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The Gambia River estuary: A reference point for estuarine fish assemblages studies in West Africa

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Abstract

The Gambia River is one of the last aquatic ecosystems in West Africa that has not yet been affected by strong environmental changes and human disturbances. In contrast to the neighbouring Casamance and Sine Saloum estuaries, the Gambia estuary is free of major climatic perturbation and remains a "normal" estuary, with a salinity range from freshwater to 39. The present paper aims to study the spatial and seasonal variability of fish assemblages in this estuary in terms of bio-ecological categories and of their relation with some environmental variables. Four surveys were conducted, from June 2001 to April 2002, in order to cover the major hydroclimatic events, at 44 sampling sites along the lower, intermediate and upper zones of the Gambia estuary (up to 220 km). Fish assemblages were sampled using a purse seine net, fish were identified to species level and environmental variables such as water depth, transparency, salinity, temperature and percentage oxygen saturation were measured. The main spatial structure of the fish assemblages and its seasonal changes were first studied using the STATIS-CoA multitable method. The combination of fish assemblages and environmental variables was then analysed using the STATICO method, designed for the simultaneous analysis of paired ecological tables. A total of 67 species were observed, belonging to all bio-ecological categories characterizing West African estuaries. The marine component of the community was largely dominant throughout the estuary, while the freshwater component was permanently observed only in the upstream zone. The main spatial structure was a longitudinal gradient contrasting marine and freshwater affinity assemblages, with strong seasonal variations. The most complete gradient was observed in December, at the beginning of the dry and cool season, while in June, at the end of the dry and warm season, there was the least structured gradient. The role of salinity, always correlated with temperature, was emphasized, while turbidity appeared to be another important factor. Oxygen and depth did not play a major role at the estuary scale. The relative importance of the bio-ecological categories varied according to the season and the distance to sea. Stable fish assemblages were observed in the lower zone at the end of the dry season, in the upper zone during the flood and in the middle zone throughout the year. In some situations, a relative inadequacy between fish assemblages and their environment was noticed. The present study contributes to the definition of the functioning of a "normal" West African estuary, the Gambia estuary, with balanced effects of marine and freshwater influences and the presence of all bio-ecological categories. The Gambia estuary can therefore be considered to be a reference ecosystem for further comparisons with other tropical estuarine ecosystems, subjected to natural or artificial perturbations.

Keywords: brackishwater fish; community composition; seasonal variations; salinity gradients; environmental factors; multivariate analysis; West Africa; The Gambia

1. Introduction

In both tropical (Blaber, 2000) and temperate areas (Elliott and Hemingway, 2002), estuaries and coastal lagoons are ecosystems of great biological importance due to their role of interface between the freshwater and the marine environment, but they are also among the most modified and threatened of aquatic environments: the effects of fishing in particular, on the structure and functioning of estuarine environments were reviewed by Blaber et al. (2000), with case studies throughout the world.

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In West Africa, several studies were conducted in recent decades, in order to evaluate the effects of different types of perturbations due to human activities or climate modifications on estuarine environments and associated fish assemblages. The effects of fishing have been considered in Togo and the Ivory Coast (Laë, 1996; Albaret and Laë, 2003) and in Ghana (Koranteng et al., 2000). The impact of pollution on the environment itself, and on different compartments of the ecosystem, has been studied in the Ivory Coast (Dufour et al., 1994; Kouassi et al., 1995; Scheren et al., 2004). The impact of pollution on the fish compartment in particular has been demonstrated in the same area by Albaret and Charles-Dominique (1982) and Guyonnet et al. (2003). The effects of the major climatic stress were also the subject of some works, in Senegal, where the consequences of a drought period on the estuarine environment and associated fish assemblages were studied in the Casamance (Albaret, 1987) and the Sine Saloum estuaries (Albaret and Diouf, 1994; Diouf, 1996; Simier et al., 2004).

Difficulties in quantifying changes in estuarine fish communities, mainly result from two reasons: complexity of system dynamics, due to the high variability at different temporal and spatial scales, and the lack of reference conditions (a comparable pristine ecosystem, or a pre-perturbation situation). The reference to a preceding unspoilt situation is seldom possible, in particular for West-African estuarine ecosystems. This impossibility is due to the lack of long-term comparable data, and also because there are very few estuaries that can be used as an example of a non-impacted ecosystem.

The Gambia River estuary could be considered as a reference point for West Africa, for several reasons. It is one of the last aquatic ecosystems of this area that has not yet been affected by strong environmental changes and human disturbances. It is moderately exploited by small-scale fisheries (Laë et al., 2004) and does not receive any severe pollution from either agriculture or industrial activities. The Gambia River still has a natural flood regime with no dams or weirs. In contrast to the neighbouring Casamance and Sine Saloum estuaries, the Gambia estuary has been free of major climatic perturbation. It was less affected by the succession of drought periods experienced by the Sahel region since 1970 and consequently remained a ‘‘normal’’ estuary, with a salinity range from freshwater to 39.

Some studies on the Gambia River were conducted in the 1960s by Daget (1960), in the 1980s by Dorr et al. (1985) and Lesack (1986), and then more recently by Albaret et al. (2004), Guillard et al. (2004) and Vidy et al. (2004). The study by Albaret et al. (2004), using purse seine net sampling in the main channel of the Gambia estuary, aimed at a detailed description of environmental conditions and of adult and sub-adult fish diversity, abundance, distribution and community structure. The fluctuations of several environmental variables and the dynamics of the fish assemblages were described on a seasonal basis. It appeared that for the Gambia estuary, the total number of species may not be a good indicator of biodiversity, and that the diversity of life cycles and ecological categories may be more appropriate for evaluating the ‘‘health’’ of West African estuarine environments.

The present paper is a continuation of this first descriptive analysis of aquatic environment and fish assemblages. It aims to study the spatial and seasonal variability of fish assemblages in the Gambia estuary in terms of bio-ecological categories and of their relation with environmental variables, in order to better explain fish community structure and dynamics. These will usefully contribute to the definition of the functioning of a ‘‘normal’’ West African estuary and to further comparisons with other tropical estuarine ecosystems, especially those that are subjected to different kinds of perturbations such as pollution, hypersalinity and overfishing.

2. Materials and methods

2.1. Study area

The Gambia River is located in West Africa. It originates in the Fouta Djalon plateau of northern Guinea and flows 1200 km through Guinea, southern Senegal and The Gambia to the Atlantic Ocean (Fig. 1). The total area of the river basin is 78,000 km^2 (Lesack, 1986). The climate is of Sahelo-Sudanian type, dominated alternately by the dry harmattan wind, which originates in the Sahara and a southwesterly monsoon of humid oceanic air. Rains occur from June to October with the highest precipitation in August. Peak river discharge occurs in late September or October, with the rise and fall of discharge being rapid, declining to almost nil from December to the beginning of July (Lesack et al., 1984). The dry season is cool from November to March, and warm from April to June. The maximum flow of the Gambia River, at the end of the rainy season, is about 1500 m^3 s^{-1}, while the minimum dry season flow is less than 4.5 m^3 s^{-1}, both measurements taken at Gouloumbo (13°28′ N–13°44′ W) in Senegal (Lamagat, pers. commun.). Due to the very low flow during the dry season and the flat nature of the country’s terrain, the Gambia River is tidal, and thus saline, for much of its length. The position of the interface between the freshwater and saltwater varies with river flow. According to Daget (1960), tidal effects can be felt up to the Senegal–The Gambia border, but true brackish waters are located only in the last 180 km where tidal flood plains of mangrove swamps are found.

The study area extends from the mouth (Banjul: 13°25′ N; 16°34′ W) up to Deer Islands (220 km upstream: 13°41′ N; 15°08′ W). It includes three out of the five zones defined by Dorr et al. (1985): the lower and upper estuary and a part of the lower river zone (freshwater zone with a tidal influence). No vertical stratification was observed for salinity, but the longitudinal distribution of salinity showed marked seasonal changes: the brackish water zone extended from about 80 km in length in September to more than 220 km in June (Albaret et al., 2004). The study focuses on the main channel and excludes all tributaries and creeks (known locally as ‘‘bolongs’’), except for one large side branch, the Bintang bolong.

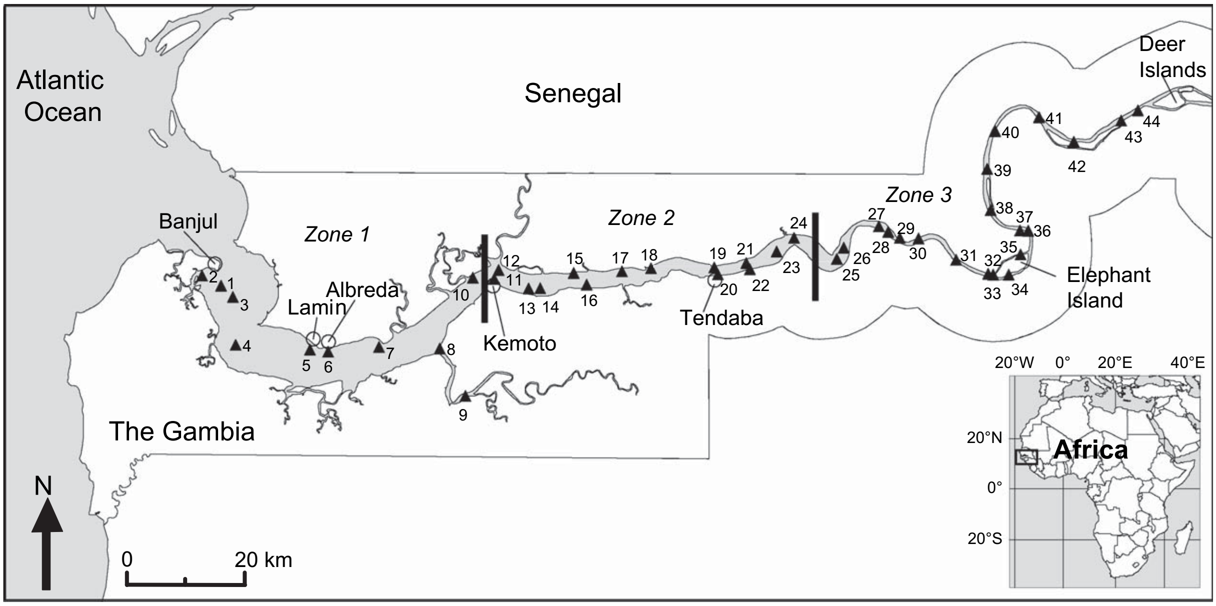

Fig. 1. Map of the Gambia estuary and the study area with location of the 44 sampling sites.

2.2. Sampling design

The surveys took place at four different hydrological periods in order to cover the major hydroclimatic events (Table 1): June 2001, September 2001, December 2001 and April 2002. A preliminary survey, conducted in November 2000, was not taken into account for the present work, because the sampling design was not totally fixed and several sampling sites were changed after it. 44 fishing sites were distributed throughout the whole study area and were located in as many types of environments as possible: right and left bank, middle of channel, various depths (up to 18 m which is the efficiency limit of the sampling technique), with or without nearby mangroves, confluences, etc. The sampling area and sites are shown in Fig. 1. The complete list of sampling sites with their geographical coordinates, distance to the sea and average depth is given by Albaret et al. (2004). All sites were sampled at each survey, except one site unusable in June 2001. According to Guillard et al. (2004), the study area was divided into three zones (Fig. 1):

1. The lower zone up to site 10 (Z1—68 km), under direct marine influence, with salinity always above 15.
2. The intermediate zone from site 11 to site 24 (Z2—52 km).
3. The zone upstream of site 25 (Z3—100 km), with the widest salinity range and therefore the greatest spatial and seasonal variations: from 0 to 25 at the lower end of the zone in the dry season.

Table 1
Summary of surveys

Survey code	Dates	Season	No. of sites
G2	2–12 June, 2001	End of dry and warm season, highest theoretical salinity	43
G3	16–25 September, 2001	Wet and flood season	44
G4	3–12 December, 2001	Start of dry and cool season	44
G5	12–24 April, 2002	Start of dry and warm season	44

2.3. Sampling technique

The fish assemblage was sampled using a purse seine net and using a protocol similar to that previously used in several West African estuarine and lagoon fish community surveys: the Ebrié lagoon in the Ivory Coast (Albaret, 1994; Ecoutin et al., 2005), the Fatala River estuary (Baran, 1995) and Sine Saloum delta in Senegal (Diouf, 1996; Simier et al., 2004). The net was 250 m long, 20 m deep and had a 14 mm mesh. It was deployed by nine trained fishermen, from a large motorized canoe without any surface fish search, in order to provide a reproducible sampling unit: one seine haul. The falling speed was increased by adding additional weights to the lead line.

2.4. Data collected

2.4.1. Biological data

For each seine haul, fish were identified to species level, counted and weighed. Among the 70 species listed by Albaret et al. (2004), only 67 were considered in the present work, because 3 species (*Hydrocynus brevis*, *Liza dumerili* and *Nematogobius maindroni*) were identified only during the preliminary survey in November 2000. These 67 species were classified into the eight bio-ecological categories defined in the West African estuarine and lagoon fish communities (Albaret, 1999). These categories are distributed on two gradients from a central point: the strictly estuarine species (Es). The gradient of marine affinity comprises four categories: the estuarine species of marine origin (Em), the marine-estuarine species (ME), the marine species accessory in

Table 2
List of the 67 species ordered by bio-ecological categories from the most freshwater-affinity to the most marine-affinity category. Co, freshwater species occasional in estuaries; Ce, freshwater species with estuarine affinities; Ec, estuarine species of freshwater origin; Es, strictly estuarine species; Em, estuarine species of marine origin; ME, marine-estuarine species; Ma, marine species accessory in estuaries; Mo, marine species occasional in estuaries

Bio-ecological categories	Species names
Co	*Alestes baremoze*
Co	*Brycinus nurse*
Co	*Clarias anguillaris*
Co	*Hyperopisus bebe*
Co	*Mormyrops anguilloides*
Co	*Synodontis batensoda*
Ce	*Chrysichthys johnelsi*
Ce	*Schilbe intermedius*
Ce	*Synodontis gambiensis*
Ec	*Chrysichthys maurus*
Ec	*Chrysichthys nigrodigitatus*
Ec	*Pellonula leonensis*
Es	*Bostrychus africanus*
Es	*Gerres nigri*
Es	*Monodactylus sebae*
Es	*Porogobius schlegelii*
Es	*Sarotherodon melanotheron*
Es	*Tilapia guineensis*
Es	*Tylochromis jentinki*
Em	*Citharichthys stampflii*
Em	*Cynoglossus senegalensis*
Em	*Dasyatis margarita*
Em	*Dasyatis margaritella*
Em	*Ethmalosa fimbriata*
Em	*Ilisha africana*
Em	*Liza falcipinnis*
Em	*Liza grandisquamis*
Em	*Plectorhinchus macrolepis*
Em	*Pomadasys jubelini*
Em	*Pomadasys perotaei*
Em	*Pseudotolithus elongatus*
Em	*Strongylura senegalensis*
Em	*Trachinotus teraia*
ME	*Arius latiscutatus*
ME	*Arius heudelotii*
ME	*Arius parkii*
ME	*Brachydeuterus auritus*
ME	*Caranx hippos*
ME	*Caranx senegallus*
ME	*Chloroscombrus chrysurus*
ME	*Drepane africana*
ME	*Elops lacerta*
ME	*Ephippion guttifer*
ME	*Eucinostomus melanopterus*
ME	*Galeoides decadactylus*
ME	*Mugil bananensis*
ME	*Mugil cephalus*
ME	*Polydactylus quadrifilis*
ME	*Pseudotolithus brachygnathus*
ME	*Pseudotolithus typus*
ME	*Pteroscion peli*
ME	*Sardinella maderensis*
ME	*Sphyraena afra*
ME	*Sphyraena guachancho*
ME	*Trichiurus lepturus*
Ma	*Batrachoides liberiensis*
Ma	*Chaetodipterus lippei*
Ma	*Hypacantus amia*
Ma	*Pentanemus quinquarius*
Ma	*Pseudotolithus senegalensis*
Mo	*Dasyatis ukpam*
Mo	*Gymnura micrura*
Mo	*Hemicaranx bicolor*
Mo	*Pisonodophis semicinctus*
Mo	*Synaptura cadenati*
Mo	*Tylosurus acus rafale*
Mo	*Umbrina ronchus*

estuaries (Ma) and the marine species occasional in estuaries (Mo). The gradient of freshwater affinity comprises the estuarine species of 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 estuarine community. The list of all 67 species, ordered by bio-ecological categories, is given in Table 2.

2.4.2. Environmental data

During the fish sampling, the following environmental data were collected for each seine haul: water depth (m) with a hand-sounder, water transparency (cm) using a Secchi disk of 30 cm diameter, surface salinity measured with an optical refractometer, surface temperature (°C) measured with a thermometer and surface percentage oxygen saturation with a YSI multi-parameter probe. A detailed description of environmental conditions is given by Albaret et al. (2004).

2.4.3. Data processing

Two series of data tables were built: one for environmental variables and one for species abundances. Each pair of tables corresponds to the information collected during a survey. All the species abundance tables shared the same species (in columns), and all the environmental variables tables had the same variables (in columns). The sampling sites (in rows) were the same for the two tables of one pair, but they varied slightly between the pairs due to the unusable haul in June 2001.

2.4.3.1. The stable part and seasonal changes in the spatial structure of fish assemblages. As a first approach, the series of site-species abundance tables was studied using STATIS-CoA, the Correspondence Analysis version (Gaertner et al., 1998) of the STATIS method (Lavit et al., 1994), previously used by Simier et al. (2004) for a similar study in the Sine Saloum estuary. This method was used (1) to describe the common structure of the series of site-species abundance tables (called the "stable part" of the spatial structuring of the fish assemblages) and (2) to study the variability of each table compared to the common structure.

As the number of rows was not the same for each survey, a preliminary stage consists of calculating for each survey (k) a matrix of scalar products between species, in order to standardize the dimensions of the k tables. The first stage (called "interstructure") of the STATIS-CoA method provides a comparison between surveys by calculating a matrix of inter-matrix scalar products. The diagonalization of this matrix is carried out. The k coefficients of the first eigenvector are then used to weight the k matrices of scalar product between species with the aim of constructing an average matrix of maximum inertia called the "compromise" table. The diagonalization of the compromise table constitutes the second stage of the STATIS-CoA analysis. It defines axes and components that express the stable part of the spatial structure throughout the surveys by giving an average position of the species on factorial axes. The third step (called "trajectories") consists of analysing the reproducibility of the compromise for each survey, showing how the shared structure is taken into account by each table. This is done by projecting the rows of the k initial tables (i.e. the sites) as supplementary elements onto the compromise axes.

2.4.3.2. The stable part and seasonal changes in the relationship between fish assemblages and environmental variables. In a second analysis, the series of species abundance tables was coupled with the series of environmental variable tables using the STATICO method (Simier et al., 1999; Thioulouse et al., 2004), in order to analyse the relations between fish assemblages and environmental conditions. Fig. 2 presents a summarized flow chart of STATICO as a three-step method:

1. Each table is first analysed by a basic analysis (CoA for species abundance tables and PCA for environmental tables).
2. Each pair of tables is then linked by a Co-inertia analysis (Dolédec and Chessel, 1994; Dray et al., 2003). Co-inertia analysis is a two-table coupling method, which allows a cross-table to be computed between the variables of the two tables (here between species and environmental variables).
3. A partial triadic analysis (PTA, Thioulouse and Chessel, 1987; Blanc et al., 1998) is used to analyse the series of species and environmental variables cross-tables. The aim of PTA is to identify the shared structure of a series of tables having same rows and same columns. This analysis belongs to the family of the STATIS methods. Like the STATIS-CoA method, PTA comprises three steps: the interstructure, the compromise and the trajectories. In this study, the "compromise" step gives an ordination of the species and of the environmental variables on shared axes, showing the stable part of the species–environment relationships. In the "trajectories" step, species and environmental variables for each survey are projected as additional elements on the compromise axes in order to summarize the reproducibility of the structure across the series of cross-tables. Moreover, sampling sites can also be projected as supplementary elements on the same axes, showing the ordinations of sites across the series of both species abundance and environmental tables.

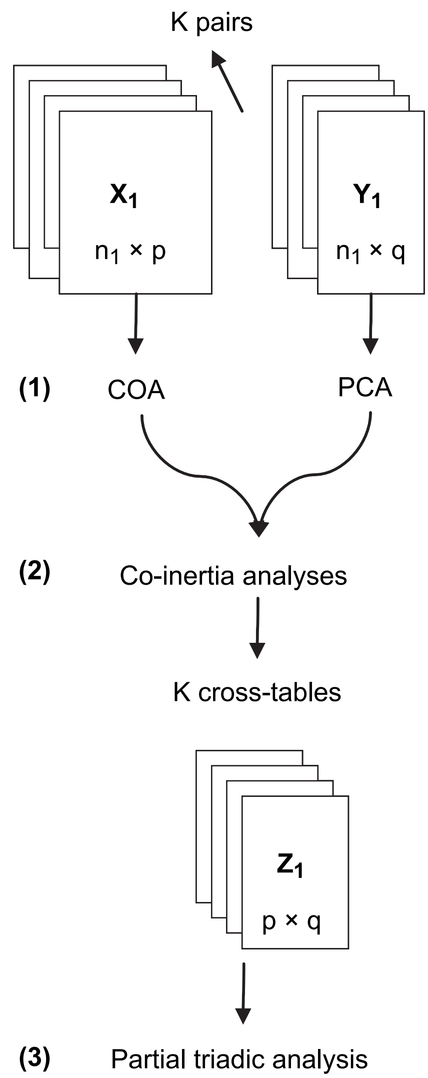

Fig. 2. STATICO flow chart. The data structure is a sequence of K paired ecological tables. X_k and Y_k are respectively the species and environmental tables in the pair. Z_k is the kth cross-table. p is the number of species, q is the number of environmental variables, nk is the number of rows in the kth pair of tables. (1) Basic analyses (PCA for environmental tables and COA for species abundance tables) are performed on each table. (2) Co-inertia analyses allow linkage of the pairs of PCA-COA, producing a sequence of cross-tables. (3) PTA is finally used to analyse this sequence.

As proposed by Ecoutin et al. (2005), species were grouped into bio-ecological categories in the graphic representations of both the STATIS and STATICO analyses, and sites were generally not represented by their codes, but were grouped together in zones.

3. Results

3.1. Spatial structure and seasonal variability of fish assemblages

3.1.1. Composition of fish assemblages

A total of 67 species were observed during this study of the Gambia estuary and all eight bio-ecological categories defined by Albaret (1999) were well represented. Table 3 gives the

Table 3
Percentage in number of individuals for each category per survey and per zone

Survey	Zone	Co	Ce	Ec	Es	Em	ME	Ma	Mo
June 2001	1	0.00	0.00	0.00	0.05	87.89	6.96	4.96	0.14
	2	0.00	0.00	0.34	0.17	95.04	4.19	0.20	0.06
	3	0.00	3.26	1.12	1.41	81.95	10.40	1.86	0.00
September 2001	1	0.00	0.03	0.19	0.41	82.95	15.04	1.36	0.03
	2	0.00	11.67	1.00	0.33	83.08	3.08	0.75	0.08
	3	33.84	31.71	2.99	0.24	28.60	2.62	0.00	0.00
December 2001	1	0.00	0.00	0.02	0.11	79.23	19.81	0.80	0.03
	2	0.00	0.36	0.28	0.55	95.79	2.54	0.23	0.25
	3	0.85	33.75	2.04	0.23	60.53	2.60	0.00	0.00
April 2002	1	0.00	0.00	0.00	0.74	65.11	28.84	5.00	0.31
	2	0.00	0.00	0.57	0.22	89.58	9.09	0.42	0.13
	3	0.31	8.35	1.72	0.96	84.50	2.78	1.27	0.12

percentage in number of individuals for each bio-ecological category per survey and per zone. Whatever the survey or the zone, the fish assemblages were clearly dominated by the estuarine species of marine origin (Em) which represented 60–96% of fish numbers, except in the upstream zone in September (only 29%). The strictly estuarine species (Es) were always present but they represented very small numbers (generally less than 1%). The estuarine species of freshwater origin (Ec) also represented small numbers of individuals (maximum 3% in September in the upstream zone). The freshwater component of the community was mainly represented by the freshwater species with estuarine affinities (Ce), permanently observed in the upstream zone: 32–34% in September and December, 8% in April and only 3% in June. This category was also present in the intermediate zone in December (0.4%) and particularly in September (12%). The Co category (freshwater species, occasional in estuaries) was only observed in the usptream zone. It was especially abundant in September (34%), and rare in April and December (less than 1%). Among the marine component of the community, marine-estuarine (ME) species were abundant (always more than 2.5% of fish numbers), especially in the downstream zone (7% in June, 15% in September, 20% in December and 29% in April). The marine species accessory in estuaries (Ma) were also especially abundant in the downstream zone (5% in April and in June) and totally absent from the upstream zone in September and December. The marine species occasional in estuaries (Mo) were always present but in very small numbers (<0.3%).

3.1.2. Spatial structure of fish assemblages

The first two axes of the compromise analysis explained 17.2% of total inertia (Fig. 3A). The compromise factor plot of fish species (Fig. 3B) showed a gradient of species, with freshwater affinity species (Co, Ce and Ec categories) on the right side, and marine affinity species (Mo, Ma, ME and Em categories) on the left side. The strictly estuarine (Es) species were scattered but the average position of the group was intermediary, between the freshwater and marine species, corresponding to its central position in the classification proposed by Albaret (1999). The Ma and Mo categories were

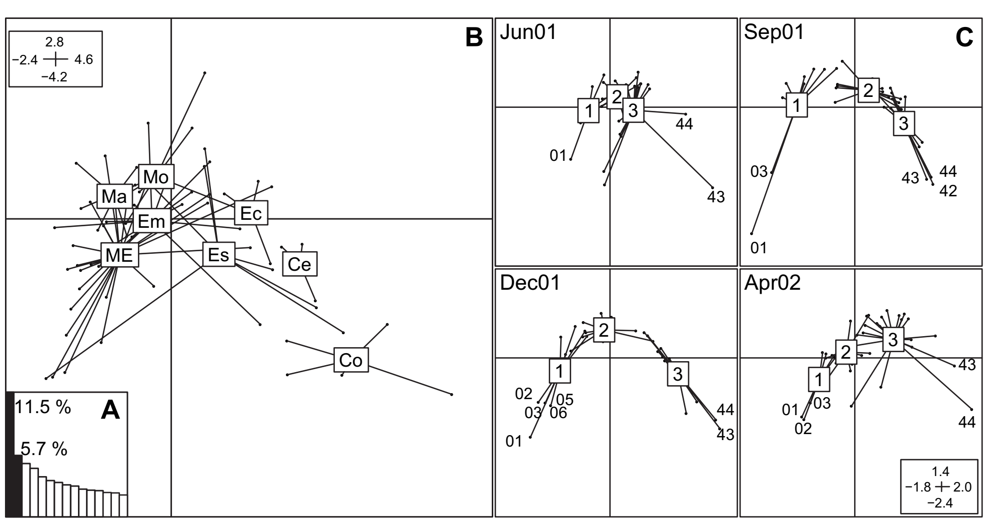

Fig. 3. STATIS-CoA of the series of fish abundance tables, compromise step. (A) Eigenvalues diagram. (B) Factor plot of species (dots) with average positions of bio-ecological categories. (C) Projection of the coordinates of the 44 sites grouped by zones (1: downstream, 2: intermediate, 3: upstream). The four surveys have been plotted on four separate graphs. For (B) and (C), the scale is given in the rectangular box. Labels are given only for outlying sites.

surprisingly not positioned at the extremity of the gradient. This could be explained by the small number of individuals observed for species belonging to these categories.

3.1.3. Seasonal variability of fish assemblages

Fig. 3C shows the trajectory factor plots of the sites. These factor plots need be interpreted in relation with the factor plot of the compromise of fish species (Fig. 3B) because the axes are the same. On the whole the factor plots showed a longitudinal gradient of sites, related to the species gradient. Whatever the date, the most upstream sites 43 and 44, were clearly apart at the freshwater extremity of the gradient. In contrast, site 1 was consistently located on the marine side, isolated in June, associated with site 3 in September, with sites 2, 3, 5 and 6 in December, and with sites 2 and 3 in April. This is related to the existence of a typical community in the lower zone of the estuary, which was limited to the immediate vicinity of the estuary mouth or extended up to 30 km upstream, depending on the season.

June had the least structured gradient: fish assemblages showed no clear longitudinal pattern and the three zones were poorly separated on the graph. At this period of the year, the freshwater component was at its minimum, with only 3% of freshwater species with an estuarine affinity (Table 3), while the marine component, in particular the marine-estuarine category, was better represented in the upstream zone (10%) than in the downstream zone (only 7%).

In September, the longitudinal gradient was clearly expanded. The influence of the flood was at its maximum, with a large proportion of freshwater species in the upstream zone (32% Ce and 34% Co), but also in the intermediate zone (12% Ce), which was projected on the ‘‘freshwater’’ side of the gradient. In contrast, in the downstream zone, the estuarine of marine origin (Em) and marine-estuarine (ME) species represented 98% of the abundances.

The most complete gradient was observed in December due to the presence of both marine and freshwater components, respectively in the downstream zone and in the upstream zone. Species of marine origin dominated in the downstream zone (20% of individuals were marine-estuarine species) and species of freshwater origin in the upstream zone (34% of individuals were freshwater species with estuarine affinity). The intermediate zone, clearly dominated by the estuarine of marine origin (Em) category (96%), was shifted to the ‘‘marine’’ side of this gradient, with only two sites presenting freshwater affinity assemblages.

In April, during the dry and warm season, the freshwater component of the gradient was considerably reduced because the abundance of freshwater species had dramatically decreased in the upstream zone, except in a few sites: only 8% of freshwater species with estuarine affinity and almost no freshwater species occasional in estuaries. In contrast, the abundance of marine species increased, with 29% of marine-estuarine species and 5% of marine species accessory in estuaries in the downstream zone, and 9% of marine-estuarine species in the intermediate zone.

3.2. Combination of fish assemblages and environmental variables

3.2.1. Spatial structure

The factor plots of the first two axes of the compromise analysis are shown in Fig. 4, for the environmental variables (Fig. 4B) and for the fish species (Fig. 4C). The eigenvalues diagram (Fig. 4A) shows that the first axis was clearly dominant (77.4%).

Salinity and temperature were opposed on the first axis. Transparency was positively correlated with salinity. This first axis was therefore a salinity gradient, with relatively cold (24 °C), saline (39) and transparent (1.8 m) water on the right, and warm (32 °C), turbid (0.1 m) and low salinity (freshwater) water on the left. The percentage oxygen saturation was not well represented on this factorial plane, but it seemed to be correlated with salinity and transparency. The depth was

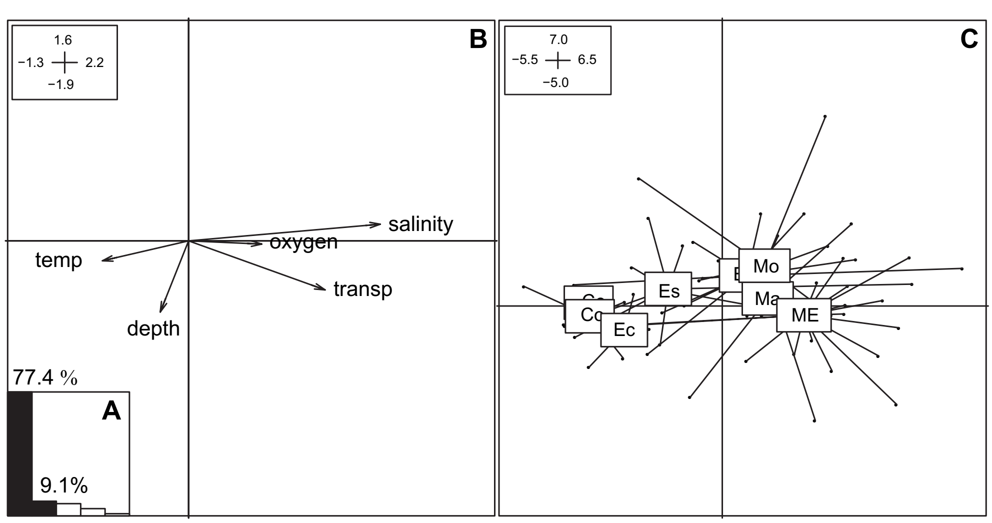

Fig. 4. Compromise step of the STATICO analysis. (A) Eigenvalues diagram. (B) Environmental variables projected on the first factorial plane (1–2). (C) Fish species projected on the same factorial plane. The scales for axes are given in the rectangular boxes.

correlated with the second axis, which was much less significant (9.1%) than the first one.

There was a clear gradient in the distribution of species, with freshwater affinity species (Co, Ce and Ec categories) on the left side and marine affinity species (Mo, Ma, ME and Em categories) on the right side, as in the previous STATIS-CoA analysis.

As a result, the stable part of the species–environment relationships mainly consisted of a combined salinity, turbidity and temperature gradient linked to a freshwater-marine gradient of the species. The freshwater component of the community was associated with warm, turbid and low salinity water, while the marine component was characteristic of colder, saline and transparent water. Environmental variables such as oxygen and depth did not play a major role in the organization of species assemblages in the Gambia estuary at an overall level.

3.2.2. Seasonal variability

For each survey, the projection on the compromise axes of the five environmental variables (left) and of the 67 species grouped by bio-ecological category (right) is shown in Fig. 5. The stable part of the species-environment dynamics revealed by the compromise analysis was well expressed by the September and December surveys. The June survey however, showed a very different gradient, the line bisecting the origin on the plane 1–2, with transparency opposed to salinity and oxygen, and no clear contrast between freshwater and marine affinity species. At an annual scale, two main environmental phenomena influencing the fish assemblages could therefore be distinguished: throughout the annual cycle, the most stable structuring factor was the salinity gradient, inversely correlated with the temperature gradient. Ecological categories, from the most marine to the highest freshwater affinity, were logically distributed along the longitudinal gradient determined by these two factors. Transparency, though positively correlated with the salinity gradient in December and September, became less correlated during the dry season (April), and inversely correlated in June.

The projection of the sampling sites on the compromise axes, in terms of both environmental and faunistic structure is shown on Fig. 6 for each survey and each zone.

In the lower zone (zone 1) the sites were mostly projected on the right-hand side of the first axis, characterized by the highest salinity and the marine affinity of fish communities. From an environmental point of view only one site (9) was regularly projected on the left-hand side of the first axis. This site was located in the Bintang ‘bolong’, a tributary of the main channel, and was less under marine influence than the others sites of the lower zone. The spatial heterogeneity of this zone was lowest in June and high during the flood in September, especially in terms of the fish assemblages. The arrows were mostly short, expressing a good coincidence between environmental and faunistic structure except in the September survey, particularly in site 1 situated at the mouth of the estuary.

The sites located in the intermediate zone (zone 2) were grouped in the central part of the first axis and in the positive part of the second axis. This position was related to the depth: the smallest values were observed in this zone (6.0 m on average, compared to 7.3 m for the lower zone and 8.0 m for the upper zone). On the first axis, the environmental points (origin of arrows) were located differently according to the date: on the left for the September survey, on the right for the April survey; and more central for the June and December surveys. Whatever the date, the faunistic points (end of arrows) were more stable than the environmental points, expressing the steady establishment of the fish assemblages in this zone, in spite of the high environmental variability (salinity in particular).

The sites from the upstream zone (zone 3) were projected on the left-hand side of the first axis, corresponding to freshwater with the warmest temperatures and freshwater affinity fish communities. In contrast to what happens in the lower zone, in September and December, sites from zone 3 were

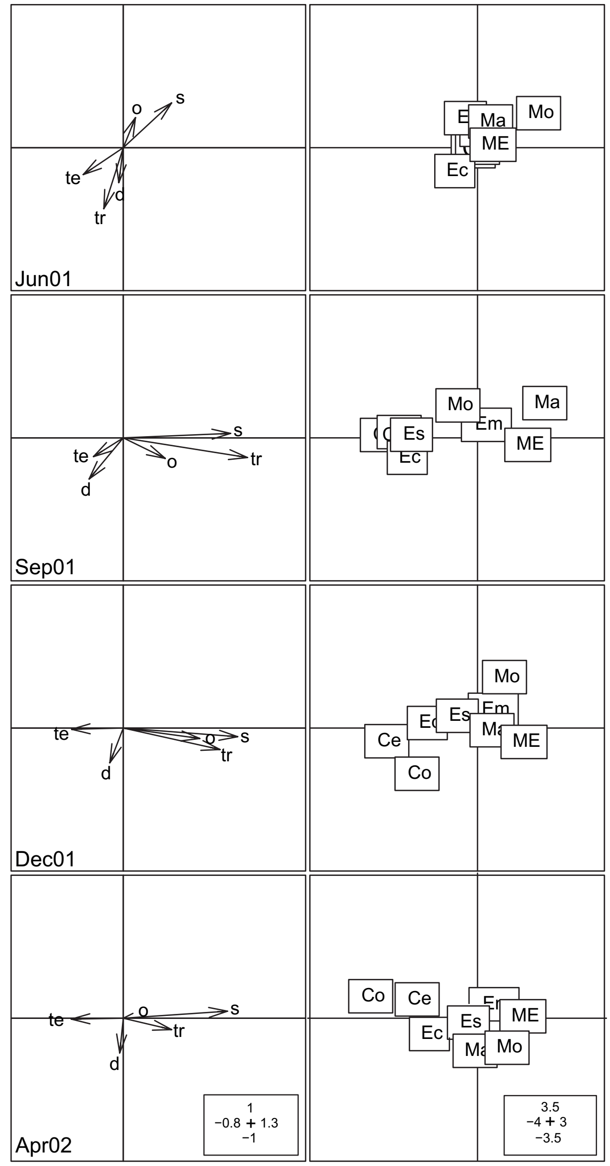

Fig. 5. Trajectories factor plots of the STATICO analysis: on the left column, projection of the five environmental variables on the first factorial plane (s, salinity; tr, transparency; o, oxygen; te, temperature; d, depth), and on the right, projection of the average positions of bio-ecological categories of species. The four surveys have been plotted on four separate graphs. The scales for axes are given in the rectangular boxes.

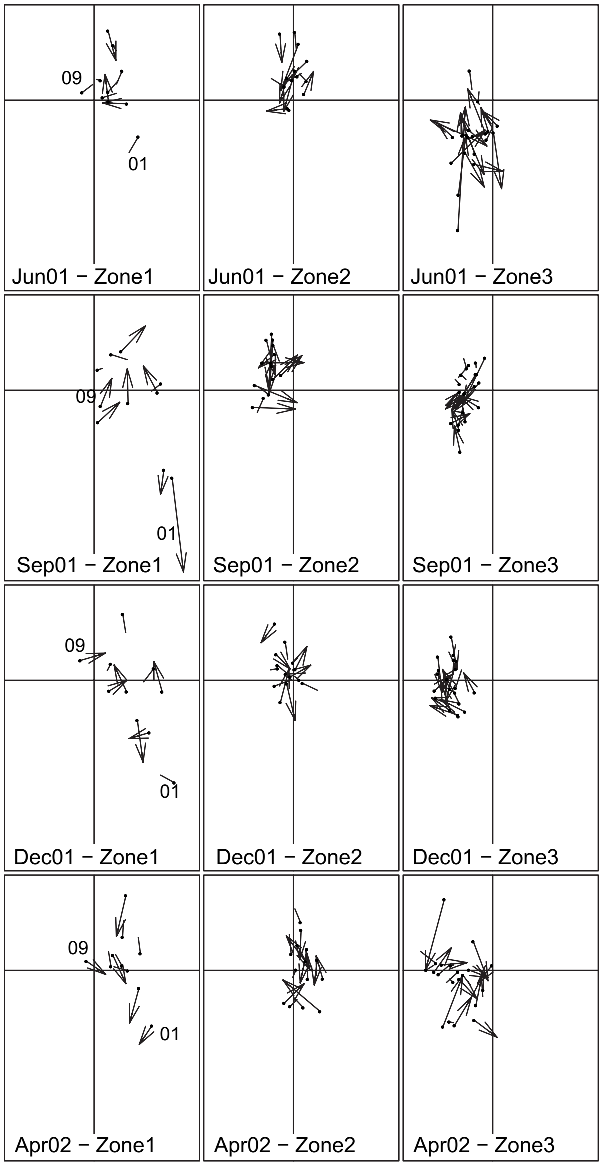

Fig. 6. Trajectories factor plots of the STATICO analysis: projection of the sampling sites on the first factorial plane of the compromise analysis, for each survey and each zone. Each site is represented by a couple of points corresponding to both environmental and faunistic tables. An arrow is drawn to enhance readability: the environmental position is at the origin of the arrow, the species position at the end. The limits of axis 1 go from −2.5 to 3; the limits of axis 2 go from −6 to 3. Labels are given only for outlying sites.

grouped together and the arrows were short, expressing a very stable environment and fauna, under the direct influence of freshwater. In June and April, however, there was a strong dispersion of the environmental points and a poor fit between the fauna and environment (long arrows).

4. Discussion

4.1. Selectivity of the purse seine sampling

The water depth in the Gambia River estuary was generally less than the seine depth (Albaret et al., 2004). Furthermore, in this study, the falling speed of the purse seine net was increased by adding additional weights to the lead line. The risk of avoidance by fish was consequently reduced and adhesion to the bottom was improved, so that fish could not escape while the seine was hauled. Thus, the purse seine sampling could be considered as a low-selective fishing gear. All species present in the sampling sites could potentially be caught, except very small fish, smaller than the mesh size (14 mm). Even flat fish such as *Cynoglossus senegalensis* and *Citharichthys stampflii* were regularly caught by the purse seine net. However, this fishing method is representative of open water areas, i.e. the main channel of the estuary, which is large enough to allow purse seine use. It is not well suited for mangrove habitats sampling, especially small mangrove channels. Thus, species living preferently in mangrove habitats were probably under-represented. A survey of the juvenile and small fish assemblage was conducted at the same period in lateral channels of the Gambia estuary using small meshed fyke-nets (Vidy et al., 2004). Most of the 51 species listed in this study were also caught by purse seine sampling. Among the most abundant species in fyke-nets, only the mudskipper *Periophthalmus barbarus* and very small species like *Aplocheilichthys spilauchen* and *Dormitator lebretoni* never occurred in purse seine sampling.

4.2. Number of species and composition of fish assemblages

The 67 species observed during this study of the Gambia estuary were collected with a sampling effort of 175 seine hauls distributed over 44 sites at four dates. If the preliminary survey is included, three more species can be added to this list. This result has to be compared first to those observed in other West African estuaries and lagoons using the same sampling technique. In the neighbouring inverse estuary of the Sine Saloum (Senegal), up to 73 species were captured in a less extensive study: 96 seine hauls over 16 sites and six surveys (Simier et al., 2004). In the Ebrié Lagoon (Ivory Coast), 64 species were listed by Ecoutin et al. (2005), for a higher number of sites but only two surveys: 53 sites in the dry season and 55 sites in the wet season. The salinity regime is one of the main differences between these three estuarine systems: in the Sine Saloum delta, the salinity was generally greater than that of seawater (range 30–55), while in the Ebrié lagoon, it was often less than 5 and never higher than 32. In the Gambia estuary, salinity values range from 0 to 39, with marked seasonal fluctuations.

A world-wide review by Blaber (2002) underlined that most medium to large subtropical and tropical estuaries have much greater numbers of fish species than temperate ones: at least 100 species, with some reaching more than 200. Estuary size and diversity of habitats appear as the most important factors in relation to species diversity: deep open water channels favour larger species, especially those of marine origin, and larger systems provide a higher diversity of habitats. The species richness appears greater in the Indo-West Pacific area (generally more than 100), even in small estuaries, than in the East and West Atlantic areas (less than 100). In a recent study of fish assemblages of the main channel of the Caete River estuary, Brazil, 82 fish species were collected in 270 samples using otter trawl (Barletta et al., 2005). In a shallow tropical estuarine system of Mexico (Castillo-Rivera et al., 2002), 66 species were recorded using seine net. The number of species recorded in the Gambia estuary (70) consequently appears relatively low regarding the world-wide average species richness of medium to large tropical estuaries, but it is consistent with the other species numbers recorded in the East and West Atlantic areas.

While the number of species is the most commonly used parameter to summarize a fish community, the observed value of this parameter is an underestimation of the true number of species. The error involved depends on sampling effort (Ramos Miranda et al., 2005), which must be taken into account when comparing fish assemblages from other parts of the world using different sampling techniques.

With respect to the composition of the assemblages in terms of the bio-ecological categories the marine component of the community (Mo, Ma, ME, Em) was largely dominant in the Gambia estuary, with 49 out of 67 species. The marine-estuarine (ME) category was the best represented in terms of numbers of species, (22 species, 11% of fish numbers) while the estuarine of marine origin category (Em), was the most abundant (15 species, 80% of fish numbers). The marine species, occasional or accessory in estuaries (Mo and Ma) are represented by 15 species, accounting for only 1.4% of the fish numbers. In the Sine Saloum estuary (Simier et al., 2004), the fish assemblages were even more largely dominated by the marine component with 69 of 73 species: ME (21 species, 79% of numbers), then Em (16 species, 18% of numbers), and especially Ma and Mo (32 species, 0.6% of numbers). Due to the lack of river freshwater input, the freshwater affinity component was totally absent from this ecosystem and the strictly estuarine species (Es) were few. Consequently, the higher number of species observed in the Sine Saloum estuary can be attributed to the marine species accessory or occasional in estuaries which had a high diversity but accounted for a very small proportion of the fish numbers. In the Ebrié lagoon, no marine occasional (Mo) species was observed and the distribution of the seven marine accessory (Ma) species was limited to the area close to the communication with the sea. In contrast, 11 freshwater species occasional in estuaries (Co) or with an estuarine affinity (Ce) were observed but they were restricted to the most distant areas from the sea.

The composition of the fish assemblages in the Gambia estuary therefore appears to be intermediate between that of the Sine Saloum estuary, almost totally dominated by the marine affinity component and with no freshwater affinity species, and of the Ebrié lagoon, with very scarce marine species and a more marked freshwater influence than the Gambia estuary. It is the only ecosystem of the three where all the eight categories defined by Albaret (1999) are present. However, as already quoted by Albaret et al. (2004), the number of fish species is incontestably the lowest of the three ecosystems when related to the sampling effort. This was unexpected, in view of several criteria favouring high biodiversity such as its tropical situation (Whitfield, 1994a,b), a wide range of hydrological situations, the diversity of habitats and the fact that the Gambia is an extensive estuary with large, permanent interfaces with the Ocean and the Gambia River which both offer a rich potential for colonization of the estuary by fish. Possible explanations for this can be the high seasonal variability of the environmental conditions and the natural disturbance imposed on the system by extensive flooding, and the lack of permanent marine conditions within the estuary, except in the immediate vicinity of the mouth. Most West African estuarine systems have highly perturbed catchments but also possess large zones under permanent marine influence that enable marine taxa (mainly ME) to colonize and settle in the estuary. In West Africa the number of marine species likely to enter estuaries considerably exceeds the number of freshwater species capable of living even temporarily in the estuary. A strong freshwater influence does not compensate for a weak marine influence and even in the strongly freshwater-influenced Gambia estuary, the species of marine origin constitute the majority of the species reported (Albaret et al., 2004).

4.3. Spatial structure and seasonal variability of fish assemblages

The main spatial structure identified by the analysis of the fish abundances and summarized in Fig. 3, was a longitudinal gradient opposing marine-affinity assemblages in the lower zone, to freshwater-affinity assemblages in the upper zone. The marine component was widely distributed throughout the year in the Gambia estuary, and generally dominant whatever the zone and the season, except in the upper zone during the flood. In contrast, the freshwater-affinity component, mainly represented by the freshwater with estuarine affinity category (Ce), had a limited spatio-temporal distribution. This component was permanent in the upper zone only, and extended to the intermediate zone during the September flood and the following months (December). This strong longitudinal organization, obviously related to the linear shape of the estuary, varied considerably depending on the season.

The most complete gradient was observed in December, at the beginning of the dry and cool season, and was related to two environmental conditions: after the end of the wet and flood season, salinity was in an ascendant phase, which explains the dominance of the marine component in the lower zone, while freshwater was still present in a large upper part of the estuary where it allowed the presence of freshwater-affinity species. As a consequence, December could be considered, in terms of bio-ecological categories, as the most complete and typical (as a representation of a ‘‘normal’’ tropical estuary model) period of the year, with a combination of strong marine influence in the lower zone and freshwater influence in the upper zone.

June, at the end of the dry and warm season, had the least structured gradient because it is a period of ecological disruptions: the first rain showers appear, but the salinity is still at its highest (no zero salinity measured in the estuary even at

220 km from the mouth) and the marine affinity species dominate fish assemblages. As a consequence of the lack of freshwater inputs at this period of the year, the freshwater-affinity component was at its lowest and the Co category was even totally absent from the fish assemblages. In addition, the proportion of marine-estuarine species was higher in the upper zone than in the lower zone. As a consequence, there was no clear longitudinal gradient, in contrast to the other dates. These results were in agreement with those from Albaret et al. (2004), who identified a stable number of about 50 species throughout the year, except in June when it dramatically decreased to 40.

Between these two dates, September and April showed intermediate spatial organizations, where a greater place was given respectively to the freshwater or marine component of the gradient. In September, at the end of the wet and flood season, a large part of the estuary was desalinated and turbid. The freshwater affinity component increased (69% of fish numbers in the upstream zone) and moved down in the estuary as far as the lower zone (Ce and Ec categories). The marine affinity component was at its lowest and was mainly located in the downstream zone. April corresponded to the dry and warm season: the percentage of marine-affinity species increased and re-settled in the lower and intermediate zones while the freshwater-affinity component was at its lowest and limited to the upper sites. These two situations were expressed in Fig. 3C: in September the lower zone was opposed to an intermediate-upper zones continuum, while in April the upper zone was distinguished from a lower-intermediate zones continuum.

The similar analysis conducted in the Sine Saloum estuary (Simier et al., 2004) revealed a very different spatio-temporal pattern, mainly related to the hydroclimatic conditions and the delta shape of the estuary. The fish assemblages were stable over an annual cycle but a strong spatial organization was identified and three kinds of assemblages were characterized: (1) the open water assemblages located in the main channel of the Saloum and subjected to large but irregular fluctuations due to the occasional presence of large schools of pelagic species; (2) the mouth assemblages, with a very low diversity; and (3) the shallow water assemblages, mainly constituted by estuarine and for many of them sedentary species, which were present throughout the year. In the Ebrié lagoon system (Ecoutin et al., 2005), like in The Gambia, there was a true wet season with the flood of the Comoé River and several coastal rivers. A freshwater-marine affinity gradient was shown from both eastern and western ends to the central area where the connection to the sea takes place. Two particular zones were identified. The Aghien lagoon, at the eastern end of the system, was characterized by freshwater affinity assemblages whatever the season, due to the permanently freshwater conditions. The other area, near the connection to the sea, was permanently under marine influence and more or less extensive according to the season. It was characterized by unstable and poorly structured assemblages of marine-affinity species, mainly schools of small pelagic species. These two extreme situations can be compared respectively to the most upstream part of the Gambia estuary (sites 43, 44) and to the mouth area (site 1, associated with sites 2, 3, 5 and 6 according to the season).

4.4. Fish assemblages and environmental variables

The effects of the physicochemical water properties (temperature, salinity, dissolved oxygen, water transparency etc.) on the distribution, abundance, and composition of fish communities in estuarine ecosystems have been studied by several authors in both temperate (Young et al., 1997; Marshall and Elliott, 1998; Paperno and Brodie, 2004) and tropical and sub-tropical environments (Blaber and Blaber, 1980; Cyrus and Blaber, 1992; Winemiller and Leslie, 1992; Castillo-Rivera et al., 2002; Rueda and Defeo, 2003; Barletta et al., 2005). Separating and evaluating the influences of each parameter remains one of the most difficult challenges because many are correlated with one another (Blaber, 2002).

In the Gambia estuary, the simultaneous analysis of fish abundances and environmental variables emphasized the preponderant role of salinity in the longitudinal structuring of fish assemblages throughout the year. Temperature was always inversely correlated with salinity. Transparency, however, appeared to be a different structuring factor, directly correlated with the salinity gradient during the flood and the following months (September, December), but becoming less correlated and even opposed to salinity during the dry season. In consequence, in September and December, the marine component of the fish assemblages corresponded to saline, transparent and relatively cold waters, while the freshwater-affinity component was observed in non-saline, turbid and warmer waters. In June, this gradient was strongly modified since the transparency became highest in the upstream zone where the salinity was the lowest. Consequently, at this period of the year, the freshwater-affinity assemblages were observed in the most transparent waters, while the marine-affinity component corresponded to relatively turbid waters. Environmental variables such as oxygen and depth did not play a major role in the overall organization of species assemblages in the Gambia estuary but may be important at a local scale.

The positive correlation between salinity and transparency found in the Gambia estuary during the wet season partly confirms for tropical areas the results from Marshall and Elliott (1998) in the temperate Humber Estuary (U.K.): negative correlation between salinity and turbidity. In the same study, multivariate analyses of the environmental influences on the fish assemblage indicated that salinity and temperature were the dominant factor influencing the distribution of species, while the effects of turbidity were negligible.

In tropical areas, with marked seasonal variability of the freshwater inputs, salinity and transparency are frequently quoted as the main environmental factors liable to influence the spatial organization of the fish assemblages and its seasonal fluctuations. Temperature is seldom a structuring factor, since it remains relatively stable during the whole year. Thus, in a tropical northern Australian estuary (Cyrus and Blaber, 1992), fish densities were related to turbidity and salinity but not temperature. There was a strong inverse relationship between turbidity and salinity. In Pueblo Viejo lagoon, a tropical estuarine system of Mexico, the major role of salinity and turbidity in affecting fish composition was also underscored by Castillo-Rivera et al. (2002). These two factors were shown to vary over a seasonal cycle, determined by freshwater inflow.

The preponderant role of seasonal salinity fluctuations in structuring fish assemblages was shown by Barletta et al. (2005) in a tropical estuary in Brazil: during the dry season, when the hydrological conditions were stable, the estuarine-dependent species were ordered along a well defined salinity gradient. When the freshwater runoff increased during the late rainy season, salinity decreased and the estuary became suitable for freshwater and brackish-water species. Salinity was also identified as the key factor responsible for the population dynamics in four types of estuaries in Nigeria: a bar-built estuary, a drowned river valley and two river delta estuaries (Amadi, 1990).

In the Sine Saloum delta, however, which is an "inverse" estuary with nearly no freshwater input (Simier et al., 2004), transparency was relatively high everywhere (from 2.1 to 3.2 m), while salinity was higher or equal to that of seawater. The seasonal variations of these factors were very slight and fish assemblages were mainly organized in space, according to the branch of the delta and, in the large Saloum main branch, to the distance from the bank.

4.5. Spatial organization vs. heterogeneity

In the Gambia estuary, the fish assemblages were characterized by the alternation, in both space and time, of stable and unstable situations, in terms of spatial homogeneity and concordance with the environmental conditions. Whatever the period of the year, the lower zone appeared to be the most heterogeneous zone from both an environmental and a fish assemblage point of view. Two explanations could be proposed: (1) the lower zone of an estuary is directly under the marine influence and consequently subjected to both short-term ebb/flood changes and monthly variations, in particular spring/neap differences (Wilson and Sheaves, 2001); (2) a high habitat diversity was observed in this zone. However, this high spatial heterogeneity was associated with a good fit between the fauna and environment, except during the flood. This concordance might be explained by the almost total absence of freshwater categories in this part of the estuary.

In contrast, the intermediate zone was spatially homogeneous, characterized by shallow water, and despite seasonal environmental fluctuations, fish assemblages remained stable, due to the permanent overwhelming predominance of estuarine species of marine origin (Em).

During and just after the wet and flood season, the upper zone was characterized by its spatial homogeneity and a good fit between environmental and fish assemblages structuring. As for the lower zone, this apparent concordance could be explained by the absence of some categories, i.e. the marine species accessory or occasional in estuaries (Ma and Mo). During the dry season, in April and especially in June, this spatial organization was deconstructed from an environmental point of view, while the fish assemblages remained more stable. At this period of the year, the upper zone of the estuary appeared to be a destructured ecosystem, in which the fish assemblages variability no longer followed the environmental variability.

5. Conclusions

Estuaries and lagoons have been supporting human populations since very ancient periods as attested in West Africa, particularly in Sénégal, by the finding of large middens of mollusc shells (Descamps et al., 1974). Nowadays, population growth is leading to an increasing pressure on these ecosystems resulting from multiple, often contradictory or even incompatible uses, such as: fishing, aquaculture, transportation, wildlife conservation, urbanization, tourism, various forms of exploitation (e.g. mangrove wood and sand) and dams. Most estuaries and lagoons in West Africa are therefore subjected to major developments such as dam building (Sénégal river), seaports (Ebrié lagoon), hydraulic works to improve water circulation or drainage (Ebrié lagoon again) and/or excessive fishing pressure. Although human activities are usually the cause of the deterioration of estuarine environments, natural changes and events can also cause profound modifications to plant and animal communities. In fact, the most delicate situations frequently result from the combination of two types of factors and from their mutual aggravation. For example, in West Africa, the chronic drought that the Sahel region has experienced is combined with several human factors to cause profound changes to the biocoenoses of some estuarine ecosystems, although in the current state of our knowledge, it is impossible to determine with any precision the relative influence of the incriminating factors. On the basis of some case studies, Albaret and Diouf (1994) listed the threats to estuarine and lagoon environments in West Africa and particularly to the diversity of fish populations.

The Gambia estuary, unlike most West African estuaries, remains moderately exploited by small-scale fisheries and does not receive any severe pollution from human activities. Neither the Gambia River nor its estuary is artificially impounded. Moreover, originating in the Fouta Djalon, the so-called "water tower" of West Africa, the Gambia River is free of major climatic perturbation such as drought. Consequently, the Gambia estuary may be considered to be the last large West African estuary free from major natural or human disturbance.

In addition, the Gambia estuary matches all the criteria of a "normal" (or "type E") estuary, characterized by Albaret (1999) as an estuary widely open to marine and freshwater domains. The fundamental fish assemblage of a type E estuary is dominated by estuarine species of marine origin (Em), and also consists of marine-estuarine species (ME), strictly estuarine species (Es) and estuarine species of freshwater origin (Ec). The present study has shown that in the Gambia estuary, the respective influences of both domains were more or less balanced depending on the hydroclimatic season and the distance to the sea. All bio-ecological categories defined in the West African estuarine fish communities were well represented.

For both reasons, the Gambia estuary therefore appears to be a reference ecosystem for the functioning of a tropical estuary, in terms of both fish assemblages and the bioecological cycles of species. The present study, which clarifies the spatial and seasonal dynamics of this ecosystem in terms of fish assemblages and their relation to environmental conditions, will be useful in further comparative studies on fish assemblages on tropical estuaries subjected to various degrees of disturbance.

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References

Albaret, J.-J., 1987. Les peuplements de poissons de la Casamance (Sénégal) en période de sécheresse. Revue d'Hydrobiologie tropicale 20, 291–310.

Albaret, J.-J., 1994. Les poissons: biologie et peuplements. In: Durand, J.-R., Dufour, P., Guiral, D., Zabi, S.G.F. (Eds.), Environnement et Ressources Aquatiques de Côte d'Ivoire. Tome 2. Les Milieux Lagunaires. Office de Recherche Scientifique et Technique Outre-Mer, Paris, pp. 239–279.

Albaret, J.-J., 1999. Les peuplements des estuaires et des lagunes. In: Lévèque, C., Paugy, D. (Eds.), Les Poissons des Eaux Continentales Africaines. Institut de Recherche pour le Développement, Paris, pp. 325–349.

Albaret, J.-J., Charles-Dominique, E., 1982. Observation d'une taille à la première maturité sexuelle exceptionnellement faible chez Ethmalosa fimbriata (Bowdich) dans une baie polluée de la lagune Ebrié (Côte d'Ivoire). Document Scientifique Centre de Recherche Océanographique, Abidjan 13, 1–22.

Albaret, J.-J., Diouf, P.S., 1994. Diversité des poissons des lagunes et des estuaires ouest-africains. In: Teugels, G.G., Guegan, J.F., Albaret, J.-J. (Eds.), Biological Diversity in African Fresh and Brackish Water. Geographical overviews. Symposium PARADI, Dakar. Annales Sciences Zoologiques du Musée Royal de l'Afrique Centrale, Tervuren 275, 165–177.

Albaret, J.-J., Laë, R., 2003. Impact of fishing on fish assemblages in tropical lagoons: the example of the Ebrié lagoon, West Africa. Aquatic Living Resources 16, 1–9.

Albaret, J.-J., Simier, M., Darboe, F.S., Ecoutin, J.-M., Raffray, J., Tito de Morais, L., 2004. Fish diversity and distribution in the Gambia estuary, West Africa, in relation to environmental variables. Aquatic Living Resources 17, 35–46.

Amadi, A.A., 1990. A comparative ecology of estuaries in Nigeria. Hydrobiologia 208, 27–38.

Baran, E., 1995. Dynamique spatio-temporelle des peuplements de poissons estuariens en Guinée—Relations avec le milieu abiotique. Université de Bretagne Occidentale—Brest.Thèses et Documents Microfichés No.142, Office de Recherche Scientifique et Technique Outre-Mer Editions, Paris, 236 pp. http://www.bondy.ird.fr/pleins_textes/pleins_textes_6/TDM/42826.pdf.

Barletta, M., Barletta-Bergan, A., Saint-Paul, U., Hubold, G., 2005. The role of salinity in structuring the fish assemblages in a tropical estuary. Journal of Fish Biology 66, 45–72.

Blaber, S.J.M., 2000. Tropical Estuarine Fishes. Ecology, Exploitation and Conservation. In: Fish and Aquatic Resources Series 7. Blackwell Science, Oxford, 372 pp.

Blaber, S.J.M., 2002. "Fish in hot water": the challenges facing fish and fisheries research in tropical estuaries. Journal of Fish Biology 61 (Supplement A), 1–20.

Blaber, S.J.M., Blaber, T.G., 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. Journal of Fish Biology 17, 143–162.

Blaber, S.J.M., Cyrus, D.P., Albaret, J.-J., Ching, C.V., Day, J.W., Elliott, M., Fonseca, M.S., Hoss, D.E., Orensanz, J., Potter, I.C., Silvert, W., 2000. Effects of fishing on the structure and functioning of estuarine and nearshore ecosystems. ICES Journal of Marine Science 57, 590–602.

Blanc, L., Chessel, D., Dolédec, S., 1998. Etude de la stabilité temporelle des structures spatiales par Analyse d'une série de tableaux faunistiques totalement appariés. Bulletin Français de la Pêche et de la Pisciculture 348, 1–21.

Castillo-Rivera, M., Zavala-Hurtado, J.A., Zarate, R., 2002. Exploration of spatial and temporal patterns of fish diversity and composition in a tropical estuarine system of Mexico. Reviews in Fish Biology and Fisheries 12, 167–177.

Chessel, D., Dufour, A.B., Thioulouse, J., 2004. The ade4 package-I—One-table methods. R News 4, 5–10.

Cyrus, D.P., Blaber, S.J.M., 1992. Turbidity and salinity in a tropical northern Australian estuary and their influence on fish distribution. Estuarine, Coastal and Shelf Science 35, 545–563.

Descamps, C., Thilmans, G., Thommeret, Y., 1974. Données sur l'édification de l'amas coquiller de Dioroum Bou Mak, région du Saloum (Sénégal). Bulletin ASEQUA 41, 67–84.

Daget, J., 1960. La faune ichtyologique du bassin de la Gambie. Bulletin de l'I.F.A.N 22 (2), 610–619.

Diouf, P.S., 1996. Les peuplements de poissons des milieux estuariens de l'Afrique de l'Ouest: l'exemple de l'estuaire hypersalin du Sine Saloum. Université Montpellier II, Montpellier. Thèses et Documents Microfichés No.156, Office de Recherche Scientifique et Technique Outre-Mer Editions, Paris, 267 pp. http://www.bondy.ird.fr/pleins_textes/pleins_textes_7/TDM_7/010008130.pdf.

Dolédec, S., Chessel, D., 1994. Co-inertia analysis: an alternative method for studying species-environment relationships. Freshwater Biology 31, 277–294.

Dorr, J.A., Schneeberger, P.J., Tin, H.T., Flath, L.E., 1985. Studies on adult, juvenile, and larval fish of the Gambian River, West Africa, 1983–1984. Report No 11, Great lakes and Marine waters center international programs. The University of Michigan, Ann Arbor, Michigan, 292 pp.

Dray, S., Chessel, D., Thioulouse, J., 2003. Co-inertia analysis and the linking of ecological tables. Ecology 84, 3078–3089.

Dufour, P., Kouassi, A.M., Lanusse, A., 1994. Les pollutions. In: Durand, J.-R., Dufour, P., Guiral, D., Zabi, S.G.F. (Eds.), Environnement et Ressources Aquatiques de Côte d'Ivoire. Tome 2. Les Milieux Lagunaires. Office de Recherche Scientifique et Technique Outre-Mer, Paris, pp. 309–334.

Ecoutin, J.-M., Richard, E., Simier, M., Albaret, J.-J., 2005. Spatial versus temporal patterns in fish assemblages of a tropical estuarine coastal lake: the Ebrié Lagoon (Ivory Coast). Estuarine, Coastal and Shelf Science 64, 623–635.

Elliott, M., Hemingway, K.L., 2002. Fishes in Estuaries. Blackwell Science, Oxford, 636 pp.

Gaertner, J.-C., Chessel, D., Bertrand, J., 1998. Stability of spatial structures of demersal assemblages: a multitable approach. Aquatic Living Resources 11, 75–85.

Guillard, J., Albaret, J.-J., Simier, M., Sow, I., Raffray, J., Tito de Morais, L., 2004. Spatio-temporal variability of fish assemblages in the Gambia estuary (West Africa) observed by two hydroacoustic methods: moored and mobile sampling. Aquatic Living Resources 17, 47–55.

Guyonnet, B., Aliaume, C., Albaret, J.-J., Casellas, C., Zerbi, A., Lasserre, G., Do Chi, T., 2003. Biology of *Ethmalosa fimbriata* (Bowdich) and fish diversity in the Ebrié Lagoon (Ivory Coast), a multipolluted environment. ICES Journal of Marine Science 60, 259–267.

Kouassi, A.M., Kaba, N., Métongo, B.S., 1995. Land-based sources of pollution and environmental quality of the Ebrié lagoon waters. Marine Pollution Bulletin 30, 295−300.

Koranteng, K.A., Ofori-Danson, P.K., Entsua-Mensah, M., 2000. Fish and fisheries of the Muni lagoon in Ghana, West Africa. Biodiversity and Conservation 9, 487−499.

Laë, R., 1996. Does overfishing lead to a decrease in catches and yields? An example of two West African lagoons. Fisheries Management and Ecology 3, 101−116.

Laë, R., Ecoutin, J.-M., Mendy, A., Raffray, J., Weigel, J.Y., Sadio, O., Djobe, O., 2004. Effects of a targeted shrimp (*Penaeus notialis*) exploitation on fish catches in the Gambia estuary. Aquatic Living Resources 17, 75−85.

Lavit, C., Escoufier, Y., Sabatier, R., Traissac, P., 1994. The ACT (Statis method). Computational Statistics and Data Analysis 18, 97−119.

Lesack, L.F.W., 1986. Estimates of catch and potential for the riverine artisanal fishery in the Gambia, West Africa. Journal of Fish Biology 28, 679−700.

Lesack, L.F.W., Hecky, R.E., Melack, J.M., 1984. Transport of carbon, nitrogen, phosphorus and major solutes in the Gambia River. West Africa. Limnology and Oceanography 29, 816−830.

Marshall, S., Elliott, M., 1998. Environmental influences on the fish assemblage of the Humber Estuary, U.K. Estuarine, Coastal and Shelf Science 46, 175−184.

Paperno, R., Brodie, R.B., 2004. Effects of environmental variables upon the spatial and temporal structure of a fish community in a small, freshwater tributary of the Indian River Lagoon, Florida. Estuarine, Coastal and Shelf Science 61, 229−241.

Ramos Miranda, J., Mouillot, D., Flores Hernandez, D., Sosa Lopez, A., Do Chi, T., Ayala Perez, L., 2005. Changes in four complementary facets of fish diversity in a tropical coastal lagoon after 18 years: a functional interpretation. Marine Ecology Progress Series 304, 1−13.

Rueda, M., Defeo, O., 2003. Spatial structure of fish assemblages in a tropical estuarine lagoon: combining multivariate and geostatistical techniques. Journal of Experimental Marine Biology and Ecology 296, 93−112.

Scheren, P.A.G.M., Kroeze, C., Janssen, F.J.J.G., Hordijk, L., Ptasinski, K.J., 2004. Integrated water pollution assessment of the Ebrié lagoon, Ivory Coast, West Africa. Journal of Marine Systems 44, 1−17.

Simier, M., Blanc, L., Pellegrin, F., Nandris, D., 1999. Approche simultanée de K couples de tableaux: application à l'étude des relations pathologie végétale—environnement. Revue de Statistique Appliquée 47, 31−46.

Simier, M., Blanc, L., Aliaume, C., Diouf, P.S., Albaret, J.-J., 2004. Spatial and temporal structure of fish assemblages in an "inverse estuary", the Sine Saloum system (Senegal). Estuarine, Coastal and Shelf Science 59, 69−86.

Thioulouse, J., Chessel, D., 1987. Les analyses multitableaux en écologie factorielle. I. De la typologie d'état à la typologie de fonctionnement par l'analyse triadique. Acta Oecologica, Oecologia Generalis 8, 463−480.

Thioulouse, J., Simier, M., Chessel, D., 2004. Simultaneous analysis of a sequence of paired ecological tables. Ecology 85, 272−283.

Vidy, G., Darboe, F.S., Mbye, E.M., 2004. Juveniles fish assemblages in the creeks of the Gambia estuary. Aquatic Living Resources 17, 56−64.

Whitfield, A.K., 1994a. Fish species diversity in Southern African estuarine systems: an evolutionary perspective. Environmental Biology of Fishes 40, 37−48.

Whitfield, A.K., 1994b. A review of ichthyofaunal biodiversity in Southern African estuarine systems. In: Teugels, G.G., Guégan, J.F., Albaret, J.-J. (Eds.), Biological Diversity in African Fresh and Brackish Water. Geographical Overviews. Symposium PARADI, Dakar. Annales Sciences Zoologiques du Musée Royal de l'Afrique Centrale, Tervuren 275, 149−163.

Wilson, J.P., Sheaves, M., 2001. Short-term temporal variations in taxonomic composition and trophic structure of a tropical estuarine fish assemblage. Marine Biology 139, 787−796.

Winemiller, K.O., Leslie, M.A., 1992. Fish assemblages across a complex, tropical freshwater/marine ecotone. Environmental biology of Fishes 34, 29−50.

Young, G.C., Potter, I.C., Hyndes, G.A., de Lestang, S., 1997. The ichthyofauna of an intermittently open estuary: implication of bar breaching and low salinities on faunal composition. Estuarine, Coastal and Shelf Science 45, 53−68.