Spatio-seasonal patterns of demersal fish communities on the French Guiana Coast

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Abstract

Estuarine and coastal areas are often considered as hotspots due to their high diversity and ecological importance. However, communities living on those areas are often submitted to fishery and climate change pressures causing modifications on fish assemblages. French Guiana's coastal shelf is characterised by warm waters with high turbidity and low salinity caused by the large river discharges from the Amazon and nearby estuaries. The high productivity of these areas supports fisheries and aquaculture activities. However, the structure and dynamics of coastal fish populations in French Guiana have seldom been studied. The aim of this study was to understand the effect of environmental conditions, as well as the influence of the coast and nearby estuaries on the spatio-seasonal variability of demersal fish communities living in shallow coastal waters (less than 20m depth). Data were collected from two fishing campaigns using a multi-filament drifting net during the rainy and dry season at 55 sampling stations along the coast. Results showed a high spatial patchiness and no clear seasonal pattern. Higher abundances and diversities were observed near estuaries where both marine and estuarine species were cohabitating. The high number of rare species and the aggregative behaviour recorded in this study suggest that those communities could be particularly affected by climate change, pollution and overfishing. In the light of increasing pressures expected in this area, new regulations and management programs should be developed to ensure food security and biodiversity conservation.

Highlights

- French Guiana coastal waters are primarily influenced by the nearby estuaries
- Demersal fish population is mostly estuarine
- Local estuaries significantly affect diversity and abundance of nearby fish communities
- Aggregation behaviour was recorded during the rainy season near estuaries
- Management programs need to be developed to protect biodiversity

Keywords

French Guiana; Coastal community; Estuary; Diversity; Tropical waters; Fisheries management

1. Introduction

Coastal waters in wet tropical areas are characterised by high precipitation and stable water temperatures that, together with important freshwater runoffs, lead to large nutrient fluxes, high productivity and sediment accumulation (Nittrouer et al., 1995). The high productivity of coastal areas supports a large number of fishing and aquaculture activities (Salas et al., 2007). Despite their important contribution to national economics, the composition of marine communities and their spatial and temporal changes are rarely studied (Barletta et al., 2010; Willems et al., 2015a). In recent years, several marine fisheries activities have shown signs of decline or collapse caused mainly by habitat loss, environmental changes and poor fisheries management (Barletta et al., 2010; Botsford et al., 1997; Hutchings and Reynolds, 2004; Sanz et al., 2017).

The Guianese shelf in northeastern South America is characterised by shallow coastal waters, lower salinities and high turbidity typical of estuarine areas (Blaber, 2002). French Guiana’s littoral is directly influenced by the Amazon, the world’s largest estuarine basin, with a high annual water flow which leads to the input of sediment creating large moving mudflats along the coast. The effects of the Amazon can be seen up to 400 km from the mouth (Froidefond et al., 2004, 2002; Hu et al., 2004). The presence of several estuaries and mangrove areas along the coastline makes these waters partly estuarine as far as their fish communities are concerned (Blaber, 2002; Lowe-McConnell, 1987). The high vegetation density of mangroves contributes to coastal protection against waves and wind as well as erosion (Barbier et al., 2011). Providing raw material and food, they also contribute to the maintenance of local fisheries by playing a crucial role as nurseries for coastal and estuarine species (Blaber, 2000), and by providing ideal feeding grounds for juveniles (Rousseau et al., 2018).

The marine shelf ecosystem of French Guiana is subjected to various pressures (increasing population, fisheries exploitation, climate change, globalisation of trade, oil and gold exploration, terrigenous and continental inputs related to human activities). Climate change and fisheries exploitation are among the most important factors causing alteration of ecosystems dynamics and demersal population assemblages (Bernard, 2006; Lampert, 2013; Poulard and Blanchard, 2005; Rivierre, 2007; Travers et al., 2007). Fisheries activities have been shown to modify the spatial distribution of fish communities, population structure and size structure (Blaber, 2000; Camara et al., 2016; Perry, 2005). Rising sea-surface temperature can lead to a diminution of the net primary production produced by phytoplankton (Behrenfeld et al., 2006) having consequences on fisheries yields and food-web dynamics (Diop et al., 2018c, 2018a, 2018b; Hoegh-Guldberg and Bruno, 2010; Lampert, 2013; Ware, 2005).

Over 3000 tons of fish worth 9 million euros are produced each year in French Guiana, constituting one of the most important economic activities. Of the different fishing activities (coastal artisanal fishery, offshore shrimp trawling and longline fishing), the most important resource (as in tons per year) is the coastal white fish dedicated to the local market and contributing to food security (Cissé et al., 2013; Vendeville and Baudrier, 2006). The small-scale coastal fishery, with landing points spread along the coast, operates up to 16 km offshore at depths of 0-20 m. This multi-species fishery exploits more than 30 coastal species (weak fish, cat fish, shark, grouper). In terms of volume the most important species includes the Acoupa weak fish (*Cynoscion acoupa* (Lacepède, 1801)), the Crucifix sea catfish (*Sciades proops* (Valenciennes, 1840)) and the Green weakfish (*Cynoscion virescens* (Cuvier, 1830)) representing around 75% of the annual catch between 2014 and 2018 (Observateurs du SIH, 2018a, 2018b, 2017, 2016, 2014). French Guiana's fast growing population has nearly doubled in 20 years; the demand for fishery products is therefore predicted to increase in the near future (IEDOM, 2018) hence potentially inducing increased pressure on the coastal fish communities. Unfortunately, only simple economic models based on coastal fishery data are currently available (Cissé et al., 2015, 2014, 2013). Very few studies have focused on the coastal demersal faunal assemblages of French Guiana, and the nearshore waters of the coastal fringe from 0 to 20 m depth, have never been studied before (Artigas et al., 2003). Recent studies have been published on fish larvae in estuaries (Rousseau et al., 2018) but nothing on adults, which are exploited in local coastal fisheries.

Understanding the effect of environmental conditions on seasonal and spatial patterns is the first step for a better understanding of the ecosystem ecology and the development of effective management of the area. Our study provides a first general overview of the effects of environmental variables on coastal demersal fish communities in French Guiana. Our aims were 1) to analyse seasonal and spatial variability of fish assemblages and 2) to identify which abiotic factors were driving these variabilities. We hypothesise that the presence of estuaries could define fish assemblages due to changes in the environmental conditions on those areas.

2. Material and methods

2.1. Study area

French Guiana is situated on the northeastern coast of South America, between the northern limit of Brazil and the southern border of Suriname (Artigas et al., 2003). The French Guianese's maritime space is about 320 km long and, because of the geological characteristics of the continental margins (from 08°33' N to 10°18' N and from 48°47' W to 51°52' W), it extends beyond 200 nautical miles from the baseline (from 04°30' N to 05°48' N and from 51°38' W to 53°56' W). The continental shelf extends out to sea with a slow and regular slope beyond the EEZ (about 126 000 km^2 of EEZ) (Durand, 1959; Gratiot et al., 2005). Heavy and continuous discharge of organic matter from the Amazon River and the major Guianese Rivers (Oiapoque, Approuague and Maroni) explain the moving mudflats found along the benthic coastal zone (0 to 20 m depth) (Anthony et al., 2013, 2010; Froidefond et al., 2004). The input of freshwater from the rivers also results in turbid and brackish coastal waters, a phenomenon emphasised during the rainy season due to the heavy tropical rainfalls increasing the water flow (Froidefond et al., 2002). Coastal habitat in the studied area is homogeneous and characterised by dynamic fluid mud banks moving along the coastline at >1 km per year (Vendeville and Baudrier, 2006). The macrofaunal community is characterised by very low diversity and richness and animals are generally small due to the instability and softness of the substrate (Jourde et al., 2017).

2.2. Sampling sites

Overall 32 stations were selected from the east to the west coast of French Guiana in proximity to the 10 m isobath (Figure 1). The stations were defined using a stratified random sampling procedure (coordinates of each station are available in the annex table A.1.). This method involved the division of the area into various homogeneous groups and randomly sampling a predefined number of stations within each group. Stations extended from as close as 4 m deep to depths of 14 m. Due to time and weather constraints, 26 and 29 stations were sampled during the rainy and dry season (respectively), with 24 common stations between the two seasons.

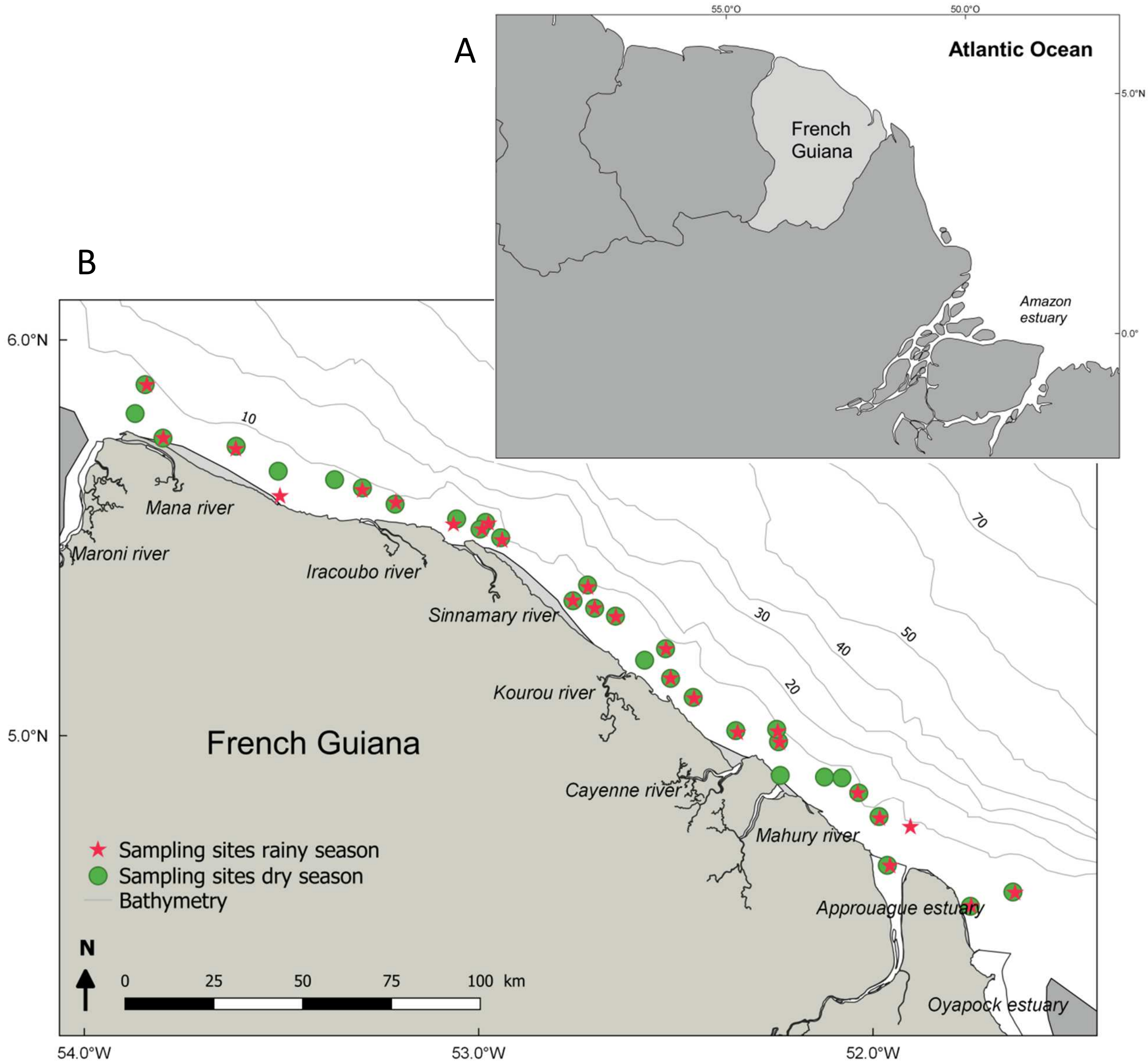

Figure 1. Study area (A) Location of French Guiana (coloured in light grey) in South America compared to the Amazon estuary in Brazil (B) French Guiana coastline from west to east representing the sampling stations for both scientific campaigns, and the major rivers and estuaries.

2.3. Sampling protocol

The survey was carried out twice, during the rainy (10 to 19th June 2015) and dry (3 to 12th November 2015) seasons. A typical Guianese professional coastal fishing vessel operating in French Guiana, BIBINE I (registration number CY 837527), was used for sampling. The vessel, built in 1998, is 11.95 m long and it can stay out at sea for up to 10 days.

At each sampling station, a drifting net (multifilament drifting net, 3 m high, with two equal portions of 60 and 70 mm side mesh size totalling 600m long) was towed for 90 minutes (measured from the moment that the trawl arrives on the bottom to the beginning of the hauling process) close to the seabed. All stations were sampled during daytime. All fish species caught were identified to species level directly onboard. Leopold (2005) was used for species identification as well as expert opinion.

GPS sampling position (latitude X and longitude Y coordinates), date, time and depth were recorded at the beginning and end of towing for each trawl sample (Table A.1). Additional environmental parameters were measured at each station with a multi-parameter probe (YSI EXO2 Sonde) and included profiles of: maximum depth of the seafloor (Zmax, in meters, m), temperature (T in Celsius degrees, °C), turbidity (Turb FNU in Formazine Nephelometric Unit, FNU), salinity and pH (Table A.3.). Environmental measures were taken at the rear end of the boat as turbulence at the front of the boat can disrupt the measurements. The net's height totalled around three meters when placed in the water, therefore mean values of the last three meters of the environmental profiles were calculated to characterise each station. Tidal height (positive for flood and negative for ebb tide) was estimated for each sampling by employing the tidal estimation of the SHOM (Service Hydrographique et Océanographique de la Marine). Distance to the coast (m) and to the estuary (m) was calculated with QGIS (2.18 Las Palmas) using the coastline and the middle of the estuary mouth respectively (Table A.3.).

2.4. Statistical methods and numerical data analysis

To evaluate the effectiveness of sampling and to estimate the validity of using species richness as a proxy for taxonomic diversity, the rarefaction curves (in terms of samples and individuals) were estimated for both seasons (Gotelli and Colwell, 2001). Rarefaction curves were drawn and the asymptote was calculated using the Lomolino model of fitspecaccum using the *vegan* package in R

(Dengler, 2009; Lomolino, 2000). In the Lomolino model the number of species (S) is expressed as in the following equation:

$$S = Asym/(1 + slope^{\log(xmid/area)})$$

with *Asym*: asymptotic maximum number of species; *slope*: maximum slope of increase in richness; *xmid*: area where half of the maximum richness is achieved.

Species occurrence is a percentage representing the number of sites where a species is sampled from the total number of sites. There are 4 frequency classes according to the scale proposed by Charbonnel et al., (1995) in Tessier et al., (2005): permanent species of the habitat (> 75%), frequent species (50-74.9%), scarce species (25-49.9%) and rare species (<25%). Frequency (F) is calculated as:

$$\mathrm{F} = \left(\frac{\mathrm{Pa}}{\mathrm{P}}\right) \times 100$$

with Pa: total number of sites containing the species; P: total number of sites.

To evaluate the spatial and seasonal variability of fish communities, four indices were calculated for each site and season (table 1).

Table 1. Definition and formula of the different diversity indices calculated in this study to characterise species diversity. Abb.: abbreviation. Archimedes' constant Pi ≈ 3.141 592…, Hmax = maximum diversity or $\log_2 S$

Index	**Abb.**	**Definition**	**Formula**	**Reference**
Abundance	A	number of individuals sampled per species in each station		
Species richness	S	number of species sampled per station		
Shannon's diversity	H'	based on species richness, as well as the distribution of individuals within the species	$\mathrm{H}' = -\sum_{\mathrm{i}=1}^{\mathrm{S}} \mathrm{p_i}\,(\log_2 \mathrm{p_i})$	(Jost, 2006; Shannon, 1948)

Pielou	J	Equality of proportional abundances	$J = \frac{H'}{H_{max}}$	(Pielou, 1966)

Seasonal differences of fish diversity (S, A, H and J) across the common stations between the two seasons (24 stations) was statistically tested using paired *t*-tests per permutation (Legendre and Blanchet, 2015).

Spatial and seasonal variability of environmental variables and fish abundances were tested using PERmutational Multivariate ANalysis Of VAriance (PERMANOVA) (Anderson, 2001). The test was run with adonis2 script (vegan package for R) with 9999 permutation and a Bray-Curtis distance. Two fixed factors were tested: season (df.= 1) and site (df.=28). PERMANOVA test was performed on root-squared transformed fish abundances and on the normalised environmental dataset.

An ordination of fish abundances Bray-Curtis matrix was conducted by applying a nonmetric multidimensional scaling (nMDS). The metaMDS function of the vegan package in R was employed with 500 random starts and two dimensions (Oksanen et al., 2010). The potential relationship between sites communities, environmental variables and species presence was fitted by adding these vectors to the ordination using enfit function of the vegan library (9999 permutations). The environmental and species variables with a p-value < 0.05 indicating a significant correlation were added to the nMDS plot.

Since no seasonal differences were detected in fish communities, the entire data set was employed for further analysis. Draftsman plot and Spearman correlation test were performed on the environmental data available (latitude, longitude, sea water temperature, pH, salinity, depth, turbidity, distance from the coast, distance from the closest estuary, tidal height). Longitude was excluded from all analysis due to its significant correlation with latitude, pH and salinity, since the inclusion of highly correlated variables tends to affect variance estimations and hence the significance levels. The strong correlation between latitude and longitude (Spearman correlation coefficient = -1, p<0.001) is probably an artefact of the stratified sampling and the shape of the coast.

A Principal Components Analysis (PCA) was employed to illustrate the main trends in our environmental (sea water temperature, pH, salinity, depth, turbidity, tidal height) and spatial (latitude, distance from the coast, distance from the closest estuary) data sets with PRIMER v.7.0.13 (©PRIMER-e). All variables were normalised by subtracting the mean and dividing by the standard deviation and the matrix samples vs variables was used to create the PCA.

Spatial correlation and the correlation between environmental variables and biological data (fish total abundance and species richness) were performed by employing a Generalised Additive Model (GAM). GAMs are generalisation of generalised linear models with their ability to model non-linearity in the relationship between the response and predictors by using non-parametric smoothers (Maravelias, 2001). Two models were computed, one to test spatial variability (distance from the coast, distance from the closest estuary and latitude) and one for the environmental parameters (temperature, salinity, pH, depth, turbidity, and tide height). A Poisson distribution was chosen since counts are assumed to follow a Poisson distribution (Yemane et al., 2010). The goodness of fit was assessed by examining the diagnostic plots and by adjusting the Akaike Information Criterion (AIC) in a step-by-step procedure. The relative proportion of the deviance explained by each predictor was estimated on the selected models. The two sites with extreme high abundance due to *Lobotes surinamensis* were excluded from the GAM abundance analysis since a preliminary test showed that those two sites could be considered as outliers.

A multivariate distance-based linear regression model (DISTLM, forward selection procedure, selection criteria: R^2) was employed to evaluate the relationship between fish assemblage data and environmental variables. The fish abundance data were firstly root-squared transformed, the resemblance matrix was constructed using a Bray-Curtis dissimilarity, the environmental and spatial variables were normalised and used as predictors. A distance-based redundancy analysis (dbRDA) was then used to visualise the DistLM model in a multi-dimensional space (Legendre and Anderson, 1999).

Map representations were made on QGIS 2.18 Las Palmas (QGIS Development Team, 2018), and all statistical analyses were performed in R v.3.4.0 (R Core Team, 2017) using the packages vegan and PRIMER v.7.0.13 (©PRIMER-e) with the Permanova add-on software (Anderson et al., 2008; Clarke and Gorley, 2015).

3. Results

3.1. Characterisation of the taxonomic diversity along the coast

Throughout both campaigns, 1807 fish were sampled, from 57 different species, for 55 samples (26 during the rainy season and 29 during the dry season). The asymptote of the number of species was not reached with the 55 samples. Ideally more stations should have been sampled. An estimated 35-37 species were not sampled according to the asymptote calculated by the Lomolino model. Fewer species were sampled during the rainy season, with an exaggerated difference in terms of species/individual sampled rather than species/samples sampled (Figure 2).

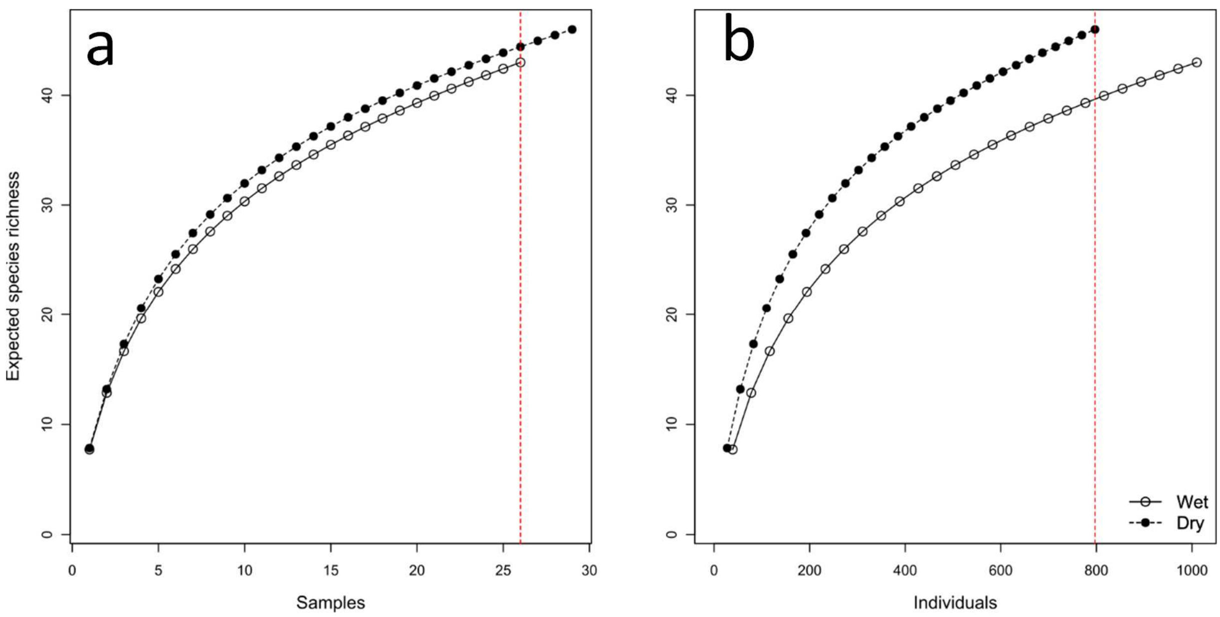

Figure 2. (a) Sample- and (b) individual-based rarefaction curves defining the number of species encountered in a number of samples and individuals. On average (for both seasons) 92.6 species are expected, to reach the asymptote when considering samples (slope 1.94) compared to 94.5 when considering individuals (slope 1.71).

The most abundant species was *Sciades proops* (the crucifix sea catfish) with 83.6% of occurrence in the samples and it can be considered as a permanent species. Only three species were present in more than 50% of the samples: *Sciades proops*, *Cynoscion virescens* (the green weakfish) and *Bagre bagre* (Linnaeus, 1766) (the coco sea catfish). Twenty five species occurred in < 5% of the samples, and 16 species were very rare, occurring each in a single sample. The species list, their occurrence, relative frequency and the total abundance of each species sampled can be found in the appendix (Table A.2.).

Species richness (S) varied between 1 and 19 species per station (Figure 3.A). Species richness is quite even along the coast of French Guiana, with most stations having between 7 and 13 species. Only 3 stations had more than 13 species. In terms of abundances (A), individuals ranged from 1 to 235 per station with a mean of 32.9 ± 41.9 individuals. Some abundance hotspots are visible on the map (Figure 3.B), indicating high variability along the coast. These hotspots were mostly situated at the Oyapock river mouth, around the Salvation Islands and around the islands of Rémire near Cayenne. One species (*Lobotes surinamensis* (Bloch, 1790)) was very abundant at two stations sampled during the rainy season (GY2D33 and GY4D12) with 208 individuals in each station and less than 179 individuals altogether on the rest of the coast (Figure 3.C).

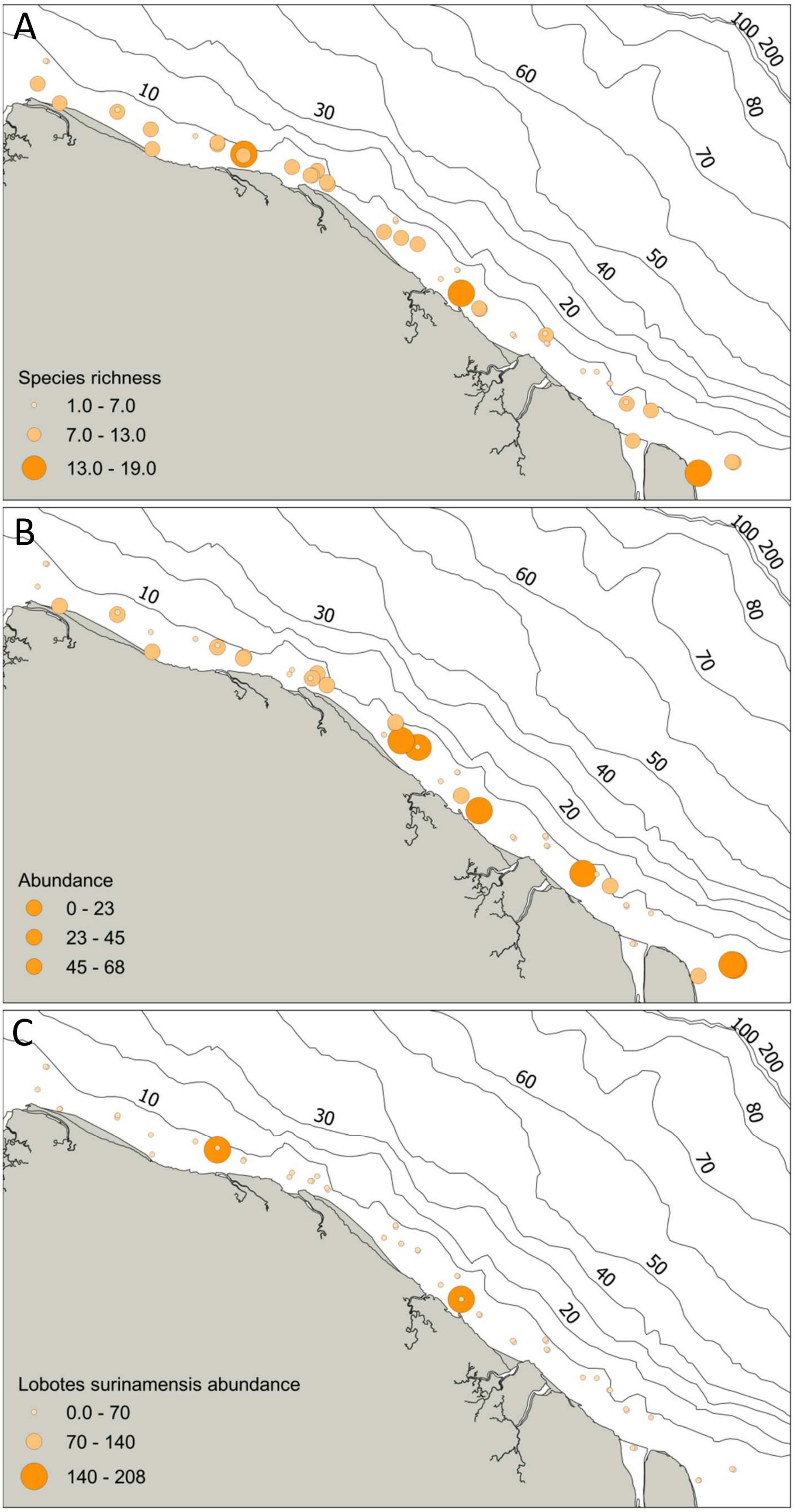
A
B
C
10
20
30
40
50
60
70
80
100
200
Species richness
1.0 - 7.0
7.0 - 13.0
13.0 - 19.0
Abundance
0 - 23
23 - 45
45 - 68
Lobotes surinamensis abundance
0.0 - 70
70 - 140
140 - 208

Figure 3. Map of the distribution of the species richness and abundance along the coastline of French Guiana with the major coastal estuaries. (A) Species richness (B) Abundance of all species except *Lobotes surinamensis* (C) Abundance of *Lobotes surinamensis*.

3.2. Environmental variables

Salinity, temperature and turbidity values were significantly different between the dry and rainy seasons (t-test, $p<0.05$). Salinity was on average higher during the dry season (mean difference -2.335, t = -3.322), while the temperature and the turbidity had higher values during the rainy season (mean diff. 1.7686, t = 5.291 and mean diff. 57.433, t = 2.268 respectively) (Figure 4). The PERMANOVA test showed significant seasonal (F= 8.04, $p<0.001$) and spatial differences (F=122.06, $p<0.001$) on the environmental variables. The mean and standard deviation, minimum and maximum values of temperature, salinity and turbidity for the dry and rainy season are presented in table 2.

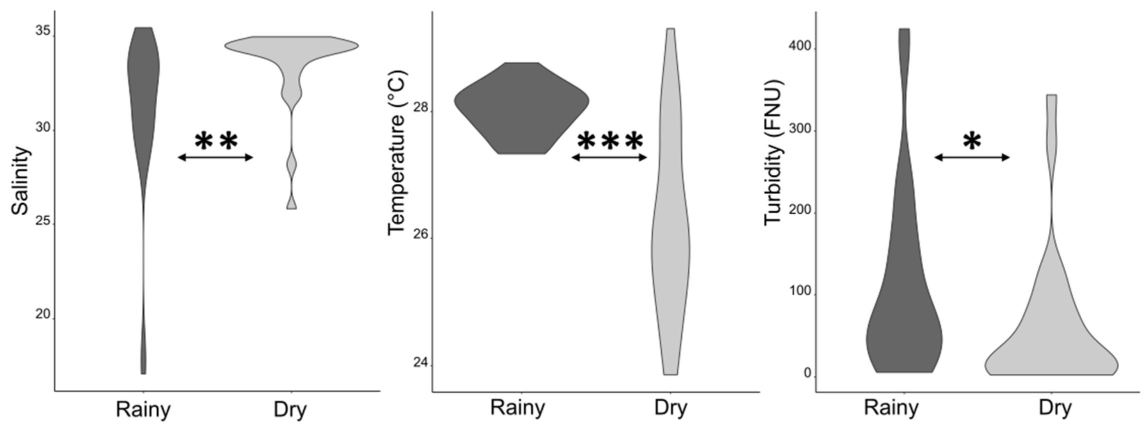

Figure 4. Violin plots representing the variations in salinity, temperature and turbidity between the rainy season and the dry season. Scales and units are different for each parameter (Signif. codes: 0 <***< 0.001 <**< 0.01 <*< 0.05 <.<0.1 < < 1). Degrees of freedom = 21.

Table 2. Mean, standard deviation and range of temperature (°C), salinity and turbidity (FNU).

	Temperature				Salinity				Turbidity			
Season	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Rainy	28.04	0.39	27.34	28.77	31.09	4.41	17.09	35.44	111.08	112.38	5.71	424.62
Dry	26.25	1.46	23.86	29.30	33.50	2.16	25.84	34.96	60.76	86.14	2.44	344.03

The PCA of the normalised environmental conditions shows that stations sampled during the dry season tend to have higher salinities and pH, while rainy season stations have higher temperatures and turbidity (Figure 5). The first two principal components of the normalised environmental dataset explained 52.5% of the total variance.

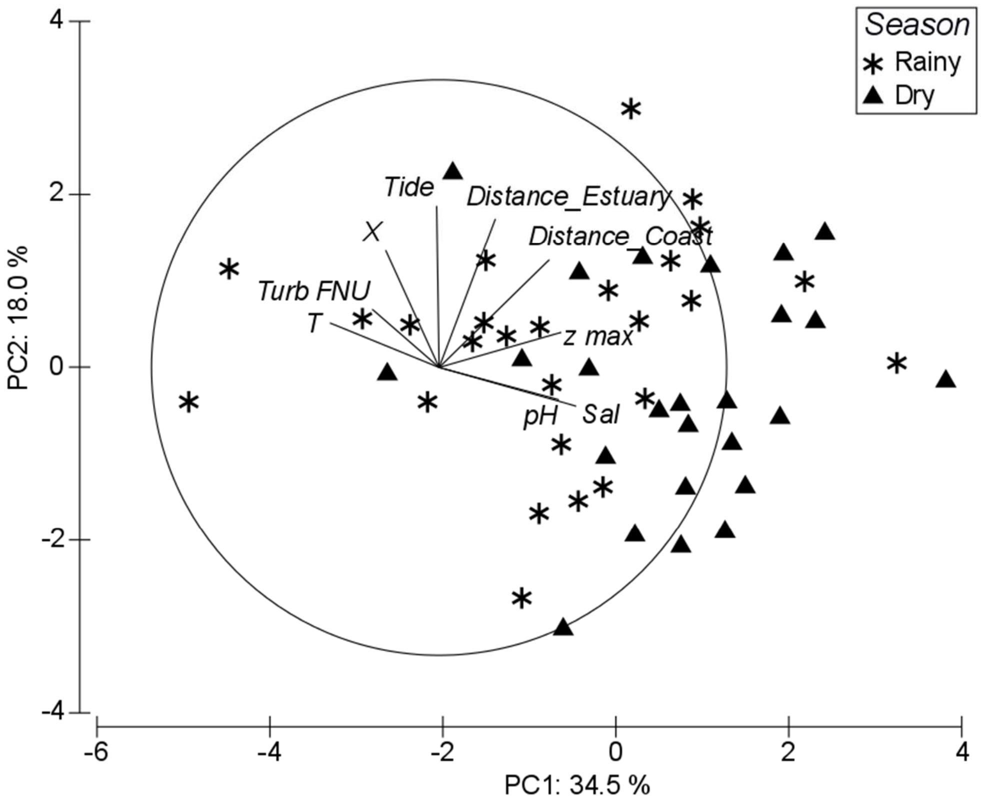

Figure 5. Principal Components Analysis (PCA) of the normalised environmental and spatial variables.

3.3. Seasonal and spatial variations of the taxonomic diversity

No significant differences in terms of species richness, evenness, diversity (Shannon) and abundance between the two seasons were detected for the common stations (T-paired test, 9999 perms) (Table 3). The results on the diversity index were strengthened by the PERMANOVA test showing no significant seasonal effect on species abundance matrix (F=1.57, p>0.05). Therefore, samples from both seasons were pooled together to investigate spatial variability.

Table 3. Paired difference *t*-tests by permutation on the diversity measures comparing the rainy and dry season (9999 permutations). df = degree of freedom, *t* = t-statistics.

	Paired t-tests			
	df	Mean diff.	*t*	*p-value*
Species richness	23	-0.83	-1.07	0.33
Pielou's evenness	21	-0.02	-0.29	0.78
Shannon	23	-0.11	-0.65	0.52
Abundance	23	11.83	0.95	0.41

Community structure differ between sites (PERMANOVA, F =1.50, p<0.001) and the nMDS analysis suggested that the main driving factors were depth and temperature (p<0.05). Nine species were significantly driving the communities' differences between sites (Figure 6). Two sites could be seen as outliers in the MDS, and can be explained by the very low abundance of species collected at these stations.

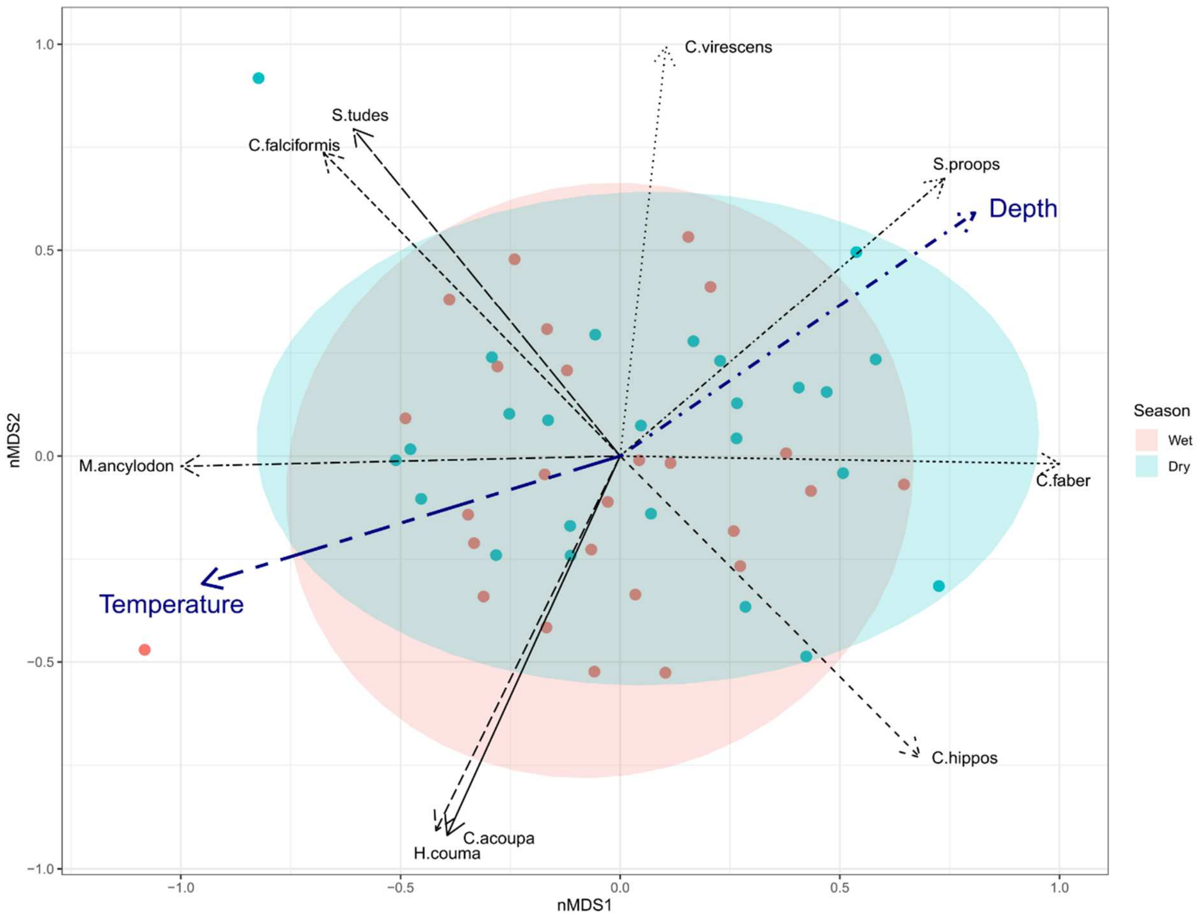

Figure 6. Non-parametric multidimentionam scaling (nMDS) plot for coastal fish assemblages during dry and wet season together.

Two sites were particularly different from the others due to extreme high abundances of *Lobotes surinamensis* (Figure 3.C) and were therefore removed for the following GAM analysis. Results of the GAM analysis on total abundance data showed that all spatial variables explained 48%, and the environmental model explained 66% of the variance (both models significantly explained abundance data; $p<0.0001$). GAM model calculated on species richness and spatial data explained 57% of the variance and the one on environmental data, 47% (both models significantly explained species richness; $p<0.0001$).

Table 4. Results of the GLM analysis of the abundance and species richness. Edf: estimated degrees of freedom.

GAM on abundance data	**edf**	**Ref.df**	**Chi.sq**	**P value**
Spatial				
Latitude	4.9	4.9	89.32	<0.0001
Distance from the coast	6.9	7.0	83.3	<0.0001
Distance from the estuary	4.3	4.7	27.6	<0.0001
Environmental				
Temperature	5.4	5.8	111	<0.0001
Tide height	4.1	4.6	5.4	0.3
Salinity	5	5	29.7	<0.0001
pH	4.7	4.9	27.4	<0.0001
Depth	1	1	1.3	0.3
Turbidity	4.3	4.7	61.3	<0.0001
GAM on species richness	edf	Ref.df	Chi.sq	P value
Spatial				
Latitude	3.4	4.1	11.9	<0.05
Distance from the coast	6.1	6.7	19.6	<0.005
Distance from the estuary	1	1	2.4	0.1
Environmental				
Temperature	2.7	3.4	12.8	<0.01
Tide height	2.8	3.3	4.6	0.3
Salinity	1.5	1.8	3.9	0.1
pH	1.7	2	3.6	0.2
Depth	1	1	2.1	0.1
Turbidity	1.3	1.6	0.2	0.8

To further investigate the relationship between species composition and environmental variables a DistLM model was performed; results were visualised by a dbRDA (Figure 7.a). Three environmental variables, depth (p < 0.001, 8 % variance explained) temperature (p < 0.005, 3.3 % variance explained) and distance to the estuary (*p* < 0.005, 3.2% variance explained), contributed to the highest and significant percent of explained variation in the fish assemblage (Figure 7.b) explaining 14.6% of the variation in community structure. All variables except latitude (X) and Tide have a significant relationship with the species multivariate data cloud when considered alone. The total variation (R^2) explained by all of the variables is 27.32 %. When adding more than three variables (T, depth and distance to estuary) the model is not statistically significant (*p*=0.118).

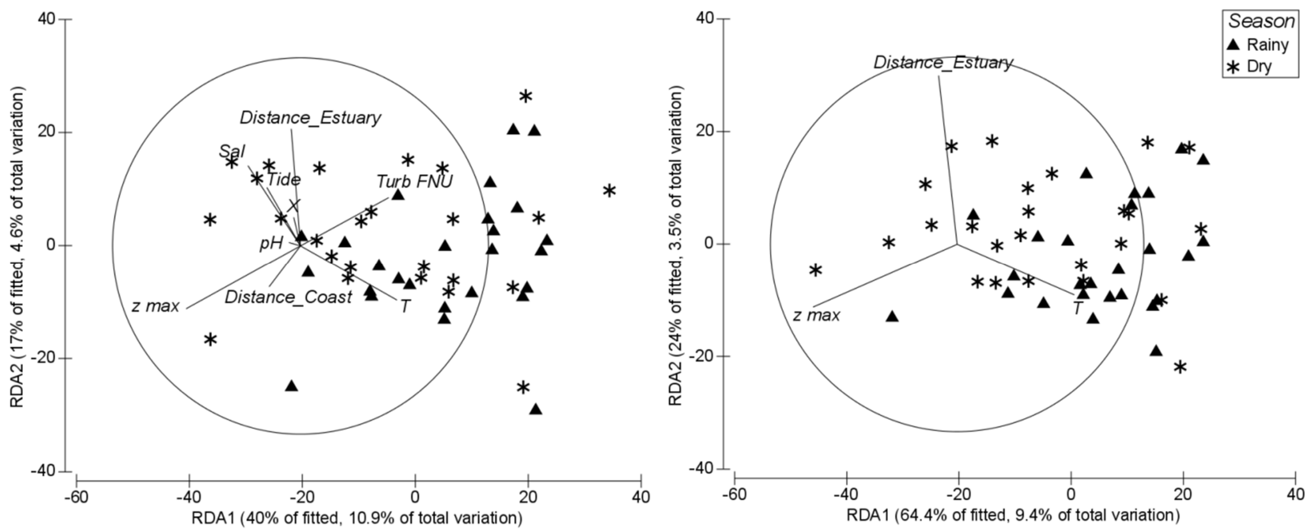

Figure 7. (a) Distance-based redundancy analysis (dbRDA) on the square root transformed species using the Bray-Curtis resemblance distance, with the normalised environmental and spatial variables as predictors. (b) dbRDA of the three significative environmental variables distance to the estuary, temperature and depth.

4. Discussion

This study is one of the first investigating the structure and dynamics of coastal fish populations of the inner shelf of French Guiana exploited by small-scale fisheries. Up to now, little was known about the factors influencing the distribution of demersal fish communities due to the lack of scientific fishing campaigns. Currently, even if bottom trawling remains one of the best ways to get representative samples of the demersal fish communities, trawls are not easy to use in the environmental context of the coastal area of French Guiana where mud banks colonise all the coastal nearshore grounds. Small trawls with small mesh size may be adapted with skates to avoid penetrating too deeply into the mud, but this reduces the probability of catching adult fish. Adapting larger and heavier trawls to mud banks seems less realistic. For these reasons, sampling was performed with drift nets operated as local small-scale coastal fisheries. Our results showed that despite a significant seasonal variability of the environmental parameters, coastal fishery communities in French Guiana are characterised by low seasonal variability and high spatial patchiness. Moreover, the dominant species are mostly estuarine and not strictly marine, suggesting that many native species may be living near to their biological tolerance limit (Kennedy, 1990; Odum, 1970; Roessig et al., 2004). Those communities are therefore particularly vulnerable in the face of environmental and climate changes, even though they tend to tolerate a higher range of variability in environmental conditions than typically freshwater or marine species (Pérez-Ruzafa et al., 2019).

A prerequisite for management and conservation of aquatic biodiversity is to fully understand the local biodiversity and its changes in space and time. No unified method is employed and several indexing, classification, ordination and multivariate techniques are commonly used (Lekve et al., 2005). Species accumulation curves are one of the methods which provide information about the species distribution of the studied community (Colwell and Coddington, 1994). Theoretically, the accumulation curve reaches an asymptote if an adequate number of samples are collected, in practice, the asymptote is often not reached even after a considerable sampling effort (Lekve et al., 2005). In our large-scale study, we did not reach the asymptotic point and estimations suggest that about 60% of the species were sampled. Species number found in our study (57 species for 55 samples) is however corroborated when compared with results from a coastal campaign in nearby Suriname (61 species in 95 trawl samples) (Willems et al., 2015b).

The dissimilarities between the sample-based and the individual-based rarefaction curves indicate an important spatial heterogeneity especially during the rainy season. The sample-based curves generally lie below the individual-based ones because they tend to aggregate individuals that are close either in time or in space (Gotelli and Colwell, 2001). While little seasonal difference was present in the sampling effort, a clear difference between rainy and dry season was evident in terms of individuals. For the same number of individuals sampled we have a difference of 5-10 species, with more species encountered during the dry season. This indicates that the difference is not due to a sampling bias, but rather to a biological meaningful pattern since differences between sample and individual rarefaction curves can be used as a measure of patchiness (Colwell and Coddington, 1994). Our results suggest that a higher patchiness was present during the rainy season probably due to some kind of aggregation behaviour for feeding or reproduction (Domeier and Colin, 1997; Johannes, 1978).

The high spatial patchiness found during our sampling was partly due to the presence of a high number of rare species (nearly 45 % of the species occurred in less than 5% of the samples). Unfortunately, no detailed data on the habitats, currents and food availability are available for the studied area. Moreover, the extensive presence of mangrove nursery areas in proximity to the sampling site can promote the presence of migrating species and increase fish diversity. Several coastal and offshore fish species, including commercial ones, use mangrove and estuaries as a calm and nutritious nursery area for larvae and juveniles (Beck et al., 2001).

However, it should be considered that the presence of rare species and diversity patchiness could also be a consequence of the sampling method and the spatial grain employed. Some species may be able to avoid, or escape from the net and benthic species can accidentally be caught in some shallow areas. The characterisation of rare species as such needs therefore to be confirmed by a multi-gear study to increase the abundance accuracy, species detectability and lower biases (Zhou et al., 2014).

Despite the high spatial variability, little or no seasonal differences were present in the community composition even if environmental conditions were significantly different between the two seasons. The increase in freshwater runoffs from tropical rains causes lower salinities and the leaching of soils and rivers into nearby coastal waters induces a higher turbidity during the rainy season (Artigas et al., 2003). Important seasonal effects on fish assemblage have been shown in tropical estuarine systems, but deeper areas far from the land have a much greater volume of water and are therefore less influenced by seasonal changes (Barletta et al., 2003; Bradley et al., 2017; Passos et al., 2016). Nonetheless, the shelf ecosystem of French Guiana is a quasi-estuarine transitional environment where environmental conditions can vary importantly over time and space (Pérez-Ruzafa et al., 2011). These transitional environments, such as estuaries or lagoons, act as buffer zones between different habitats or migrating routes for fish species (Franco et al., 2006; Pérez-Ruzafa et al., 2011). The presence of several estuarine fish (such as *Sciades proops, Bagre bagre,* or *Cynoscion acoupa*) in our data set confirms the strong influence of freshwater input in the area. Estuarine species are eurytypical given their ability to tolerate large variations of salinity, temperature or turbidity. Salinity and turbidity have been shown to be a structuring factor of estuarine fish assemblages especially for larvae and juveniles (Barletta et al., 2005; Tito De Morais and Tito De Morais, 1994). Fish communities sampled in proximity to the estuaries gave results which were significantly different from the others and the distance from the coastline and estuaries were important factors explaining fish distribution and abundances. This demonstrates that local and regional estuaries have a major influence on the environmental conditions and fish distribution and the abundance of tropical coastal areas.

The most abundant and widely distributed species recorded in this study was the crucifix sea catfish (*Sciades proops*). This coastal species inhabits estuaries and mudflats and is particularly adapted to warm, muddy and brackish waters (Leopold, 2005). A high tolerance to salinity and temperature, a particular reproductive behaviour and the presence of a complex hearing apparatus makes catfish the most successful group of fish from freshwater to the marine environment (Dantas et al., 2010). Their diet composed of mostly shrimps, as well as fish and other invertebrates with moderate influence of the season on the feeding regime, shows that they are an opportunistic species (Ton et al., 2016). The crucifix catfish, as many other catfish species in northeast Brazil, varies in density and biomass in correlation with salinity and dissolved oxygen, depending on the season (Barletta et al., 2010). *S. proops* is one of the most fished species in French Guiana, with 300 tons caught in 2017 (Observateurs du SIH, 2018a).

Together with *S. proops*, two other species showed a large distribution range; the coco sea catfish (*Bagre bagre*) and the green weakfish (*Cynoscion virescens*). Both species are common and abundant species not only in French Guiana waters but also in the Caribbean and Guiana shelf region, and down to the Amazon and northeast region of Brazil. *Bagre bagre* is considered to be anadromous and migrates towards estuaries during reproduction. Despite this species mainly feeds on fish and crustaceans, the feeding strategy is generalist (Pinheiro-Sousa et al., 2016; Tavares and Beneditto, 2017). *Cynoscion virescens* is an important predator living on muddy and sandy bottoms in coastal and estuarine ecosystems (Vergara-Chen et al., 2009). Despite their ecological and economic importance, little is known about their biology and data are often restricted to fishery campaigns (FAO/WECAFC, 2001). Both species are considered as “Least concern” by the IUCN red list, however their stock assessment is not available yet and *Cynoscion virescens* seems to suffer from overfishing pressure in the nearby Suriname (Charlier et al., 2000 in FAO/WECAFC, 2000).

Observation of some particularly interesting behaviour was recorded for the Atlantic tripletail (*Lobotes surinamensis*) that appeared in exceptionally high concentrations during the rainy season in proximity to estuarine outlets. Tripletail is a tropical and subtropical migratory species showing an aggregation behaviour during spring and summer often targeted by anglers in the USA (Franks et al., 2003; Parr, 2011; Strelcheck et al., 2004). This species is highly influenced by seasonality with a clear regime shift, based exclusively on fish during the dry season to a more opportunistic feeding regime (Strelcheck et al., 2004) with a diversification of crabs, shrimps and fish during the rainy season (Ton et al., 2016). It is also known that this species spawns offshore and becomes sexually mature during the rainy season (Franks et al., 2001; Strelcheck et al., 2004; Ton et al., 2016). Our results therefore reflect seasonal aggregation behaviour probably linked to some reproductive and possibly feeding strategies. Unfortunately, no data on the sexual developmental stage are available and further studies are needed to better understand this phenomenon in French Guiana waters.

This study presents original results on the French Guiana coastal communities. However, surveys were carried out only during one dry and one rainy season so that no information on the inter-annual variability is available. It is well known that coastal communities are subject to important inter-annual changes affecting both species diversity and abundance (Selleslagh and Amara, 2008) as well as climate change which can only be studied in the long-term (Harley et al., 2006). A multi-annual study employing a similar protocol is then necessary to evaluate the inter-annual variability, as well as the effects of long-term environmental changes, on the French Guiana coastal fish communities (Magurran et al., 2010).

Conclusions

Tropical coastal ecosystems are facing increasing levels of pressure from a multitude of sources. Unfortunately, very little is still known about fish community compositions and dynamics despite the ecological and economical importance of those assemblages. This study underlined the importance of French Guiana coastal waters for its ability to sustain high fish abundances and diversity. The considerable spatial variability and the presence of several rare species make these communities highly susceptible to environmental changes and human pressure.

To date, no regulations and management programs on fishing zones and capture size have been implemented to regulate coastal fisheries in French Guiana. Despite regular recording of fish landings and some occasional onboard observation of discards (as much as 20% of the catches, pers. obs.), no monitoring programs on by-catch and discards are available. Considering the disproportionate vulnerability and importance of rare species to maintain ecological processes (Mouillot et al., 2013), a precautionary principle needs to be applied for the conservation of the ecosystem (Leitão et al., 2016). Our primary results suggest that coastal areas close to estuaries constitute important hotspots for both diversity and abundance which may host seasonal aggregative behaviour for important commercial species. We suggest that more data (such as sex, age, or other biological parameters) should be collected through monitoring programs and scientific fishing campaigns for a better understanding of French Guiana's species ecology and distribution. The implementation of a seasonal closure of fisheries in these hotspots could potentially help to reduce the pressure on reproductive and vulnerable species. This type of seasonal fishing closure has proven more effective than complete closure in nearby Brazil (De Figueiredo Silva et al., 2012). Those management practices allow for a better control and a good balance between the sustainable use of the resource and the needs of local communities.

In light of the profound impact of climate change on tropical marine ecosystems, there is an urgent need to account for these changes and develop adaptive strategies (Cinner et al., 2018). This is particularly important given the significant demographic growth of French Guiana. Currently, the coastal small-scale fisheries contribute substantially to the local economy, to the primary sector and to food security (Cissé et al., 2015, 2013), hence the importance of a better understanding of fish stocks in French Guiana.

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Appendices

Table A.1. Location (GPS bearings in decimal degree), name and depth (in meters) of the stations sampled during the two coastal campaigns carried out in French Guiana during the rainy and dry season in 2015.

Number	Season	Station	Latitude	Longitude	Depth
1	Rainy	GY1D1	-51.75117	4.56833	3.37
2	Rainy	GY1D2	-51.64000	4.60200	6.38
3	Rainy	GY1D3	-51.95683	4.67017	3.94
4	Rainy	GY1DExtra	-51.90517	4.76850	4.38
5	Rainy	GY2D12	-52.03867	4.85500	7.86
6	Rainy	GY2D13	-51.98300	4.79017	5.84
7	Rainy	GY2D21	-52.34333	5.00800	4.77
8	Rainy	GY2D22	-52.23633	4.98267	7.92
9	Rainy	GY2D23	-52.24150	5.01067	9.06
10	Rainy	GY2D31	-52.45383	5.09417	3.51
11	Rainy	GY2D32	-52.52500	5.21861	6.64
12	Rainy	GY2D33	-52.51333	5.14467	1.90
13	Rainy	GY3D11	-52.65194	5.29972	8.64
14	Rainy	GY3D12	-52.70583	5.32167	4.43
15	Rainy	GY3D13	-52.76083	5.34056	2.57
16	Rainy	GY3D1Extra	-52.72278	5.37472	6.09
17	Rainy	GY3D21	-53.06389	5.53389	2.08
18	Rainy	GY3D22	-52.94056	5.49306	6.22
19	Rainy	GY3D23	-52.97500	5.53639	5.24
20	Rainy	GY3D2Extra	-52.99111	5.52111	3.65
21	Rainy	GY4D11	-53.21000	5.58917	2.84
22	Rainy	GY4D12	-53.29500	5.62056	5.30
23	Rainy	GY4D13	-53.50389	5.60556	1.98
24	Rainy	GY4D21	-53.61583	5.72472	9.75
25	Rainy	GY4D22	-53.79944	5.75222	3.27
26	Rainy	GY4D23	-53.84139	5.88611	13.23
Number	**Season**	**Station**	**Latitude**	**Longitude**	**Depth**
1	Dry	GY1D1	-51,75333	4,56778	4.37
2	Dry	GY1D2	-51,64528	4,60389	5.97
3	Dry	GY1D3	-51,96389	4,67139	4.00
4	Dry	GY2D11	-52,12306	4,89556	NA
5	Dry	GY2D12	-52,03611	4,85528	7.88
6	Dry	GY2D13	-51,98472	4,79472	NA
7	Dry	GY2D1Extra	-52,07889	4,89361	NA
8	Dry	GY2D21	-52,34806	5,01278	4.44
9	Dry	GY2D22	-52,23972	4,98472	6.90

10	Dry	GY2D23	-52,24444	5,01611	4.52
11	Dry	GY2D31	-52,45611	5,09667	4.56
12	Dry	GY2D32	-52,52611	5,21944	8.78
13	Dry	GY2D33	-52,51333	5,14472	2.22
14	Dry	GY2D3Extra	-52,57917	5,19056	6.07
15	Dry	GY3D11	-52,65306	5,30167	7.40
16	Dry	GY3D12	-52,70583	5,32167	5.86
17	Dry	GY3D13	-52,76083	5,34056	2.99
18	Dry	GY3D1Extra	-52,72389	5,38028	7.91
19	Dry	GY3D21	-53,05583	5,54806	0.90
20	Dry	GY3D22	-52,94417	5,49944	5.90
21	Dry	GY3D2Extra	-52,99667	5,52139	4.29
22	Dry	GY4D11	-53,21194	5,58528	NA
23	Dry	GY4D12	-53,29472	5,62639	7.17
24	Dry	GY4D13	-53,50833	5,66861	6.69
25	Dry	GY4D1Extra	-53,36528	5,64722	6.65
26	Dry	GY4D21	-53,61500	5,73167	2.25
27	Dry	GY4D22	-53,80056	5,75222	2.75
28	Dry	GY4D23	-53,84583	5,88722	12.80
29	Dry	GY4D2Extra	-53,87111	5,81417	4.43

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Table A.2. List of species identified from the trawl samples during both sampling campaign. Presence represents the number of stations where the species was encountered. *N* is the number of specimens collected per species. Environment: Marine (M)/Freshwater(F)/Brackish(B), information extracted from FishBase (Froese and Pauly, 2019)

Order	Family	Species	Presence	Relative frequency	*n*	Environment
Carcharhiniformes	Carcharhinidae	*Carcharhinus falciformis*	18	32.7	70	M
		Carcharhinus leucas	1	1.8	1	M/F/B
		Carcharhinus limbatus	4	7.3	5	M/B
		Carcharhinus spp	1	1.8	1	-
	Sphyrnidae	*Sphyrna lewini*	1	1.8	1	M/B
		Sphyrna tudes	8	14.5	16	M
Clupeiformes	Clupeidae	*Harengula jaguana*	4	7.3	6	M/B
		Odontognathus mucronatus	1	1.8	1	M/F/B
		Opisthonema oglinum	1	1.8	1	M
		Pellona flavipinnis	9	16.4	18	F/B
	Engraulidae	*Anchoa spinifer*	8	14.5	9	M/F/B
		Anchovia surinamensis	5	9.1	15	F/B
		Anchoviella cayennensis	3	5.5	5	M/B
		Anchoviella lepidentostole	3	5.5	6	M/F/B
		Lycengraulis grossidens	1	1.8	1	M/F/B
		Lycengraulis spp.	1	1.8	1	-
Myliobatiformes	Gymnuridae	*Gymnura micrura*	2	3.6	3	M/B
	Urotrygonidae	*Urotrygon microphthalmum*	1	1.8	1	M
Perciformes	Carangidae	*Caranx hippos*	5	9.1	6	M/B
		Oligoplites saliens	11	20	18	M/B
		Selene vomer	7	12.7	9	M/B
		Trachinotus cayennensis	2	3.6	2	M/B

	Centropomidae	*Centropomus ensiferus*	2	3.6	2	M/F/B
		Centropomus undecimalis	1	1.8	1	M/F/B
	Ephippidae	*Chaetodipterus faber*	9	16.4	12	M/B
	Haemulidae	*Genyatremus luteus*	15	27.3	29	M/B
	Lobotidae	*Lobotes surinamensis*	22	40	595	M/B
	Mugilidae	*Mugil cephalus*	1	1.8	3	M/F/B
	Sciaenidae	*Cynoscion acoupa*	22	40	37	M/F/B
		Cynoscion jamaicensis	1	1.8	1	M/B
		Cynoscion microlepidotus	2	3.6	5	M/B
		Cynoscion spp.	1	1.8	1	-
		Cynoscion steindachneri	4	7.3	4	M/F/B
		Cynoscion virescens	28	50.9	92	M/B
		Lonchurus lanceolatus	2	3.6	2	M/B
		Macrodon ancylodon	19	34.5	37	M/B
		Micropogonias furnieri	25	45.5	136	M/B
		Nebris microps	2	3.6	2	M/B
		Paralonchurus brasiliensis	1	1.8	1	M/B
		Stellifer rastrifer	2	3.6	55	M/B
	Scombridae	*Scomberomorus brasiliensis*	13	23.6	35	M
		Scomberomorus cavalla	1	1.8	1	M
	Stromateidae	*Peprilus paru*	3	5.5	4	M/B
Pleuronectiformes	Achiridae	*Achirus achirus*	7	12.7	13	M/F/B
Rajiformes	Dasyatidae	*Hypanus guttatus*	11	20	14	M
	Myliobatidae	*Rhinoptera bonasus*	11	20	18	M/B
Siluriformes	Ariidae	*Amphiarius phrygiatus*	1	1.8	1	M/B
		Amphiarius rugispinis	3	5.5	10	M/B
		Aspistor quadriscutis	19	34.5	34	M/F/B
		Bagre bagre	28	50.9	65	M/B
		Notarius grandicassis	3	5.5	4	M/B
		Sciades couma	15	27.3	35	F/B

		Sciades passany	1	1.8	2	M/B
		Sciades proops	46	83.6	331	M/F/B
	Aspredinidae	*Aspredo aspredo*	2	3.6	3	F/B
	Auchenipteridae	*Pseudauchenipterus nodosus*	7	12.7	24	F/B
Torpediniformes	Narcinidae	*Narcine brasiliensis*	2	3.6	2	M
Total					1807	

Table A.3. Mean, standard deviation (SD), minimum and maximum of the environmental parameters used in this study.

	Dry				Rainy			
	Mean	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Temperature	26.246	1.457	23.859	29.304	28.040	0.388	27.336	28.766
Salinity	33.504	2.162	25.843	34.962	31.094	4.413	17.088	35.442
pH	7.898	0.105	7.670	8.040	7.603	0.352	6.797	7.987
Zmax	5.508	2.525	0.893	12.802	5.417	2.754	1.898	13.225
Turbidity	60.765	86.143	2.442	344.033	111.077	112.376	5.709	424.622
Tide	-0.094	2.329	-3.270	2.990	-0.002	2.258	-3.420	3.210
Distance_Coast	8129.863	3365.352	1925.319	15902.594	7596.915	3633.979	1952.615	16386.580
Distance_Estuary	14751.630	6611.978	1442.477	27278.890	14687.760	6597.301	1636.987	26665.250