Available online at www.sciencedirect.com
SCIENCE DIRECT®

Estuarine, Coastal and Shelf Science 64 (2005) 623–635

ESTUARINE COASTAL AND SHELF SCIENCE
www.elsevier.com/locate/ECSS

Spatial versus temporal patterns in fish assemblages of a tropical estuarine coastal lake: The Ebrié Lagoon (Ivory Coast)

Jean-Marc Ecoutin [a,*], Emilie Richard [b], Monique Simier [b], Jean-Jacques Albaret [a]

[a] *IRD, BP 1386, Institut de Recherche pour le Developpement, 18524 Dakar, Senegal*
[b] *IRD, Centre de Recherche Halieutique Méditerranéenne et Tropicale, Avenue J. Monnet, B.P. 171, 34203 Sète Cedex, France*

Received 14 December 2004; accepted 5 April 2005
Available online 21 June 2005

Abstract

The fish assemblages of the Ebrié lagoon (Ivory Coast) were sampled by experimental fishing over the entire lagoon using a purse seine net. The sampling was conducted in the two main hydroclimatic seasons for this ecosystem, i.e. in the dry season (March–April) and in the wet season (August–September). The results obtained showed a fish assemblage organized around a consistently occurring group of twenty species. When analysed in terms of ecological categories, the seasonal influence led to a cycle in the assemblages from freshwater to marine around this permanent species pool, with a seasonal renewal of the assemblage. At the scale of the lagoon, there were variations in the composition of the assemblages that clearly distinguished the western part from the eastern one. The limit was situated at the Vridi canal, a wide artificial channel permanently connecting the lagoon to the sea. To the west, the assemblage was characterised by a strong spatial uniformity and low seasonal variability. To the east, the assemblage formed two different entities; one assemblage with pronounced freshwater affinities occurring in a side arm and the other assemblage with great seasonal variability under the alternating influence of seawater in the dry season and freshwater in the wet season. This part of the lagoon functioned somewhat like a typical estuary.

Keywords: fish assemblages; tropical lagoon; spatio-temporal pattern; correspondence analysis; West Africa

1. Introduction

In estuarine and lagoon environments, that are extremely variable because they are subjected to freshwater and marine influences at various time scales, the equilibria are unstable and therefore easily changed by human activities or major climatic disturbances (Blaber, 2000). A better understanding is needed in order to produce conservation management plans and for sustainable management (Blaber, 2002).

Many authors have suggested that fish communities, as indicators of environmental changes, are good tools for determining the state of health of ecosystems (Paller et al., 1996; Whitfield, 1996; Soto-Galera et al., 1998; Attrill, 2002; Whitfield and Elliott, 2002). The basis for using biological monitoring of fishes to assess environmental condition is that the relative health of a fish community is a sensitive indicator of direct or indirect stress on the entire aquatic system (Fausch et al., 1990). Knowledge of the composition and dynamics of the permanently resident fish communities in estuarine and lagoon environments and those that use these environments on a temporary basis, would allow such ecosystems to be monitored both spatially and temporally.

Recent studies on the fish assemblages of tropical estuarine and lagoon environments have demonstrated the great species richness of these ecosystems, situated at the interface between the freshwater and marine

* Corresponding author.
E-mail address: ecoutin@ird.sn (J.-M. Ecoutin).

0272-7714/$ - see front matter
doi:10.1016/j.ecss.2005.04.002

domains (Albaret, 1999; Blaber, 2002 for review). In a given geographical region, the fish communities of estuarine environments consist of a constantly occurring pool of marine coastal species, strictly estuarine species and species of freshwater origin. Depending on the degree of connection with adjacent environments (size, shape, seasonal changes and history of the connections), the fish community of a given estuary or lagoon can be close in its composition and structure to those typical of the neighbouring environments. The marine and freshwater influences are not however symmetrical and do not have the same weight. Some studies have for example emphasized the fundamental role of the marine influence on the composition and species richness of estuarine and lagoon environment assemblages, that is mainly related to the size and permanence of the connection to the sea (Cowley and Whitfield, 2001; Blaber, 2002; Vorweck et al., 2003).

The temporary or more lasting occurrence of rare or infrequent, freshwater or marine, migratory species makes the structure of fish assemblages in estuarine and lagoon environments more complex. To make the analysis easier, various authors have recommended an approach based on classifications into ecological categories taking into account the geographical origin, the length of occurrence, the seasonality and the likelihood of the species breeding (Whitfield, 1999; Blaber, 2000; Garcia et al., 2003). Analysis of the spatial or temporal changes in these ecological categories provides a new means of identifying the structure of these assemblages, at a higher level of integration than that of the species. It allows comparison to be made between environments with differing fish species composition. A classification into eight categories was proposed by Albaret (1999) for West Africa. In addition to the degree of euryhalinity, which depending on the individual case was either a main or secondary criterion, the classification was based on the characteristics of the reproductive cycle of each species, including: the distribution, breeding site, and location and respective abundance of ecophases. The concepts of spatial stability and temporal variability are discussed on the basis of this classification from a study of the fish assemblages of the Ebrié lagoon in the Ivory Coast.

A first multidisciplinary review of information acquired on the Ebrié lagoon was conducted by Durand et al. (1994). With 153 species of fish recorded (Albaret, 1994), this estuarine and lagoon environment has one of the most diverse estuarine-associated fish populations in Africa or even in the world (Albaret, 1999; Blaber, 2002). A study of the assemblages in an urban bay in the maritime part of this lagoon showed that at both an annual and long-term scale (1962–1981), there was a group of twenty species that formed a remarkably stable permanent core of the assemblage in an environment that is extremely variable at various scales (Albaret and Ecoutin, 1990). In addition to this constant component, an increase in the marine component of the assemblage was identified and was interpreted as the result of a drought in the region during the study period. An increase in the marine component of the lagoon assemblages was also demonstrated in the ecological impact study of the temporary reopening of a former connection to the sea (Albaret and Ecoutin, 1989). The area close to the capital Abidjan (Fig. 1) has been the subject of special studies because of its ecological importance as a breeding area and migratory route for young fish recruited in the lagoon and because of the effects on both the fish communities and populations of the chemical, organic and bacteriological pollution that occurs here (Albaret and Charles-Dominique, 1982; Albaret and Ecoutin, 1990; Dufour et al., 1994; Guyonnet et al., 2003).

This article, using data collected in the 1980s on the fish assemblages of the Ebrié lagoon (Albaret, 1994), concentrates on the analysis of the spatial structure of these assemblages at the scale of the entire lagoon. The distribution and spatial organisation of the communities in the lagoon at the two main hydroclimatic seasons in

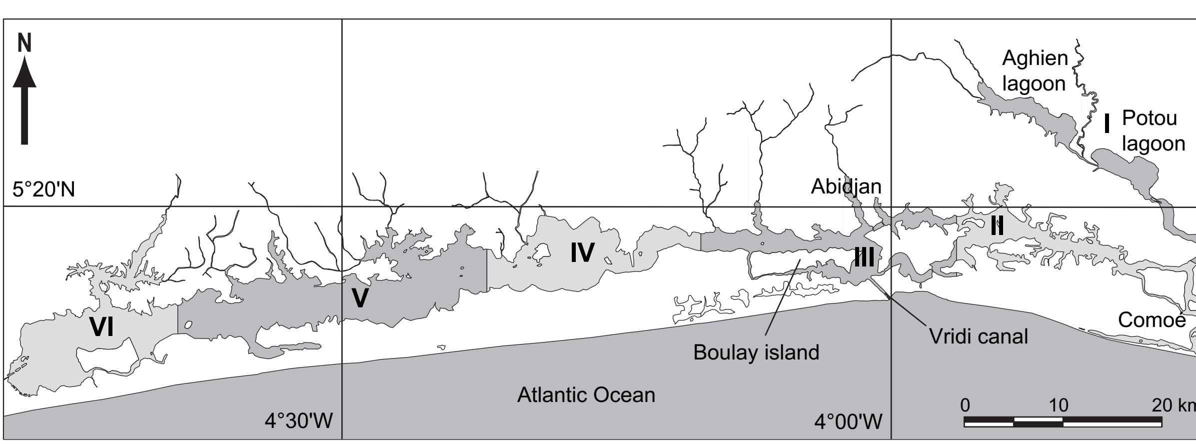

Fig. 1. Map of the Ebrié lagoon. Labels I to VI represent the six sectors defined by Durand and Skubich (1982) and derived from the hydroclimate, primary and secondary production and the fisheries.

the year (the dry season and the wet season) is described. The importance of permanent core of the assemblage identified by Albaret and Ecoutin (1990) is discussed, leading us to identify several areas in the lagoon characterised by fish assemblages whose nature and functioning are sufficiently distinct for them to be considered as functional units.

2. Materials and methods

2.1. Study area

The Ebrié lagoon is the largest coastal lagoon in West Africa (566 km^2, Durand et al., 1994). This lagoon is subjected to a double influence: a marine influence via the Vridi canal that provides a permanent connection to the sea, and a freshwater influence mainly from high river flow on the Comoé River and secondarily from direct rainfall and high river flow on coastal rivers (Fig. 1).

Studies on the hydroclimate, primary and secondary production and the fisheries on Ebrié lagoon resulted in the definition of six sectors (Fig. 1; Durand and Skubich, 1982). The constant communication with the sea produces typical estuarine characteristics, at least in sectors II, III and IV located near the Vridi canal. These parts of the lagoon, under the direct influence of both the sea and the flow of the Comoé River, are temporally variable (daily and seasonal variations) and heterogeneous. In contrast, sectors V and VI are oligohaline, stable and homogeneous (Durand and Guiral, 1994). Sector I, situated at the east of the Ebrié lagoon, is a side arm formed of two units. The first, the Aghien lagoon, is stable and uniform, being subjected to no marine influence or influence from high river flow on the Comoé, although the river is very close. The second, the Potou lagoon, is in contrast greatly influenced by such floods (Durand and Guiral, 1994).

The dry season in the Ebrié lagoon occurs between January and April. In this season freshwater inputs from rivers and direct rainfall are negligible. Evaporation is at its highest and the marine influence dominates, leading to the highest temperature and salinity values (Durand and Guiral, 1994). After a rainy season lasting about 4 months from May to August, the lagoon flood season extends from September to December. The high river flow of the Comoé, a river draining a large catchment extending into the Sahel region of Burkina Faso affects all the eastern part of the lagoon (Fig. 1). The wet season, including the rainy and subsequent flood periods, is the season when the freshwater inputs are the highest, and when local rainfall occurs. Surface salinities are close to or equal to zero over much of the lagoon; with the exception of the area close to the Vridi canal, that is subject to the daily influence of tides, and has surface salinity values slightly higher than 6 (Durand and Guiral, 1994).

2.2. Data collection

In 1980 and 1981 a sampling programme was conducted in the Ebrié lagoon with the aim of determining the overall composition of the fish assemblages (Albaret, 1994). This programme included about 60 sampling sites over the whole lagoon. Each site was sampled at two hydrobioclimatic seasons for the lagoon: the dry season and the wet season in order to determine the spatio-temporal variations in the Ebrié system.

For characterising the dry season assemblage, the sampling was conducted in February and March 1981. For the wet season, the data from the October 1980 and August-September 1981 samplings were combined into a single table. This season therefore included the end of the rainy season and the beginning of the flood season.

The experimental fishing was conducted by a crew of professional fishermen using a purse seine 300 metres long, 18 metres deep and with a mesh size of 14 mm. This fishing method gave a good sampling reproducibility in very varied environments, and the fish were collected in a good condition (Albaret, 1994). As used in this study (used blindly, without looking for fish shoals, by encircling an area of lagoon at a predetermined site), the purse seine is a low-selective gear providing great reproducibility between successive fishing operations.

Several environmental variables were measured at each seine haul: depth, water transparency, salinity, temperature and dissolved oxygen. Depth (m) was measured with a depth-meter, water transparency (m) with a Secchi disk. Salinity, temperature (°C) and dissolved oxygen (percentage saturation) were measured at the surface and bottom, respectively with an optical refractometer, a thermometer and a YSI hand-held field instrument.

Fish were identified to species level and counted by species. The composition of the assemblages was determined using the species classification proposed by Albaret (1999), which defines eight bio-ecological categories ordered on two gradients from a central point, the strictly estuarine species (Es). The gradient of marine affinity comprises four categories: the estuarine species of marine origin (Em), the marine-estuarine species (ME), the marine species accessory in estuaries (Ma) and the marine species occurring occasionally 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, occurring occasionally in estuaries (Co). Four of these categories (Ec, Es, Em and ME) compose the fundamental lagoon and estuarine community.

2.3. Data analysis

The numbers per species and per seine haul are included in two tables consisting of 53 lines for sites and

55 columns for species in the dry season and 54 columns for species in the wet season. Correspondence Analyses (CA) were conducted on each table using the logarithms of numbers to homogenise the variances between non-shoaling species that were caught in small numbers and shoaling species, which could be locally abundant.

The statistical analyses were conducted using ADE-4 software (Thioulouse et al., 1997).

3. Results

3.1. The dry season assemblages

3.1.1. Environmental conditions

The environmental characteristics of the six sectors in the Ebrié lagoon in the dry season are shown in Table 1. There was a wide range of surface and bottom salinities, from 0 to 32. The salinity was highest in sector III, close to the Vridi canal, and decreased toward both the east end (sector I) and west end (sectors V and VI). The transparency was also highest in sector III and lowest in sector I. The temperatures were high everywhere (about 30 °C). There was little vertical stratification in either salinity or temperature, reflecting a good mixing of the water column.

3.1.2. Composition of the fish assemblages

In our sampling, the 55 species were distributed irregularly in 7 of the 8 ecological categories defined by Albaret (1999), excluding the Mo category (Table 2). The two categories containing the species of freshwater origin – Freshwater occasional (Co, 2 species) and Freshwater with estuarine affinity (Ce, 6 species) – only occurred in sector I, with the exception of *Schilbe mandibularis*, that also occurred in sector VI. The accessory Marine forms (Ma, 5 species) were only captured in sector III, or in sector II for 2 observations of the same species (*Scomberomorus tritor*).

The species belonging to the four other categories (Ec, Es, Em, ME) that form the fundamental assemblage of estuarine and lagoon environments (Albaret, 1999), were recorded in all or some of the six lagoon sectors. Ten species belonging to each of these categories were even recorded in all six sectors.

The most frequent species was *Elops lacerta* (a fish-eating predator of the Marine Estuarine category) recorded in 83% of the fish samples. The most abundant was *Ethmalosa fimbriata* (a small, Estuarine of marine origin, pelagic filter-feeder) accounting 38% of fish captured.

3.1.3. Spatial structure of the fish assemblages

The first two axes of the CA explained a relatively low percentage of total inertia (26.7%). Because of the large number of eigenvalues (52), it can be considered as a good summary of the fish assemblage structure in the Ebrié lagoon during the dry season.

The plot of the sampling sites (Fig. 2) and species (Fig. 3) on the first two axes of the CA shows an arch effect (Legendre and Legendre, 1998), reflecting a very strong environmental gradient that structured the assemblage at this season.

The plot of the sampling sites distinguished three main groups: the sites in sector III and the most westerly sector II which were close together (dry season DS1 group); some sites in the Aghien lagoon (DS2) and finally the sites in sectors IV, V and VI, those of the Potou lagoon and a part of sector II (DS3). The first two groups showed a great heterogeneity within sectors, in

Table 1
Environmental characteristics of the six sectors of the Ebrié lagoon in the dry season (st., number of sites)

		Sect. I (11 st.)	Sect. II (12 st.)	Sect. III (9 st.)	Sect. IV (11 st.)	Sect. V (5 st.)	Sect. VI (5 st.)
Depth (m)	Mean (±SD)	3.92 (2.29)	4.36 (2.66)	4.19 (2.31)	2.10 (0.39)	3.98 (2.28)	3.94 (1.26)
	Range	1.7–10.0	1.7–10.0	1.2–7.5	1.5–2.5	2.5–8.0	2.5–5.5
Transparency (m)	Mean (±SD)	0.94 (0.42)	2.06 (0.49)	2.19 (1.27)	1.52 (0.41)	2.08 (0.28)	1.64 (0.29)
	Range	0.6–1.6	1.4–2.9	0.8–5.0	1.2–2.5	1.8–2.5	1.4–2.1
Surface salinity	Mean (±SD)	0 (0)	11.96 (3.12)	25.44 (4.90)	4.45 (2.56)	1.30 (1.10)	3.10 (0.70)
	Range	0–0	8.0–16.5	17.0–30.0	1.0–10.0	0.3–3.2	2.2–3.8
Bottom salinity	Mean (±SD)	0 (0)	14.50 (4.35)	27.72 (5.12)	4.80 (2.95)	1.26 (1.02)	3.24 (0.99)
	Range	0–0	8.0–21.0	19.0–32.0	2.0–12.0	0.3–3.0	1.5–3.9
Surface temperature (°C)	Mean (±SD)	30.0 (0.33)	30.50 (0.96)	29.26 (1.18)	29.39 (0.72)	30.10 (0.55)	30.66 (0.23)
	Range	29.5–30.5	29.4–32.7	28.1–32.2	28.4–30.5	29.5–31.0	30.5–31.0
Bottom temperature (°C)	Mean (±SD)	29.67 (0.66)	30.24 (1.27)	28.28 (1.72)	29.57 (0.78)	29.94 (0.76)	30.12 (0.57)
	Range	28.2–30.4	28.0–32.8	25.9–31.2	28.6–31.0	29.2–31.0	29.5–30.6
Surface oxygen (%)	Mean (±SD)	61.09 (5.05)	57.00 (3.02)	63.75 (8.33)	66.00 (3.83)	72.20 (2.05)	66.20 (4.21)
	Range	52–69	50–62	54–81	61–75	69–74	62–73
Bottom oxygen (%)	Mean (±SD)	46.7 (16.69)	28.17 (18.23)	43.63 (11.89)	63.57 (3.31)	55.60 (18.20)	44.80 (11.37)
	Range	7–63	2–53	26–63	60–69	28–72	28–58

Mean value ± standard deviation (SD), and range (minimum-maximum) are given for depth (m), water transparency (m), and surface and bottom values of salinity, temperature (°C) and percentage oxygen saturation (%).

Table 2
Distribution per bio-ecological category and per sector of the 55 fish species collected in the Ebrié lagoon during the dry season

Ecological Category	Species	Code	Sector												Total	
			I		II		III		IV		V		VI		Oc	Nb
			Oc	Nb	Oc	Nb	Oc	Nb	Oc	Nb	Oc	Nb	Oc	Nb		
Co	*Chromidotilapia guentheri*	PGU	1	1											1	1
	Hepsetus odoe	HOD	2	2											2	2
Ce	*Brycinus longipinnis*	ALO	5	23											5	23
	Brycinus macrolepidotus	AMA	2	4											2	4
	Heterobranchus isopterus	HIS	1	2											1	2
	Parailia pellucida	PHP	1	2085											1	2085
	Schilbe intermedius	SIN	3	24											3	24
	Schilbe mandibularis	EME	5	240									1	2	6	242
Ec	*Chrysichthys auratus*	CFI	5	39					4	60	1	7	3	165	13	271
	Chrysichthys maurus	CWA	9	852	3	38	2	13	6	161	4	72	4	673	28	1809
	Chrysichthys nigrodigitatus	CNI	9	126							1	1	5	1345	15	1472
	Hemichromis fasciatus	HFA	4	5	3	64	1	1	4	12	4	46	5	11	21	139
	Pellonula leonensis	PEF	5	218									1	2	6	220
	Tilapia mariae	TMA	3	35											3	35
Es	*Eleotris senegalensis*	ESE	2	2	1	1									3	3
	Enneacampus kaupi	SKA			1	1									1	1
	Gerres nigri	GNI			4	23	6	304	6	22	1	3	3	18	20	370
	Gobioides sagitta	GAN	2	2											2	2
	Gobionellus occidentalis	OOC			2	10	2	26	4	9					8	45
	Monodactylus sebae	PSB			9	330	1	1			1	1	4	11	15	343
	Porogobius schlegelii	ACS	1	2	4	6	3	18	6	10	5	22	1	1	20	59
	Sarotherodon melanotheron	THE	4	21	3	134	1	5	5	14	3	82	2	385	18	641
	Tilapia guineensis	TGU	8	38	7	122	2	6	6	40	5	237	5	96	33	539
	Tylochromis jentinki	TJE	8	31	3	3			3	3	4	75	5	224	23	336
Em	*Citarichthys stampflii*	CST	5	15	10	415	7	121	11	212	4	30	1	2	38	795
	Cynoglossus senegalensis	CYS	3	6	3	4	3	9	1	4			1	1	11	24
	Dasyatis margaritella	DAM					1	1							1	1
	Ethmalosa fimbriata	EFI	1	5	11	6227	7	1118	11	782	3	49	2	58	35	8239
	Hemiramphus balao	HBA					1	1							1	1
	Liza falcipinnis	LFA			1	1			3	6	1	2	1	1	6	10
	Liza grandisquamis	LGR			1	3	5	82			1	2			7	87
	Mugil curema	MCU					1	1	1	1					2	2
	Plectorhinchus macrolepis	PLM	1	1	2	2									3	3
	Pomadasys jubelini	PJU	3	7	9	30	4	61	8	47	1	1	1	1	26	147
	Pseudotolithus elongatus	PEL	3	16	1	4									4	20
	Strongylura senegalensis	BES	1	1	1	1					1	1			3	3
	Trachinotus teraia	TFA	3	38	6	198			1	1	2	2	4	9	16	248
ME	*Brachydeuterus auritus*	BAU					2	22							2	22
	Caranx hippos	CHI			9	91	5	17	2	2					16	110
	Caranx senegallus	CAS			6	143	1	3	1	1					8	147
	Chloroscombrus chrysurus	CHL			5	24	7	99							12	123
	Elops lacerta	ELA	11	209	10	252	4	38	10	109	4	94	6	267	45	969
	Epinephelus aeneus	EAE					5	12							5	12
	Eucinostomus melanopterus	GME			6	35	8	70	7	25	3	8	3	57	27	195
	Galeoides decadactylus	GDE			1	1	4	14							5	15
	Polydactylus quadrifilis	POQ	5	11	3	18			3	4			2	9	13	42
	Sardinella maderensis	SEB			1	1610	2	52							3	1662
	Selene dorsalis	VSE					1	6							1	6
	Sphyraena afra	SPI	6	34	10	32	1	1	2	2	1	2	1	2	21	73
	Trichiurus lepturus	TLE					2	43							2	43
Ma	*Hyporamphus picarti*	HPI							1	1					1	1
	Lagocephalus laevigatus	LLA					1	1							2	1
	Pagrus caeruleostictus	PEH					1	1							1	1
	Scomberomorus tritor	CTR			2	6	2	4							4	10
	Trachinotus ovatus	LGL					4	24							4	24

Code: abbreviation used in Fig. 3. Oc: number of samples where the species was present. Nb: total number of individuals.

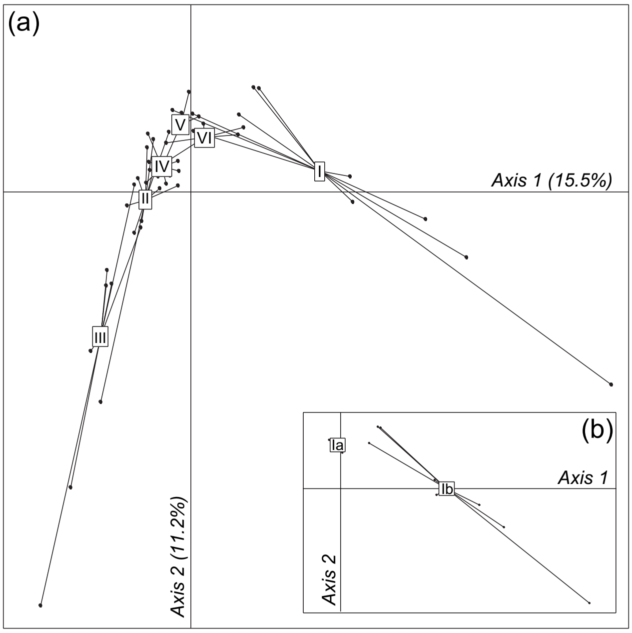

Fig. 2. Scatterplot of the 53 samples of the dry season on the first two axes of the Correspondence Analysis. (a) All 53 sites are linked to the center of gravity of their sector (in square). (b) The 11 sites of sector I are grouped by subsector: Ia: Potou, Ib: Aghien.

contrast to the third group that was more homogenous. The division of sector I into two distinct groups of sites is clearly visible (Fig. 2b). Most of the sites in the freshwater Aghien lagoon contrasted with those of the Potou lagoon, which were situated on this plot close to the sites in sectors V and VI. When these two latter zones were separated into two independent units, the results obtained for the Potou lagoon reposition it within the three western sectors groups (IV, V and VI).

The plot of the species on the same two axes (Fig. 3) related to the centre of gravity of their ecological category, completes this spatial description by linking the three spatial entities identified above to clearly distinct ecological categories. The species were distributed along a gradient from the most freshwater to those of the Marine accessory category. The most freshwater and the most marine ecological categories had the highest dispersion of species, in contrast to the estuarine type categories that were more uniform.

The assemblage in the DS1 spatial group was composed of Ma and ME species with a pronounced marine affinity. It also included species belonging to the Em, Es and even Ec categories, species that all have a high salinity tolerance or tolerance of salinity variation. The two ecological categories Ce and Co were recorded exclusively in the Aghien zone (Table 2). In association with certain Ec species, they formed the basic assemblage of the Aghien system (DS2) which can be considered, at this season, to be a strict freshwater type. Finally, the assemblage of the DS3 cluster was mainly composed of species belonging to the Ec, Es and Em categories. ME species were commonly associated with this assemblage, even in the most westerly sites in sector VI.

With the exception of the very freshwater assemblage of the Aghien lagoon, the dry season assemblages in the Ebrié lagoon were arranged along two major geographical orientations starting from a coastal marine type assemblage in sector III under the influence of the Vridi canal. This assemblage changed toward the east (from sector II to the Potou lagoon) and toward the west (from sectors IV to VI) to form a more stable assemblage with great spatial homogeneity. Although the assemblage of the Potou lagoon to the east was similar to that in sectors V and VI to the west, the gradient required to reach it was very different in its spatial trend, being gradual to the east from sector III, passing through sector II, but had a marked step to the west between the sites in sectors III and IV.

3.2. The wet season assemblages

3.2.1. Environmental conditions

The environmental characteristics of the Ebrié lagoon in wet season are shown in Table 3. At this season, the entire lagoon has zero or very low surface salinities, with only the sites in sector III close to the Vridi canal reaching a surface salinity of about 6. Almost all the sites in sectors I and II were completely freshwater both at the surface and bottom. The surface and bottom salinities in sector III sites that are far from the Vridi canal, and in sectors IV to VI were between 0.5 and 4. The transparency was low in sectors I and II, was higher in sectors V and VI but remained close to the values recorded in the dry season. With the exception of sector III, the temperatures were notably lower than in the dry season. As in the dry season, there was no vertical stratification, with the exception of the salinity in sector III.

3.2.2. Composition of the fish assemblages

A total of 54 species belonging to 7 of the 8 ecological groups were captured during the sampling, with no species belonging to the Marine occasional category (Mo) being recorded, as during the dry season. The number and proportion of forms with a freshwater tendency increased compared to the dry season (4 species in the Co category, 5 in the Ce category). With one exception (again *Schilbe mandibularis*), these 9 species were only recorded in sector I (Table 4). In contrast, the number and proportion of species belonging to the Ma category decreased, with only 4 species at a low occurrence and low abundance.

As in the dry season, ten species were recorded at least once per sector, but only 5 were the same as those recorded in the dry season.

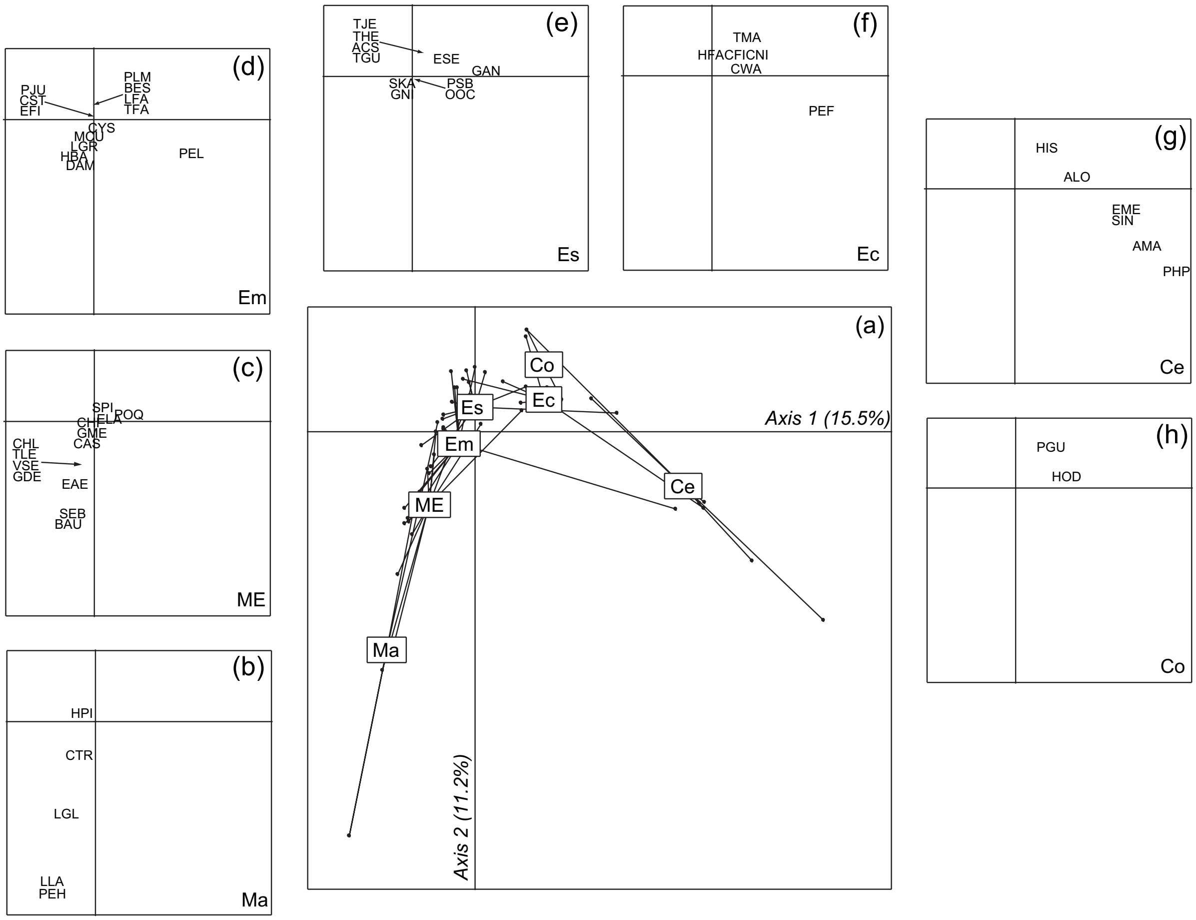

Fig. 3. Scatterplot of the 55 species of the dry season on the first two axes of the Correspondence Analysis. (a) Species have been plotted together and grouped by bio-ecological categories. (b) to (h) Species have been plotted on separate graphs for each category.

The most frequent species was *Elops lacerta* that was recorded in 90% of samples, whereas the most abundant species was *Ethmalosa fimbriata* (56% of total numbers).

3.2.3. Spatial structure of the fish assemblages

At this hydroclimatic season, the first two axes of the CA explained 27.4% of the total inertia, a similar percentage to that of the dry season. The plot of the sites

Table 3
Environmental characteristics of the six sectors of the Ebrié lagoon in the wet season (st., number of sites)

		Sect. I (11 st.)	Sect. II (12 st.)	Sect. III (9 st.)	Sect. IV (11 st.)	Sect. V (5 st.)	Sect. VI (5 st.)
Depth (m)	Mean (±SD)	3.72 (1.57)	3.23 (1.79)	3.74 (1.88)	2.14 (0.61)	4.42 (2.04)	3.9 (1.75)
	Range	1.4–7.0	1.5–8.0	1.3–7.5	1.3–3.5	3.0–8.0	2.0–6.0
Transparency (m)	Mean (±SD)	0.48 (0.04)	1.0 (1.12)	1.2 (0.28)	0.89 (0.32)	1.86 (0.60)	1.84 (0.53)
	Range	0.4–0.5	0.4–3.5	1.0–1.7	0.5–1.5	1.0–2.7	1.1–2.5
Surface salinity	Mean (±SD)	0.00 (0.00)	0.00 (0.00)	4.93 (1.49)	1.7 (0.63)	2.3 (0.45)	0.8 (0.27)
	Range	0–0	0–0	2.7–6.6	0.8–2.8	2.0–3.0	0.5–1.0
Bottom salinity	Mean (±SD)	0.00 (0.00)	1.96 (6.78)	9.11 (8.74)	2.03 (0.48)	2.5 (0.5)	0.7 (0.45)
	Range	0–0	0–23.5	3.5–29.9	1.2–2.9	2.0–3.0	0.0–1.0
Surface temperature (°C)	Mean (±SD)	26.6 (0.25)	27.1 (0.36)	29.3 (0.88)	26.5 (0.83)	25.7 (0.37)	25.5 (0.80)
	Range	26.2–27.1	26.6–27.9	27.3–30.2	25.0–27.7	25.2–26	24.8–26.4
Bottom temperature (°C)	Mean (±SD)	26.4 (0.30)	27.3 (0.90)	27.9 (1.88)	26.7 (0.52)	25.4 (0.34)	25.5 (0.76)
	Range	26–27.1	26.7–30.0	24.5–30.0	25.8–27.7	25.0–25.7	24.8–26.3
Surface oxygen (%)	Mean (±SD)	65.3 (4.45)	63.3 (2.01)	74.1 (5.51)	70.9 (3.83)	72.4 (5.03)	73.6 (5.32)
	Range	58–71	58–66	64–83	65–78	66–78	66–79
Bottom oxygen (%)	Mean (±SD)	39.6 (20.18)	54.7 (16.26)	54.4 (23.46)	62.2 (13.85)	63.8 (9.76)	69.0 (4.00)
	Range	1–62	5–65	15–85	26–74	50–76	64–74

Mean value ± standard deviation (SD), and range (minimum-maximum) are given for depth (m), water transparency (m), and surface and bottom values of salinity, temperature (°C) and percentage oxygen saturation (%).

Table 4
Distribution per bio-ecological category and per sector of the 54 fish species collected in the Ebrié lagoon during the wet season

Cat Ecol	Species	Code	Sector I		II		III		IV		V		VI		Total	
			Oc	Nb	Oc	Nb	Oc	Nb	Oc	Nb	Oc	Nb	Oc	Nb	Oc	Nb
Co	*Hepsetus odoe*	HOD	1	1											1	1
	Marcusenius bruyerei	MBR	5	28											5	28
	Marcusenius furcidens	MFU	1	1											1	1
	Petrocephalus bovei	PBO	3	13											3	13
Ce	*Brycinus longipinnis*	ALO	8	21											8	21
	Brycinus macrolepidotus	AMA	1	1											1	1
	Parailia pellucida	PHP	7	208											7	208
	Schilbe intermedius	SIN	3	48											3	48
	Schilbe mandibularis	EME	8	123	6	26									14	149
Ec	*Chrysichthys auratus*	CFI	10	663	9	64	2	5	1	14			2	5	24	751
	Chrysichthys maurus	CWA	11	1996	11	399	6	87	11	131	2	46	1	11	42	2670
	Chrysichthys nigrodigitatus	CNI	8	536	10	128	1	1	4	9	2	6	3	30	28	710
	Hemichromis fasciatus	HFA			2	3			3	5	3	13	2	27	10	48
	Pellonula leonensis	PEF	6	31	12	74	3	7	4	19	3	8	1	29	29	168
Es	*Eleotris senegalensis*	ESE	3	5	1	4	1	1							5	10
	Eleotris vittata	EVI			1	4			1	2					2	6
	Gerres nigri	GNI	3	22	6	22	6	398	8	40	5	193	5	369	33	1044
	Gobioides sagitta	GAN	1	3			1	1							2	4
	Gobionellus occidentalis	OOC					1	1	1	1					2	2
	Monodactylus sebae	PSB	2	3	7	33	3	8							12	44
	Porogobius schlegelii	ACS	3	5	6	14	3	21	5	9	3	5			20	54
	Sarotherodon melanotheron	THE	3	37	1	1	1	2	2	3			2	2	9	45
	Tilapia guineensis	TGU	4	36	7	33	1	1	6	10	4	40	5	48	27	168
	Tylochromis jentinki	TJE	5	30	2	3	2	4	6	42	4	47	5	76	24	202
Em	*Citarichthys stampflii*	CST	5	7	4	55	9	178	9	194	4	25	4	14	35	473
	Cynoglossus senegalensis	CYS	6	44	8	29	2	4	5	10	1	1			22	88
	Ethmalosa fimbriata	EFI			10	9744	7	846	4	130	5	2570	5	457	31	13747
	Liza falcipinnis	LFA			2	7	1	1	1	1	1	2	2	2	7	13
	Liza grandisquamis	LGR					6	51	2	8					8	59
	Mugil curema	MCU					2	3							2	3
	Plectorhinchus macrolepis	PLM	1	2	1	1	1	2							3	5
	Pomadasys jubelini	PJU	3	6	7	22	5	33	9	32	3	19	4	64	31	176
	Pseudotolithus elongatus	PEL	1	2	5	105	1	1							7	108
	Strongylura senegalensis	BES			2	2					2	2	1	2	5	6
	Trachinotus teraia	TFA	2	3	3	7	2	2	2	3	1	1	2	3	12	19
ME	*Arius latiscutatus*	AGA			1	1									1	1
	Caranx hippos	CHI					5	30	4	14					9	44
	Caranx senegallus	CAS					5	147							5	147
	Chloroscombrus chrysurus	CHL					4	132							4	132
	Elops lacerta	ELA	9	60	11	67	9	88	10	321	5	93	5	203	49	832
	Ephippion guttifer	EGU					1	1							1	1
	Epinephelus aeneus	EAE					5	14							5	14
	Eucinostomus melanopterus	GME			1	1	7	185	4	14	5	27	4	104	21	331
	Galeoides decadactylus	GDE					2	12							2	12
	Polydactylus quadrifilis	POQ	4	6	8	21	3	9	6	11			1	3	22	50
	Pteroscion peli	PTP					1	2							1	2
	Sardinella maderensis	SEB					3	193							3	193
	Selene dorsalis	VSE					6	85							6	85
	Sphyraena afra	SPI	2	3	6	8	1	1	1	1	1	3			11	16
	Trichiurus lepturus	TLE					1	18							1	18
Ma	*Lagocephalus laevigatus*	LLA					1	2							1	2
	Lichia amia	LIA					2	3							2	3
	Lutjanus goreensis	LGO					4	7							4	7
	Trachinotus ovatus	LGL					1	1							1	1

Code: abbreviation used in Fig. 5. Oc: number of samples where the species was present. Nb: total number of individuals.

on the first two axes (Fig. 4 a)again shows an arch effect, reflecting a strong environmental gradient.

This plot distinguishes four main groups of sites: the whole of sector III (WS1 group) despite a contrast between the north and south of Boulay island, the main part of the Aghien lagoon (WS2), sector II and the Potou lagoon (WS3) and finally sectors IV, V and VI (WS4).

Groups WS1 and WS2 had a high within-sector spatial heterogeneity whereas WS4 (sectors IV, V, VI) and to a lesser extent WS3, were quite uniform. As in the dry season, most of the sites situated in Aghien lagoon were distinguished from those of the Potou lagoon (Fig. 4b). In contrast, sector III was no longer associated with the more western sites in sector II, nor with those of sector IV. In the wet season, the sites in this sector were clearly isolated from those of the other sectors of the lagoon and were divided into two groups in relation to their geographical position with respect to Boulay island (Figs. 1 and 4c). The sites in the Potou lagoon were mostly associated with those in the upper parts of sector II. Sectors V and VI were similar, whereas the sites in sector IV were in an intermediate position between most of the sites of the lagoon.

The plots of the species points on the same two axes in relation to their ecological category (Fig. 5) divided the species into distinct assemblage structures, that were associated with the distribution of the sites into four groups on the sites plot. The assemblage in sector III (WS1) was composed of Ma species, characteristic of this sector, and also ME, some of which only occurred in this sector, or even only in those of the sites south of Boulay island, the most influenced by the connection to the sea via the Vridi canal (Fig. 1). This assemblage also included species in categories Em and Es and some Ec. The assemblage of the Aghien lagoon (WS2) consisted of species of freshwater origin (ecological categories Ce and Co) to which were added most of the species of type Ec and some Es species. Sector II and the Potou lagoon (WS3) were mainly populated by Ec species, plus Es and some Em and ME. The assemblage in sectors IV, V and VI was composed of species belonging to three of the basic categories for lagoon and estuarine assemblages, i.e. Ec, Es, and Em together with a few ME species.

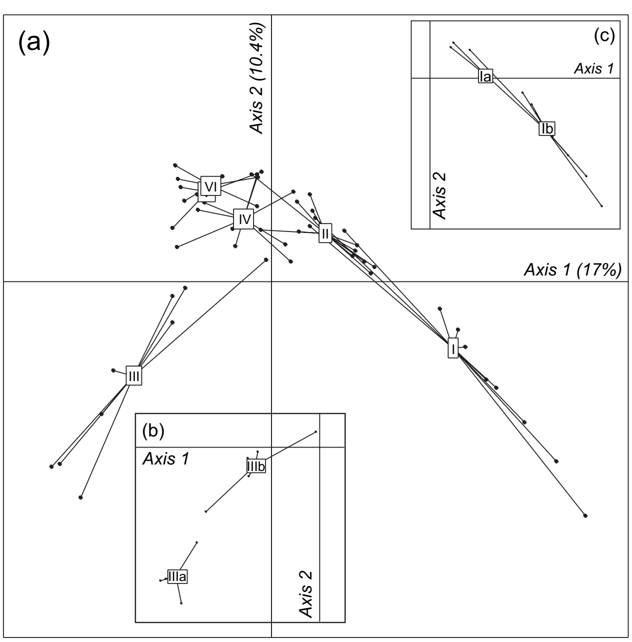

Fig. 4. Scatterplot of the 53 samples of the wet season on the first two axes of the Correspondence Analysis. (a) Lines link all sites to the center of gravity of their sector. (b) The 9 sites of sector III are grouped according to their position (IIIa: south of Boulay Island, IIIb: north of Boulay Island). (c) The 11 sites of sector I are grouped by subsector: Ia: Potou, Ib: Aghien.

The assemblages recorded in the wet season for the lagoon consisted of four distinct groups: a characteristic freshwater assemblage in the Aghien lagoon, a marine assemblage under the direct influence of exchanges with the sea in the sites close to the Vridi canal, a uniform assemblage occurring in the most westerly two sectors (V and VI) of the lagoon associated with some of the sites in sector IV; and finally a grouping of sites including most of the Potou sites and those of sector II, that were clearly distinct from the adjacent zones. The intermediate zones between these groups were very restricted; the sites situated to the north of Boulay island were not associated either with those to the south of the island or with those in the adjacent sector IV.

3.3. A permanent fish assemblage

Twenty species form the basis of a relatively stable assemblage both at a spatial scale and over the annual cycle over most of the lagoon. This group (Table 5) is composed of 4 Estuarine of freshwater origin species, 6 strictly Estuarine species and 6 Estuarine of marine origin species, that all complete their entire life cycle in the lagoon. In addition there are 4 Marine-Estuarine species regularly recorded at most of the sampling sites.

4. Discussion

The analysis of the lagoon fish assemblages in two characteristic seasons, dry and wet, demonstrated the existence of a basic assemblage that occurred throughout the lagoon, with the exception of two clearly distinct zones.

The first one, very spatially distinct, with a zero salinity throughout the year is the Aghien lagoon (DS2, WS2). It is occupied in all seasons by an assemblage with a very pronounced freshwater affinity, composed mainly of species belonging to the Freshwater occasional, Freshwater with estuarine affinities or Estuarine of freshwater origin ecological categories. All these species also have a wide biogeographical distribution in West

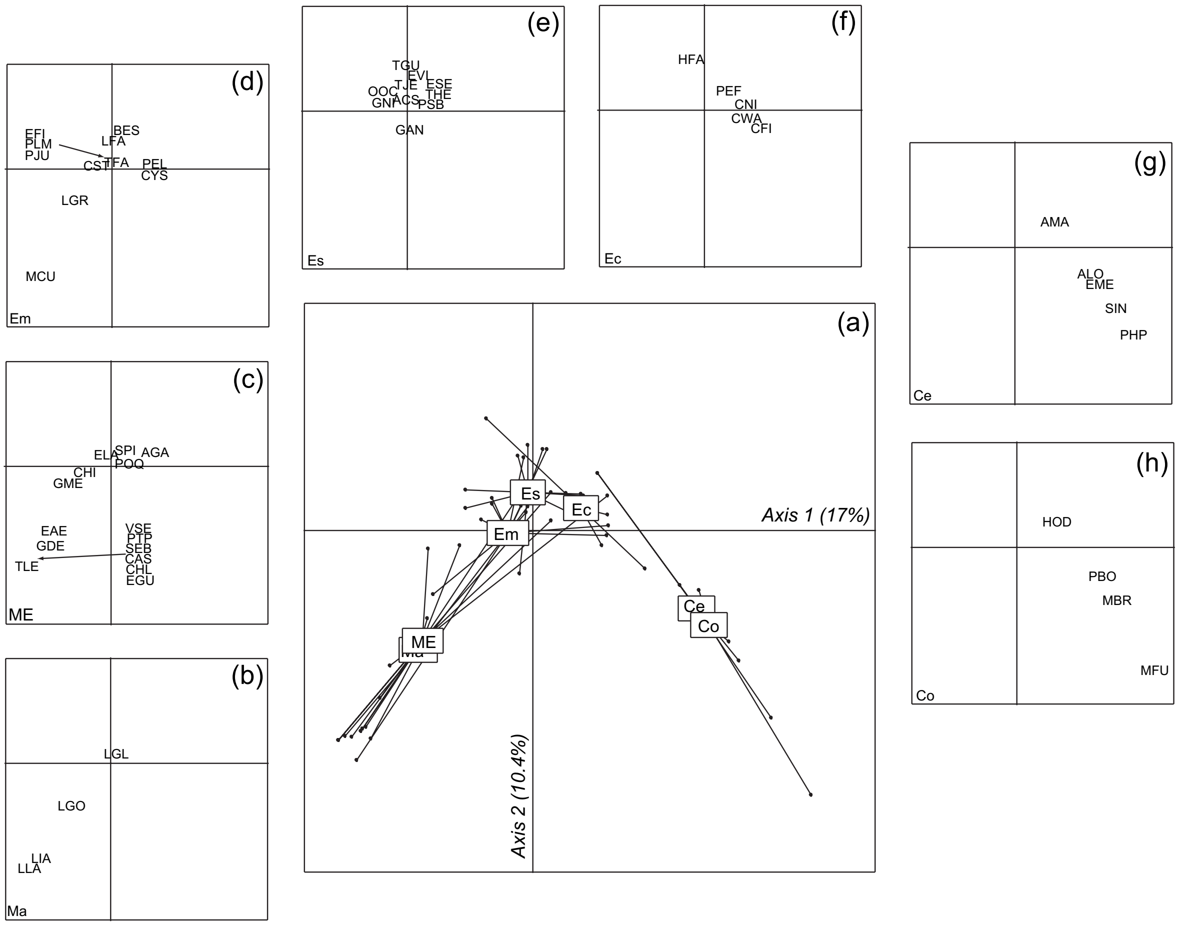

Fig. 5. Scatterplot of the 54 species of the wet season on the first two axes of the Correspondence Analysis. (a) Species have been plotted together and grouped by bio-ecological categories. (b) to (h) Species have been plotted on separate graphs for each category.

Table 5
Species composition of the permanent fish assemblage of the Ebrié lagoon

Ecological category	Code	Species
Estuarine species of freshwater origin	Ec	*Chrysichthys auratus*
		Chrysichthys maurus
		Chrysichthys nigrodigitatus
		Hemichromis fasciatus
Strictly Estuarine species	Es	*Gerres nigri*
		Monodactylus sebae
		Porogobius schlegelii
		Sarotherodon melanotheron
		Tilapia guineensis
		Tylochromis jentinki
Estuarine species of marine origin	Em	*Citarichthys stampflii*
		Cynoglossus senegalensis
		Ethmalosa fimbriata
		Liza falcipinnis
		Pomadasys jubelini
		Trachinotus teraia
Marine-Estuarine species	ME	*Elops lacerta*
		Eucinostomus melanopterus
		Polydactylus quadrifilis
		Sphyraena afra

African rivers (Lévêque et al., 1992), where they complete their whole life cycle.

The second zone varies in area depending on the season. It is very extensive in the dry season, when it covers all of sector III and some adjacent sites in sector II (DS1), but in the wet season, it is restricted to the areas close the Vridi canal (WS1). It is populated by an unstable and poorly structured assemblage consisting of marine or estuarine with a marine affinity species and is more like a transition zone assemblage. It is dominated by small shoaling pelagic species that enter the lagoon in successive waves, as has been observed in Senegal (Diouf, 1996) and Gambia (Albaret et al., 2004).

The identification of an assemblage of twenty species, stable both at a spatial scale and over the annual cycle, is in agreement with the conclusions of the study by Albaret and Ecoutin (1990) who demonstrated the existence, in a polluted bay close to Abidjan, of a basic assemblage consisting of the same species. In this bay, the permanent inhabitants remained stable over the annual cycle and in the long term (1962–1981), in an environment with an extreme variability at various scales.

In addition to this permanent core assemblage that occurs throughout the Ebrié lagoon, the structures of the assemblages clearly differentiate the eastern part from the western part; the separation occurring at the Vridi canal, a wide artificial channel that permanently connects the lagoon to the sea. There can be more or less variations in the composition of this residual fauna, depending on the hydro-climatic season.

To the east, the assemblage differs greatly depending on the season. In the wet season, there is a uniform assemblage consisting mostly of freshwater species over the whole of sector II and the Potou lagoon. This differs from that of the marine interface zone and sector III to the north of Boulay island. In the dry season, under the effect of a more pronounced marine influence, the assemblage in sector II becomes closer to that of sector III and diverges from that of the Potou lagoon. In the part of sector II closest to the sea there is strong marine tendency, the ecological ME and Em categories being well represented and the freshwater component being reduced. Sector II therefore functions like a typical estuary, influenced by the high river flow on the Comoé River in the wet season and by inputs of seawater via the Vridi canal in the dry season. In sector I, the composition and the structure of the assemblages in the Aghien and Potou lagoons differ from one another in all seasons, although the environmental conditions are similar with an almost zero salinity throughout the year. In the wet season, under the influence of the flood on the Comoé River, the Potou lagoon becomes closer to the estuarine zone. In the dry season, it tends to become a strictly lagoon ecosystem, with an assemblage closer to that recorded in the western part.

To the west, there is a low spatio-temporal variability in all the sectors VI, V and IV. Here the assemblage is composed in both seasons by the permanent core lagoon assemblage, together with some other species belonging mainly to the 3 Estuarine type ecological categories (Em, Es, Ec), depending on season.

Tropical lagoons, and especially large ones, are not necessarily uniform units in terms of their fish assemblages. The situation in the Ebrié lagoon is even more complex because of the central position of the Vridi canal that provides a communication with the sea and also because a large river draining the Sahel region enters the eastern end of the lagoon. Before the Vridi canal was dug in 1951, the natural outlet for the lagoon and Comoé River was at the eastern end of the lagoon (the Grand Bassam channel). The western part of the Ebrié lagoon is scarcely subjected to seasonal freshwater influence, as it is not affected by the high river flow of the Comoé River, and has only a slight and short term influence from small coastal rivers entering this zone. Because of the structure of the assemblage and the reduced variability in environmental conditions, this ecosystem can be defined as a coastal lake according to the definition of Blaber (2002). Although the marine influence is very slight, it is still identifiable by the presence of species belonging to the Marine Estuarine category.

This new hydrological configuration due to human intervention has transformed the entire eastern part of the lagoon that now functions as an estuarine prolongation of the Comoé River and subjects the assemblages of the Potou lagoon to the seasonal effect of the flood; this small lagoon should therefore be considered as a side arm of the estuary. In its hydrological functioning, sector II conforms with the definition of an open estuary given by Blaber (2002) or that of a typical estuary (Elliott and McLusky, 2002). In this model, the atypical zone close to the Vridi canal corresponds to a permanent mouth of this estuary with a typical assemblage subjected to the double influence at different time scales of the tides and seasons. This type of unstable assemblage, that is constantly being renewed, has already been observed in West Africa in similar situations in the Sine Saloum (Diouf, 1996) and in the Fatala estuary (Baran, 1995).

Analysed in terms of ecological categories, the seasonal influence leads to a cycle ranging from freshwater to marine around the permanent estuarine component of the assemblage. At a larger scale and because of the permanent connection to the sea via the Vridi canal, the marine component of this assemblage under seasonal influence should not lose its dominance. It could even increase at the expense of the freshwater influence as a result of great hydrological and climatic disturbances, such as drought and dam construction, that this part of West Africa is experiencing. Drought is the main factor implicated in the trend toward marine type assemblages in a bay of the Ebrié lagoon over a period of 20 years (Albaret and Ecoutin, 1990).

The alternating shift between freshwater or marine tending categories, observed in this study at a seasonal scale, also occurs with non-periodical climatic events at longer time scales, but with fast-acting shifts. For example, Garcia et al. (2001, 2003) demonstrated an effect of the El niño/La niña anomalies, observed between 1995–1998 and that led to very pronounced changes in rainfall and salinity, on the structure of the fish assemblages recorded in the estuary of the Patos lagoon in Brazil. Over a period of one year, which is the time taken for the oscillation between the two reverse anomalies, the assemblage changed from one with a freshwater tendency toward ecological categories with a strong marine affinity.

From a study on the assemblages of the Cinega Frande de Santa Marta lagoon (Colombia) at two different annual climatic seasons in 1993–1994 and in 1997, Rueda and Defeo (2003) showed that out of a total of 39 species identified, 7 were dominant in all four periods analysed, but 19 of the 39 species captured were present in each period. On the base of their ecological classification based on biological and ecological features, these authors showed that there was a shift between freshwater and marine tendencies between the two major annual seasons. This shift was more pronounced when the difference between the salinities in these two climatic seasons was greater.

Irrespective of the geographical or spatial scale used, the analysis of the estuarine and lagoon assemblages using ecological categories of species, allows the structures of the assemblage to be monitored and compared in an integrative way. This requires some profound thinking on the definition of the ecological categories. According to various studies, it seems that classifications can define 7 to 8 ecological groups (Albaret, 1999; Whitfield, 1999), that can be used to construct the structure of assemblages in estuarine and lagoon environments, ecosystems that are known for their great heterogeneity, and to monitor changes at both spatial and temporal scales.

As a conclusion, the Ebrié system presents a wide variety of habitat types, of fish assemblages and of estuarine functioning. Moreover, this wide variety of estuarine functioning is increased partly because of severe increase in urban, port-related and agricultural pollution (Scheren et al., 2004) and also because of the high, diversified and structured fishery exploitation (Ecoutin et al., 1994). In terms of management at both the local and regional scale, these differences of structure and of functioning of the assemblages require that each spatio-temporal unit of the Ebrié lagoon has to be specifically taken into account. This constitutes an additional constraint for managers who have to make the trade-off between the use of the ecosystem, in the wider meaning, and the need to maintain its sustainable functioning (Blaber et al., 2000; Blaber, 2002).

References

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 II – Les milieux Lagunaires. ORSTOM, Paris, pp. 239–279.

Albaret, J.J., 1999. Les peuplements des estuaires et des lagunes. In: Leveque, C., Paugy, D. (Eds.), Les Poissons des Eaux Continentales Africaines: Diversité, Écologie, Utilisation Pour L'Homme. IRD, Paris, pp. 325–350.

Albaret, J.J., Charles-Dominique, E., 1982. Observation d'un phénomène de maturation sexuelle précoce chez l'ethmalose, Ethmalosa fimbriata Bowdich, dans une baie polluée de la lagune Ebrié (Côte d'Ivoire). Document Scientifique Centre Recherches Océanographiques, Abidjan 13, 23–31.

Albaret, J.J., Ecoutin, J.M., 1989. Communications mer – lagune. Impact d'une réouverture sur l'ichtyofaune de la lagune Ebrié Côte-d'Ivoire. Revue d'Hydrobiologie Tropicale 22, 77–81.

Albaret, J.J., Ecoutin, J.M., 1990. Influence des saisons et des variations climatiques sur les peuplements de poissons Côte-d'Ivoire. Acta Oecologica 11, 557–583.

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.

Attrill, M.J., 2002. Community-level indicators of stress in aquatic ecosystems. In: Adams, S.M. (Ed.), Biological Indicators of Aquatic Ecosystem Stress. American Fisheries Society Bethesda, Maryland, pp. 289–320.

Baran, E., 1995. Dynamique Spatio-Temporelle des Peuplements de Poissons Estuariens en Guinée: Relations avec le Milieu Abiotique. TDM 142, ORSTOM, Paris, 236 pp.

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

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

Blaber, S.J.M., Cyrus, D.P., Albaret, J.J., Chong Ving Ching, J., 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.

Cowley, P.D., Whitfield, A.K., 2001. Fish population size estimates from a small intermittently open estuary In South Africa, using mark-recapture techniques. Marine and Freshwater Research 52, 283–290.

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. TDM 156, ORSTOM, Paris, 267 pp.

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 II – Les Milieux Lagunaires. ORSTOM, Paris, pp. 309–333.

Durand, J.R., Guiral, D., 1994. Hydroclimat et hydrochimie. In: Durand, J.R., Dufour, P., Guiral, D., Zabi, S.G.F. (Eds.), Environnement et Ressources Aquatiques de Côte-d'Ivoire. Tome II – Les Milieux Lagunaires. ORSTOM, Paris, pp. 59–89.

Durand, J.R., Skubich, M., 1982. Les lagunes ivoiriennes: the lagoons of Ivory Coast. Aquaculture 27, 211–250.

Durand, J.R., Dufour, P., Guiral, D., Zabi, S.G.F., 1994. Environnement et Ressources Aquatiques de Côte-d'Ivoire. Tome II – Les Milieux Lagunaires. ORSTOM, Paris, 546 pp.

Ecoutin, J.M., Durand, J.R., Laë, R., Hié Daré, J.P., 1994. L'exploitation des stocks. In: Durand, J.R., Dufour, P., Guiral, D., Zabi, S.G.F. (Eds.), Environnement et Ressources Aquatiques de Côte d'Ivoire, Tome II – Les Milieux Lagunaires. ORSTOM, Paris, pp. 399–444.

Elliott, M., McLusky, D.S., 2002. The need for definitions in understanding estuaries. Estuarine, Coastal and Shelf Science 55, 815–827.

Fausch, K.D., Lyons, J., Karr, J.R., Angermeir, P.L., 1990. Fish communities as indicators of environmental degradation. In: Marshall Adams, S. (Ed.), Biological Indicators of Stress in Fish. American Fisheries Society Symposium 8. American Fisheries Society Bethesda, Maryland, pp. 123–144.

Garcia, A.M., Vieira, J.P., Winemiller, K.O., 2001. Dynamics of the shallow-water fish assemblage of the Patos Estuary (Brazil) during cold and warm ENSO episodes. Journal of Fish Biology 59, 1218–1238.

Garcia, A.M., Vieira, J.P., Winemiller, K.O., 2003. Effects of 1997–1998 El Niño on the dynamics of the shallow-water fish assemblage of the Patos Lagoon Estuary (Brazil). Estuarine, Coastal and Shelf Science 57, 489–500.

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.

Legendre, P., Legendre, L., 1998. Numerical Ecology, 2nd English edition. Elsevier Science BV, Amsterdam, xv+853 pp.

Lévêque, C., Paugy, D., Teugels, G.G., 1992. Faune des Poissons d'Eaux Douces et Saumâtres de l'Afrique de l'Ouest. Tome I et II. Collection Faune tropicale XXVIII, MRAC/ORSTOM, 902 pp.

Paller, M., Reichert, M., Dean, J.M., 1996. Use of the fish communities to assess environment impacts in South Carolina coastal plain streams. Transactions of the American Fisheries Society 125, 633–644.

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, doi:10.1016/j.jmarsys.2003.08.002.

Soto-Galera, E., Diaz-Pardo, E., Lopez-Lopez, E., Lyons, J., 1998. Fish as indicators of environmental quality in the Rio Lerma Basin, México. Aquatic Ecosystem Health and Management 1, 267–276.

Thioulouse, J., Chessel, D., Dolédec, S., Olivier, J.M., 1997. ADE4: a multivariate analysis and graphical display software. Statistics and Computing 7, 75–83.

Vorweck, P.D., Whitfield, A.K., Cowley, P.D., Paterson, A.W., 2003. The influence of selected environmental variables on fish assemblage structure in a range of southeast African estuaries. Environmental Biology of Fishes 66, 237–247.

Whitfield, A.K., 1996. Fishes and the environmental status of South African estuaries. Fisheries Management and Ecology 3, 45–57.

Whitfield, A.K., 1999. Ichthyofaunal assemblages in estuaries: a South African case study. Reviews in Fish Biology and Fisheries 9, 151–186.

Whitfield, A.K., Elliott, M., 2002. Fishes as indicators of environmental and ecological changes within estuaries: a review of progress and some suggestions for the future. Journal of Fish Biology 61 (Suppl. A), 229–250.