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Fish diversity and distribution in the Gambia Estuary, West Africa, in relation to environmental variables

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Abstract – The Gambia Estuary, a "normal" estuary with a decreasing salinity gradient from the mouth towards the head, is moderately exploited by small-scale fisheries and does not receive any severe pollution from either agriculture or industrial activities. Neither the Gambia River nor its estuary are artificially impounded. As the last large West African estuary free of major human disturbance, it is of considerable interest for comparative studies on the effect of major environmental perturbations in West African estuarine ecosystems. The aquatic environment and fish communities of the Gambia Estuary (about 250 km long) were studied by purse seine sampling at different periods in the river cycle, covering all hydro-climatic seasons that are characteristic of West African estuaries. Emphasis was placed on the diversity, composition, structure and distribution of fish assemblages in relation to fluctuations in physico-chemical factors such as water temperature, salinity and turbidity. Results on the aquatic environment, mainly the salinity range (from freshwater to 39) and dissolved oxygen (never a limiting factor for fish in the estuary) and on the main characteristics of the fish fauna (high diversity of life cycles, all the ecological categories represented) indicated that the Gambia Estuary was free of major climatic perturbation and reinforced the choice of this system as a reference for the study of the effects of major perturbations on estuarine tropical fish communities.

Key words: Fish community / Aquatic environment / Estuary / Gambia / West Africa

Résumé – Diversité et répartition des peuplements de poissons dans l'estuaire de la Gambie, Afrique de l'Ouest, en relation avec des variables environnementales. L'estuaire du fleuve Gambie, de type « normal » (présentant un gradient de salinité décroissant de l'aval vers l'amont) est modérément exploité par la pêche, exempt de pollution agricole ou industrielle grave, et sans barrage sur l'ensemble de son cours : il constitue le dernier milieu estuarien d'Afrique de l'Ouest préservé de perturbations naturelles ou d'origine anthropique importantes. Il présente donc un intérêt considérable pour l'évaluation comparative des effets de perturbations majeures sur la faune aquatique, subies par d'autres milieux similaires de la région. Les peuplements de poissons de la totalité de la zone estuarienne de la Gambie (environ 250 km de long) ont été étudiés au moyen de pêches expérimentales réalisées à la senne tournante coulissante, à des périodes caractéristiques du cycle hydro-climatique. La diversité, la nature, la structure et la dynamique des communautés ichtyologiques ont été précisées et reliées aux principales variables de l'environnement aquatique telles que la salinité et la turbidité. Les données concernant l'environnement aquatique, principalement la gamme de salinité (de l'eau douce à une salinité de 39) et l'oxygène dissous (qui n'est jamais un facteur limitant pour les poissons dans l'estuaire), et les principales caractéristiques de l'ichtyofaune (diversité des cycles biologiques, présence de toutes les catégories écologiques possibles) ont montré que l'estuaire de la Gambie ne subissait pas de stress climatique majeur ; ces résultats justifient le choix de ce système comme milieu de référence pour l'étude des effets des perturbations sur les communautés de poissons estuariens tropicaux.

1 Introduction

Throughout the world, estuaries are among the most modified and threatened environments (Blaber et al. 2000). Scientific interest is increasingly focusing on the effects of major natural or human perturbations on aquatic ecosystems, yet in this field of research few studies have been conducted on estuarine systems, particularly in the tropics. This view is highlighted by Gray (2001) as follows, "... assessment is urgently

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needed of the spatial scales and dynamics of species richness from point samples to assemblages, habitats and landscapes, especially in coastal areas and in the tropics where threats to biodiversity are greatest".

The effects of fishing on tropical estuarine environments have been reviewed by Blaber et al. (2000). In terms of the effects of major climatic stress, some preliminary work has been conducted in West Africa on the consequences of a drought period on the estuarine environment and associated fish assemblages (Albaret 1987; Albaret and Diouf 1994; Diouf 1996).

The main reasons why so few studies have been conducted on estuarine fish community changes are 1) the complexity, linked most of the time to the high variability at different temporal and spatial scales, and 2) the lack of reference conditions on the previous, pre-perturbation situation or a comparable pristine ecosystem. In the case of tropical estuarine ecosystems the reference to a previous pristine situation is rarely possible because of the lack of long-term comparable data and, as previously stated, there are very few estuaries or coastal lagoons that can be used as an example of an undisturbed ecosystem. To some extent, the Gambia River Estuary may be considered an exception. It is the last and only large estuary in the subregion not to have been affected by extensive and/or intensive human disturbances. Originating in the Fouta Djalon, the so-called water tower of West Africa, the Gambia River has been less affected by the succession of drought periods experienced by the Sahel region since 1970. In contrast to the neighbouring Casamance and Sine Saloum estuaries, the Gambia has remained a "normal" estuary with no reversed salinity gradient and no hyperhaline zone. Although there have been many proposed development projects, none has come to fruition and the Gambia River still has a natural flood regime with no dams or weirs. The Gambia is not a very industrialised country and there is no major source of pollution. Fishing activities appear to be conducted at a moderate level of exploitation (Laë et al. 2004).

For all the above reasons, the Gambia Estuary was chosen as a reference study to ascertain the effect of major perturbations on tropical fish communities. Prior to the initiation of this programme, very limited research effort had been applied in this area, e.g. the study conducted in the early 1980s by Berry et al. (1985) and the work of Lesack (1986) and Lesack et al. (1984).

This paper firstly describes the aquatic environment and the fluctuations of the main hydrological variables in the Gambia Estuary on a seasonal basis, and secondly describes the seasonal dynamics of the purse seine net fish assemblage in order to better understand the role of environmental factors in determining fish diversity, abundance, distribution and community structure.

This work is part of a series on the effects of environmental factors on fish and fishing in the Gambia Estuary. It complements studies of Gambia Estuary fish assemblages using hydro-acoustic (Guillard et al. 2004) and fyke net sampling (Vidy et al. 2004), as well as a description of fishing activities in the estuary by Laë et al. (2004).

2 Materials and methods

2.1 Study area

The Gambia River, with a catchment area of 78 000 km^2 (Lesack 1986), originates in the Fouta Djalon plateau of northern Guinea and flows 1200 km through southern Senegal and The Gambia to the Atlantic Ocean (Fig. 1). The lower Gambia, encompassing the whole Gambian part of the river, has a virtually zero drainage gradient over the last 500 km. Tidal effects are perceptible up to Yarboutenda at the Senegal, the Gambia border. However, in accordance with Daget (1960), true brackish waters are located "only" in the last 180 km where there are tidal flood plains colonised by mangrove swamps.

The study area for the present paper includes the lower, middle and upper part of the Gambia Estuary from the mouth (Banjul) up to Deer Island located more than 220 km upstream. The study focused on the primary estuary, i.e. on the main channel excluding all tributaries and creeks (known locally as "Bolongs").

Rains occur from June to October with the highest precipitation recorded in August. Peak river discharge occurs during September, with the rise and fall of discharge being rapid, declining to almost nil from December to the beginning of July (Lesack et al. 1984). Further descriptions of the Gambia River hydrology and geomorphology are given in Michel (1963), Lesack et al. (1984), Berry et al. (1985) and Lamagat et al. (1990).

2.2 Sampling design

One preliminary and four detailed surveys were performed in order to cover the major hydroclimatic cycle events as follows:

- Gambia 1: November 2000 (Preliminary survey) – Declining river flows entering estuary.
- Gambia 2: June 2001 – End of the dry season, maximum estuary salinities.
- Gambia 3: September 2001 – Rainy season and river flooding, minimum estuary salinities.
- Gambia 4: December 2001 – Dry and cool season.
- Gambia 5: April 2002 – Dry and warm season.

The study area covered three out of the five zones as defined in the University of Michigan survey (Dorr et al. 1985), viz. the lower estuary, upper estuary and a part of the lower river zone (freshwater zone where there is still a tidal influence).

A combination of (non-probabilistic) purposive and stratified sampling (Scherrer 1984) based on the above spatial zonation (Dorr et al. 1985) was used to define sampling sites. The sampling sites were located in as many biotopes (or 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 Figure 1, with the name, code, position, average depth and type of bottom sediment at the 44 sites given in Table 1.

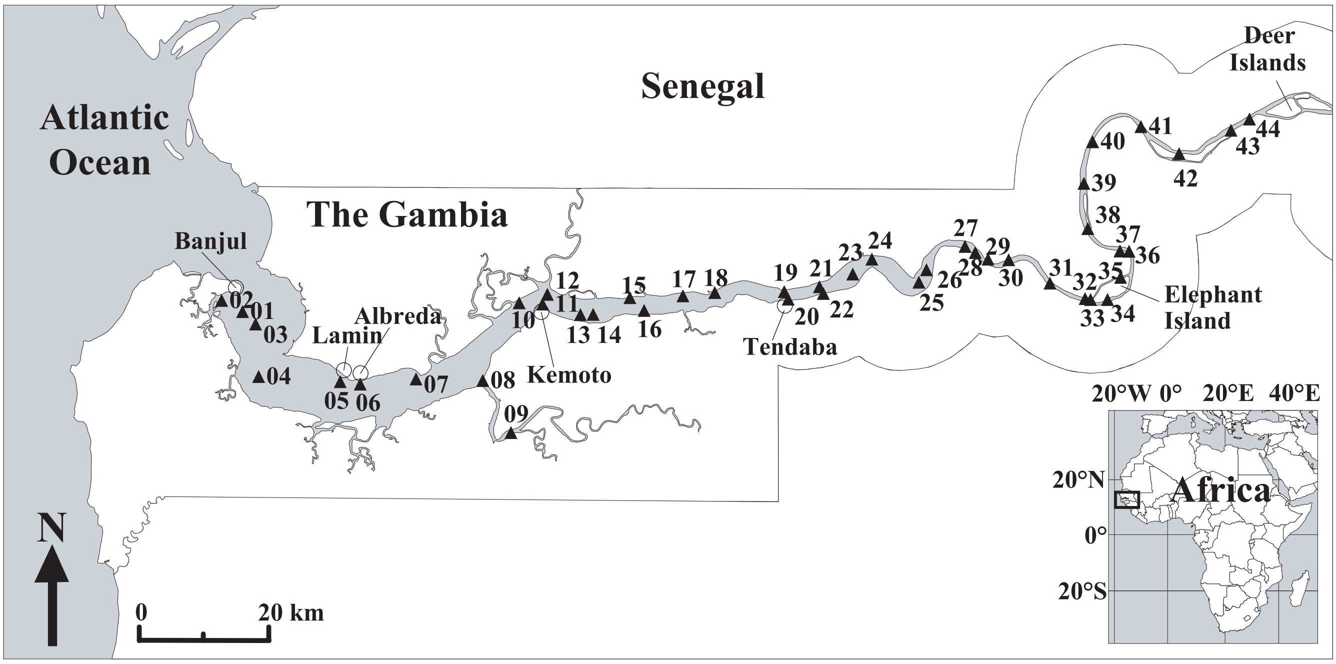

Fig. 1. Map of The Gambia and of the study area with location of the 44 sampling sites. Codes are in Table 1.

2.3 Sampling technique

Fish assemblage sampling requires an efficient, reproducible and broadly selective fishing gear. These criteria were met using a purse seine net and a protocol similar to that previously used in several estuarine West African fish community surveys (Albaret 1994; Baran 1995; Diouf 1996). The net is 250 m long, 20 m deep and has a 14 mm mesh. It was deployed by 9 trained fishermen, from a large motorized canoe without any surface fish search. Each fishing operation (haul) was considered to be a well-defined unit of effort.

2.4 Data collected

Three types of complementary data were simultaneously collected: acoustic data (not used in this paper, see Guillard et al. 2004), biological data and environmental data.

2.4.1 Biological data

In the field, fish were identified to species level, counted and weighed (total weight in g). They were then individually measured (mm fork length) and weighed (individual weight in g for fifty individuals per species at most, global weight in g for the rest of the sample in the case of very abundant species).

2.4.2 Environmental data

The precise location of the fishing and environmental sampling sites (as close as possible to each other) was determined using a GPS and the following environmental data were collected: depth (with a hand-sounder), direction and strength of the water current (with a flow-meter), surface and bottom salinity measured with both a refractometer and a YSI multi-parameter probe, surface and bottom temperature (°C) measured with a thermometer and a YSI multi-parameter probe, surface and bottom percentage oxygen saturation with a YSI multi-parameter probe, water transparency (cm) measured using a Secchi disk (diameter 30 cm).

2.4.3 Data processing

All biological and environmental data were combined into a relational database. Using their geographical co-ordinates, sampling sites were entered onto a Geographical Information System and their distance from the sea was calculated. Each environmental parameter was plotted for each survey as a longitudinal profile, according to distance from the sea. The abundance distribution of the main fish species in the Gambia Estuary was also presented as a scatter plot of Ln $(n + 1)$ transformed data as function of the distance to the river mouth. A lowess (locally weighted regression) curve (Cleveland 1979) was fitted by least squares ("Gaussian") to the data to summarize the distribution patterns. The smooth curve locally minimizes the variance of the residuals or prediction error. Only the points in that vicinity determine the curve value at each particular location along the x-axis. The span (i.e. the value between 0 and 1 controlling the amount of smoothing) was fixed to 0.5.

All five surveys were used for environmental and for species presence/absence data analysis. Data from the preliminary survey (November) were not included in the abundance distribution analysis.

Table 1. The 44 sites ordered from the mouth to upstream. Distance to the sea (km), name, code, geographical coordinates (decimal degrees), mean depth (m, with SD, standard deviation) and type of bottom sediment (sa: sand, vv: mud, vm: soft mud, vd: hard mud, sv: sand+mud).

Dist. sea (km)	Name	Code	Latitude N	Longitude W	Mean Depth (SD)	Sediment
4.2	Banjul 2	01	13° 25′ 50	16° 34′ 31	12.0 (1.4)	vd
5.6	Chilabong bolon	02	13° 26′ 42	16° 36′ 08	6.2 (0.2)	vm
7.5	Dog Island	03	13° 24′ 45	16° 33′ 19	10.4 (0.6)	sa
15.2	Maredina bolon	04	13° 20′ 08	16° 32′ 92	2.8 (0.5)	sa
28.1	Lamine Village	05	13° 19′ 65	16° 25′ 95	8.5 (1.6)	sv
31.2	Lamine Point	06	13° 19′ 45	16° 24′ 24	5.4 (0.5)	vd
39.9	Sika	07	13° 19′ 89	16° 19′ 45	7.0 (2.2)	sv
50.1	Bintang Point	08	13° 19′ 75	16° 13′ 75	7.6 (1.0)	vm
59.1	Bintang Amont	09	13° 15′ 42	16° 11′ 32	6.9 (1.0)	vd
63.4	Tabirere Creek	10	13° 26′ 22	16° 10′ 63	6.3 (0.9)	vm
68.7	Muta Point	11	13° 26′ 11	16° 08′ 63	8.0 (0.9)	vm
68.7	Suara Point	12	13° 26′ 92	16° 08′ 20	4.5 (0.9)	vm
73.7	Suara Island 1	13	13° 25′ 24	16° 05′ 38	7.0 (0.4)	vm
75.7	Suara Island 2	14	13° 25′ 25	16° 04′ 28	6.6 (0.7)	vm
82.3	Selekini Point	15	13° 26′ 64	16° 01′ 16	5.0 (0.9)	vm
84.5	Tankular Amont	16	13° 25′ 59	15° 59′ 93	6.9 (0.7)	vm
90.9	Jali Point	17	13° 26′ 80	15° 56′ 61	4.4 (0.4)	vd
95.8	Mandori Creek	18	13° 27′ 09	15° 53′ 88	7.0 (0.5)	vd
106.4	Tendaba	19	13° 27′ 16	15° 47′ 95	3.2 (0.6)	vv
106.7	Tendaba silos	20	13° 26′ 52	15° 47′ 60	9.2 (1.4)	vm
112.0	Katchiang	21	13° 27′ 57	15° 44′ 92	3.4 (0.6)	vm
112.4	Bambako	22	13° 27′ 00	15° 44′ 59	8.5 (0.7)	vd
117.3	Kunda	23	13° 28′ 63	15° 42′ 08	6.0 (0.5)	vd
120.8	Krule Point	24	13° 29′ 87	15° 40′ 44	5.1 (0.8)	vm
129.1	Devils Point	25	13° 27′ 95	15° 36′ 41	8.3 (2.8)	vd
131.4	Balingo	26	13° 28′ 97	15° 35′ 76	8.4 (3.1)	vd
139.5	Bambatenda	27	13° 30′ 93	15° 32′ 46	4.8 (1.4)	vd
141.4	Tambakoto	28	13° 30′ 41	15° 31′ 58	6.1 (0.8)	vd
143.6	Sankuia	29	13° 29′ 86	15° 30′ 49	7.1 (1.8)	vm
146.5	Wale	30	13° 29′ 80	15° 28′ 72	7.3 (1.6)	vm
155.4	Tudenda	31	13° 27′ 87	15° 25′ 20	6.2 (0.7)	vm
161.2	Elephant Aval	32	13° 26′ 57	15° 22′ 18	11.4 (3.0)	vd
161.9	Elephant Pointe	33	13° 26′ 51	15° 21′ 72	7.9 (1.1)	vd
164.6	Elephant Jassang	34	13° 26′ 51	15° 20′ 27	10.8 (1.1)	vd
167.5	Bambali Amont	35	13° 28′ 35	15° 19′ 16	8.9 (1.5)	vd
171.7	Sofanyama	36	13° 30′ 51	15° 18′ 43	12.5 (1.7)	vv
173.3	Samba	37	13° 30′ 54	15° 19′ 19	6.8 (1.0)	vv
180.7	Sea horse I. Aval	38	13° 32′ 42	15° 21′ 96	7.8 (1.4)	vm
186.8	Sea horse I. Amont	39	13° 36′ 17	15° 22′ 28	6.5 (1.0)	sa
193.3	Balangar	40	13° 39′ 64	15° 21′ 55	8.8 (1.2)	vm
201.5	Bantanta creek	41	13° 40′ 90	15° 17′ 42	7.5 (0.6)	vd
209.0	Milieu Papa Island	42	13° 38′ 65	15° 14′ 13	7.9 (0.9)	sa
218.2	Carrol’s wharf	43	13° 40′ 58	15° 09′ 70	5.8 (3.5)	vm
220.9	Deer Islands	44	13° 41′ 53	15° 08′ 11	8.2 (1.3)	sa

3 Results

3.1 Aquatic environment

3.1.1 Salinity

The mean overall surface and bottom salinities for all sites and seasons combined were 13 and 14 respectively. Salinity values ranged from freshwater to a salinity rate slightly higher than sea water (maximum 39) at three downstream sites at the end of the dry season (June) (sites 03, 05, 06, Fig. 1). Differences between surface and bottom salinity values were generally less than 2 but the longitudinal distribution of salinity showed marked seasonal changes (Fig. 2a). The brackish water zone extended from about 80 km in length in September to more than 220 km in June (bottom salinity was 5 at the most upstream site). In the rainy and flood seasons, at least two-thirds of the estuary was totally fresh, oligohaline (salinity from 0.5 to 5) or mesohaline (5 to 18) according to Por's classification (Por 1972). In the dry season, most of the estuary up to Elephant Island (162 km from mouth) became polyhaline (18 to 30) or mixoeuhaline (30 to 40).

3.1.2 Turbidity

In general, water was very turbid in the Gambia Estuary. Water transparency values ranged from 0.1 m to 1.8 m with an overall mean value of 0.6 m. During the wet season, the longitudinal distribution of transparency values (Fig. 2b) showed a rapid decrease from the estuary mouth upstream, reaching values of approximately 0.2 m in the upper parts of the estuary. During the dry season, however, higher transparency values were noted in the upper part of the estuary (mean value 1.2 m). Transparency values showed large spatial variability, except for the constantly very high turbidity in upper part of the estuary during the wet season. This was related to the imperfect mixing of water masses of different origin in the lower estuary.

3.1.3 Temperature

The surface temperature of the Gambia Estuary was generally less than 1 °C higher than the bottom temperature (mean surface temperature 27.4 °C, mean bottom temperature 26.9 °C). In April and June the water temperature gradually increased from the mouth upstream which was not the case at other periods when no clear pattern appeared in the longitudinal distribution (Fig. 2c). The water temperature was lowest in November and December, with a minimum of 23.8 °C noted at Devil's Point (site 25, 129 km from the sea). It was highest both in June and September with a maximum bottom temperature of 30.0 °C in June at Mootah Point (site 11, 69 km from the sea).

3.1.4 Dissolved oxygen

Dissolved oxygen was never a limiting factor for fish in the Gambia Estuary even in the bottom water layer. Oxygen values were noticeably lower during the peak flood in September,

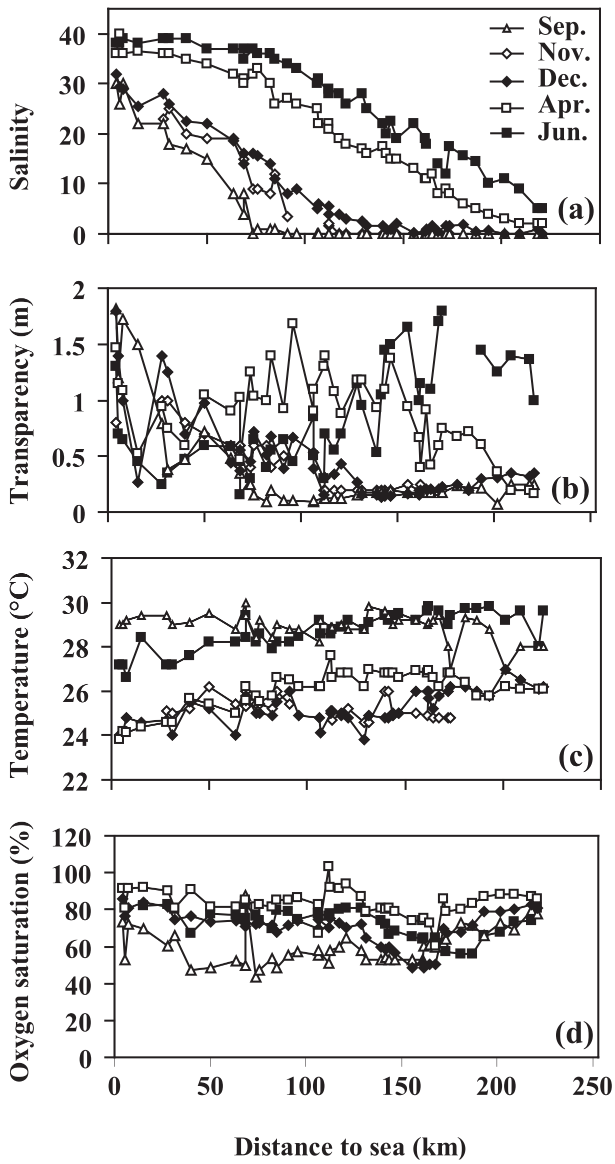

Fig. 2. Longitudinal distribution of environmental parameters for each survey. (a) Bottom salinity. (b) Transparency (m). (c) Bottom temperature (°C). (d) Percentage oxygen saturation (%).

especially in the lower and intermediate parts of the estuary (Fig. 2d). On the contrary, oxygen values were higher in April, during the dry and cool season.

3.2 Species richness and faunal composition

Seventy fish species, belonging to 32 families, were recorded during this study (Table 2) and many families were represented by a single species. The average number of species per family was low (2.18). This ratio was the lowest during November and highest in the dry season (April). The families with the highest species diversity were Carangidae and Sciaenidae (6 species each), Mugilidae (5 species), Clupeidae and Haemulidae (4 species each). With the exception of June when only 40 taxa were recorded, the species richness per survey

Table 2. List of the 70 fish species listed by order and family. Cat.: bioecological category (Co: continental species, occasional in estuaries; Ce: estuarine species from continental origin; Ec: estuarine species from continental 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), Occ.: occurrence (number of samples where the species was present), %Occ.: percentage of occurrence, Numbers: total number of individuals, and Biomass (g).

Order	Family	Name	Cat.	Occ.	%Occ.	Numbers	Biomass
Anguilliformes	Ophichthyidae	*Pisonodophis semicinctus*	Mo	3	1.4	3	609
Batrachoidiformes	Batrachoididae	*Batrachoides liberiensis*	Ma	6	2.9	6	261
Beloniformes	Belonidae	*Strongylura senegalensis*	Em	4	1.9	4	210
		Tylosurus acus rafale	Mo	1	0.5	1	242
Characiformes	Alestiidae	*Alestes baremoze*	Co	8	3.8	13	487
		Brycinus nurse	Co	6	2.9	8	309
		Hydrocynus brevis	Co	1	0.5	1	386
Clupeiformes	Clupeidae	*Ethmalosa fimbriata*	Em	97	46.6	12 583	503 141
		Ilisha africana	Em	93	44.7	6760	107 393
		Pellonula leonensis	Ec	30	14.4	79	918
		Sardinella maderensis	ME	60	28.8	3819	66 180
Elopiformes	Elopidae	*Elops lacerta*	ME	61	29.3	141	10 161
Osteoglossiformes	Mormyridae	*Hyperopisus bebe*	Co	4	1.9	6	1549
		Mormyrops anguilloides	Ce	2	1.0	3	556
Perciformes	Carangidae	*Caranx hippos*	ME	5	2.4	16	1262
		Caranx senegallus	ME	17	8.2	79	6664
		Chloroscombrus chrysurus	ME	20	9.6	169	5140
		Hemicaranx bicolor	Mo	14	6.7	40	2563
		Lichia amia	Ma	1	0.5	1	54
		Trachinotus teraia	Em	13	6.3	21	35 369
	Cichlidae	*Sarotherodon melanotheron*	Es	4	1.9	6	520
		Tilapia guineensis	Es	4	1.9	4	417
		Tylochromis jentinki	Es	2	1.0	2	483
	Drepaneidae	*Drepane africana*	ME	11	5.3	29	1616
	Eleotridae	*Bostrychus africanus*	Es	1	0.5	1	28
	Ephippidae	*Chaetodipterus lippei*	Ma	3	1.4	6	273
	Gerreidae	*Eucinostomus melanopterus*	ME	5	2.4	10	336
		Gerres nigri	Es	4	1.9	43	2524
	Gobiidae	*Nematogobius maindroni*	Es	1	0.5	1	1
		Porogobius schlegelii	Es	3	1.4	3	5
	Haemulidae	*Brachydeuterus auritus*	ME	9	4.3	18	269
		Plectorhinchus macrolepis	Em	2	1.0	2	2552
		Pomadasys jubelini	Em	11	5.3	33	2416
		Pomadasys perotaei	Em	5	2.4	14	622
	Monodactylidae	*Monodactylus sebae*	Es	45	21.6	150	10 685
	Mugilidae	*Liza dumerili*	Em	1	0.5	1	45
		Liza falcipinnis	Em	39	18.8	259	14 503
		Liza grandisquamis	Em	67	32.2	851	53 373
		Mugil bananensis	ME	1	0.5	1	73
		Mugil cephalus	ME	1	0.5	2	186
	Polynemidae	*Galeoides decadactylus*	ME	31	14.9	236	7676
		Pentanemus quinquarius	Ma	49	23.6	445	17 027
		Polydactylus quadrifilis	ME	81	38.9	162	74 808

Table 2. Continued.

Order	Family	Name	Cat.	Occ.	%Occ.	Numbers	Biomass
	Sciaenidae	*Pseudotolithus brachygnathus*	ME	48	23.1	142	16 849
		Pseudotolithus elongatus	Em	201	96.6	19 336	1 223 993
		Pseudotolithus senegalensis	Ma	34	16.3	180	6107
		Pseudotolithus typus	ME	15	7.2	55	7766
		Pteroscion peli	ME	10	4.8	83	744
		Umbrina ronchus	Mo	1	0.5	1	15
	Sphyraenidae	*Sphyraena afra*	ME	11	5.3	16	2177
		Sphyraena guachancho	ME	5	2.4	7	552
	Trichiuridae	*Trichiurus lepturus*	ME	13	6.3	25	4909
Pleuronectiformes	Cynoglossidae	*Cynoglossus senegalensis*	Em	97	46.6	216	30 294
	Paralichthyidae	*Citharichthys stampflii*	Em	17	8.2	23	374
	Soleidae	*Synaptura cadenati*	Mo	2	1.0	2	13
Rajiformes	Dasyatidae	*Dasyatis margarita*	Em	7	3.4	11	9875
		Dasyatis margaritella	Em	3	1.4	5	2700
		Dasyatis ukpam	Mo	2	1.0	2	15 500
	Gymnuridae	*Gymnura micrura*	Mo	2	1.0	3	7838
Siluriformes	Ariidae	*Arius heudelotii*	ME	15	7.2	52	10 114
		Arius latiscutatus	ME	73	35.1	489	63 875
		Arius parkii	ME	37	17.8	115	10 557
	Bagridae	*Chrysichthys johnelsi*	Ce	14	6.7	15	502
		Chrysichthys maurus	Ec	46	22.1	109	6940
		Chrysichthys nigrodigitatus	Ec	60	28.8	113	28 662
	Clariidae	*Clarias anguillaris*	Co	1	0.5	2	4400
	Mochokidae	*Synodontis batensoda*	Co	25	12.0	617	27 929
		Synodontis gambiensis	Ce	89	42.8	1980	101 591
	Schilbeidae	*Schilbe intermedius*	Ce	43	20.7	266	5638
Tetraodontiformes	Tetraodontidae	*Ephippion guttifer*	ME	15	7.2	37	2588

remained relatively stable throughout the seasonal cycle at between 49 (November) and 52 species (April). Family richness was also lower in June (22) and never exceeded 28 (November).

The Gambia Estuary fish fauna was dominated by the sciaenid *Pseudotolithus elongatus* (Table 2). The next three most abundant species were the clupeids *Ethmalosa fimbriata*, *Ilisha africana* and *Sardinella maderensis*. *Synodontis gambiensis*, the first continental species, was the fifth most abundant and fourth in terms of biomass. Two other Siluriforms, *S. batensoda* and *Schilbe intermedius*, were also in the ten most abundant species.

Some typical estuarine families were unusually scarce in the Gambia Estuary, e.g. the gerreids *Gerres nigri* and *Eucinostomus melanopterus* that are usually among the most abundant, widely distributed and frequently occurring species in West Africa. In the Gambia Estuary, both species were scarce with respectively 4 (1.9%) and 5 (2.4%) occurrences and only a few individuals captured. In the same way, only five species of mugilids (three *Liza* and two *Mugil*) were recorded out of the 7 usually documented from other estuaries in the sub-region. Moreover, three typically common mugilids, *Liza dumerili*, *Mugil cephalus* and *Mugil bananensis* were represented by only a single individual. *Mugil curema*, another very common and widespread mullet was not recorded in the Gambia Estuary.

3.3 Species assemblages and distribution

The species of the Gambia Estuary fish community were sorted into the 8 bio-ecological categories defined in the West African estuarine fish communities (Albaret 1999). These eight bio-ecological 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 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 continental origin (Ec), the continental species with estuarine affinities (Ce), and the continental species, occasional in estuaries (Co). Four of these categories (Ec, Es, Em and ME) compose the fundamental estuarine community. All categories, from the "occasional marine" (Mo) to the "occasional continental" (Co) species, were represented in the Gambia Estuary (Table 2). There were no distinct seasonal patterns in the number of species in each ecological category, except perhaps for the absence of Co species in June when the marine influence and salt intrusion was at its highest, and the higher number of ME species in April (Fig. 4). The main species of each category are discussed hereafter. These species have been selected because of their abundance in the fish community and as representatives of different ecological categories.

3.3.1 Marine component of the community (Em, ME, Ma, Mo categories)

These categories dominated, with a total number of 49 species (Fig. 3a), although a large part of the estuary becomes oligohaline or completely fresh for extended periods each year. Though relatively well represented (7 species), the "occasional Marine" (Mo) were rarely recorded and numerically of very limited importance. The "marine estuarine" (ME) group was particularly diverse (22 species). Fishes from this group do not usually reproduce in estuarine ecosystems but use them widely as a nursery, e.g. *Elops lacerta*, *Sardinella maderensis* and *Chloroscombrus chrysurus*.

S. maderensis is a ME species that is mainly represented in estuaries by immature juveniles. The main concentrations were recorded in the lower estuary from the mouth up to Albreda, only 30 km from the ocean (Fig. 5). A low abundance of *S. maderensis* was noted during the rainy season, even near the mouth. In contrast, the species was abundant and distributed over a large part of the estuary during the dry season with a maximum distribution range during June when it reached Sea Horse Island, 187 km from the sea.

There was also a high number (15) of "estuarine of marine origin" species (Em), i.e. permanent inhabitants of estuarine communities that can complete their entire life cycle within estuaries. The clupeid *Ethmalosa fimbriata* and the sciaenid *Pseudotolithus elongatus* were the best representatives of the Em category in the Gambia Estuary. Though less numerous than the ME, the Em species were much more abundant in terms of individual numbers (Fig. 3b) and biomass (Fig. 3c). The 3 dominant species in numbers, biomass and occurrence (*P. elongatus*, *E. fimbriata*, *Ilisha africana*, see Table 2) belong to this category, which accounted for four times as many individuals as the seven others together.

The sciaenid *P. elongatus* was the dominant species in the fish community, in numbers (19 336 fish caught) and biomass (1224 kg). It had a remarkably wide spatio-temporal distribution in the estuary (96.6% occurrence). It was abundant in every season and at all sites, from the estuary mouth to the upper reaches and was captured in large numbers in relatively clear as well as in the more turbid waters and in all salinities from sea water to totally fresh water (Fig. 5). Even during the maximum flood period (September), this marine species was abundant in the upper reaches of the estuary. In addition, it breeds in the Gambia Estuary and all stages of the life cycle were represented in the system.

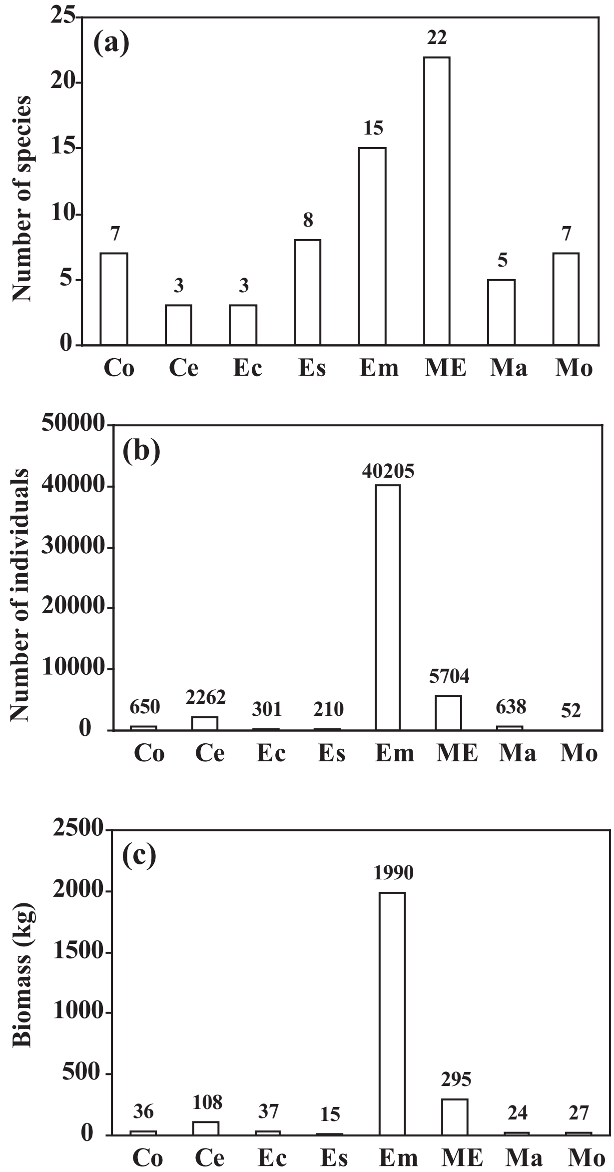

Fig. 3. Distribution of fish assemblages per bioecological category (Co: continental species, occasional in estuaries; Ce: estuarine species from continental origin; Ec: estuarine species from continental origin; Es: strictly estuarine species; Em: estuarine species from marine origin; ME: marine-estuarine species; Ma: marine species accessory in estuaries; Mo: marine species occasional in estuaries): (a) number of species, (b) number of individuals, (c) biomass (kg).

E. fimbriata, was second in terms of total fish numbers, biomass and occurrence, with biomass and occurrence less than half that of *P. elongatus*. Both juveniles and adults were recorded in seine net samples throughout the estuary. However, *E. fimbriata* shows a clear seasonal pattern: present in the lower reaches all year round and moving upstream only during the dry season (Fig. 5). By December, a few subadult *Ethmalosa* were captured in the most upstream site (more than 220 km from the Ocean) in totally fresh water, but it was only in April, in a mesohaline environment (about 5 to 20) that the species became abundant in the middle and upper part of the estuary.

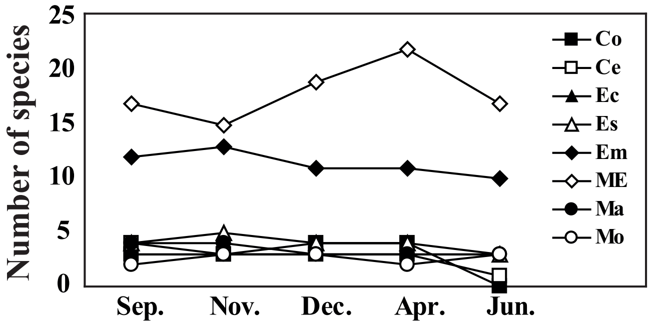

Fig. 4. Time evolution of the number of species per bioecological category for the five campaigns: Co: continental species, occasional in estuaries; Ce: estuarine species from continental origin; Ec: estuarine species from continental origin; Es: strictly estuarine species; Em: estuarine species from marine origin; ME: marine-estuarine species; Ma: marine species accessory in estuaries; Mo: marine species occasional in estuaries.

Ilisha africana also had a wide distribution in the Gambia Estuary, mainly during the dry season when the marine influence was highest. In April, this species was captured up to Wale (almost 150 km from the Ocean). However, the species was more abundant in the lower part of the estuary downstream of Suara Island (Fig. 5). In September, it was captured only in the lower part of the estuary.

3.3.2 Strictly estuarine component of the community (Es category)

Eight "strictly estuarine" (Es) species were recorded with *Monodactylus sebae* and *Gerres nigri* being the most abundant taxa in this category (Table 2). Three of them belong to the cichlid family (*Sarotherodon melanotheron*, *Tilapia guineensis* and *Tylochromis jentinki*) and the other three are small Eleotrids (*Bostrychus africanus*) and gobiids (*Nematogobius maindroni* and *Porogobius schlegelii*). All these species were not abundant and had very low occurrence (except for *M. sebae*, 21.6%). They did not follow any clear spatio-temporal distribution pattern in the Gambia Estuary.

3.3.3 Continental component of the community (Ec, Co and Ce categories)

Only 3 "estuarine of continental origin" (Ec) species were recorded, of which the catfish, *Chrysichthys nigrodigitatus*, was the most abundant and most frequently occurring. Like the "occasional Marine" (Mo) species, the "occasional Continental" (Co) were rarely recorded and were numerically of very limited importance.

Large populations of this estuarine catfish, of continental origin (Ec), live and reproduce in the estuaries and lagoons of West Africa. In the Gambia Estuary, it ranked eleventh in total biomass but only twenty-third in numbers. In addition to its overall abundance, it was a very frequent species, tenth in terms of occurrence (29% occurrence). *C. nigrodigitatus* was present in most of the estuary, down to Sika Point (40 km from the sea) during the wet season but limited to the middle and upper estuary (upstream of Tendaba, 107 km from the sea) during the dry season (Fig. 5).

S. gambiensis and *S. batensoda* (Mochokidae) had different distribution patterns in the Gambia Estuary. *S. gambiensis* is a species of continental origin with a strong estuarine affinity (Ce). It is the first species from this category in the Gambia Estuary. It does not reproduce in the estuary but had a wide spatio-temporal distribution (Fig. 5) and was one of the more abundant species. It came in fourth place in biomass and ranked fifth in numbers and occurrence (43%). During the wet season (September) *S. gambiensis* followed the river flood as far downstream as Mootah Point (69 km from the sea). By December the species had started moving back upstream and was confined to the upper reaches during the dry season.

S. batensoda is a freshwater species found only occasionally in the estuarine environment (Co). It was not as abundant as *S. gambiensis*, ranked seventh in numbers, eleventh in biomass and only twenty-second in occurrence. Its distribution area was much more limited than that of *S. gambiensis*. It was only abundant during the wet season and generally restricted to the upper estuary. It was never caught downstream of Bambako (site 22) with the highest numbers recorded in the three upper sites (42 to 44) during the maximum flood period in September. In the dry season, it was almost totally absent from the study area and was caught only once, in the most upstream zone (April).

4 Discussion

Most of the fish taxa living permanently or temporarily in West African estuaries and lagoons have wide tolerance limits to the fluctuating conditions found in these systems. It is widely acknowledged that many interacting physical and biological factors influence the occurrence, distribution, abundance and diversity of estuarine tropical fishes (Whitfield 1998; Blaber 2000). Among the physico-chemical factors, water salinity, temperature, turbidity, depth, current strength, dissolved oxygen, and their regular or irregular fluctuations at different time scales, have been identified as determinants in estuarine fish ecology (Whitfield 1998; Albaret 1999; Blaber 2000).

The most essential adaptation by fish, which enter estuarine systems, is an ability to adjust to changes in salinity (Panikkar 1960). Most estuarine fish are able to cope with salinity fluctuations but their ability to do so varies from species to species and hence influences their distribution (Blaber 2000). In a large open estuary such as the Gambia, the salinity at a given site and the magnitude of fluctuation depends mainly upon the balance between freshwater inflow (long-term, seasonal changes) and tidal regime (short-term changes). The Gambia River originates in the Fouta Djalon, and its estuary receives a large freshwater input for a protracted period each year. Unlike nearby estuaries of the Sene-Gambian area, the Sine Saloum to the North, the Casamance to the South, the Gambia has no hyperhaline waters in its upper reaches. Whatever the season the salinity gradient always decreases from the mouth upstream. The longitudinal distribution of salinity showed seasonal changes (Fig. 2a), the shape

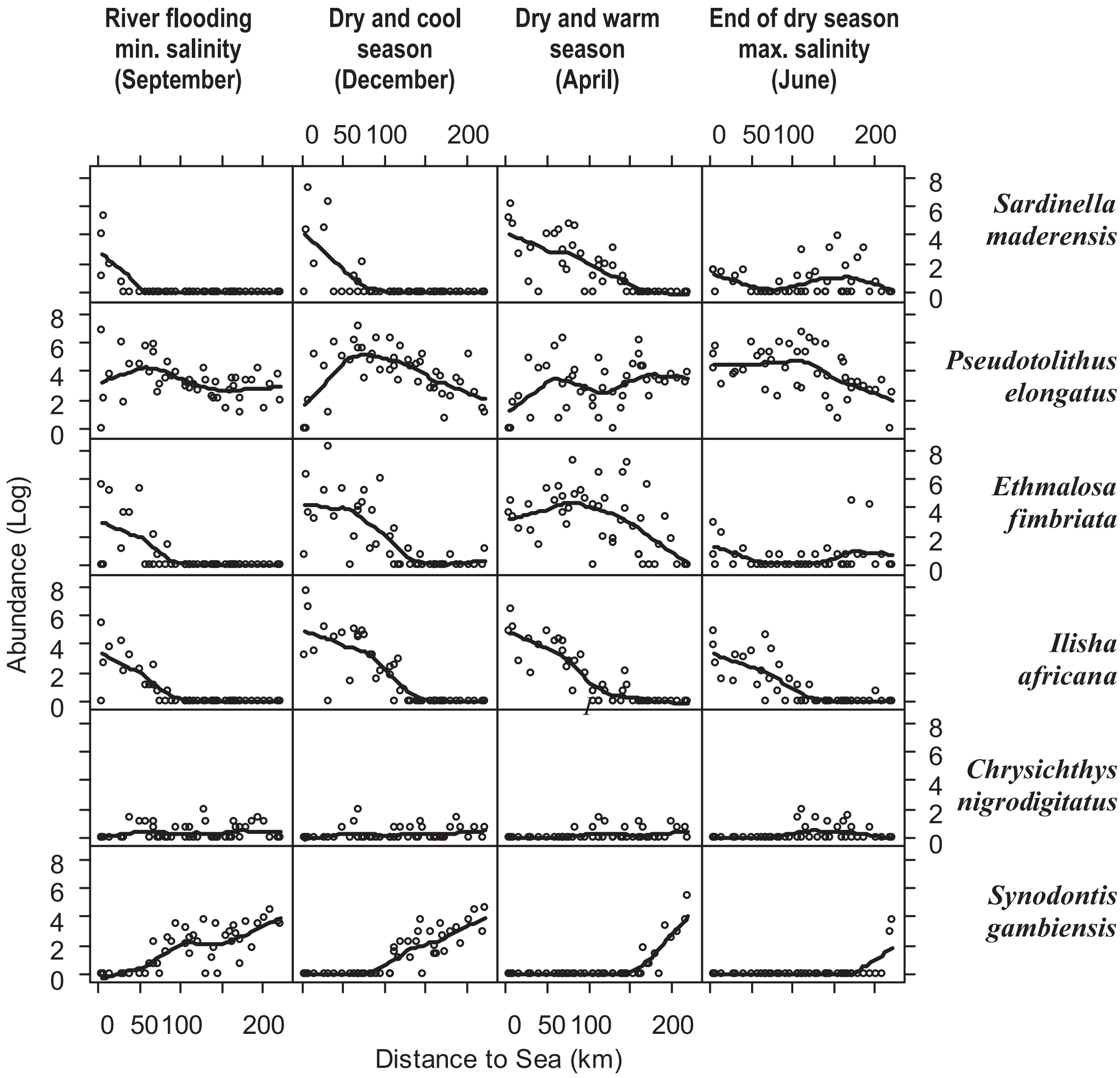

Fig. 5. Spatial (distance to sea in km) and seasonal (periods of the hydrological cycle) distribution of abundances of *Sardinella maderensis*, *Pseudotolithus elongatus*, *Ethmalosa fimbriata*, *Ilisha africana*, *Chrysichthys nigrodigitatus* and *Synodontis gambiensis*. The periods of the hydrological cycle are (from left to right): the rainy season (river flooding and minimum estuary salinity), the dry and cool season, the dry and warm season, the end of the dry season (maximum estuary salinity). Each point represents the log-transformed value of the fish abundance in relation to the distance to the sea. The smooth curve is the locally weighted regression (Lowess) with a span value of 0.5.

of the 5 profiles fitting the "Type 3" shape category of the classification proposed by Savenije and Pagès (1992). "Type 3" has a concave shape and the salinity gradient at the mouth is small. In the Gambia Estuary, freshwater intrusion increased during the flood season, then decreased during the dry period until the end of June, yet the shape type remained unchanged. The Gambia Estuary is a well-mixed (no thermal or saline spatial or temporal vertical stratification) and oxygenated system. Considerable seasonal variation in river flow results in marked changes to the aquatic environment. Despite the recent and severe drought in the sub-region, the Gambia Estuary has remained a "normal" estuary, unlike the neighbouring Casamance and Sine Saloum, which have become "reversed" estuaries. This point has reinforced the choice of the Gambia system as a reference for estimating the impact of changing freshwater inputs on West African estuarine fish communities.

Another important environmental finding was the generally high turbidity of the Gambia Estuary. Turbidity is known to have a major influence on estuarine fish occurrence and distribution. Turbidity affects estuarine fishes in three main ways: it may afford greater protection for juvenile fish from predators; it is generally associated with areas where there is an abundance of food; and it may provide an orientation mechanism for migration to and from the estuary (Blaber 2000). However, excessively high water turbidity has been shown to negatively affect fish egg survival, hatching success, feeding efficiency (mainly of filter feeders), growth rate and population size (Whitfield 1998). Whatever its origin in the Gambia Estuary, high primary production, suspended inorganic matter, or a combination of the two, turbidity will need to be taken into account in future comparative work because of its fundamental influence on fish distribution within the estuarine environment.

According to a number of criteria, the Gambia Estuary should have very high species diversity. Biogeography plays an important role in species richness (Blaber 1981) and tropical and subtropical estuaries have higher species richness than temperate systems (Whitfield 1994a,b). The Gambia is a large estuary (several km wide in the lower reaches and more than 200 km long) with an extensive, permanent interface with the Atlantic Ocean in the mouth region and the Gambia River in the upstream region. Both offer a rich potential for colonization of the estuary by fish. The morpho-edaphic diversity, including the presence of extensive mangroves and a range of hydrological situations, are further factors favouring high biodiversity (Albaret 1999).

All the West African estuarine ecological categories are represented in the fish fauna of the Gambia Estuary, which clearly belongs to the "Type E" theoretical model used to explain the evolution and classification of West African estuarine ecosystems (Diouf 1996; Albaret 1999). "Type E" ecosystems are exposed to balanced marine and continental influences and all types of bio-ecological life cycles are likely to be found in them. Similarly, all of the main fish families likely to be found in tropical estuaries are represented in the Gambia system.

Despite the above favourable analysis, the Gambia Estuary was found to have a moderate or even low number of fish species when compared with other West African estuaries studied using a similar sampling method and effort (Albaret 1999). The main explanations for this apparent paradox are probably to be found in the natural disturbance imposed on the system by regular extensive flooding and to the lack of persistent marine conditions within the estuary. Most large West African estuaries have highly perturbed catchments but also possess large, marine zones that enable marine taxa (mainly ME but also Ma and Mo species) to colonize the estuary.

Fish community ecological categories in the estuarine environments of West Africa (Albaret 1999) are not symmetrical, with four categories to the right of the "marine" branch and only three on the left "continental" branch. Moreover the number of marine species likely to enter estuaries considerably exceeds the number of freshwater species capable of colonising estuaries. A strong continental influence does not compensate for a weak marine influence in terms of overall estuarine species richness. Figure 3a clearly shows that even in the very continental influenced Gambia Estuary, the species of marine origin constitute the majority of the species reported (49 against 13).

When compared with the Sine Saloum fish community (Diouf 1996) it appears that extreme categories Mo and Ma are mainly responsible for the lower species diversity recorded in the Gambia Estuary but that all the species forming the "estuarine fundamental community" (Albaret 1999) are present in this system. In terms of species number alone, the Gambia Estuary cannot be considered a biodiverse environment, but in terms of the ecological categories and life cycles it has a biodiversity close to or greater than that of many other estuarine systems in West Africa. In conclusion, it would appear that for the Gambia Estuary, total species richness 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.

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References

Albaret J.J., 1987, Les peuplements de poissons de la Casamance (Sénégal) en période de sécheresse. Rev. Hydrobiol. Trop. 20, 291-310.

Albaret J.J., 1994, Les poissons : biologie et peuplements. In: Durand J.R., Dufour P., Guiral D., Zabi S.G. (Eds.), Environnement et ressources aquatiques de Côte d'Ivoire. Tome 2. Les milieux lagunaires. ORSTOM, Paris, pp. 239-279.

Albaret J.J., 1999, Les peuplements des estuaires et des lagunes. In: Lévêque C., Paugy D. (Eds.), Les poissons des eaux continentales africaines : diversité, biologie, écologie et utilisation par l'homme. Éditions de l'IRD, Paris, pp. 325-349.

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. Ann. Museum R. Afr. Centr. Zool. 165-177.

Baran E., 1995, Dynamique spatio-temporelle des peuplements de poisons estuariens en Guinée. Relations avec le milieu abiotique. Thèses et Documents microfiches No. 142, ORSTOM, Paris.

Berry T.D., Moll R.A., Krausse G.L., 1985, Physical and chemical environment of the Gambia River, West Africa, 1983-1984. Report No. 9, Great lakes and Marine waters center international programs, The University of Michigan, Ann Arbor, Michigan, p. 202.

Blaber S.J.M., 1981, The zoological affinities of estuarine fishes in South-East Africa. S. Afr. J. Sci. 77, 305-307.

Blaber S.J.M., Albaret J.J., Chong Ving Ching, et al. 2000, Effects of fishing on the structure and functioning of estuarine and nearshore ecosystems. ICES J. Mar. Sci. 57, 590-602.

Blaber S.J.M., 2000, Tropical Estuarine Fishes. Ecology, Exploitation and Conservation. Fish and Aquatic Resources Ser. 7, Blackwell Science.

Cleveland W.S., 1979, Robust locally weighted regression and smoothing scatterplots. J. Am. Statist. Assoc. 74, 829-836.

Daget J., 1960, La faune ichtyologique du bassin de la Gambie. Bull. IFAN 22, No. 2, 610-619.

Diouf P.S., 1996, Les peuplements de poissons des milieux estuariens d'Afrique de l'Ouest : l'exemple de l'estuaire hyperhalin du Sine-Saloum. Thèses et Documents microfiches No. 156, ORSTOM, Paris.

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.

Gray J.S., 2001, Marine diversity paradigms: the patterns of species richness examined. Sci. Mar. 65 (suppl. 2), 41-56.

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

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. Aquat. Living Resour. 17, 75-85.

Lamagat J.P., Albergel J., Bouchez J.M., Descroix L., 1990, Monographie hydrologique du fleuve Gambie. ORSTOM; Organisation pour la Mise en Valeur du fleuve Gambie (OMVG), Dakar, Sénégal.

Lesack L.F.W., 1986, Estimates of catch and potential for the riverine artisanal fishery in the Gambia, West Africa. J. Fish Biol. 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. Limnol. Oceanogr. 29, 816-830.

Michel P., 1963, Les bassins des fleuves Sénégal et Gambie. Étude géomorphologique. Paris, Mémoires ORSTOM No. 63.

Panikkar N.K., 1960, Physiological aspects of adaptation to estuarine conditions. Australian Fisheries Council Proceedings 32, 168-175.

Por F.D., 1972, Hydrobiological notes on the high-salinity waters of the Sinai Peninsula. Mar. Biol. 14, 111-119.

Savenije H.H.G., Pagès J., 1992, Hypersalinity: adramatic change in the hydrology of Sahelian estuaries. J. Hydrol. 135, 157-174.

Scherrer B., 1984, Biostatistique. In G. Morin (Ed.), Montréal, Paris.

Vidy G., Darboe F.S., Mbye E.M., 2004, Juveniles fish assemblages in the creeks of the Gambia Estuary. Aquat. Living Resour., 17, 56-64.

Whitfield A.K., 1994a, Fish species diversity in Southern African estuarine systems: an evolutionary perspective. Env. Biol. 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.), Diversité biologique des poissons des eaux douces et saumâtres d'Afrique : Synthèses géographiques. Ann. Mus. R. Afr. centr., Zool., Tervuren, 275, 149-163.

Whitfield A.K., 1998, Biology and Ecology of Fishes in Southern African Estuaries. Ichthyological. Monographs of the J.L.B. Smith Institute of Ichthyology, No. 2.