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Spatial and temporal structure of fish assemblages in an "inverse estuary", the Sine Saloum system (Senegal)

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Abstract

As a consequence of the Sahelian drought, the Sine Saloum, a large estuarine system located in Senegal (West Africa), has become an "inverse estuary" since the late sixties, i.e. salinity increases upstream and reaches 100 in some places. To study the fish assemblages of such a modified system, a survey was conducted in 1992, collecting fish every two months with a purse seine at eight sites spread over the three main branches of the estuary. A total of 73 species belonging to 35 families were identified. Eight species comprised 97% of the total numbers of fish. The predominant species was a small clupeid, *Sardinella maderensis*, representing more than half of the total biomass and nearly 70% of the total number of fish. The spatio-temporal structure of the fish assemblages was studied using the STATIS-CoA method, which combines the multitable approach with the correspondence analysis method. Whatever the season, a strong spatial organization of fish assemblages was observed, mainly related to depth and salinity. Three types of assemblages were identified. In shallow water areas, fish assemblages were dominated by Mugilidae, Gerreidae and Cichlidae and were stable with time. In open water areas, large fluctuations in the species composition were observed, due to the occasional presence of large schools of pelagic species: in the southern area, where salinity and water transparency were the lowest, the main species were *Ilisha africana*, *Brachydeuterus auritus* and *Chloroscombrus chrysurus*, associated with a few Sciaenidae and Tetraodontidae, while the poorest areas were characterized by only two dominant species, *S. maderensis* and *Scomberomorus tritor*.

Keywords: inverse estuary; high salinity; fish assemblages; spatio-temporal pattern; multivariate analysis; West Africa

1. Introduction

Tropical lagoons and estuaries are the subject of an increasing scientific interest because of the expansion of human activities in these areas and the awareness of their economic and ecological importance. Estuarine fish assemblages have been studied since the late seventies (Warburton, 1978; Yanez-Arancibia et al., 1985; Winemiller and Leslie, 1992; Whitfield et al., 1994; Blaber, 2000). They are characterized by a high diversity including species of both marine and freshwater origin, with migrant or sedentary behaviour, inhabiting estuaries as larvae, juveniles or adults. Estuaries are widely recognized as nurseries for young fishes, offering food and shelter for larval and juvenile stages (Blaber and Blaber, 1980; Yanez-Arancibia et al., 1993; Whitfield, 1999). As estuaries are at the interface between marine and freshwater systems, the spatial organization of their fish assemblages presents complex patterns (Blaber et al., 1989). Many authors have also shown that they exhibit strong short and long-term variability, due to environmental fluctuations (Day and Yanez-Arancibia, 1985; Day et al., 1989; Kupschus and Tremain, 2001). Both spatial and temporal studies of fish assemblages are therefore needed to understand fully the functioning

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of those systems (Robertson and Duke, 1990; Tzeng and Wang, 1992; Laroche et al., 1997; Blanc et al., 2001).

In West Africa, several studies on estuarine and lagoon fish assemblages have been undertaken during the last two decades (Albaret and Diouf, 1994; Albaret, 1999). These studies are mainly concerned with environments receiving freshwater input, such as the Ebrié lagoon in Ivory Coast (Albaret and Ecoutin, 1989; Albaret, 1994), the Fatala River estuary in Guinea (Baran and Poizat, 1994; Baran, 1995) and the Rio Grande de Buba in Bissau Guinea (Kromer, pers. comm.). Some northern West African coastal environments, however, receive little or no freshwater input, except local rainfall, and, under the intense evaporation regime of the area, have become highly saline or even hyperhaline. Some studies on fish assemblages of these environments have been published: Banc d'Arguin in Mauritania (Sevrin-Reyssac and Richer de Forges, 1985), Casamance River (Albaret, 1987) and Sine Saloum Delta (Diouf, 1996) both in Senegal. The present study is a contribution to a better knowledge of the organization and dynamics of fish assemblages in high-salinity environments and particularly in inverse estuaries (Pritchard, 1967). It deals with the Sine Saloum Delta, a large estuarine system situated south of Dakar (Senegal), which became permanently inverted in the late sixties due to the increasing lack of rain in the Sahelian area (Barusseau et al., 1985; Pagès and Citeau, 1990). In the upper part of the estuary, high salinities (>60) are observed all year long, and reach more than 130 at the end of the dry season. This is the hyperhaline area according to the estuarine waters classification by Por (1972). As a consequence of the very high salinity, species richness, diversity and abundance are drastically limited in such an extreme environment. Furthermore, fish assemblages of the hyperhaline area were shown to be stable in space and with time by Diouf (1996).

The results presented in this paper concern the intermediate and lower parts of the Sine Saloum estuary. From an environmental point of view, this wide area is mainly under oceanic influence, with salinity varying between seawater and around 60, according to the season and the distance from the mouth. This corresponds to the metahaline zone first proposed by Hedgpeth (1951), which is known to be suitable for a high species richness and abundance (Hedgpeth, 1967; Hodgkin and Kendrix, 1984). The aim of the present study is to describe the spatio-temporal organization of the fish assemblages observed in this part of the Sine Saloum Delta. First, general information about the fish assemblages is given in terms of species richness, fish numbers and biomass. Second, the spatial structure of fish distribution and its seasonal variations are determined.

2. Materials and methods

2.1. Study area

The Sine Saloum Delta is located 100 km south of Dakar, between 13°55′ and 14°10′ North and 16°03′ and 16°50′ West. The system comprises three main branches: from north to south, the Saloum, the Diomboss and the Bandiala (Fig. 1). In the study area, the Saloum and the Diomboss are wide and deep, while the Bandiala is narrower and shallower. The south-western area of the Sine Saloum system is characterized by a dense network of small seawater creeks locally named "bolongs" and are covered with tall mangrove, mainly *Rhizophora* and *Avicennia*, which becomes shorter in the central zone. The mangrove thins in the northern area and totally disappears in the upstream Saloum.

In the Sine Saloum region, the climate is characterized by an extended dry season, cool from November to March, and warm from April to June, and by a short wet and warm season from July to October. Since the 1920s, the annual rainfall has been decreasing in this region, first slowly until 1961, and then more drastically in recent decades (Pagès and Citeau, 1990). The combined effects of reduced freshwater inputs, intense evaporation and a low gradient in the lower estuary, have resulted in a high overall salinity and an inversion of the salinity gradient. Thus, in the Saloum, and to a lesser extent in the Diomboss, salinity increases upstream whatever the season. In the Bandiala, salinity decreases during and just after the rainy season due to local freshwater inputs. A detailed description of environmental conditions in the Sine Saloum system can be found in Diouf (1996).

2.2. Sampling methods

Based on abiotic and biotic environmental criteria (physico-chemistry, sediment, plankton and use of remote sensing), eight ecological zones were defined in the Sine Saloum Delta by Diouf (1996): three in the Bandiala, one in the Diomboss and four in the Saloum. Except for the most upstream zone of the Saloum, corresponding to the hyperhaline area, which was not included in this study, one or two sampling sites were chosen per zone, resulting in a total of eight sites: three were located in the Bandiala (sites B1–B3), one in the Diomboss (site D1) and four in the Saloum (sites S1–S4). They were visited every two months in 1992: in February (dry and cool season), April (beginning of the dry and warm season), June (end of the dry and warm season), August (wet and warm season), October (end of the wet season) and December (beginning of the dry season). Each site was sampled twice for a given date: one haul in the mid-channel, and the other one close to the bank. To identify the position of the haul, an

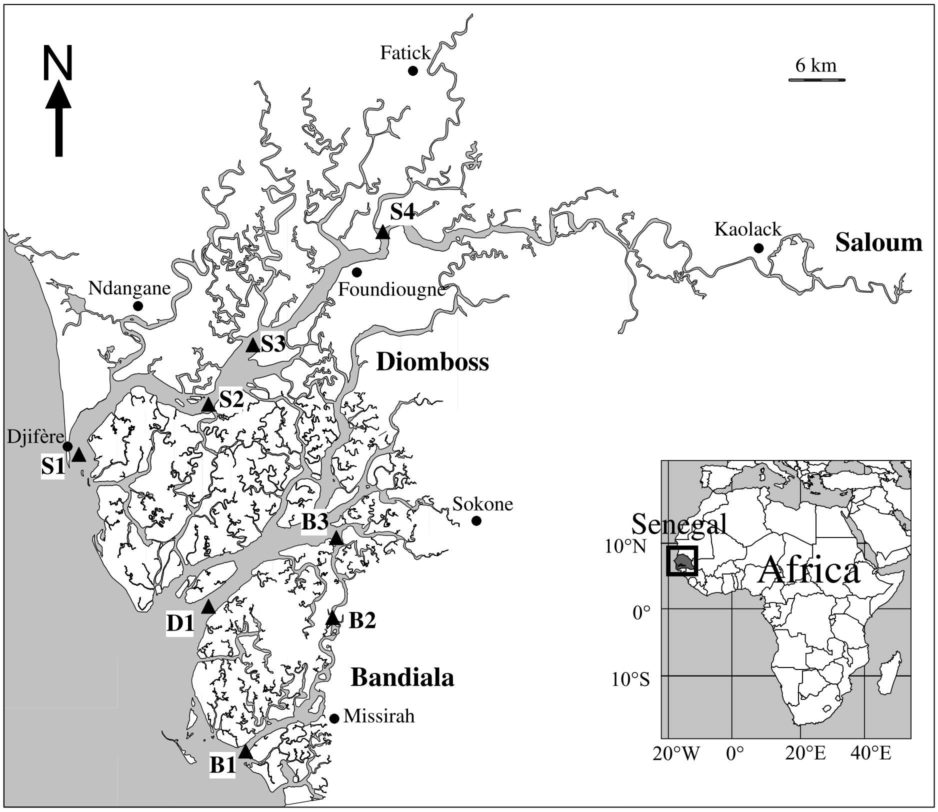

Fig. 1. Map of the Sine Saloum estuary and location of sampling sites.

additional character was added at the end of the site code: "c" for mid-channel samples and "b" for those close to the bank. As a result, the study provided 96 samples (6 dates × 8 sites × 2 hauls). Fish were collected using a purse seine 250 m long, 20 m height and 14 mm mesh size. Fishing efficiency was improved by adding additional weights to the lead line (500 g m^{-2}). The falling speed was thus increased, consequently reducing the risk of avoidance by fish, and adhesion to the bottom was improved, so that fish could not escape while the seine was hauled. All sampling was done by the same experienced fishing team. Thanks to these precautions, sampling was quite exhaustive and reproducible. Fish were identified to species level, counted and weighed by species to the nearest gram. The depth was measured at each seine haul and other environmental variables at each site: water transparency, salinity, temperature, dissolved oxygen and chlorophyll content. Except for depth and transparency, all variables were measured at the surface and bottom. Depth (m) was measured with a depth-meter, water transparency (m) with a Secchi disk, salinity with an optical refractometer, temperature (°C) with a thermometer, dissolved oxygen (percentage of saturation) with a YSI hand-held field instrument and total chlorophyll content (μg l^{-1}) with a fluorimeter. A qualitative description of the state of the mangrove was recorded once for each site.

2.3. Data analysis

As a preliminary analysis of the fish assemblages, species richness, total number of fish and biomass were examined. A natural logarithm transformation was used to normalize the distributions and stabilize the variances for fish numbers and biomass (Sokal and Rohlf, 1995). Three-way ANOVAs were processed to test differences between branches (Saloum/Diomboss/Bandiala), positions (bank/channel) and sampling dates, taking into account the second- and third-order interactions. When an ANOVA showed a significant difference on main effects, a Tukey's studentized range test (HSD) was performed to determine which means were significantly different at the 0.05 level of probability.

Then, the composition of the assemblages was discussed using the species classification proposed by Albaret (1999), which defines eight bio-ecological categories ordered on two gradients from a central point, the strictly estuarine species (Es). The gradient of marine affinity comprises four categories: the estuarine species from marine origin (Em), the marine–estuarine species (ME), the marine species accessory in estuaries (Ma) and the marine species occasional in estuaries (Mo). The gradient of freshwater affinity comprises the estuarine species from freshwater origin (Ec), the freshwater species with estuarine affinities (Ce), and the freshwater species, occasional in estuaries (Co). Four of these categories (Ec, Es, Em and ME) compose the fundamental lagoon and estuarine community.

The spatio-temporal patterns of the fish assemblages were studied next, by multivariate analysis of the log transformed fish abundance matrix (73 species × 16 locations × 6 dates). As pooling all the data in a single table might result in a confusing mixture of spatial and temporal effects (Gaertner et al., 1998), the use of a multitable method, which allows the simultaneous analysis of several data tables, was preferred. The principle of this type of method is to find and analyse the common structure of a series of data sets sharing the same rows, columns, or both, and to study the variability of each table compared to this common structure. Multitable methods have been used in aquatic ecology by several authors (Amanieu et al., 1981; Dolédec, 1988; Aliaume et al., 1993; Haury, 1996; Blanc and Beaudou, 1998; Cillauren et al., 1998; Gaertner et al., 1999; Licandro and Ibanez, 2000; Anneville, 2002; Lekve et al., 2002). In the present study, the correspondence analysis (CoA) version of the STATIS method (Lavit et al., 1994), proposed as the STATIS-CoA method by Gaertner et al. (1998, 2002) was used, since the data set was composed of fish abundances. The data matrix was treated as a series of six tables defined by the sampling date, with the 16 locations (sites—positions) as rows and the 73 species as columns. First, for each date, a matrix of scalar products between species was calculated. Then, an average table, called "compromise", was computed by weighting the six matrices in order to give a greater importance to those having similar patterns. The analysis of this compromise table expressed the stable part of the spatial organization of fish assemblages, by giving an average position of species on factorial axes. The projection of the rows and columns of the six by-date tables, as supplementary elements onto the compromise axes, allowed the representation of temporal variations of locations and species around the common organization. In addition to the STATIS-CoA, a hierarchical agglomerative clustering by Ward's method was used to classify species according to their average positions on the compromise axes. Ward's method (also known as minimum-variance clustering) attempts to optimize the minimum variance within clusters using the within-groups sum of squares.

All the species were analysed, because, by computing an average table, the multitable approach avoids the frequently noticed bias of CoA caused by rare species. The multivariate analyses were performed using the ADE-4 software (Thioulouse et al., 1997) freely available on the web (http://pbil.univ-lyon1.fr/ADE-4/).

3. Results

3.1. Environmental characteristics

The environmental characteristics of the 16 locations are given in Table 1 and Fig. 2. As surface and bottom values of salinity, temperature and chlorophyll content were very similar, only surface values are presented here.

Mangrove was most luxuriant in the Bandiala (sites B1–B3) and in the intermediate zone of the Saloum (site S2) whereas it was residual in sites D1 of the Diomboss and S3 of the Saloum, patchy at the mouth (site S1), and almost totally absent in the upper Saloum (site S4). Near the bank, average depth of the sampling locations ranged from 3.8 m (B3b) to 6.4 m (B1b), while in the middle of the channel, it was generally greater than 9 m (average value of 16.5 m in B1c), except in the upper Bandiala (average values of 6.4 m in site B3c and 6.7 m in B2c). The mean water transparency was high in all sites, ranging from 2.1 m in site B1 to 3.2 m in site D1. The mean surface salinity was generally greater than that of seawater, with a minimum average value of 36 in the mouth

Table 1
Description of the eight sampling sites. Mean value, standard deviation (SD) and range are given for depth (m) in the mid-channel and near the bank, water transparency (m), and surface values of salinity, temperature (°C) and total chlorophyll content (µg/l)

Branch		Bandiala			Diomboss	Saloum			
Site		B1	B2	B3	D1	S1	S2	S3	S4
Distance to the sea (km)		3	22	30	8	1	19	29	48
Mangrove		Luxuriant	Luxuriant	Luxuriant	Residual	Patchy	Luxuriant	Residual	None
Depth (channel)	Mean (±SD)	15.3 (1.6)	6.7 (1.5)	6.4 (0.5)	13.5 (3.1)	13.6 (4.7)	9.5 (0.6)	10.6 (1.0)	13.6 (3.5)
	Range	12.5–16.5	4.5–8.0	5.6–6.8	8.0–16.0	10.5–21.7	8.7–10.0	10.0–12.5	8.0–17.5
Depth (bank)	Mean (±SD)	6.4 (2.3)	4.6 (1.0)	3.8 (0.5)	5.3 (2.0)	5.4 (1.5)	5.2 (1.3)	6.0 (0.8)	4.8 (1.6)
	Range	4.0–9.0	3.0–5.6	3.0–4.3	2.4–6.8	3.0–7.5	2.7–6.3	4.5–6.8	3.0–7.3
Transparency	Mean (±SD)	2.1 (0.6)	2.2 (0.7)	2.9 (0.4)	3.2 (1.0)	2.8 (1.1)	2.7 (0.6)	2.4 (0.6)	2.5 (0. 4)
	Range	1.5–3.0	1.0–3.0	2.5–3.4	2.5–5.0	1.7–4.7	2.0–3.3	1.2–3.0	2.0–2.9
Salinity	Mean (±SD)	36.0 (4.0)	37.7 (3.78)	38.3 (3.4)	38.5 (2.1)	37.0 (1.9)	40.5 (3.2)	44.7 (3.2)	50.7 (4.7)
	Range	30–40	33–42	35–43	35–40	35–40	36–46	39–47	43–55
Temperature	Mean (±SD)	26.4 (3.1)	27.3 (3.1)	27.1 (3.0)	26.6 (3.0)	25.6 (3.7)	26.4 (3.5)	26.6 (3.2)	26.7 (3.4)
	Range	22.5–29.6	22.8–29.9	22.3–30.3	23.2–30.7	20.8–30.0	21.8–31.1	23.0–30.9	23.2–30.4
Chlorophyll	Mean (±SD)	4.5 (3.1)	2.9 (1.6)	2.1 (1.0)	2.8 (1.5)	2.1 (1.6)	3.1 (1.9)	2.6 (1.5)	2.3 (1.3)
	Range	0.7–10.1	0.4–5.1	0.4–3.4	1.0–4.2	0.7–4.5	1.0–5.4	0.9–4.8	1.0–4.3

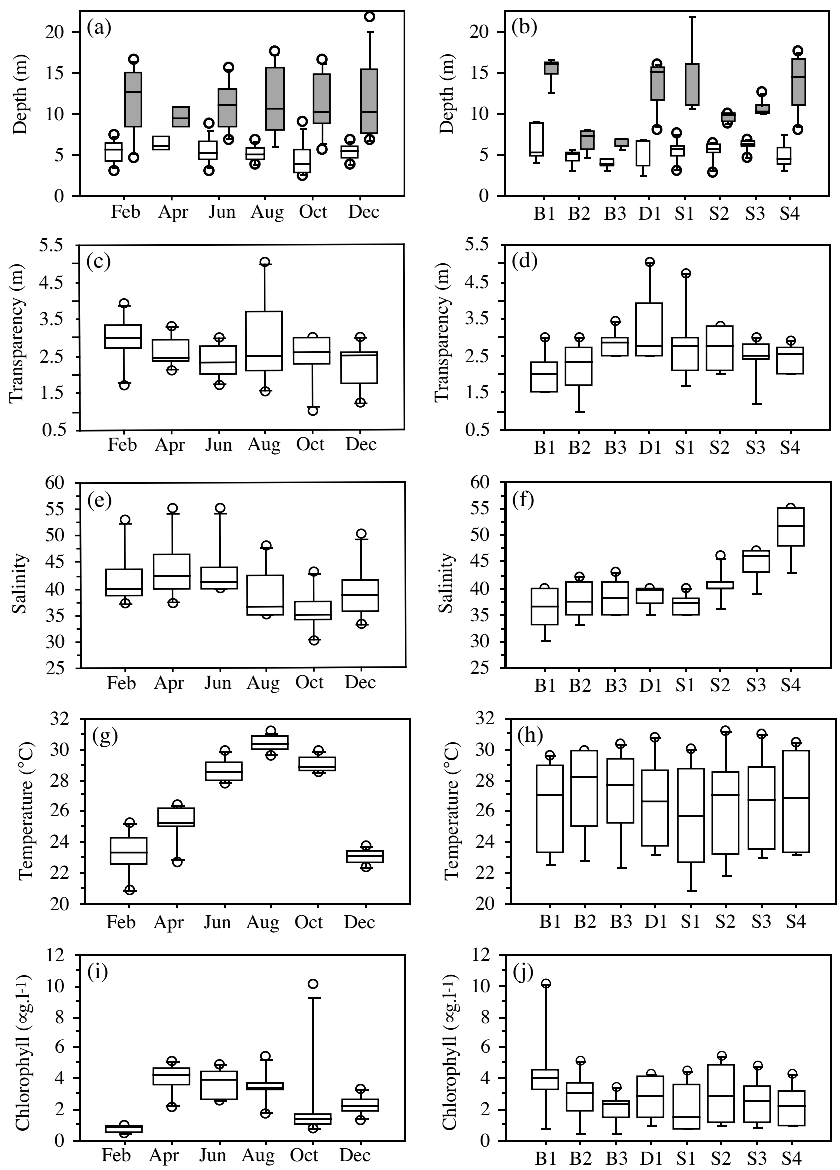

Fig. 2. Box and whisker plots showing the seasonal (left) and spatial (right) variations in the main environmental parameters. The bottom and top edges of the boxes are located at the sample 25th and 75th percentiles. The center horizontal line is drawn at the 50th percentile (median). The whiskers are drawn, respectively, from the box to the 10th and 90th percentiles. Circles correspond to values lower than the 10th percentile or greater than the 90th percentile. (a), (b): depth (m); (c), (d): transparency (m); (e), (f): surface salinity; (g), (h): temperature (°C); (i), (j): chlorophyll content (μg l^{-1}). In (a) and (b), white boxes correspond to bank samples and grey boxes to mid-channel samples.

of the Bandiala (B1) and a maximum of 50.7 in the upper Saloum (S4), where the highest value recorded reached 55. Throughout the year, the highest values of salinity were recorded in April, at the end of the dry season and the lowest in October, at the end of the wet season (Fig. 2e). The mean surface temperature ranged between 25.6 °C in the mouth of the Saloum (S1) and 27.3 °C in the Bandiala (B2). The seasonal evolution of temperature (Fig. 2g) clearly showed an annual cycle with a maximum in August and a minimum in February. The chlorophyll content was particularly high in site B1 (4.5 μg l^{-1}), and around 2–3 μg l^{-1} in the other sites.

3.2. Fish richness and abundance

A total biomass of around 1.7 t, representing 74 610 individuals belonging to 73 species, and 35 families was collected over the 96 samples. One sample (D1c in February) was completely empty. Excluding this empty haul, the number of species per sample ranged from 1 to 22, with an average value of 7.8 (standard deviation 4.9). Eight samples, four of which are in site S4c in the upper Saloum (February, April, June and August), contained only one species, *Sardinella maderensis*. The highest number of species was observed in February in site B3c.

The ANOVA performed on species richness showed a significant effect of branch and position with interaction, and no difference between dates (Table 2). According to the Tukey's HSD test, the overall richness was higher in the Bandiala (10) than in the Saloum (7) and the Diomboss (4.6), and in the bank samples (9.5) than in the mid-channel ones (6). When considering separately bank and mid-channel samples (Fig. 3a and b), bank samples had higher numbers of species at each date, especially in June and August. At the site level, the difference between bank and channel samples was very significant in the lower and intermediate Saloum (12 vs. 4), less in the upper Saloum (5.3 vs. 2) and the Diomboss (6.2 vs. 3), while in the Bandiala, species richness was nearly the same or even lower in bank samples than in mid-channel ones (9.5 vs. 10.3).

The total number of fish ranged from a minimum of 1 (sites D1b in August and S3c in April) to a maximum of 14 314 in October in site S2b. The average value was equal to 777.2 with a standard deviation of 1942.03. The log transformed number of fish varied significantly between dates (Table 2), showing lower values in June and August than in October, December and April. The variability due to the branch (higher numbers in the Bandiala than in the Diomboss) and to the interaction between branch and date was also significant, but there was no effect of the position of the haul (Fig. 3c and d).

The biomass per haul varied between 0.01 kg in August in site D1b and 218.6 kg in April in site S3c, with an average value of 17.8 kg (standard deviation: 32.9). The log transformed biomass varied significantly with branch (Table 2): it was higher in the Bandiala than in the Diomboss. All the other effects and interactions were also significant except the position of the haul.

The temporal and spatial patterns of change in the numbers and biomass were very similar (Fig. 3b–e), with the seasonal minimum of abundance during the warm season (June and August), and the spatial minimum in the Diomboss (D1) and the upper Saloum (S4).

3.3. Composition of the fish assemblages

The high values of number of fish and biomass observed in some samples were mainly due to *Sardinella maderensis*, which represented 69.4% of the total numbers and nearly 52% of the total biomass (Table 3). This was followed by two other small Clupeidae, *Ethmalosa fimbriata* (11.5% of the abundance, 9.5% of the biomass) and *Ilisha africana* (5.2% of the abundance and 3.1% of the biomass). These three pelagic species were often caught in large schools of several hundreds or sometimes thousands of individuals, which explains their importance in terms of number of fish. Among the other abundant species were two Gerreidae, *Gerres nigri* (3.3%) and *Eucinostomus melanopterus* (2%), a Haemulidae, *Brachydeuterus auritus* (2.5%), a Carangidae, *Chloroscombrus chrysurus* (2%), and a Polynemidae,

Table 2
Results of the three-way analysis of variance testing for significant differences in species richness, total numbers (log-transformed) and total biomass (log-transformed), between branches, positions and dates. Second- and third-order interactions and residual values are given

	Source	DF	Sum of squares	Mean square	F value	$P > F$
Species richness	Branch	2	317.760	158.880	9.623	0.0002
	Position	1	160.661	160.661	9.731	0.0028
	Date	5	118.569	23.714	1.436	0.2244
	Branch × position	2	306.010	153.005	9.268	0.0003
	Branch × date	10	50.927	5.093	0.308	0.9762
	Position × date	5	53.657	10.731	0.650	0.6626
	Branch × position × date	10	169.344	16.934	1.026	0.4333
	Residual value	60	990.583	16.510		
Total number (log-transformed)	Branch	2	23.025	11.513	4.971	0.0101
	Position	1	0.388	0.388	0.168	0.6837
	Date	5	64.801	12.960	5.596	0.0003
	Branch × position	2	16.964	8.482	3.662	0.0316
	Branch × date	10	64.359	6.436	2.779	0.0069
	Position × date	5	27.082	5.416	2.339	0.0525
	Branch × position × date	10	45.533	4.553	1.966	0.0534
	Residual value	60	138.968	2.316		
Total biomass (log-transformed)	Branch	2	31.428	15.714	7.893	0.0009
	Position	1	2.615	2.615	1.313	0.2564
	Date	5	46.397	9.279	4.661	0.0012
	Branch × position	2	21.803	10.902	5.476	0.0065
	Branch × date	10	67.356	6.736	3.383	0.0015
	Position × date	5	32.597	6.519	3.274	0.0011
	Branch × position × date	10	66.400	6.640	3.335	0.0017
	Residual value	60	119.456	1.991		

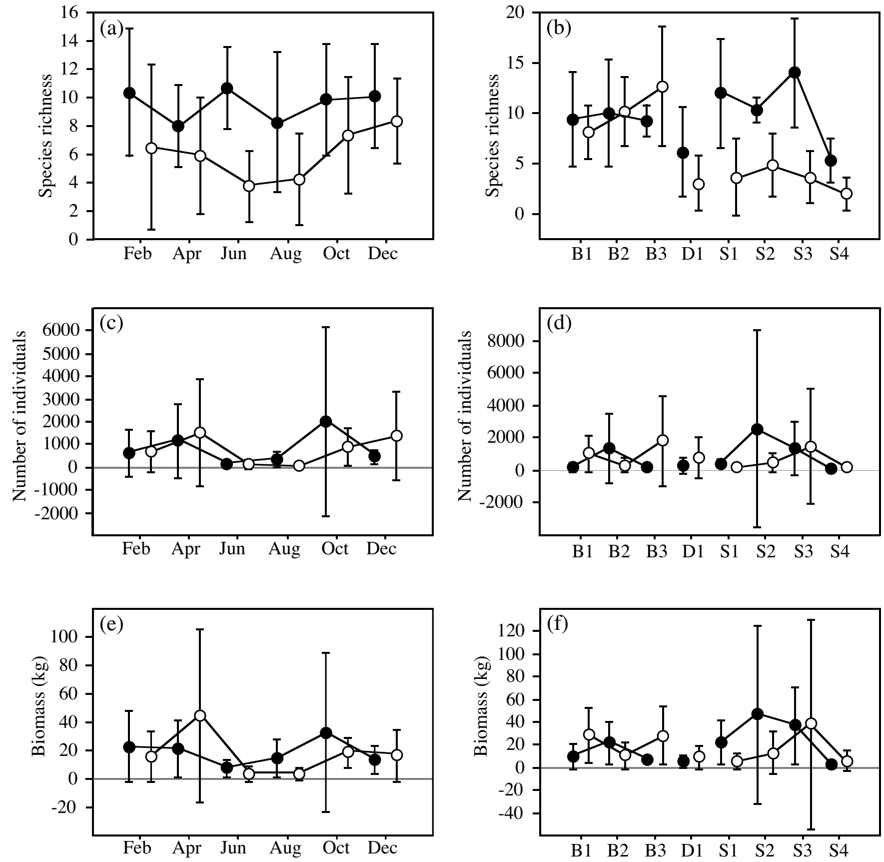

Fig. 3. Seasonal (left) and spatial (right) variations in average values of (a), (b): species richness; (c), (d): total fish number; (e), (f): total fish biomass (kg). Solid symbols correspond to samples close to the bank and open symbols to mid-channel ones. Error bars correspond to 95% confidence intervals.

Galeoides decadactylus (1%). These eight species constituted nearly 97% of the total fish number, the remaining 3% being shared by the 65 other species. In terms of biomass, these eight species represented 76.5% of the total biomass, the rest being constituted by large species, such as *Drepane africana* (2%), *Liza dumerili* (2%), *Pseudotolithus brachygnathus* (1.9%), *Rhinoptera bonasus* (1.7%), *Tilapia guineensis* (1.6%), *Ephippion guttifer* (1.5%), *Scomberomorus tritor* (1.3%) and *Pomadasys jubelini* (1%).

In terms of bio-ecological categories, the fish assemblages were greatly dominated by marine–estuarine (ME) species (21 species accounting for 79% of the total numbers and 66% of the biomass) and, to a lesser extent, estuarine forms of marine origin (Em) (16 species accounting for 18% of the total abundance and 22% of the biomass). Only four species were strictly estuarine (Es); they accounted for 3% of the numbers and 7% of the biomass. The freshwater species (Ec, Ce and Co) were totally absent, while the marine ones (Ma and Mo) were largely represented by 32 species. However, these marine species only accounted for 0.6% of the total abundance and 5% of the biomass.

3.4. Spatial structure of the fish assemblages

In the first step of the STATIS-CoA analysis, i.e. the construction of the compromise matrix, the contribution of the six sampling dates (weights—Table 4) were well balanced (between 0.36 for February and 0.43 for June), indicating that no date was either favoured or ignored in the constitution of the average matrix. Moreover, the fit of each date to the compromise (Cos^2—Table 4), was relatively constant. The slightly lower values ($0.21 < Cos^2 < 0.29$) obtained for the dry season months (February, April and December) indicated that their structure was not as well reflected by the compromise as for the wet season ($0.37 < Cos^2 < 0.41$). The compromise matrix, however, provided a good approximation of the spatial organizational pattern of the fish assemblages over the one-year sampling period.

In the second step of the STATIS-CoA, i.e. the analysis of the compromise matrix, the first two axes represented, respectively, 15% and 9% of the total variability, which is a good ratio in relation to the high dimension of the compromise matrix (73×73). The projection of the 73 species onto the compromise axes

Table 3
List of the 73 fish species sorted by family

Family	Species	Code	Category	Occurrence	Abundance	Biomass
Acanthuridae	*Acanthurus monroviae*	AMO	Mo	1	2	132
Antennariidae	*Antennarius pardalis*	APA	Mo	4	16	3416
Ariidae	*Arius heudelotii*	AHE	ME	1	1	176
	Arius latiscutatus	AGA	ME	9	17	5259
	Arius parkii	ARP	ME	4	7	2517
Batrachoididae	*Batrachoides liberiensis*	BLI	Ma	7	7	1833
Belonidae	*Tylosurus crocodilus*	TCR	Mo	1	1	550
Carangidae	*Alectis alexandrinus*	SAL	Mo	1	1	526
	Caranx hippos	CHI	ME	6	16	2102
	Caranx rhonchus	CRH	Mo	4	5	98
	Caranx senegallus	CAS	ME	1	4	5000
	Chloroscombrus chrysurus	CHL	ME	34	1531	38475
	Lichia amia	LIA	Ma	2	3	176
	Selene dorsalis	VSE	ME	1	1	10
	Trachinotus teraia	TFA	Em	2	2	5691
	Trachurus trecae	TTR	Mo	3	87	2612
Chaetodontidae	*Chaetodon hoefleri*	CHO	Mo	1	1	10
Cichlidae	*Sarotherodon melanotheron*	THE	Es	1	7	554
	Tilapia guineensis	TGU	Es	13	97	25802
Clupeidae	*Ethmalosa fimbriata*	EFI	Em	24	8603	162831
	Ilisha africana	IAF	Em	19	3914	53747
	Sardinella aurita	SAU	Ma	1	120	780
	Sardinella maderensis	SEB	ME	82	53055	891681
Cynoglossidae	*Cynoglossus monodi*	CYM	Mo	1	1	28
	Cynoglossus senegalensis	CYS	Em	21	28	4309
Dasyatidae	*Dasyatis margarita*	DMA	Em	11	17	20778
	Dasyatis margaritella	DAM	Em	2	3	1805
Drepaneidae	*Drepane africana*	DAF	ME	9	91	35014
Elopidae	*Elops lacerta*	ELA	ME	2	5	1050
	Elops senegalensis	ELS	Ma	2	2	483
Ephippidae	*Chaetodipterus goreensis*	CHG	Mo	2	4	82
	Chaetodipterus lippei	CLI	Ma	5	8	1088
Exocoetidae	*Fodiator acutus*	FAC	Ma	3	3	67
Gerreidae	*Eucinostomus melanopterus*	GME	ME	52	1463	32851
	Gerres nigri	GNI	Es	57	2433	86124
Haemulidae	*Brachydeuterus auritus*	BAU	ME	40	1854	23963
	Plectorhinchus macrolepis	PLM	Em	8	10	13556
	Pomadasys incisus	PIN	Ma	5	19	324
	Pomadasys jubelini	PJU	Em	26	245	17913
	Pomadasys perotaei	PPE	Em	18	177	11785
	Pomadasys rogerii	PRO	Mo	1	1	115
Hemiramphidae	*Hemiramphus brasiliensis*	HBR	Em	4	33	1995
Lobotidae	*Lobotes surinamensis*	LSU	Mo	1	1	8100
Lutjanidae	*Lutjanus goreensis*	LGO	Ma	1	1	100
Monodactylidae	*Monodactylus sebae*	PSB	Es	8	10	683
Moronidae	*Dicentrarchus punctatus*	DPU	Mo	1	2	155
Mugilidae	*Liza dumerili*	LDU	Em	29	391	33965
	Liza falcipinnis	LFA	Em	19	71	5622
	Liza grandisquamis	LGR	Em	6	85	12243
	Mugil bananensis	MBA	ME	18	86	8292
	Mugil cephalus	MCE	ME	4	30	3396
	Mugil curema	MCU	Em	10	25	2385
Myliobatidae	*Rhinoptera bonasus*	RBO	Mo	2	2	29500
Paralichthyidae	*Citharichthys stampflii*	CST	Em	7	11	216
Polynemidae	*Galeoides decadactylus*	GDE	ME	41	744	21963
	Polydactylus quadrifilis	POQ	ME	1	2	1091
Psettodidae	*Psettodes belcheri*	PBE	Mo	6	9	1604
Rhinobatidae	*Rhinobatos cemiculus*	RCE	Ma	5	7	13960
Sciaenidae	*Argyrosomus regius*	ARE	Mo	2	7	179
	Pseudotolithus brachygnathus	PBR	ME	13	107	32403
	Pseudotolithus elongatus	PEL	Em	8	187	27062
	Pseudotolithus senegalensis	PSN	Ma	1	1	54

Table 3 (*continued*)

Family	Species	Code	Category	Occurrence	Abundance	Biomass
	Pteroscion peli	PTP	ME	3	15	512
Scombridae	*Scomberomorus tritor*	CTR	Ma	33	135	21794
Serranidae	*Epinephelus aeneus*	EAE	ME	13	19	4762
Sparidae	*Diplodus bellottii*	DBE	Mo	2	2	84
	Diplodus vulgaris	DVU	Mo	1	1	22
	Lithognathus mormyrus	LMO	Mo	1	1	120
	Pagrus caeruleostictus	PEH	Ma	1	1	153
Syngnathidae	*Hippocampus algiricus*	HPU	Ma	5	6	43
Tetraodontidae	*Ephippion guttifer*	EGU	ME	10	12	25649
	Lagocephalus laevigatus	LLA	Ma	3	4	90
Trichiuridae	*Trichiurus lepturus*	TLE	ME	4	24	2161

Code: abbreviation used in Figs. 4, 5 and 8. Category: ecological category code (Ec: estuarine species from freshwater origin, Es: strictly estuarine species, Em: estuarine species from marine origin, ME: marine–estuarine species, Ma: marine species accessory in estuaries, Mo: marine species occasional in estuaries). Occurrence: number of samples where the species was present. Abundance: total number of individuals. Biomass: total biomass (g).

(Fig. 4) was compared to the projection on the same axes of the 96 samples with their average by-location position (Fig. 6), in order to summarize the spatial pattern of the fish assemblages shared by the six sampling dates. The hierarchical agglomerative clustering of the species coordinates (Fig. 5) defined five groups of species which are identified in Fig. 4. Three of them (Groups I–III, composed of 18, 5 and 5 species, respectively) were characteristic of certain areas of the Sine Saloum Delta. The last two groups (Groups IV and V, composed of 30 and 15 species, respectively), projected in the middle of the graph, were not clearly associated with any definite area of the Sine Saloum Delta.

3.4.1. Group I

The first group, on the left side of the first axis (Fig. 4) was composed of the four strictly estuarine species (Es) identified in this study. Among them were the two Cichlidae, *Tilapia guineensis* and *Sarotherodon melanotheron*, the only West African Monodactylidae, *Monodactylus sebae*, and *Gerres nigri*, a very common Gerreidae species in the Sine Saloum estuary and most West African estuarine environments. The other Gerreidae, *Eucinostomus melanopterus*, considered as a marine–estuarine species (ME), also belonged to this assemblage, as did the six Mugilidae species: *Liza grandisquamis*, *Liza dumerili*, *Liza falcipinnis*, *Mugil bananensis*, *Mugil curema* and *Mugil cephalus*, which are marine–estuarine (ME) or estuarine of marine origin (Em). The smooth flounder *Citharichthys stampflii* and two Rajiformes, the blackchin guitarfish (*Rhinobatos cemiculus*) and the daisy stingray (*Dasyatis margarita*), were associated with this group, which comprised also a few less common species, such as the white grouper, *Epinephelus aeneus*, the African sicklefish, *Drepane africana*, the hairy toadfish *Batrachoides liberiensis*, and the frogfish *Antennarius pardalis*. This fish assemblage was typical of bank and channel samples from the upstream Bandiala (B2 and B3), and of bank samples from the Saloum (S1b–S4b) (Fig. 6). The main environmental characteristic of these locations was their shallow depth (Fig. 2): coordinates of the samples on the first axis and the logarithm of depth were well correlated ($r = 0.6$).

Table 4
Description of the structure defined for each sampling date in the STATIS-CoA analysis

Date	Weight	Cos^2
February	0.362	0.219
April	0.398	0.288
June	0.430	0.371
August	0.426	0.407
October	0.426	0.375
December	0.404	0.280

Weights: contribution to the construction of the compromise. Cos^2: fit to the structure of the compromise summarized by its two first axes.

3.4.2. Group II

The second group, on the right side of the first axis (Fig. 4), comprised the razor fish *Ilisha africana*, the bigeye grunt *Brachydeuterus auritus* and the Atlantic bumper *Chloroscombrus chrysurus*. Other less abundant species were associated with them, such as the largehead hairtail *Trichiurus lepturus* and the croaker *Pseudotolithus elongatus*. All were marine–estuarine (ME) or estuarine of marine origin (Em) species. This second group was located at B1c and B1b in the mouth of the Bandiala (Fig. 6), where the lowest surface salinity (36), water transparency (2 m) and the highest chlorophyll content (4.5 $\mu g\ l^{-1}$ at surface) were observed.

3.4.3. Group III

On the lower side of the second axis (Fig. 4), two species were projected: the marine–estuarine (ME) small Clupeidae *Sardinella maderensis*, described above as the most abundant species in the Sine Saloum estuary, and the Scombridae *Scomberomorus tritor*, a marine accessory species (Ma), far less abundant with 0.2% of the total fish number. Three rare species, *Acanthurus monroviae*, *Lutjanus goreensis* and *Lichia*

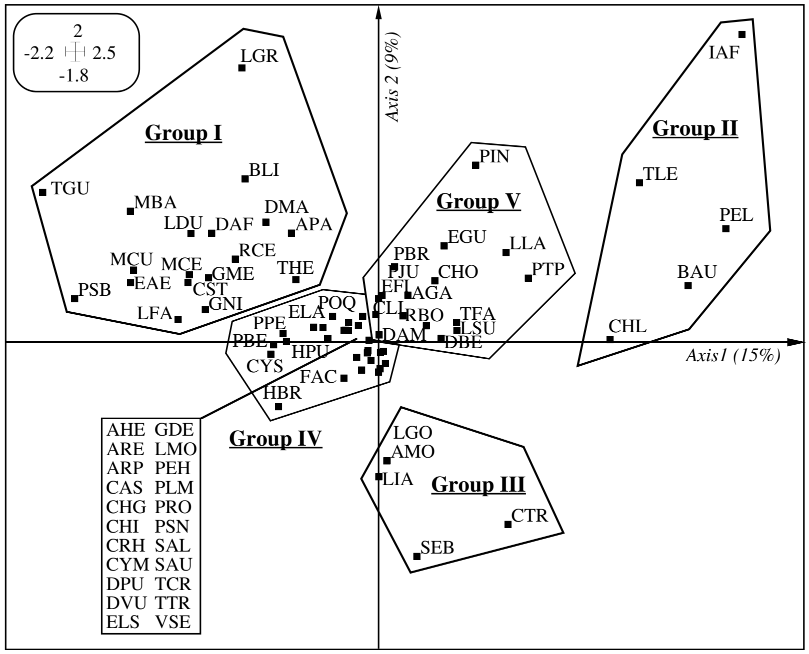

Fig. 4. Scatterplot of the average positions of the 73 species on the first two axes of the STATIS-CoA compromise analysis (see Table 3 for species abbreviations). To enhance readability, codes for species projected at the center of the graph are listed in a box. The minimum and maximum values on the axes are given by the scale box in the upper left corner.

amia were associated with this group. All three were marine species, accessory or occasionally present in estuaries (Ma and Mo). This group was characteristic of the mouth of the Diomboss (D1c and D1b) and the mid-channel of the Saloum (S1c–S4c) (Fig. 6), i.e. open water areas, with depth generally greater than 8 m (except in D1b), high transparency (2.4–3.2 m) and high salinity (37–50.7). The coordinates of samples on the second axis were correlated with species richness ($r = 0.55$), fish number ($r = 0.31$) and biomass ($r = 0.33$), showing that locations belonging to Group III were the poorest in the Sine Saloum Delta.

3.4.4. Groups IV and V

The species placed in Groups IV and V by the hierarchical aggregative clustering did not contribute to the spatial organization pattern of the fish assemblages described above, except a few species from Group V which were projected close to Group II (Fig. 4) because they were caught most of the time near the Bandiala mouth (site B1). Among them were the two Tetraodontidae *Ephippion guttifer* and *Lagocephalus laevigatus*, the Sciaenidae *Pteroscion peli*, and one Haemulidae, *Pomadasys incisus*.

Some species were abundant (*Ethmalosa fimbriata*, which was the second most abundant species, *Galeoides decadactylus*, *Pomadasys jubelini*, *Pomadasys perotaei*, *Pseudotolithus brachygnathus*), or occurred regularly (*Cynoglossus senegalensis*, *Arius latiscutatus*, *Plectorhinchus macrolepis*). They were ubiquitous species, widely distributed all year long through the various habitats of the Sine Saloum Delta. Conversely, many species belonging to Groups IV and V were rare species, and as a consequence it was not possible to identify their spatio-temporal pattern. Among the 19 species caught only once during the sampling period, 14 belonged to Group IV and two to Group V. Most of them (10) were marine species occasional in estuaries (Mo), the others were marine species accessory in estuaries (Ma) and marine–estuarine species (ME).

3.5. Stability in time of the spatial structure

The temporal variability of locations and species is shown in Figs. 7 and 8, respectively, by plotting rows and columns of the six by-date tables onto the compromise axes.

3.5.1. Group I

Almost all samples from Group I (B2, B3 and bank of the Saloum) were grouped together (Fig. 7a), showing very stable species assemblages from date to date. Deviations from the average position of the group, observed in few cases, mainly resulted from drastic fluctuations in the abundance of *Sardinella maderensis*. This species, although not characteristic of Group I, was generally part of the species composition, but was sometimes absent (B3b in February and October, S4b in June) or, on the contrary, largely predominant (98% for S4b in February). A majority of species from Group I showed stable spatio-temporal patterns, e.g. *Eucinostomus melanopterus*, *Gerres nigri*, *Liza falcipinnis* and

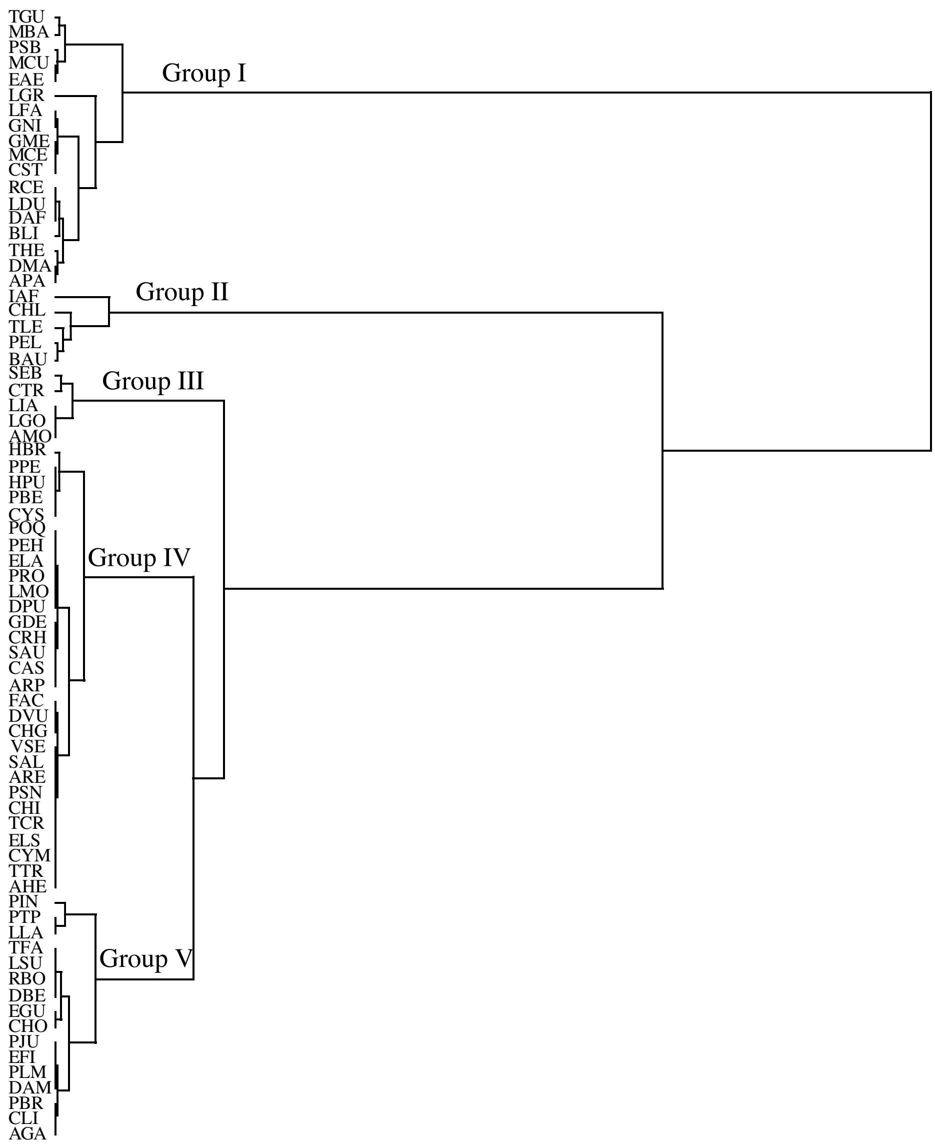

Fig. 5. Hierarchical cluster analysis of the 73 species by Ward's method using their average positions on the compromise axes.

Tilapia guineensis (Fig. 8a). At some dates, however, some species were caught in different areas. For example, in December, *Batrachoides liberiensis* was only present in the mouth of the Bandiala and consequently associated with Group II and *Citharichthys stampflii*, caught in the Diomboss, was projected close to Group III. *Sarotherodon melanotheron*, observed only once, in location S4b in June, was clearly associated with Group I.

3.5.2. Group II

The samples from the mouth of the Bandiala (B1b and B1c) were all projected on the right side of the first axis (Fig. 7b), because of the low abundance of Group I species in this area whatever the season. However, their position along the second axis varied from date to date, reflecting variations of the abundance of *Ilisha africana*, the most characteristic species of the mouth of the Bandiala. Thus, location B1c was projected close to Group III in February and June, due to the absence of *I. africana*, whereas it was characterized by a high abundance of this species in every other month. The five species from this group showed stable patterns, except *Trichiurus lepturus* which was associated with Group I in December, because it was caught in location B2b (Fig. 8b).

3.5.3. Group III

The Diomboss (D1c and D1b) and the central channel of the Saloum (S1c–S4c) showed the highest temporal variability, particularly in locations S1c and S3c. Samples which contained only *Sardinella maderensis* and *Scomberomorus tritor* (August samples and most of the April and June samples) were projected in

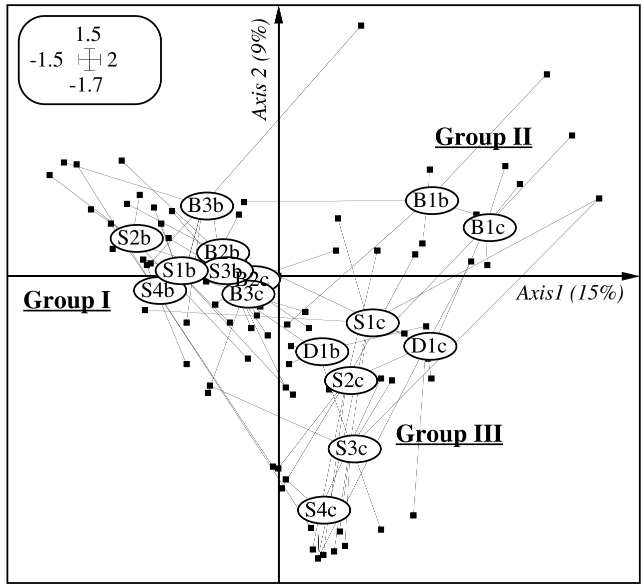

Fig. 6. Scatterplot of the 96 samples on the first two axes of the STATIS-CoA compromise analysis. Lines link samples to the center of gravity of the corresponding sampling location (in circle).

the lowest part of the graph (Fig. 7c). Variability around this position was due to the presence of other species like *Brachydeuterus auritus*, *Chloroscombrus chrysurus* and *Ilisha africana* (Group II) and Gerreidae (Group I). In the upper Saloum (S4c), the only species caught from February to August was *S. maderensis*, while a few other species were observed just after the wet season (October and December) (Fig. 8c).

3.5.4. Groups IV and V

The wide spatial and temporal distribution of the most abundant species belonging to Groups IV and V (*Ethmalosa fimbriata*, *Galeoides decadactylus*) were expressed by the projection of their by-date positions all around the origin of the axes (Fig. 8d and e). The species from Group V which were projected close to Group II in Fig. 4 (*Ephippion guttifer*, *Pomadasys incisus*, *Lagocephalus laevigatus*, and *Pteroscion peli*) occurred regularly in different sites but mostly near the mouth of the Bandiala (Fig. 8e).

4. Discussion

Most high-salinity waters occur in tropical or subtropical areas, but these environments are rare, particularly those with a real hyperhaline zone. Some of them have been the subject of environmental or faunistic studies including the Laguna Madre of Texas (Hedgpeth, 1967), Laguna Madre de Tamaulipas in Mexico (Hildebrand, 1958), Shark Bay in Western Australia (Logan, 1961), St Lucia and other South African lagoons (Whitfield et al., 1981; Whitfield and Bruton, 1989) and the Banc d'Arguin in Mauritania (Sevrin-Reyssac and Richer de Forges, 1985). Most of the time, when these areas are in open contact with the sea, salinity is below 80. In the inverse estuaries of West Africa, however, such as the Casamance River estuary (Savenije and Pagès, 1992; Albaret, 1987) and the Sine Saloum Delta (Pagès and Citeau, 1990), the salinity can reach more than 130.

In such high-salinity environments, modifications in the biodiversity, species composition, seasonal dynamics, trophic organization and demographic characteristics of fish assemblages have been reported. A drastic decrease in species richness and diversity is often the most notable consequence of high salinity. This phenomenon, however, only concerned the upstream hyperhaline areas, which had few species, with always less than 10 species and ultimately only one. A reduced fish assemblage was typical of this upstream area, comprising very few species able to adapt their eco-physiological abilities and some of their life history attributes, such as feeding and reproduction (Albaret, 1987).

4.1. Species richness and abundance

The total species richness of high-salinity environments can be equal to or even higher than that of "normal" estuaries: 108 species in St Lucia lagoon (Blaber, 1988), more than 70 in Laguna Madre, Texas (Hedgpeth, 1967) and 111 in Laguna Madre de Tamaulipas in Mexico (Chavez, 1979). By comparison, in West Africa, the average estuarine species richness was estimated to be 97 by Baran (2000) from 10 case studies in various types of estuarine environments.

Diouf (1996) reported 114 species in the whole Sine Saloum system, over a two-year sampling period

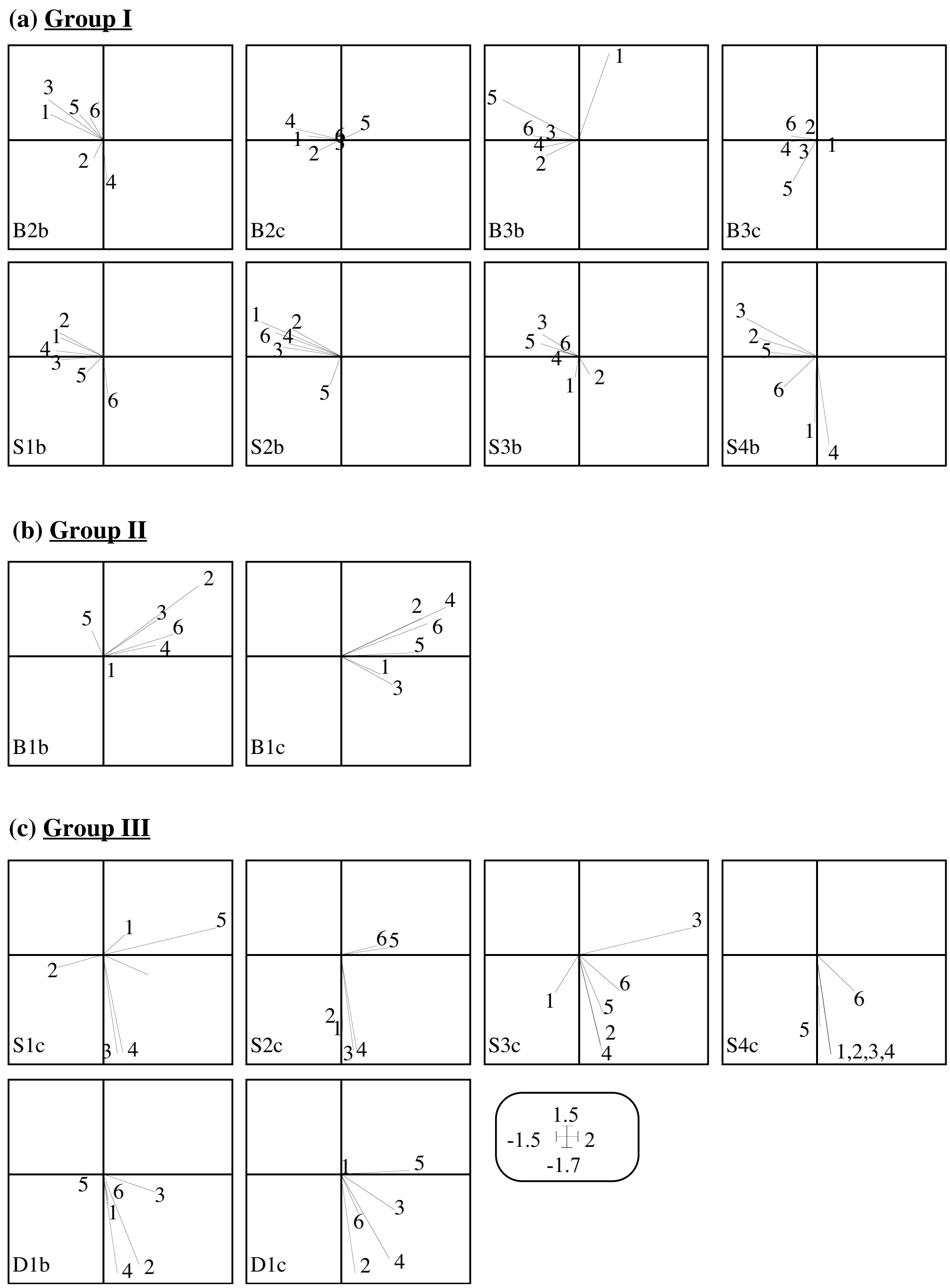

Fig. 7. Scatterplot of samples on the first two axes of the STATIS-CoA compromise analysis. Coordinates of samples are the same as in Fig. 4, but the 16 sampling locations have been plotted on 16 separate graphs, arranged by groups of locations: Group I (a), Group II (b) and Group III (c). Numbers 1–6 refer to successive sampling dates, respectively, February, April, June, August, October and December.

involving several fishing techniques and with additional observations from small-scale and game fisheries. Among these species, 73 were caught during the present study. The high species richness of the study area was in accordance with the observations of Hedgpeth (1967) and Hodgkin and Kendrix (1984), who reported the highest number of species for salinities between 25 and 50. Periods of moderately high salinities could favour higher diversity.

For the Sine Saloum Delta, at least three explanations can be proposed for this high value: (1) the settlement in the estuary by many marine species could be made easier by the permanent broad communication with the ocean, related to the large number of river branches in the Sine Saloum system, and conversely the almost entire absence of freshwater influence (Blaber, 1985; Whitfield et al., 1994); (2) the high diversity of habitats (three main branches, many small seawater

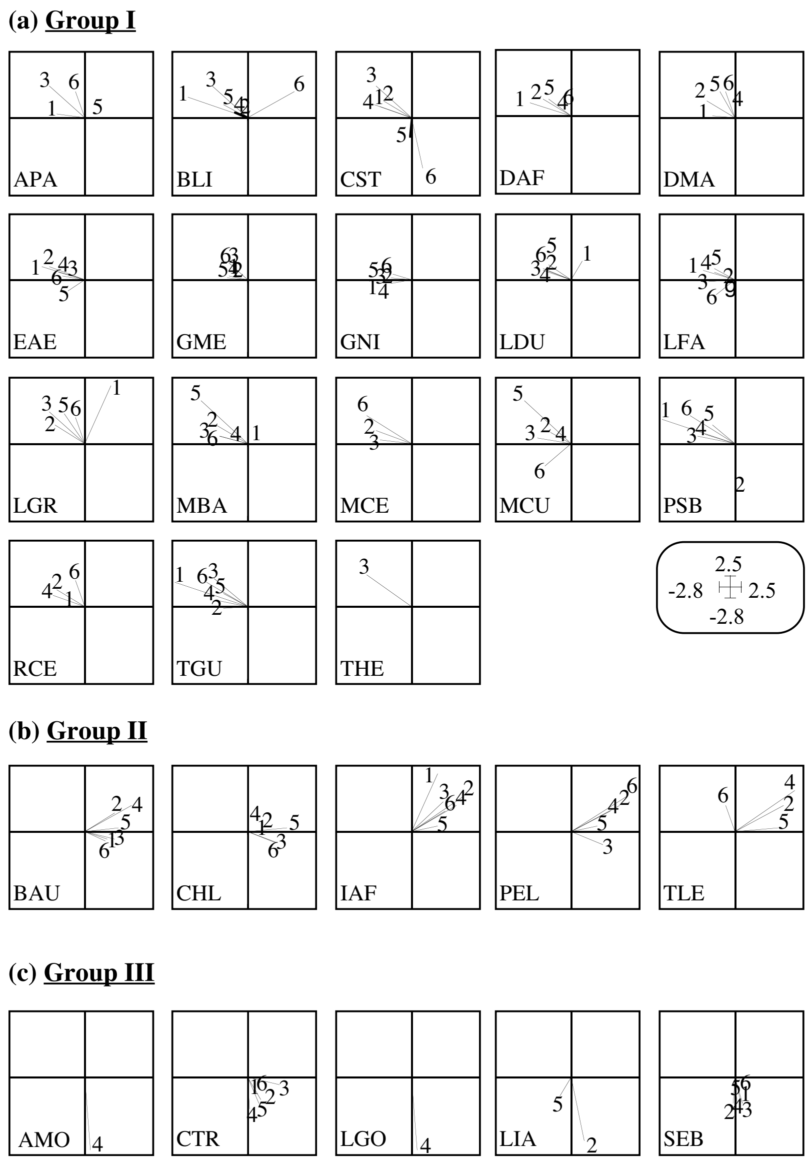

Fig. 8. Scatterplot of the by-date positions of species, projected as supplementary elements on the first two axes of the STATIS-CoA compromise analysis. Graphs are arranged by group of species: Group I (a), Group II (b), Group III (c), Group IV (d) and Group V (e). Numbers 1–6 refer to successive sampling dates, respectively, February, April, June, August, October and December. A species absent at a given date is not plotted on the graph.

creeks, presence of mangrove, diversity of bottom sediments) could allow the colonization of the estuary by many different species; and (3) the lack of freshwater flow in the system could limit the export of nutrients to the sea and consequently increase the trophic capacity of the estuary.

4.2. Spatio-temporal variability of species richness and abundance

The lowest species richness and abundance were observed in sites S4 in the upper Saloum and D1 in the Diomboss. In site S4, located at the edge of the hyperhaline area, the high salinity, reaching 55 at the end of the dry season, was clearly a limiting factor for many species. In site D1, located at the mouth of the Diomboss, with a wide communication with the ocean, species were mainly passing through and few of them settled in this area. In contrast, the highest species richness was observed in site B3, located at the confluence between the upper Bandiala and the Diomboss, and also at the opening of several small seawater creeks. This diversity of influences probably favoured settlement of many species in this area. Except in the upper Bandiala (sites B2 and B3), species richness was generally higher near the bank than in the mid-channel samples. This may be due to a greater habitat diversity near the banks, allowing the presence of many fish species finding food

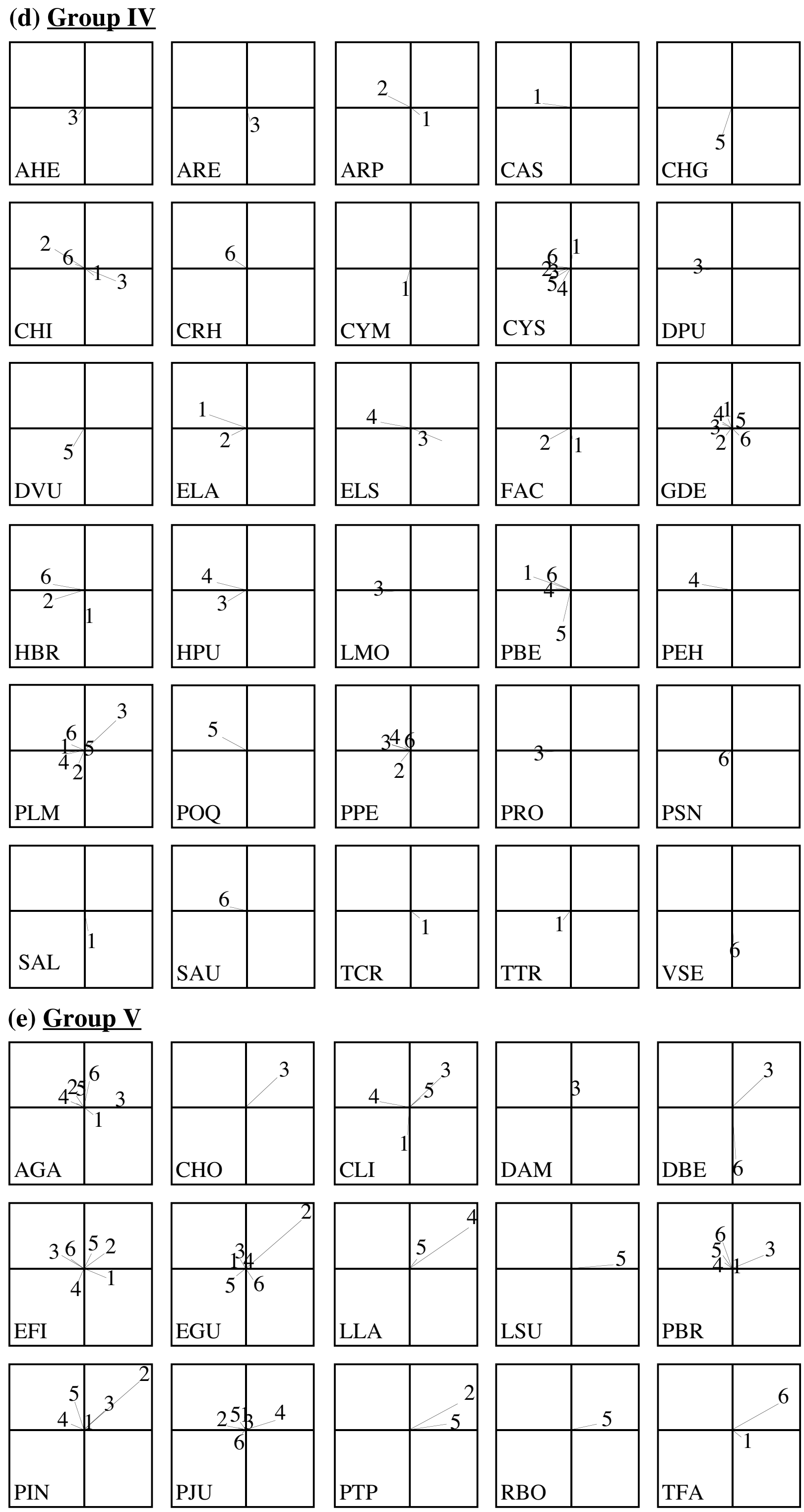

Fig. 8 (*continued*)

and shelter in the mangrove (such as Cichlidae), of species feeding on mud flats such as benthophagous (Gerreidae) and detritivorous (Mugilidae) species, and of associated predators like *Epinephelus aeneus* and *Lutjanus goreensis*. Conversely, in the mid-channel, the lack of shelter, the current strength and the trophic conditions do not favour the settlement of as numerous species: most of the fish caught in the channel were small migrating pelagic species. In the Bandiala, however, which is much narrower and shallower than the other branches, the difference between bank and channel samples was not so clearly marked. This was particularly the case in the very sinuous upper Bandiala where the channel comes close to the mangrove in the curves.

The total fish number varied mainly through time, with minimum values observed just before and during the wet season (June and August). This phenomenon could be explained by the migration of many individuals of some species (sub-adults or adults) to the sea for spawning at the beginning of the wet season, leading to an overall decrease of their abundance in many sites of the estuarine system. In October, at the end of the wet season, as the juveniles of sea spawning species appeared in the estuary (Vidy, 2000), the total abundance increased. High average numbers and biomass, generally associated with high variability, were influenced by the occasional presence of very large schools of small pelagic species, mainly *Sardinella maderensis*.

4.3. Composition of fish assemblages

Although many species could settle temporarily or permanently in the estuary, few were dominant in terms of abundance, as previously observed in many other estuary or lagoon ecosystems (Albaret and Ecoutin, 1990; Flores-Verdugo et al., 1990; Tzeng and Wang, 1992; Baran, 1995; Laroche et al., 1997; Maes et al., 1998). Environmental conditions favoured the establishment of a rich and diversified fish fauna, mainly composed of species of marine origin (Em, ME, Ma, Mo). Most of them were juvenile forms of species from the continental shelf, which used the Sine Saloum Delta as a regular or occasional nursery.

The most abundant species were essentially small pelagic Clupeidae like *Sardinella maderensis*, *Ethmalosa fimbriata* and *Ilisha africana*, characterized by a high capacity for osmoregulation which allows them to have a broad spatio-temporal distribution in this estuary as in other African estuarine ecosystems (Albaret and Ecoutin, 1990; Potter et al., 1990). Two of them, *S. maderensis* and *E. fimbriata* were even able to cross the "obstacle" of very high salinity and were part of the reduced fish assemblage of the hyperhaline area, together with other species such as *Sarotherodon melanotheron* (Es), *Gerres nigri* (Es), *Liza dumerili* (Em), and *Liza falcipinnis* (Em). These few species constituted the "resistance community" first identified in the estuary of the Casamance River by Albaret (1987).

In terms of overall species richness, these species of marine origin balanced the complete absence of species of freshwater origin at all seasons. Thus, several estuarine species of freshwater origin (Ec), which are generally common in brackish waters of West Africa, were not present in the Sine Saloum, such as the three Bagridae *Chrysichthys nigrodigitatus*, *Chrysichthys auratus* and *Chrysichthys maurus* and the Cichlidae *Tilapia mariae*. Freshwater species with estuarine affinities (Ce) such as *Chrysichthys johnelsi*, *Schilbe intermedius*, *Parailia pellucida*, *Brycinus longipinnis* and *Hepsetus odoe*, or occasionally present in estuaries (Co) such as *Brycinus nurse*, *Papyrochranus afer*, *Hyperopisus bebe*, *Hydrocynus brevis* and *Synodontis batensoda*, were absent.

4.4. Spatio-temporal variability of the fish assemblages

The spatial organization of the fish assemblages was mainly influenced by three factors: the estuary branch, the distance to the sea and the distance to the bank. At the level of the estuarine complex as a whole, the three branches showed different types of spatial organization. In the Bandiala, the fish assemblages in bank and channel samples were similar but there were notable differences between the mouth (B1) and the upstream sites (B2, B3). In the Diomboss, considered by Diouf (1996) as a whole homogeneous ecological zone, the influence of the distance to the sea could not be measured, because only one site was sampled; as in the Bandiala, there was no difference between bank and channel samples. In the Saloum branch, on the contrary, the fish assemblages from the bank were completely different from the channel ones: the bank assemblages were similar to those from the upstream Bandiala, while the channel ones were comparable to those from the Diomboss. Although the Saloum branch was much longer than the two other ones, the distance to the sea did not appear to be a structuring factor of its fish assemblages, with the exception of the hyperhaline area.

As no major seasonal hydrological phenomenon, such as flooding, occurred in the Sine Saloum estuary, this spatial organization was very stable throughout the year. The bank assemblages were particularly stable, while large fluctuations occurred in the channel, due to the occasional presence of large schools of small migrating pelagic species.

5. Conclusion

In many West African estuaries receiving freshwater inputs, for most of the year, hydroclimatic conditions remain relatively stable or rather progressively change under the influence of the ocean. As a consequence, fish assemblages can reach a certain degree of organization (though not very high), which is highest at the end of the dry season. When the flood occurs, the development of the fish assemblages is suddenly stopped. Environmental conditions and consequently fish assemblages are drastically modified with many marine species leaving the estuary or becoming scarce, and freshwater species replacing them. Thus, assemblages in the wet season appear to be completely disorganized.

This phenomenon was observed in the Ebrié Lagoon by Albaret and Ecoutin (1990) and in the Fatala River estuary by Baran (1995). In the Sine Saloum Delta, in the absence of flooding, only small-scale seasonal variations were observed, resulting from the migration of some species between the continental shelf and the estuary. These species belonged to the estuarine of marine origin (Em) and mainly marine–estuarine (ME) categories.

Compared to other West African estuaries, the Sine Saloum system is clearly a "Type I" (inverse) estuary, at the end of the theoretical evolution pattern of West African estuaries proposed by Albaret (1999). In this type of estuary, fish assemblages are characterized by the almost complete absence of freshwater species and the reduction of the abundance of marine species, while the number of marine species remains high. Despite the high salinity, most of the main functions of the estuary were preserved; in particular the nursery function was especially well-developed for many species. This was a consequence of the relative stability of environmental conditions and of the trophic richness due to mangrove and to the low export of nutrients resulting from the absence of flooding.

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