opposite sites (site A and site C) where environmental conditions were the most
324 contrasted. The species were separated in the estuary along a gradient linked to environmental
325 conditions (mainly salinity and turbidity gradient) according to their ecological guild. Overall, the
326 larval fish assemblages comprised resident species (estuarine/marine and mangrove species). Other
327 species, probably transient species, complete the composition: marine species associated with high
328 salinity downstream (site A), and more estuarine species and freshwater species correlated with
329 lower salinity of upstream (site C). This spatial distribution and structure of the communities have
330 commonly been observed on estuarine larval and adult fish assemblages worldwide (e.g., Barletta-
331 Bergan et al. 2002b; Blaber and Barletta 2016; Ramos et al. 2017).

332 In summary, the study showed that the larval fish community in the Mahury estuary was
333 structured according to environmental conditions. Salinity and turbidity were the most important
334 variables influencing the larval fish species composition and abundance. Species richness and
335 abundance gradually changed in the Mahury estuary from upstream to downstream with higher
336 values in the lower estuary where the salinity and turbidity were the most important. Seasonal
337 fluctuations in salinity also determined the larval fish assemblages (to a lesser extent) with the

338 smallest number of species during the early dry season and the lowest abundance of larvae during
339 the wet season. According to the fluctuation of these environmental variables, the community
340 structure finally highly followed the abundance variations of dominant species which mainly
341 comprised resident species (estuarine/marine and mangrove species).

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- 601 Wolanski, E., and Elliott, M. 2016. *Estuarine ecohydrology: an introduction (Second Edition)*. Elsevier,
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603 Table 1. Abundance (number of individuals adjusted to a constant volume of 100 m³) of taxa sampled
 604 in three sites of the Mahury mangrove estuary and their relative contributions compared to the total
 605 catch in each site.

Order/Family/Species	Total catch		Percent (>0.1%)			Ecological guild
	Ind.100m ⁻³	%	Site A	Site B	Site C	
Perciformes	51.3					
Eleotridae	<i>Eleotris sp1</i>	7 650.5 16.9	1.7	28.8	31.6	MS
Gobiidae	<i>Ctenogobius stigmaticus</i>	6 711.6 14.9	24.4	10.5	2.7	MS
Sciaenidae	<i>Sciaenidae unid.</i>	3 377.3 7.5	13.0	3.3	2.0	ND
Gobiidae	<i>Gobionellus oceanicus</i>	2 249.6 5.0	8.3	3.6	0.7	MS
Eleotridae	<i>Eleotridae sp2</i>	1 172.6 2.6	0.2	8.2	1.2	MS
Sciaenidae	<i>Micropogonias sp.*</i>	417.9 0.9	1.8	0.2	<0.1	E-M
Sciaenidae	<i>Stellifer rastrifer</i>	375.1 0.8	1.7	<0.1	<0.1	M
Sciaenidae	<i>Cynoscion acoupa*</i>	323.6 0.7	0.8	1.0	0.3	E-M
Carangidae	<i>Oligoplites saliens*</i>	246.3 0.5	0.6	0.7	0.3	M
Eleotridae	Eleotridae sp4	134.7 0.3	-	<0.1	1.1	MS
Gobiidae	<i>Gobiidae unid.</i>	121.3 0.3	0.3	0.4	<0.1	MS
Gobiidae	Gobiidae sp2	63.8 0.1	0.1	0.3	<0.1	MS
Eleotridae	<i>Eleotridae unid.</i>	46.5 0.1	<0.1	0.1	0.2	MS
Sciaenidae	<i>Stellifer microps</i>	41.8 <0.1	<0.1	0.3	<0.1	E-M
Centropomidae	<i>Centropomidae sp1*</i>	38.4 <0.1	0.1	<0.1	<0.1	E-M
Carangidae	<i>Carangidae ind.*</i>	31.3 <0.1	<0.1	0.1	<0.1	ND
Gobiidae	<i>Gobiidae sp3</i>	30.5 <0.1	<0.1	<0.1	<0.1	MS
Centropomidae	<i>Centropomidae sp2*</i>	30.4 <0.1	0.1	<0.1	<0.1	E-M
Gobiidae	<i>Gobiidae sp1</i>	18.1 <0.1	<0.1	<0.1	-	MS
Carangidae	<i>Oligoplites sp.*</i>	17.5 <0.1	<0.1	<0.1	<0.1	M
Lutjanidae	<i>Lutjanus jocu*</i>	12.9 <0.1	<0.1	<0.1	<0.1	M

Carangidae	<i>Oligoplites sp1*</i>	10.2	<0.1	<0.1	<0.1	<0.1	M
Carangidae	<i>Caranx sp.*</i>	8.3	<0.1	<0.1	<0.1	-	M
Haemulidae	<i>Genyatremus luteus*</i>	7.3	<0.1	<0.1	-	-	M
Centropomidae	Centropomidae unid.*	5.3	<0.1	<0.1	<0.1	<0.1	E-M
Gobiidae	<i>Gobioides broussonnetii</i>	5.1	<0.1	<0.1	-	-	MS
Sciaenidae	<i>Cynoscion sp.*</i>	4.5	<0.1	-	<0.1	<0.1	E-M
Eleotridae	<i>Eleotridae sp3</i>	4.5	<0.1	<0.1	<0.1	-	MS
Sciaenidae	<i>Plagioscion squamosissimus*</i>	4.1	<0.1	<0.1	<0.1	-	E-F
Sciaenidae	<i>Cynoscion virescens*</i>	4.1	<0.1	<0.1	-	<0.1	E-M
Sciaenidae	<i>Sciaenidae sp1</i>	2.3	<0.1	<0.1	-	-	ND
Carangidae	<i>Trachinotus cayennensis</i>	1.2	<0.1	<0.1	-	-	E-M
Ephippidae	<i>Chaetodipterus faber</i>	1.0	<0.1	<0.1	-	-	M
Centropomidae	Centropomidae sp3	1.0	<0.1	<0.1	-	-	E-M
Carangidae	<i>Selene vomer</i>	0.9	<0.1	<0.1	-	-	M
Clupeiformes		42.8					
Engraulidae	<i>Anchoviella lepidentostole</i>	6 732.1	14.9	24.8	7.3	5.3	E-M
Engraulidae	<i>Anchoviella guianensis</i>	4 302.9	9.5	3.5	10.9	18.5	E
Unidentified	<i>Clupeiformes unid.</i>	1 508.8	3.3	0.4	2.9	8.9	ND
Engraulidae	<i>Lycengraulis sp.</i>	1 128.7	2.5	3.3	1.8	1.8	ND
Engraulidae	<i>Anchovia surinamensis</i>	981.9	2.2	1.7	3.2	2.0	E-F
Clupeidae	Clupeidae unid.	971.8	2.2	0.4	3.4	4.0	ND
Clupeidae	<i>Harengula sp.</i>	898.6	2.0	0.6	1.7	4.7	E-M
Engraulidae	Engraulidae unid.	747.4	1.7	0.8	1.5	3.3	ND
Engraulidae	<i>Anchoa spinifer</i>	571.6	1.3	2.3	0.2	0.5	E-M
Pristigasteridae	<i>Pellona sp.*</i>	540.0	1.2	0.2	1.1	3.0	E
Clupeidae	<i>Sardinella sp.</i>	442.5	1.0	0.1	1.1	2.3	E-M
Engraulidae	<i>Lycengraulis batesii</i>	400.4	0.9	0.8	0.8	1.1	E-F
Engraulidae	<i>Lycengraulis grossidens</i>	84.0	0.2	0.3	<0.1	0.2	E-M

Engraulidae	<i>Anchovia clupeoides</i>	12.4	<0.1	<0.1	<0.1	<0.1	E
Engraulidae	<i>Pterengraulis atherinoides</i>	7.6	<0.1	<0.1	<0.1	<0.1	E-F
Siluriformes		2.8					
Auchenipteridae	<i>Pseudauchenipterus nodosus</i>	1 085.0	2.4	2.7	2.4	2.0	E-M
Auchenipteridae	<i>Auchenipterus nuchalis</i>	56.4	0.13	<0.1	0.3	0.2	E-M
Aspredinidae	<i>Aspredo aspredo</i>	41.8	<0.1	0.2	<0.1	<0.1	E-M
Unidentified	<i>Siluriformes unid.</i>	39.8	<0.1	<0.1	0.2	0.1	ND
Auchenipteridae	<i>Auchenipteridae unid.</i>	10.1	<0.1	<0.1	<0.1	-	E-M
Ariidae	<i>Sciades herzbergii*</i>	6.1	<0.1	<0.1	-	-	E-M
Aspredinidae	<i>Aspredinichthys tibicen</i>	4.5	<0.1	<0.1	-	-	E-F
Loricariidae	<i>Hypostomus sp.*</i>	3.4	<0.1	<0.1	<0.1	-	E-F
Ariidae	<i>Cathorops spixii</i>	1.1	<0.1	<0.1	-	-	E-M
Loricariidae	<i>Loricariidae unid.*</i>	1.1	<0.1	-	-	<0.1	E-F
Tetraodontiformes		2.2					
Tetraodontidae	<i>Colomesus psittacus</i>	967.0	2.1	2.8	2.1	1.0	E-M
Tetraodontidae	<i>Sphoeroides testudineus</i>	21.5	<0.1	<0.1	<0.1	-	E-M
Pleuronectiformes		0.3					
Achiridae	<i>Achiridae unid.*</i>	118.9	0.3	0.3	0.3	0.2	E-M
Achiridae	<i>Apionichthys dumerili*</i>	15.9	<0.1	<0.1	<0.1	<0.1	E-M
Unidentified	<i>Pleuronectiformes unid.*</i>	5.5	<0.1	<0.1	<0.1	<0.1	ND
Achiridae	<i>Achirus lineatus*</i>	5.2	<0.1	<0.1	<0.1	<0.1	E-M
Paralichthyidae	<i>Citharichthys spilopterus*</i>	3.8	<0.1	<0.1	<0.1	-	E-M
Bothidae	<i>Bothidae*</i>	1.1	<0.1	-	<0.1	-	ND
Paralichthyidae	<i>Syacium gunteri*</i>	1.0	<0.1	<0.1	-	-	E-M
Cynoglossidae	<i>Symphurus plagusia*</i>	0.9	<0.1	<0.1	-	-	M
Achiridae	<i>Trinectes sp.*</i>	0.9	<0.1	<0.1	-	-	ND
Elopiformes		0.3					
Elopidae	<i>Elops saurus</i>	78.8	0.2	0.2	0.3	<0.1	E-M

Megalopidae	<i>Megalops atlanticus*</i>	57.0	0.1	0.1	0.2	<0.1	M
Anguilliformes		<0.1					
Ophichthidae	<i>Myrophis plumbeus</i>	31.7	<0.1	0.1	<0.1	<0.1	E-M
Unidentified individuals		<0.1					
Unidentified	<i>Unidentified individuals</i>	28.4	<0.1	<0.1	<0.1	<0.1	ND
Unidentified	<i>Pseudoleptocephalus unid.</i>	0.9	<0.1	<0.1	-	-	ND
Mugiliformes		<0.1					
Mugilidae	<i>Mugil curema*</i>	18.0	<0.1	<0.1	<0.1	<0.1	E-M
Gymnotiformes		<0.1					
Hypopomidae	Hypopomidae unid.	17.1	<0.1	<0.1	<0.1	<0.1	F
Characiformes		<0.1					
Characidae	<i>Pristella maxillaris</i>	7.1	<0.1	-	<0.1	<0.1	F
Curimatidae	<i>Curimata cyprinoides</i>	2.0	<0.1	<0.1	-	<0.1	F
Lebiasinidae	<i>Nannostomus beckfordi</i>	1.2	<0.1	-	-	<0.1	F
Characidae	<i>Copella carsevennensis</i>	1.0	<0.1	<0.1	-	-	F
Syngnathiformes		<0.1					
Syngnathidae	<i>Syngnathus pelagicus</i>	3.7	<0.1	-	<0.1	<0.1	E-M
Syngnathidae	<i>Syngnathidae sp1</i>	1.2	<0.1	-	-	<0.1	E-M
Cyprinodontiformes		<0.1					
Poeciliidae	<i>Tomeurus gracilis</i>	4.4	<0.1	<0.1	-	<0.1	F
Beloniformes		<0.1					
Belonidae	<i>Pseudotylorus microps</i>	2.4	<0.1	-	-	<0.1	F
	No. of larvae	45 148		17 359	14 299	13 489	
	No. of species	67		60	48	46	

606 **Nota.** Data are based on catches between February 2014 and February 2015. Taxa not caught in a site are
607 indicated by – . For each taxa, the ecological guild according to its preferred adult habitat is indicated: M,
608 marine; E–M, estuarine–marine; E, estuarine; MS, mangroves; E–F, estuarine–freshwater; F, freshwater.
609 Economic species are marked by *.

610 Table 2. Sums of squares, mean squares and significant levels for PERMANOVA tests of the
 611 environmental data, the number of species and the abundance of fish larvae caught in plankton net
 612 in the three study sites between February 2014 and February 2015.

Source of variation	d.f.	Fish data						Environmental data			
		No. of taxa			Total abundance			All environmental data			
		SS	MS	F	SS	MS	F	d.f.	SS	MS	F
Main effect											
Site	2	1.93 x 10 ⁸	9.63 x 10 ⁷	17.64***	3 130.9	1 565.5	12.78***	2	111.69	55.85	56.95***
Season	3	4.30 x 10 ⁷	1.43 x 10 ⁷	2.63*	547.33	182.44	1.49	3	355.66	118.55	120.88***
Two-way interaction											
Site x Season	6	6.63 x 10 ⁷	1.10 x 10 ⁷	2.02*	1 898.1	316.35	2.58*	6	21.00	3.50	3.57***
Residual	105	5.73 x 10 ⁸	5.46 x 10 ⁶		12 862	122.5		96	94.15	0.98	
Pair-wise tests											
Site		<u>A</u> > <u>B & C</u>			<u>A</u> > <u>B & C</u>			<u>A</u> ≠ <u>B</u> ≠ <u>C</u>			
Season		<u>3</u> < <u>1 & 2 & 4</u>						<u>1</u> ≠ <u>2</u> ≠ <u>3</u> ≠ <u>4</u>			

613 **Nota.** *P<0.05; **P<0.01; ***P<0.001

614 Multiple comparisons are shown. A, B and C are used for site A, B and C respectively. Numbers are used for
 615 seasons. 1, rainy season; 2, minor rainy season; 3, early dry season; 4, dry season.

616 Figure 1. Location of study sites (A, B and C) sampled monthly between February 2014 and February
617 2015 in the Mahury estuary. Map source: DEAL French Guiana.

618 Figure 2. Relative abundance (%) of each ecological guild of the larval fish assemblages in the three
619 studied sites which were distributed from downstream (site A) to upstream (site C), considering all
620 species collected. Abbreviations used: M, marine; E–M, estuarine–marine; E, estuarine; MS,
621 mangroves; E–F, estuarine–freshwater; F, freshwater.

622 Figure 3. Average abundance (\pm SD) and number of taxa collected each month on the three study
623 sites during monthly monitoring carried out from February 2014 to February 2015 on the Mahury
624 estuary. Abundance is represented by histogram and the number of taxa by dots linked by a
625 continuous line.

626 Figure 4. Ordination plot resulting from the principal component analysis (PCA) examining the
627 variability of the environmental conditions of the three study sites sampled monthly between
628 February 2014 and February 2015 in the Mahury estuary. To visualise easily the difference between
629 site conditions, enclosing envelopes were drawn with all the transects of each site. Abbreviations
630 used: T°C for temperature; DO for dissolved oxygen.

631 Figure 5. Mean monthly variations (\pm SD) of (a) temperature, (b) conductivity, (c) dissolved oxygen
632 and (d) turbidity related to the monthly variations in precipitation of samples in the Mahury
633 mangrove estuary during the study period. Precipitations values are averages of daily measurements.
634 Precipitation is represented by histogram and measured variables by points. Pearson correlation
635 between the precipitation and each variable is indicated. Solid lines refer to variables measured at
636 the surface and for plot D the dotted line refers to the variable measured at the bottom.
637 Precipitation: Météo France data.

638 Figure 6. Ordination plot resulting from the canonical correspondence analysis (CCA) carried out on
639 the whole data set collected monthly on the three study sites between February 2014 and February

640 2015, examining the relationship between environmental conditions and species abundances in the
641 Mahury estuary. All species are represented on figure A and only species explained more than 50%
642 by the environmental variables (7 species) are shown in figure B. To visualise easily the difference
643 between site conditions, enclosing envelopes were drawn with all the transects of each site.
644 Abbreviations used: T°C for temperature; DO for dissolved oxygen.

645 Figure 7. Average abundance (\pm SD) collected monthly from 5 main species on the 3 study sites from
646 February 2014 to February 2015. The ecological guild of each species according to its preferred adult
647 habitat is indicated in brackets (E–M, estuarine–marine; E, estuarine; MS, mangroves).













