**SPATIO-TEMPORAL DYNAMICS OF LARVAL FISH IN A
TROPICAL ESTUARINE MANGROVE: EXAMPLE OF THE
MAHURY RIVER ESTUARY (FRENCH GUIANA)**

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EXAMPLE OF THE MAHURY RIVER ESTUARY (FRENCH GUIANA)

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ABSTRACT

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

RESUME (French)

11 La structure et la dynamique spatio-temporelle de l'ichtyoplancton de l'estuaire du Mahury (Guyane
12 française) ont été étudiées ainsi que les paramètres environnementaux pouvant les influencer. Trois
13 sites constitués de mangroves, répartis d'amont en aval, ont été échantillonnés. Plus de 45 000 larves
14 ont été collectées appartenant à 31 familles et 67 taxa. Le peuplement est dominé en nombre par
15 peu d'espèces : les Engraulidae constituent la famille la plus abondante, suivie par les Gobiidae,
16 Eleotridae et Sciaenidae. Comme pressenti, les taxa les plus abondants sont des espèces
17 estuariennes et vivant dans les mangroves, avec des espèces plutôt associées à des conditions d'eau
18 douce dans la partie supérieure de l'estuaire et des espèces avec une affinité pour les eaux marines
19 dans la partie inférieure. Les densités de la plupart des espèces sont plus influencées par le site que
20 par la saison. Les variations temporelles des espèces dominantes sont en lien avec leur cycle
21 biologique, avec une majorité des espèces de poissons ayant un cycle de vie se déroulant
22 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

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

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

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

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

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

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

Statistical analyses

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

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

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

RESULTS

Larval fish communities

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

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

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

Spatial and temporal variability of communities

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

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

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

Study of environmental conditions

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

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

interaction of sites and seasons (PERMANOVA; $F=3.6$; $p<0.001$ – Table 2). The principal variables responsible for these differences are temperature, conductivity, and turbidity. Correlation tests on monthly rainfall data (data from Météo-France) and temperature, conductivity, and dissolved oxygen show high seasonality among these three parameters (Figure 5), with average maximal temperature ($30.4\pm0.1^{\circ}\text{C}$), conductivity ($29290\pm6737\ \mu\text{S cm}^{-1}$) and dissolved oxygen values ($93.3\pm2.9\%$) are attained in October during the dry season (Figure 5) and minimal values ($25.1\pm0.1^{\circ}\text{C}$, $106\pm60\ \mu\text{S cm}^{-1}$ and $66.8\pm1.3\%$) in January-February, during the minor rainy season. Turbidity is influenced more by upstream – downstream position than by season (Figure 5).

Relationship between environmental factors and community structure

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

DISCUSSION

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

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

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

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

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

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

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

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

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

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

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

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

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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	<i>Eleotridae sp4</i>	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	<i>Gobiidae sp2</i>	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 clupeioides</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 tibi</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>Pseudotyloturus 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	

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

Table 2. Sums of squares, mean squares and significant levels for PERMANOVA tests of the environmental data, the number of species and the abundance of fish larvae caught in plankton net 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>			

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

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

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

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

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

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

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

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

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

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

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