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Factors Structuring the Ichthyofauna Assemblage in a Mangrove Lagoon (Guadeloupe, French West Indies)

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ABSTRACT

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The ichthyofauna of the Manche-à-Eau mangrove lagoon was regularly sampled in 2002 with a fixed net at seven stations during 4 months corresponding to two hydrological seasons. Physicochemical variables (depth, temperature, salinity, dissolved oxygen, pH) and population descriptors (species and family richness, density and biomass) were measured. The Whitefield and the well-being indexes were calculated to appreciate species equilibrium. Canonical correspondence analysis and generalized linear models were used to link species assemblages to physicochemical variables and to search for a special link with salinity. A total of 30,733 individuals belonging to 34 species and 23 families were collected. The Gerreidae, Clupeidae, Engraulidae, Scianidae, and Sparidae represented almost 98% of the total number of individuals. Our results show that organization of the fish assemblages in the lagoon is poorly dependent on salinity, whereas dissolved oxygen, temperature, and pH could have a stronger role. Looking at response curves to salinity change, most fishes species appeared to be visitors, either temporarily present or regular migrators. Only a few species compose the year-round resident population. They have a high patrimonial value and could be considered bioindicator species for long-term studies (*e.g.,* of global change and natural or anthropogenic disturbances). The Euclidean distance and biomass variables were not useful descriptors of confinement and biological zonation in the lagoon, whereas the negative gradient of specific richness, number of individuals, Whitefield index, and index of well-being better described confinement. On the basis of these last parameters, biological zonation in the Manche-à-Eau lagoon was established and is provided.

ADDITIONAL INDEX WORDS: *Biological zonation, confinement, fishes, organization, salinity.*

INTRODUCTION

Mangrove lagoons found in tropical and subtropical regions are ecologically important systems. The physical environment of mangrove wetlands provides food sources and habitat for fish and wildlife, plays a role in estuarine nutrient processes, and acts as a hydrological buffer with a strong self-purification capability. These characteristics, along with the enhanced biodiversities observed in warm tropical ecosystems (Gaston and Williams, 1996), make mangrove wetlands very sensitive to modifications. They represent one of the most fragile ecosystems on earth, and areas of mangrove wetlands are in constant regression.

From place to place, mangrove wetlands function differently depending on the precise water balance between rivers, sea level, and vegetation. However, mangrove wetlands have a common socioeconomic importance. Because of human demographic shifts to coastal areas in the 20th century, the coastal zones and mangrove wetlands are home to nearly 65% of the global population (Kjerfve, Drude de Lacerda, and Diop, 1997). Such increases in human pressure and the urbanization of mangrove wetland areas are even more substantial on small islands, where land is scarce and a well-developed public policy for home accessibility exists.

One of the most valuable resources of mangrove wetlands is their high fish diversity. Mangrove wetlands act as nurseries and growth facilities and are home to many different life stages (Kathiresa and Bingham, 2001; Ley, McIvor, and Montague, 1999). Mangrove ecosystems are particularly useful to migrant fish species because the wetlands can provide high food densities and can reduce the effectiveness of predators via high turbidity or structural complexity of mangrove roots (Beck *et al.,* 2001; Louis, 1983; Sheridan and Hays, 2003), strongly facilitating reproductive success. This scenario suggests that migrant fish are attracted to mangroves at one stage of their life cycle (*e.g.,* juvenile for growing and adult for breeding) more strongly than they are to adjacent habitat, such as seagrass, coral reefs, and the

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open ocean. Thus, discrimination between mangrove migrant species and mangrove resident species is one of the most important goals in the evaluation of mangroves as welcome sheltered habitat with high trophic richness for reproductive or feeding activities of fish. The regular migratory and occasional species spend one genesic (to breed) or trophic (to feed) ecophase there (Bouchereau and Chaves, 2002, 2003; Caberty, Chaves, and Bouchereau, 2004; Capapé *et al.,* 2002; Chaves and Bouchereau, 2000, 2004; Chaves, Bouchereau, and Vendel, 2000).

The brackish waters of mangrove wetlands are the result of mixing processes that occur between freshwater and seawater, with complex patterns resulting from tides and hydrological flow regimes that vary greatly both daily and seasonally. Salinity has been widely used in hydrology to track the strength of mixing processes and seawater intrusions. It has long been considered a fundamental ecological parameter explaining the tolerance and distribution of the flora and fauna species assemblages (Kiener, 1978; Petit, 1962; Potts and Parry, 1964; Remane and Schlieper, 1956; Sacchi, 1967; Vatova, 1963). However, the importance of salinity in structuring fish assemblages and other biological compartments in paralic ecosystems (including mangrove wetlands) was called into doubt with the increasing knowledge of the life cycles of species—many spend just an ecophase there and their others life stages in totally different biotopes and salinities (Frisoni *et al.,* 1983; Guelorget and Perthuisot, 1983; Guelorget *et al.,* 1982; Hartog, 1971). The questions increased with the numerous observations of supposedly stenohaline marine organisms, such as echinoderms that tolerate more than 60 g/L in the Salwa Gulf between Saudi Arabia and the Qatar Peninsula (Basson *et al.,* 1977), or other species that live in 5 g/L in the Vonitza Bay, Greece (Guelorget and Perthuisot, 1983).

The goals of this study were to (i) evaluate the relative importance of salinity and other abiotic factors in explaining the patterns of fish assemblages in a mangrove lagoon (the Manche-à-Eau lagoon) over time, (ii) to discriminate between migrant or transient and resident species through response models (generalized linear models [GLMs]), (iii) to propose the biological zonation in this ecosystem, and (iv) to identify the major driving descriptors (gradients) of species organization.

MATERIALS AND METHODS

Study Site Description

The Manche-à-Eau lagoon (MAE) is located at the northeast of the Island of Basse-Terre (16°16′N; 61°33′W) in Guadeloupe, French West Indies, in the Caribbean Sea (Figure 1). This semiclosed 0.26-km^2 lagoon receives continental freshwaters from diffuse peripheral running waters and marine waters via a semidiurnal tide of low amplitude (40 cm). The average depth ranges from 1.5 to 2.0 m (Assor, 1987), and the movements of the water masses are slow and complex. This lagoon is linked with the Grand-Cul-de-Sac-Marin (GCSM) lagoon by a channel, the Rivière-Salée, which delimits the two main islands of the Guadeloupe archipelago: the Basse-Terre and the Grande-Terre (Figure 1). The lagoon is completely fringed by a typical vegetation of mangrove trees (*Rhizophora mangle, Avicennia germinans,* and *Laguncularia racemosa*).

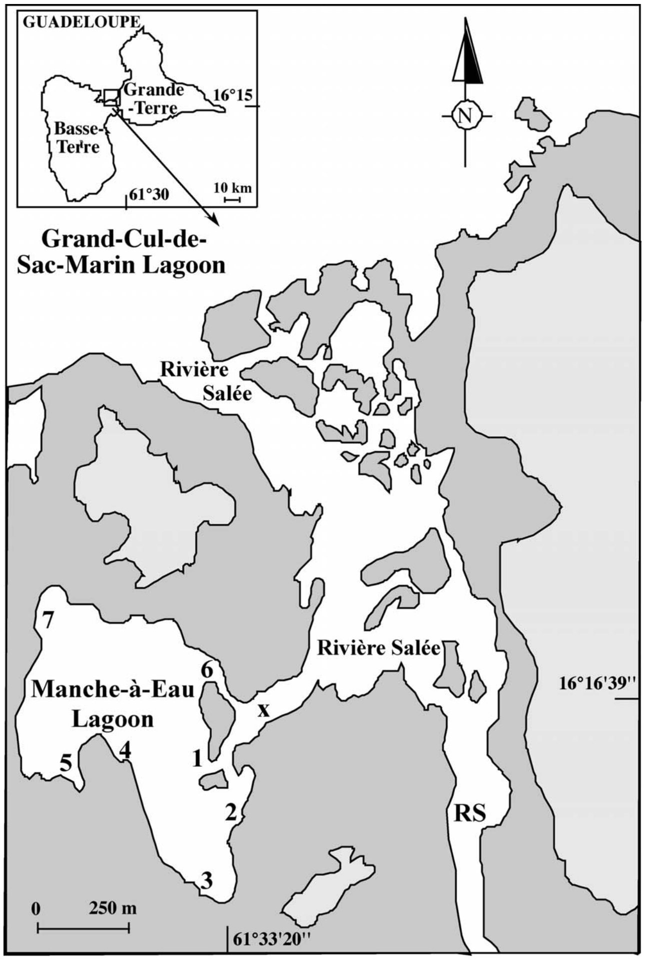

Figure 1. Guadeloupe's position in the French West Indies and location of the Manche-à-Eau lagoon with its connection to the Grand Cul-de-Sac Marin lagoon. Sampling stations are numbered 1 to 7, and the 'x' symbol represents the starting point for the ED measurements.

Sampling

We sampled seven stations (S1–S7) in the lagoon (Figure 1) with a type of passive fishing gear called *capéchade* (Quignard and Farrugio, 1981), which includes a 45-m-long stopping net (the *paradière*) suspended with floats. Fish are driven to three bow nets sustained with arches forming funnels with mesh sizes decreasing from 8 to 6 mm (Bouchereau, Joyeux and Quignard, 1989). A fishing operation is 24 h long from 1000 h to 1000 h the next day, one end beginning near the coast, the other toward deeper water so that the net covers from 0 to about 1.70 m depth. We sampled four times during 2002, twice in each of the two main hydrological periods (Bleuse and Mandar, 1996): the dry season (5–8 February, 8–11 April) and the rainy season (2–4 July, 9–12 December). Fish were sorted from other biological groups and detritus and preserved in 8% seawater formalin. All individuals were identified to species levels according to Randall (1968) and the Food and Agriculture Organization (Fisher, 1978) species identification sheets (Humann, 1989), counted, measured (total [TL] or fork length [FL] to the inferior millimeter, grouped in size classes of 1 mm), and weighed to further evaluate densities in number and biomass. Size was used to discriminate juveniles from adults according to size at first maturity when necessary. Data on ecological preferences were retrieved when necessary from Fishbase (Frœse and Pauly, 2004). The Euclidean distance (ED) from the main entrance (cross in Figure 1) of the lagoon and the station locations (Figure 1) was measured as the straight-line distance through the water compartment between the entrance and the sampling stations ported on a 1:25,000 map from the Institut Géographique National (*série bleue* 4603GT, Pointe-á-Pitre/Sainte-Anne).

At each station at the end of each fishing operation and during each sampling period, we measured depth (cm) and, at the bottom level of the water column, temperature (°C), salinity (g/L), dissolved oxygen (mg/L), and pH with a multiparameter analyzer (multiprobe analyzer; Bioblock Multiline P4, Straubing, Bayern, Germany). A reference station (RS) in the Rivière-Salée was also sampled only for these abiotic parameters (Figure 1). Therefore, seven stations sampled four times provided 28 absolute data points for each variable studied.

Data Analysis

Descriptors of the Assemblage

In addition to calculating species and family richness at each sampling station and during each period, we quantified fish community assemblages according to two synthetic indexes: the Whitfield index (WI = number of fish species/number of fish families; Whitefield, 1994) and the index of well-being (IWB; Gammon, 1976, 1980; Hughes and Gammon, 1987), the computational formula of which is

$$\mathrm{IWB} = 0.5 \ln N + 0.5 \ln B + \mathrm{Hn} + \mathrm{Hw}$$

where N is the relative number of all species, B is the relative weight of all species, and Hn and Hw are Shannon diversity indexes based on number and weight (both calculated in $\log_e$), respectively.

Because the IWB incorporates abundance, mass, and two diversity measures in an approximately equal fashion, it often represents fish assemblage quality more realistically than a single diversity or abundance measure (Gammon, 1980). Originally used to study streams and lake habitats (USEPA, 1993), this composite index was generalized by environmental agencies to operate ecological surveys (Ohio Environmental Protection Agency, 1989). It was employed here for a more complex habitat of larger scale than usual, which included migrant or transient species. We used it to access relative community fitness through time and space. A modified version (Yoder, 1987) of this index includes an extraction of highly tolerant species, hybrids, and exotic species, which are eliminated from two components of the formula but not from the computations of the diversity indexes (modified index of well-being). In this study, we used the original version, which includes all species in all components of the index. For reference, a score of 10 or above is considered excellent.

We propose the biological zonation in the MAE on the basis of the "confinement concept" defined by Guelorget and Perthuisot (1983). After combining all temporal data for a given site, values of the following community descriptors—mean specific richness (mSR), species richness (SR), number of individuals (NI), weight (W), mean WI (mWI), and mean IWB (mIWB)—were calculated and sorted in descending order, except for those of the ED, which were arranged in ascending order.

Links Between Fish and Environment

We quantified the links between absolute values of environmental variables and the observed abundances of fish by canonical correspondence analysis (CCA; Ter Braak, 1986a, 1986b, 1987). In this technique, which is an extension of reciprocal averaging (Hill, 1973), the ordination axes are a linear combination of the environmental variables. Species and environmental variables use the same space, which is defined by the chi-squared distance. In the ordination plots, environmental variables are represented by vectors, for which direction and length are determined by the correlation of the environmental variable with the ordination axes and by the eigenvalues of the axes. CCA selects the linear combination of variables that maximizes dispersion of species in the ordination space, which is termed constrained ordination (for more information, see Hill, 1973; Jongman, Ter Braak and Tongeren, 1987, 1995; Leps and Smilauer, 2003; Ter Braak, 1985, 1986a, 1986b, 1987). We assessed the multicolinearity among environmental variables using the variance inflation factor, VIF = 1/(1—R_j^2) (Montgomery and Peck, 1982), where R_j is the coefficient of multiple linear correlation between environmental variable j and the other environmental variables included in the analysis.

Identification of Migrant, Transient, or Resident Species

Generalized linear models (GLMs) are an extension of the linear modeling process that allows models to be fit to data that follow probability distributions other than the normal distribution. These methods relax the requirement of equality or constancy of variances. These tools are much recommended when the distribution of counts is discrete rather than continuous and limited to nonnegative values (Cameron and Trivedi, 1998; Winkelmann, 1997). A fitness function could be obtained by a GLM calculated for each species corresponding to the link between species abundance and a single predictor, such as salinity. The existence and strength of this link between species abundances and salinity gradient are interpreted as indicative of the species dependence to salinity considered as a marker of hydrodynamism processes, and thus the status of species confronted by water mass intrusion. In such biotopes, species independent of water mass intrusion are proposed to be resident and those strongly dependent are proposed to be transient or migrant. These GLM analyses were performed on fish abundances with CANOCO software (Ter Braak, 1987). We selected a logarithm link function for our analysis, which was the default link function for a Poisson distribution belonging to the exponential family. A Poisson model is similar to an ordinary linear regression, with two exceptions: First, it assumes that the errors follow a Poisson, not a normal, distribution; second, rather than modeling Y as a linear function of the regression coefficients, it models the natural log of the response variable, $\ln(Y)$, as a linear function of the coefficients. We used the Fischer test (for $n > 100$) to assess the correlation and the Pearson X^2 p-test to evaluate the validity of each regression analysis.

RESULTS

Species Equilibrium

A total of 30,733 individuals belonging to 34 species (Table 1) and 23 families (Table 2) were collected during the study period. Five families represent almost 98% of the total number (Table 3): Gerreidae (53.26%), Clupeidae (34.38%), Engraulidae (5.58%), Scianidae (3.64%), and Sparidae (1.07%). The 18 other families compose less than 1%, led by the Atherinidae (0.95%). Most individuals of the Gerreidae, Clupeidae, Engaulidae, and Atherinidae were juvenile, whereas the Sciaenidae and the Sparidae were a mixture of mainly adults and juveniles. In the other families, all size classes can be found with no modal length value.

When considering the four different sampling times (Table 4), the numerically dominant family in February, April, and December was the Gerreidae; in July it was the Clupeidae. The Engraulidae and the Sciaenidae were always next in numerical dominance. The other families were weakly represented. The number of families varied between 6 (S7 in February, S5 in April) and 13 (S1 in December). Stations S1 (9–13) and S6 (7–12) were the richest stations over the year and S3 (7–9) and S5 the poorest (6–10). December was the richest period in families (8–13) and February the poorest (6–10).

The ED varied (Table 5; Figure 1) between 1.5 (S1) and 10.5 (S7). Three groups with increasing values are visible: (i) S1 (1.5), S6 (2.2), and S2 (3.0); (ii) S4 (4.6); and (iii) S3 (6.5), S5 (9.5), and S7 (10.5).

Extreme values (Table 5) of mSR (S5–S1, 10.75–15.50), SR (S5–S1, 14–25), NI (S5–S2, 330–2413), and weight (W; S5–S1, 3.087–22.222) varied relatively more than those of mean WI (S1–S5, 1.476–1.536) and mIWB (S3–S1, 6.55–8.37). Except for ED (at S7), the other descriptors at stations S1 and S2 near the entrance points of marine water had values opposite those (S5, S3) from the most fringing area.

According to the time sampled, ED and IWB were significantly well correlated ($0.72 < r < 0.88$); the slope of the regression curves (Figure 2) was weak (-0.091) in December after the rainy season and increased from February (-0.176) to July (-0.197).

Links Between Fish and the Environment

Restricted Salinization Process

The range of salinities of incoming waters varied between 30.85 and 35.75 g/L during the study, showing strong variations because of complex hydrological processes and water mass exchanges (Table 6). During the dry season (February–April), the incoming waters had higher salinities than those located in the undisturbed area of the lagoon, whereas during the rainy season, the incoming waters had lower salinities. The results of the CCA analysis (Table 7; Figures 3a and 3b) showed stations that are positioned in a space defined primarily by pH ($r = -0.85$ in February and $r = -0.68$ in April on the first axis), whereas the second axis is mainly correlated with oxygen in February ($r = -0.86$) and depth in April ($r = 0.68$). The strong negative correlation between salinity and ED ($r = -0.73$ in February and $r = -0.83$ in April) revealed that the incoming of water significantly increased the natural salinity of the lagoon. During these months, the extent of the salinization process (Figures 3a and 3b) concerned only stations 1 and 2 located near the mouth of the lagoon.

Extended Desalinization Process

During the rainy season (July–December; Figures 3c and 3d), the stations are positioned in a space defined primarily by the depth on axis 1 ($r = 0.60$ in July and $r = 0.51$ in December) and salinity ($r = -0.88$ in July) and distance ($r = -0.45$ in December) on axis 2. The positive correlation (Table 7) between salinity and ED (0.46 in July and 0.25 in December) show that the incoming waters decreased the existing salinity of the lagoon markedly. This extended desalinization process affects stations 1, 4, 5, 6, and 7 in July and stations 1, 4, 6, and 7 in December, which are those situated in the middle of the lagoon (Figure 1).

Identification of Migrant, Transient, or Resident Species

The examination of species occurrence through time (Tables 1 and 2) and the results of the salinity fitness function (GLM models) showed (Figure 4) that a strong temporal pattern that could be linked to increasing salinities existed for the main contributing species. These species were *Harengula clupeola, Anchoa lyolepis, Diapterus rhombeus,* and *Eucinostomus gula.* They are migrant species belonging to the main families Gerreidae, Clupeidae, and Engraulidae. Species that did not show such a strong link between occurrences and salinity were *Apogon conklini, Atherinomorus stipes, Caranx latus, Harengula humeralis, Eucinostomus argenteus, Eugerres brasilianus, Gerres cinereus, Bairdiella ronchus, Archosargus rhomboïdalis, Sphyræna barracuda,* and *Sphœroides testudineus.* Except for *A. conklini, B. ronchus,* and *S. testudineus,* which are rather sedentary, those species are regular migrants or occasional visitors (*S. barracuda*). The number of occurrences of the 19 other species was not high enough to exhibit a significant pattern with a GLM model.

Spatial and Population Descriptors

After classification of the stations according to their descriptor values in increasing or decreasing order (Table 8) and enumeration of the most represented in each row from 1 to 7, it became clear that the stations closest to the entry of

Table 1. *Species occurrence in the seven stations during the four sampling months (F) February, (A) April, (J) July, (D) December, in the Manche-à-Eau lagoon.*

Species	Month																											
	F							A							J							D						
	Station																											
	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7
Acanthurus chirurgus (Bloch, 1787)									+																			
Albula vulpes (Linnaeus, 1758)								+												+								
Apogon conklini (Silvester, 1915)	+	+	+	+	+	+	+								+		+	+		+	+							
Atherinomorus stipes (Müller and Troschel, 1848)	+	+	+	+	+	+	+	+					+		+			+		+	+	+			+	+	+	+
Caranx latus Agassiz, 1831	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+		+	+	+	+	+
Chloroscombrus chrysurus (Linnaeus, 1776)																											+	
Oligoplites saurus (Bloch and Schneider, 1801)									+						+	+	+	+				+	+			+		
Selene vomer (Linnaeus, 1758)															+													
Centropomus undecimalis (Bloch, 1792)									+																			+
Harengula clupeola (Cuvier, 1829)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+
Harengula humeralis (Cuvier, 1829)	+	+	+	+	+	+	+	+	+		+		+	+	+			+	+		+							
Opisthonema oglinum (Lesueur, 1818)	+	+	+	+	+	+	+						+				+	+						+				
Dasyatis americana Hildebrand and Schrœder, 1928																						+					+	
Elops saurus Linnaeus, 1766																							+	+			+	
Anchoa lyolepis (Evermann and Marsh, 1900)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+		+
Chætodipterus faber (Broussonet, 1782)																						+						
Diapterus rhombeus (Cuvier, 1829)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Eucinostomus argenteus Baird and Girard, 1855	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Eucinostomus gula (Quoy and Gaimard, 1824)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Eugerres brasilianus (Cuvier, 1830)	+	+	+	+	+	+	+	+	+		+		+	+	+	+	+		+	+			+	+			+	+
Gerres cinereus (Walbaum, 1792)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+
Gobionellus oceanicus (Pallas, 1770)									+							+												
Lophogobius cyprinoides (Pallas, 1770)	+	+	+	+	+	+	+																					
Hæmulon aurolineatum Cuvier, 1830	+	+	+	+	+	+	+																					
Hæmulon bonariense Cuvier, 1830	+	+	+	+	+	+	+	+			+						+								+			
Hyporamphus unifasciatus (Ranzani, 1842)															+							+						
Adioryx coruscus (Poey, 1860)																		+										
Lutjanus griseus (Linnaeus, 1758)	+	+	+	+	+	+	+	+	+		+		+	+											+		+	
Megalops atlanticus Valenciennes, 1847																							+					
Mugil curema Valenciennes, 1836																							+					
Bairdiella ronchus (Cuvier, 1830)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+
Archosargus rhomboidalis (Linnaeus, 1758)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+			+	+	+	+
Sphyræna barracuda (Edwards, 1771)	+	+	+	+	+	+	+				+		+	+	+	+	+	+	+			+	+	+	+	+	+	+
Sphæroides testudineus (Linnaeus, 1758)	+	+	+	+		+		+		+				+	+	+						+		+	+		+	+

marine water (S1, S2, S6) formed a group. Those occupying ranks 4 and 5 (S4, S7) were located in the extension of the general circulation of the entrances or exits of water according to the currentology studied by Assor (1987). Finally, stations S3 and S5, which corresponded to ranks 6 and 7, were located in areas of little current. This classification was similar whenever a negative gradient of the descriptor existed: mSR, SR, NI, and mIWB.

DISCUSSION

Seasonal Influence on Salinity

Throughout the year, salinity variations in the MAE were greater (minimum 28.30 g/L; maximum 35.40 g/L) than those observed by Blanc *et al.* (2001) in the GCSM lagoon (mean 35.40 g/L; SD 1.9), which is a large bay (110 km^2) limited seaward by a 30-km-long barrier reef and landward by an important mangrove forest surrounded by several lagoons.

Canonical correspondence analyses revealed the existence of a marked seasonality in salinity patterns, despite the lack of clear freshwater inputs via rivers or point source drainage areas. The dry season (beginning in February or April in Guadeloupe) resulted in a perceptible salinization of the lagoon, possibly by mean of seawater inputs or evaporation. During this time of year, the areas influenced by increased salinity were located close to the channel, which reveals that marine water inputs were prominent before evaporation.

In the rainy season (July and December), desalinisation was spatially more extensive and reached S4; S5 showed a significant reinforcement of water exchange. These results,

Table 2. *Total number of individuals per species found during the four sampling months for the entire study period and relative frequency in percentage (%).*

Species	Code	Feb	Apr	Jul	Dec	Total	%
Acanthurus chirurgus (Bloch, 1787)	Acch	0	1	0	0	1	0.0
Albula vulpes (Linnaeus, 1758)	Alvu	0	4	1	0	5	0.0
Apogon conklini (Silvester, 1915)	Apco	2	0	7	0	9	0.0
Atherinomorus stipes (Müller and Troschel, 1848)	Atst	20	10	170	91	291	1.0
Caranx latus Agassiz, 1831	Cala	9	52	46	29	136	0.4
Chloroscombrus chrysurus (Linnaeus, 1776)	Chch	0	0	0	1	1	0.0
Oligoplites saurus (Bloch and Schneider, 1801)	Olsa	0	4	5	10	19	0.1
Selene vomer (Linneaus, 1758)	Sevo	0	0	1	0	1	0.0
Centropomus undecimalis (Bloch, 1792)	Ceun	0	2	0	1	3	0.0
Harengula clupeola (Cuvier, 1829)	Hacl	599	1537	4434	3927	10,497	34.2
Harengula humeralis (Cuvier, 1829)	Hahu	4	19	32	0	55	0.2
Opisthonema oglinum (Lesueur, 1818)	Opog	5	2	2	5	14	0.1
Dasyatis americana Hildebrand and Schræder, 1928	Dahi	0	0	0	2	2	0.0
Elops saurus Linnæus, 1766	Elsa	0	0	0	6	6	0.0
Anchoa lyolepis (Evermann and Marsh, 1900)	Anly	531	522	503	159	1715	5.6
Chætodipterus faber (Broussonet, 1782)	Chfa	0	0	0	1	1	0.0
Diapterus rhombeus (Cuvier, 1829)	Dirh	690	4210	2977	2386	10263	33.4
Eucinostomus argenteus Baird and Girard, 1855	Euar	127	210	108	293	738	2.4
Eucinostomus gula (Quoy and Gaimard, 1824)	Eugu	1062	1405	585	1927	4979	16.2
Eugerres brasilianus (Cuvier, 1830)	Eubr	10	163	42	72	287	0.9
Gerres cinereus (Walbaum, 1792)	Geci	22	36	17	25	100	0.3
Gobionellus oceanicus (Pallas, 1770)	Gooc	0	4	2	0	6	0.0
Lophogobius cyprinoides (Pallas, 1770)	Locy	1	0	0	0	1	0.0
Hæmulon aurolineatum Cuvier, 1830	Hæau	2	0	0	0	2	0.0
Hæmulon bonariense Cuvier, 1830	Hæbo	3	3	1	1	8	0.0
Hyporamphus unifasciatus (Ranzani, 1842)	Hyun	0	0	1	4	5	0.0
Adioryx coruscus (Poey, 1860)	Adco	0	0	1	0	1	0.0
Lutjanus griseus (Linnaeus, 1758)	Lugr	2	11	0	4	17	0.1
Megalops atlanticus Valenciennes, 1847	Meat	0	0	0	1	1	0.0
Mugil curema Valenciennes, 1836	Mucu	0	0	0	1	1	0.0
Bairdiella ronchus (Cuvier, 1830)	Baro	222	506	282	108	1118	3.6
Archosargus rhomboidalis (Linnaeus, 1758)	Arrh	60	94	91	85	330	1.1
Sphyræna barracuda (Edwards, 1771)	Spba	19	5	16	17	57	0.2
Sphæroides testudineus (Linnaeus, 1758)	Spte	14	13	11	25	63	0.2
Total		3404	8813	9335	9181	30,733	100

coupled with the large range of salinity variations observed during this study, clearly point out the high sensitivity and short reaction time of such hydrological systems. The MAE lagoon quickly and widely reacted to seasonal water exchanges. Despite this marked chemical variation and the obvious changes in salinity gradients, our results indicate that salinity was not a global driving force in structuring the fish assemblages.

Table 3. *Number (N) and frequency (%) of individuals found per family during the study period.*

Families	*N*	%	Families	*N*	%
Acanthuridae	1	0.00	Gobiidae	7	0.02
Albulidae	5	0.02	Haemulidae	10	0.03
Apogonidae	9	0.03	Hemiramphidae	5	0.02
Atherinidae	291	0.95	Holocentridae	1	0.00
Carangidae	157	0.51	Lutjanidae	17	0.06
Centropomidae	3	0.01	Megalopidae	1	0.00
Clupeidae	10,566	34.38	Mugilidae	1	0.00
Dasyatidae	2	0.01	Sciaenidae	1118	3.64
Elopidae	6	0.02	Sparidae	330	1.07
Engraulidae	1715	5.58	Sphyraenidae	57	0.19
Ephippidae	1	0.00	Tetraodontidae	63	0.20
Gerreidae	16,367	53.26	Total	30,733	100.00

What Does Salinity Explain?

Salinity has long been considered the fundamental ecological parameter affecting distribution of the floral and faunal assemblages in paralic ecosystems (Kiener, 1978; Petit, 1962; Remane and Schlieper, 1956; Sacchi, 1967; Vatova, 1963). However, from the physicochemical variables considered in the CCA in this study, salinity was not a major explanatory factor of the structure of the ichthyofauna in the MAE, whatever the season. In contrast, dissolved oxygen, pH, and temperature were more important (73, 46 and 64% respectively) than salinity (26%).

Our data show that the organisation of the aquatic populations in the MAE lagoon-estuary ecosystem is relatively independent of salinity gradients, as were the floristic and faunistic assemblages in the lagoon-estuary Mediterranean ecosystems described by Guelorget and Perthuisot (1983). The same findings were reported by Bouchereau and Chaves (2003) for a tropical estuarian ecosystem. Pérez-Ruzafa, Mompean, and Marcos (2007) showed for 40 Atlanto-Mediterranean coastal lagoons that species richness was negatively related to the absolute difference in salinity between lagoon waters and the sea.

Bouchereau and Chaves (2003), Bouchereau *et al.*

Table 4. *Relative number (%) of individuals per major fish family at the seven stations sampled in the Manche-à-Eau lagoon in February (Fe), April (Ap), July (Jl), and December (De).*

	Relative no. (%)																											
	Station 1				Station 2				Station 3				Station 4				Station 5				Station 6				Station 7			
Family	Fe	Av	Jl	De	Fe	Av	Jl	De	Fe	Av	Jl	De	Fe	Av	Jl	De	Fe	Av	Jl	De	Fe	Av	Jl	De	Fe	Av	Jl	De
Clupeids	28	29	57	81	14	11	68	2	10	11	11	3	17	31	83	34	5	7	64	32	21	36	0	9	38	4	29	75
Engraulids	15	8	13	0	37	3	1	2	1	3	1	0	1	21	12	1	4	2	6	1	2	5	1	0	5	1	0	9
Gerreids	29	36	15	17	46	84	27	92	84	84	86	93	72	45	2	61	82	73	22	64	63	53	89	80	49	91	63	10
Scianids	22	24	7	0	0	1	3	3	2	1	1	4	8	1	0	0	2	9	3	1	6	1	3	0	3	0	0	0
Sparids	1	2	1	1	1	0	0	0	1	0	0	0	1	1	0	1	3	2	2	1	5	3	3	3	4	1	5	1
Others	5	1	6	1	1	0	1	1	2	0	1	1	1	1	2	3	3	8	3	1	3	2	4	7	1	3	3	4

(2000a, 2000b), CHAVES and BOUCHEREAU (2004), GARNEROT *et al.* (2004), MARIANI (2001), and PÉREZ-RUZAFA *et al.* (2006) showed that hydrodynamism linked to the renewal rate originating from marine water governs the organisation of the ichtoyfauna in lagoon-estuary ecosystems. This applies to other biological compartments as well, such as flora, meiofauna, and benthic macrofauna in soft or hard substrates. They occupy the paralic ecosystems according to the "confinement concept" defined by GUELORGET and PERTHUISOT (1983).

BLANC *et al.* (2001) observed that the spatial distribution of fish species in the GCSM lagoon is not linked to spatial variation of salinity. Species did not show preferences induced by salinity gradients and could have been influenced by other factors, such as water turbidity, dissolved oxygen (LOUIS, BOUCHON, and BOUCHON-NAVARRO, 1995) or habitat complexity (GARCIA-CHARTON and PÉREZ-RUZAFA, 1998). However, all those authors did not link their results to the confinement concept or biological zonation.

Flora and fauna continue to be classified on the basis of a salinity scale. One can wonder why this persists because the idea has been so many times discredited. The main reason for this persistence is probably the high variability of salinity in these biotas compared with average seawater and easy accessibility, which makes it easy to measure this parameter. However, many marine species that spend all or just an ecophase of their life cycle in paralic ecosystems are distributed independent of salinity. For instance, the monocotyledon *Ruppia spiralis,* which is never found in the open sea, can be found at salinities ranging from 1.5 to 23 g/L in the polders of the Netherlands (HARTOG, 1971), at 33 g/L in the Urbino lagoon (FRISONI *et al.,* 1983), between 60 and 80 g/L in the Bahiret-El-Biban in Tunisia (GUELORGET *et al.,* 1982), and at >80 g/L in the Salin-de-Giraud in France (GUELORGET and PERTHUISOT, 1983). Among mollusks, *Hydrobia acuta, Pirenella conica,* or *Cerastoderma glaucum* are only observed in paralic ecosystems regardless of salinity. In addition, marine organisms such as some types of echinoderms, which have long been considered stenohaline organisms, are able to live in variable salinities. For example, three stelleride species, *Astropecten phragmosus, Astropecten polyacanthus* and *Asterina burtoni,* tolerate more than 60 g/L in the Salwa Gulf in Saudi Arabia and the Qatar Peninsula (BASSON *et al.,* 1977); in the latter, the grouper *Epinephelus tauvina* can be observed in waters with salinity as high as 70 g/L (GUELORGET and PERTHUISOT, 1983). Other organisms live at the opposite extreme, such as the sea urchin *Paracentrotus lividus,* which lives in waters of 5 g/L, as observed in the Vonitza Bay and Amvrakikos Gulf in Greece (GUELORGET and PERTHUISOT, 1983). These examples show that osmoregulation is not a decisive problem, even for species considered to be the most stenohaline.

Response Curve, Mangrove Resident or Migrant Species

As discussed above, salinity had little influence on organisation of the fish community in the MAE. Regarding the numerous publications on their ecology, both allochthonous and autochthonous fish species were found coexisting in this mangrove lagoon. Most of the known ecological guilds (ELLIOTT and DEWAILLY, 1995) are represented in our species list.

The few species (*H. clupeola, A. lyolepis, D. rhombeus,* and *E. gula*) that occurred in high density and were influenced by high salinities (as shown by their salinity response func-

Table 5. *Expression of the Euclidean distance (ED) and population descriptors for stations 1 to 7 (all sampling data combined for a given station).*

Position of Stations	ED	mSR	SR	NI	W	mWI	mIWB	View on IWB*
1 (16°16′36″ N; 61°33′23″ W)	1.5	15.50	25	1845	22,222	1.476	8.37	Good
2 (16°16′31″ N; 61°33′19″ W)	3.0	14.25	24	2413	14,203	1.500	7.83	Good
3 (16°16′25″ N; 61°33′23″ W)	6.5	11.75	17	807	7287	1.514	6.55	Fair
4 (16°16′36″ N; 61°33′30″ W)	4.6	13.00	22	864	5382	1.492	7.21	Fair
5 (16°16′34″ N; 61°33′35″ W)	9.5	10.75	14	330	3087	1.536	6.71	Fair
6 (16°16′43″ N; 61°33′20″ W)	2.2	14.25	22	871	19,706	1.506	7.65	Good
7 (16°16′48″ N; 61°33′37″ W)	10.5	12.00	18	553	5786	1.507	6.73	Fair

mSR denotes mean species richness; SR, species richness; NI, number of individuals; W, weight; mWI, mean Whitefield index; mIWB, mean index of well-being.

* According to Gammon (1980).

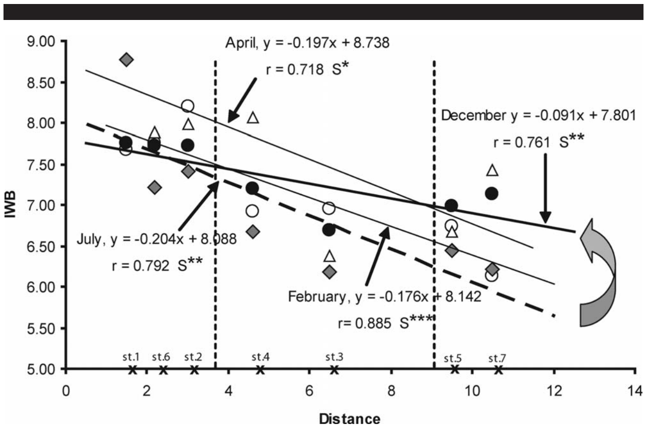

Figure 2. Index of well-being (IWB) *vs.* the ED in February, April, July, and December at each station (st.$_{(1-7)}$). The respective regression lines and their equations are shown with the correlation coefficient (r): ** $p > 0.05$; *** $p > 0.01$; the curved arrow points out the distinct slope shift that occurred in December just after the rainy season.

tion) represent regular migrants coming into the lagoon as juveniles. They spend a trophic (Bouchereau *et al.,* 2006; Chaves and Bouchereau, 1999, 2004; Chaves and Correa, 2000; Chaves and Otto, 1999; Chaves, Rickli, and Bouchereau, 1998) or genesic (Chaves and Bouchereau, 2000; Capapé *et al.,* 2002) ecophase of their life cycle in the mangrove. They belong to the Engraulidae, Clupeidae, and Gerreidae families, and they use the high level of trophic richness and the peculiar nature of the mangrove lagoon. They are planktonovores, omnivores, or first-order carnivores. The young individuals of these pelagic or demersal species are recruited in the lagoon according to the different spawning periods happening in sea. In the MAE lagoon, they represent an important food resource for many fish species (Caberty, Chaves, and Bouchereau, 2004).

The other group of species, with poor salinity response function (*A. conklini, A. stipes, C. latus, H. humeralis, E. argenteus, E. brasilianus, G. cinereus, B. ronchus, A. rhomboidalis, S. barracuda,* and *S. testudineus*), is made up of sedentary and carnivorous species of second order (predators). The sedentary species in the Apogonidae, Tetraodontidae, Sciaenidae, and Sparidae families spend their whole life in the lagoon. The predatory species are opportunist visitors that raid the lagoon regardless of their size and age; they belong mainly to the Carangidae, Muraenidae, and Sphyraenidae. Some are occasional (Atherinidae planktonovores). Finally, the few remaining species, *E. argenteus, E. brasilianus,* and *G. cinereus,* even if they are relatively less abundant in their respective family (Gerreidae), also can be considered regular migrants.

The 19 other species exhibiting no significant salinity response function belong to the Acanthuridae, Albulidae, Centropomidae, Dasyatidae, Elopidae, Ephippidae, Gobiidae, Haemulidae, Hemiramphidae, Holocentridae, Lutjanidae, Megalopidae, and Mugilidae. Some belonging to Gobiidae are sedentary and numerous but are poorly selected by fishing gear. The densities of sub-cryptobenthic species like Gobiidae are underestimated because they are caught more often with other experimental fishing gear than the *capéchade.* Some are occasional, belonging to Dasyatidae. The remaining species are too scarce to be taken into account by the response function analyses.

Table 6. *Comparisons of incoming and local salinities. RS = reference station of the Rivière Salée; MAE = Manche-à-Eau lagoon; S = salinisation process; D = desalinisation process.*

Month	RS (main channel)	Process	MAE (station 3)
February	35.75	S ●→	35.35
April	31.00	S ●→	30.85
July	31.25	D ●→	33.70
December	33.60	D ●→	33.90

Functionnal Links Between Adaptative Strategies of Species and Mangrove Lagoon

Among the fish species living in the MAE mangrove lagoon, most are either occasional visitors or regular migratory visitors. Only a few species represent the population of full-time residents, and they have developed successful strategies to survive in this inconstant ecosystem. They compose the real patrimonial richness that characterizes the mangroves. Because of their small size, sub-cryptobenthic status, and level of parental care, they should receive more scientific attention for protection and be preserved or restored. These species can serve as bioindicator, or sentry, species for long-term studies (*e.g.,* of global change and natural or anthropogenic disturbances). Moreover, the functions and roles of the mangrove biotopes should be reviewed. Their famous biodiversity is high when considering the number of species collected over years of sampling, but in this study, all of the fish species

Table 7. *Absolute correlation values between variables O_2 (dissolved oxygen), pH, T (temperature), Z (depth), S (salinity), and ED (distance from the station to the mouth of the lagoon).*

Correlation-Rank	February		April		July		December	
First	O_2	0.8567	Ph	0.6804	T	0.8022	S	0.5112
Second	Ph	0.8504	Z	0.6801	S	0.7473	O_2	0.4516
Third	Z	0.7535	O_2	0.5928	Z	0.5960	ED	0.4506

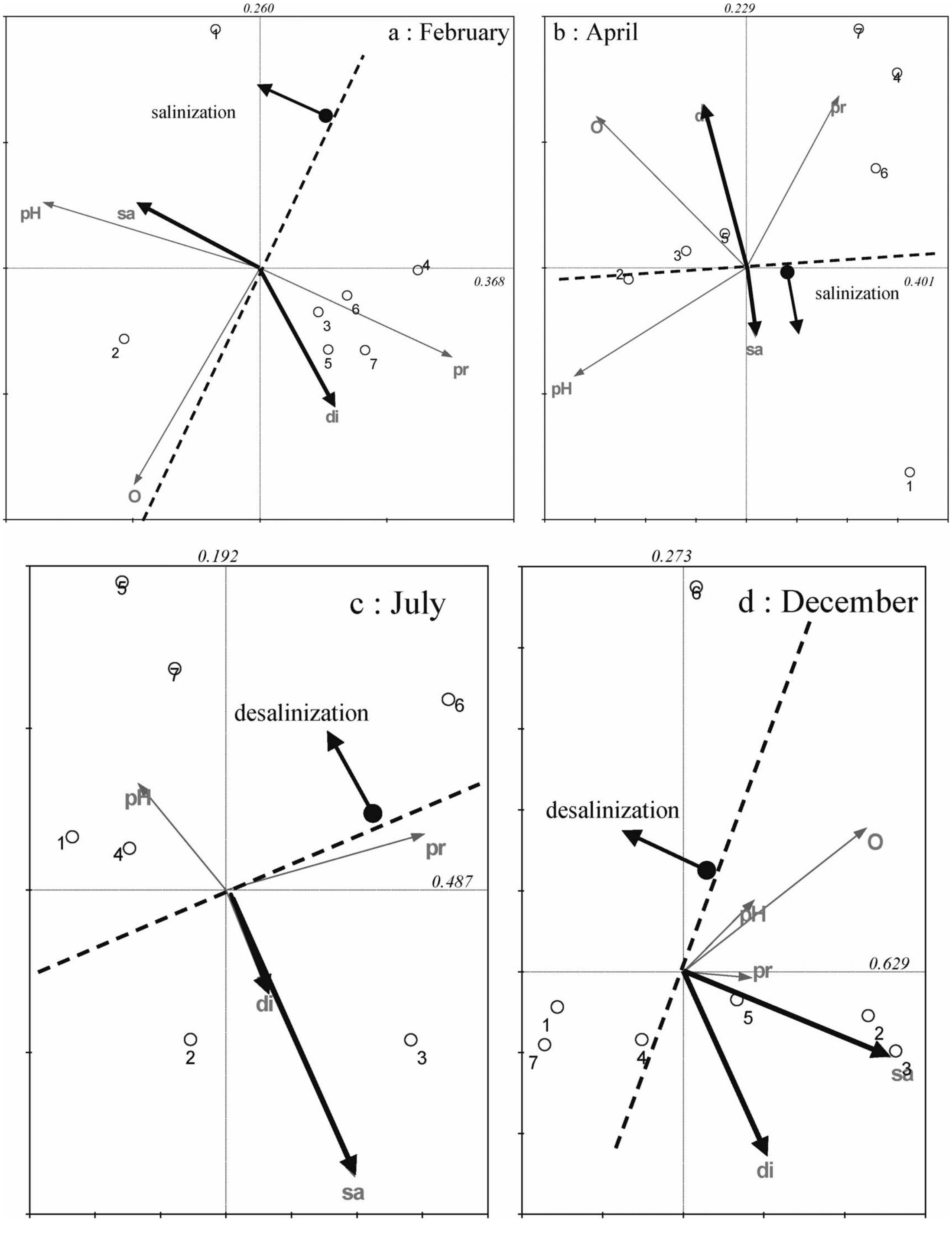

Figure 3. Canonical correspondence analyses. The positions of environmental variables (vectors) and stations (dots) in the space of the first two canonical axes show two situations: salinisation in the dry season, (a) February and (b) April and desalinisation in the rainy season, (c) July and (d) December. ED denotes Euclidean distance; Z, depth; S, salinity; O, dissolved oxygen.

that we expected to observe (>54 observed by CABERTY, CHAVES, and BOUCHEREAU [2004] and LOUIS [1983]) were not present at the same time. If biodiversity is important in mangrove wetlands in terms of quantity of species, factors other than salinity must be considered when trying to understand the organisation and functioning of the fish assemblage. The low number of native species and the multiple functional roles of the mangrove (*e.g.,* nursery, food resource, and permanent habitat) must be taken into account for long-term management of lagoon ecosystems.

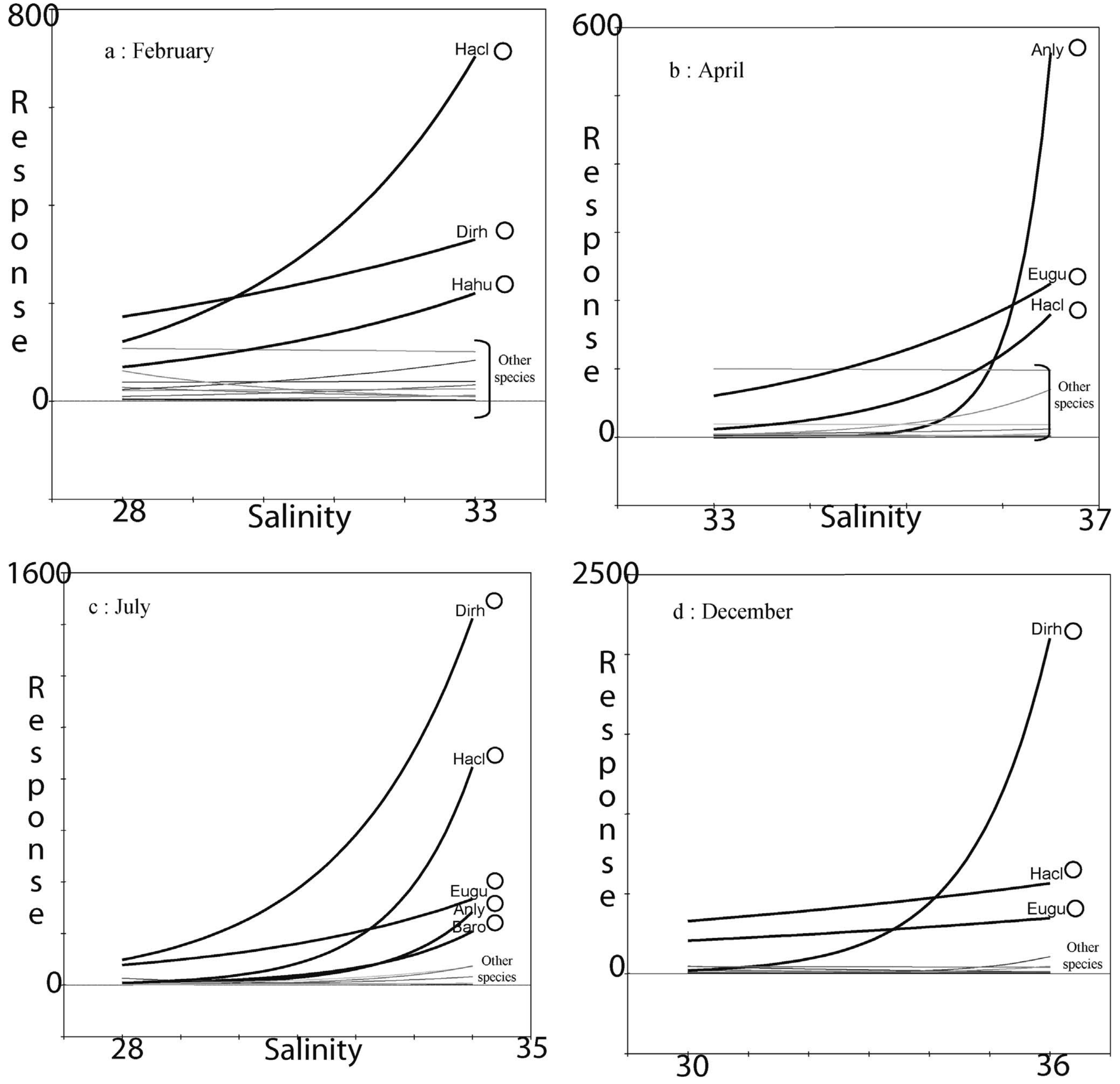

Figure 4. Species response curves to salinity (GLMs) according to the date sampled: (a) February, (b) April, (c) July, (d) December. See code of species in Table 2.

Biological Zonation

The fitting of the stations (Table 8) and the regroupings authorized by the local hydrodynamism would place stations S1, S2, and S6 in zones II, II/III, and II, respectively; S4 and S7 in zones III and III/IV, respectively; and S3 and S5 in zones IV/V and V, respectively (Figure 5), according to the Guelorget and Perthuisot (1983) confinement scale. Indeed, it is near S1, S2, and S6, close to the Rivière- Salée classified in zone II, that the water from marine origins is most quickly renewed. Moreover, sea urchins, whose distribution was limited to zones II and III (after Guelorget and Perthuisot, 1983), were observed there in the fixed nets (*capéchades*). At station S2, many *Anomalocardia brasiliana* and some *Chione cancellata, Lucina pectinata, Pena* sp. and *Tachycardium* sp. valves can be found in the sediment, and *Brachydontes exustus, Crassostrea rhizophora, Isogomon alatus,* and some *Isogomon radiatus* were found on the mangrove tree roots (O. Gros, personal communication). This presence

Table 8. *Biological zonation and classification of stations. We based our interpretation on this work and the works of Guelorget and Perthuisot (1983) and Monti, Frenkiel, and Mouëza (1991). ED = Euclidean distance; mSR = mean species richness; SR = species richness; NI = number of individuals; W = weight; mWI = mean Whitefield index; mIWB = mean index of well-being); S = station most cited (n times) according to its occurrence in the rank corresponding to the descriptor value ranked in ascending (Δ) or descending (∇) order.*

Rank	ED	mSR	SR	NI	W	mWI	mIWB	*n* Times	S	Present Work	1983	1991
1	1	1	1	1	1	1	1	7	1	II	II	II
2	6	2–6	2	2	6	4	2	3.5	2	II	III/IV	II
3	2		4–6	6	2	2	6	3	6	II	II	II
4	4	4		4	3	6	4	4.5	4	III	III/IV	III
5	3	7	7	3	7	7	7	5	7	III/IV	—	IV
6	5	3	3	7	4	3	5	3	3	IV/V	V	VI
7	7	5	5	5	5	5	3	5	5	V	V	VI
Gradient	Δ	∇	∇	∇	∇	∇	∇			Confinement		

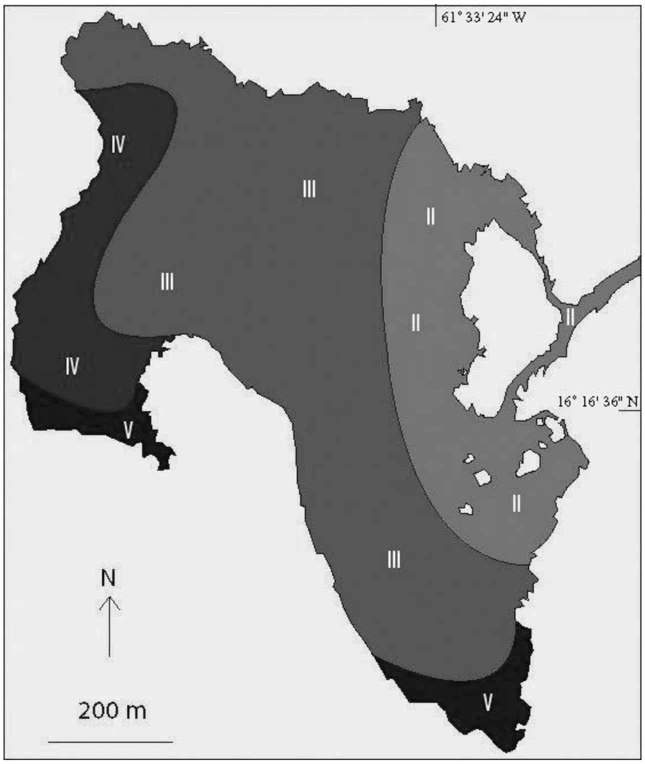

Figure 5. The biological zonation of the Manche-à-Eau lagoon according to the confinement concept of Guelorget and Perthuisot (1983).

of pelecypods in zone II announced their next high abundance in zone III, after Guelorget and Perthuisot (1983). At stations S4 and S7 in zone III, Monti, Frenkiel, and Mouëza (1991) observed the strongest production of Veneridae bivalves (*A. brasiliana*) within the MAE, which is a suitable characteristic for zone III as defined by Guelorget *et al.* (1982). The most confined stations, S3 and S5, were placed in zones IV/V, and V. Gaujous (1981) and Guelorget *et al.* (1990) observed a very great scarcity of macrobenthic species and individuals there. Monti, Frenkiel, and Mouëza (1991) qualified those locations as azoic. However, no cyanobacterial mats, which are typical of zone VI, were observed, except on the barks of *A. germinans* trunks. The distance of a station from the mouth of the system was independant of confinement (*e.g.,* station 7) and biomass production was shared in two groups of stations rather than a spread group along a continuous gradient. Fish production was high at S1, S2, and S6 close to the entrance of marine water (zone II), whereas that of mollusks was maximum (Monti, Frenkiel, and Mouëza, 1991) at S7 in zone III. For these reasons, ED and weight are not good descriptors for confinement and biological zonation. Because of the positionning of S4 at rank 2 by the Whitefield index and at rank 4 by the well-being index, we prefer to use the latter. It indicates very good sensitivity for describing species organisation. However, both descriptors must also be used with species richness and density to study confinement and biological zonation in a paralic ecosystem.

The descriptors offering the most expressive gradients are those related to SR, NI, and IWB. The good or fair water quality in the MAE expressed by IWB is also to be related to the general circulation of marine water. Just as relative ED was not a factor in structuring the assemblage of a biological compartment, the biomass also was not a good descriptor of biological zonation. However, the latter indicates the zones of strong ichthyic productivity and thus of possible halieutic exploitation. This is in agreement with the confinement concept, which postulates that it is the renewal rate from marine water in a given point of the paralic ecosystem that controls the organisation and structuring of the different populations. Indeed, in the MAE, according to local hydrodynamism and independent of salinity, one or several points close to the principal entries of marine water (S5) can be more confined than others more geographically distant stations (S7). Station S7 was highly influenced by water coming in via the second entrance, in contrast to S5 and S3. This is why the biodiversity in species and number of individuals and the quality of water were lower at S5 and S3 and why MONTI, FRENKIEL, and MOUËZA (1991) qualified those locations azoic.

CONCLUSION

Salinity was not at all a suitable physisicochemical parameter to explain the organisation of the fish assemblage in the paralic ecosystem of the mangrove lagoon in Manche-à-Eau. Other ichthyofauna descriptors, such as species richness, density, biomass, the Whitfield index and the index of well-being confirm and improve the preliminary zonation pattern proposed by GUELORGET and PERTHUISOT (1983) in the MAE and make it possible to establish with certainty the biological zonation (Figure 5) in it, even if this study is based on only 1 year of samples. This moderately confined lagoon (zones II and III occupy more of the lagoon surface than zones IV and V) has high water quality, welcomes many species, and has productivity in the different biological compartments, particularly fish and bivalves.

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☐ RÉSUMÉ ☐

Pour étudier l'influence des facteurs sur l'organisation de l'assemblage de poissons dans la lagune, son ichthyofaune a été régulièrement échantillonnée, en 2002, avec un filet fixe à sept stations sous quatre conditions hydrologiques différentes. Les descripteurs physico-chimiques (profondeur, température, salinité, oxygène dissous, pH) et populationnels (richesses spécifique et familiale, densité, biomasse) ont été mesurés, les indices de diversité de Shannon et de bien-être calculés, et analysés (analyse canonique des correspondances, modèles linéaires généralisés utilisant le logiciel « canoco »). Ont été collectés 30733 individus appartenant à 34 espèces et 23 familles. Les Gerreidés, Clupeidés, Engraulidés, Scianidés et Sparidés représentaient 98% d'entre eux. Les paramètres physico-chimiques ont montré que l'organisation de l'assemblage des poissons était très peu dépendante de la salinité, tandis qu'oxygène dissous, température et pH avaient un rôle plus fort. La plupart des espèces de poissons sont visiteuses de la lagune, soit occasionnellement comme prédatrices ou perdues, soit régulièrement comme migratrices cycliques. Seulement quelques-unes font partie du peuplement des sédentaires. Ces dernières ont une grande valeur patrimoniale et sont des espèces biointégratrices pour des études de suivi du milieu (changement global, perturbations naturelles ou anthropiques). Distance euclidienne et biomasse ne sont pas des descripteurs utiles du confinement et de la zonation biologique, tandis que les gradients négatifs de richesses spécifique et familiale, la densité numérique, les indices de Whitefield et de bien-être le décrivent mieux. La zonation biologique de la lagune à mangrove de la Manche-à-Eau a été établie.