

ROLE OF THE NON-NATIVE FISH *OREOCHROMIS NILOTICUS* IN THE LONG-TERM VARIATIONS OF ABUNDANCE AND SPECIES COMPOSITION OF THE NATIVE ICHTHYOFAUNA IN A CARIBBEAN ESTUARY

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ABSTRACT

Changes in native fish abundance (catch per unit effort–CPUE) and species composition were assessed before and after the introduction of *Oreochromis niloticus* Linnaeus, 1757 (Nile tilapia) in the Caribbean estuary Ciénaga Grande de Santa Marta (CGSM), northern Colombia. Multiple regression analysis was used to relate the abundance of *O. niloticus* to that of non-native fishes and environmental variables such as salinity, dissolved oxygen, pH, local rainfall, and river discharge. Species composition and abundance of native fishes were found to vary with environmental conditions in different zones but on a large scale, overall abundance remained approximately constant over all studied periods. Abundance of the native catfish *Cathorops mapale* Betancur-R. and Acero-P., 2005 was negatively related to the abundance of *O. niloticus*, and both varied with salinity. Overall fish diversity varied in periods when *O. niloticus* was present, which coincided with low salinity conditions. Our findings indicate that environmental fluctuations constrain the long-term establishment of *O. niloticus* in the estuary and thus its possible effects on abundance and species composition of the native ichthyofauna. However, it is feasible that the arrival of a more tolerant strain of *O. niloticus*, its future adaptation to the variable environment, or a longer duration of freshwater conditions in the estuary, could favor its long-term proliferation. In such a case, the occurrence of negative impacts on the native fishes cannot be disregarded. This is, to our knowledge, the first study investigating the impacts of *O. niloticus* on the ichthyofauna of a Caribbean estuary.

The introduction of new species into aquatic ecosystems has become common practice, but also a serious ecological problem: although it is intended as a solution to overcome shortage in food supply in many tropical countries, such introductions are recognized as one of the primary threats to biodiversity (Sala et al., 2000; Bax et al., 2003; Sala and Knowlton, 2006; Rahel, 2007). Species introductions may result in biological invasions that dramatically affect native species through predation or grazing, competition for food or space, and hybridization with native species. These and other impacts may eventually lead to alterations in the structure and function of the ecosystems and cause the loss of valuable resources (Mack et al., 2000; Mooney and Cleland, 2001; Hoffmeister et al., 2005). The introduction of non-native species in Africa and the Great Lakes of North America, for example, is considered one of the main causes for the collapse of the fisheries in those regions (Ogutu-Ohwayo and Hecky, 1991; Hall and Mills, 2000).

Colombia's fish fauna includes at least one third of the total number of fish species known in South America (Mojica et al., 2002), however, it also has one of the highest numbers of non-native fish species with at least 153 recorded (Gutierrez, 2004). Many of these fishes were intentionally introduced to increase local fishery production, for use in the ornamental fish trade, or for aquaculture purposes. Many others were accidentally introduced as a result of inadequate management of intentional

introductions. Although there have been numerous warnings about the potential consequences of the increasing number of non-native fishes on the native Colombian ichthyofauna, there are as yet no published studies directly addressing those impacts, even though some non-native fishes already constitute important fishery resources in several regions of the country (Diaz and Alvarez, 1998; Álvarez and Salazar, 2001; Gutierrez, 2004).

The Ciénaga Grande de Santa Marta (CGSM) is located along the north coast of Colombia as part of the delta of the Magdalena River, which is one of the largest deltas in the Caribbean Sea. The CGSM estuary is the main source of food and income for the region due to its large size (ca 1280 km²) and productivity (Sánchez and Rueda, 1999; Gocke et al., 2003). The most important natural factors influencing the distribution and abundance of resources in the CGSM are the freshwater input from the Magdalena River (Wiedemann, 1973; Kaufmann and Hevert, 1973) and saltwater input from the Caribbean Sea (Sanchez and Rueda, 1999; Rueda, 2001; Blanco et al., 2006, 2007). Interruption of fresh and marine water input, pollution, deforestation, erosion, and over-fishing in CGSM has led to the loss of many valuable resources during the last 40 yrs (Botero and Mancera, 1996; Botero and Salzwedel, 1999; Rueda and Defeo, 2003). Former waterways were re-established by dredging in 1998 with the goal of recovering former ecological conditions. Since that time, non-native fishes such as the snakeskin gourami (*Trichogaster pectoralis* Regan, 1910), the Nile tilapia (*Oreochromis niloticus* Linnaeus, 1757), the hybrid red tilapia (*Oreochromis* sp.), and the tambaqui (*Colosoma macropomum* Cuvier, 1818) increased their presence in the system (Sanchez, 1996; Bateman, 1998). Since 1999, *O. niloticus* has become one of the principal fishery resources, accounting for almost 60% of all catches in 1999 and 2000 (INVEMAR, 2006), but decreasing to < 10% thereafter. This drastic variation in abundance of *O. niloticus* seems to be related to environmental fluctuations (e.g., salinity) in the estuary (Blanco et al., 2007).

The goal of our study was to determine whether the observed spatio-temporal variation in species composition and abundance of native fish were related to the presence or abundance of the non-native fish *O. niloticus* or to environmental variability or both. We used descriptive and multivariate analysis to identify spatio-temporal trends in the fluctuations of native fish abundance and species composition before and after the introduction of *O. niloticus*. We also used multiple regression analysis to test for possible correlations between changes in native fish abundances and abundance of *O. niloticus*, salinity, pH, dissolved oxygen, and freshwater input (local rainfall and river discharge). We predicted that changes in the catches of the most abundant native fishes would be strongly related to the variation of the catches of *O. niloticus*. To our knowledge, this is the first study investigating the possible impacts of the *O. niloticus* on the native ichthyofauna of a Caribbean estuary.

METHODS

STUDY SITE.—The CGSM is located between 10°43′–11°00′N and 74°16′–74°35′W in the delta of the Magdalena River on the north coast of Colombia (Fig. 1). Its major connection to the Caribbean Sea is Boca de la Barra, an 80–100 m wide artificial outlet (Santos-Martinez and Acero, 1991). The system receives freshwater from several rivers originating in the Sierra Nevada de Santa Marta mountain system and from the Magdalena River through a complex of channels and swamps termed Pajarales (Fig. 1; Botero and Salzwedel, 1999). The mean annual water temperature is 30 °C and the depth in the system varies between 1 and 7 m. The

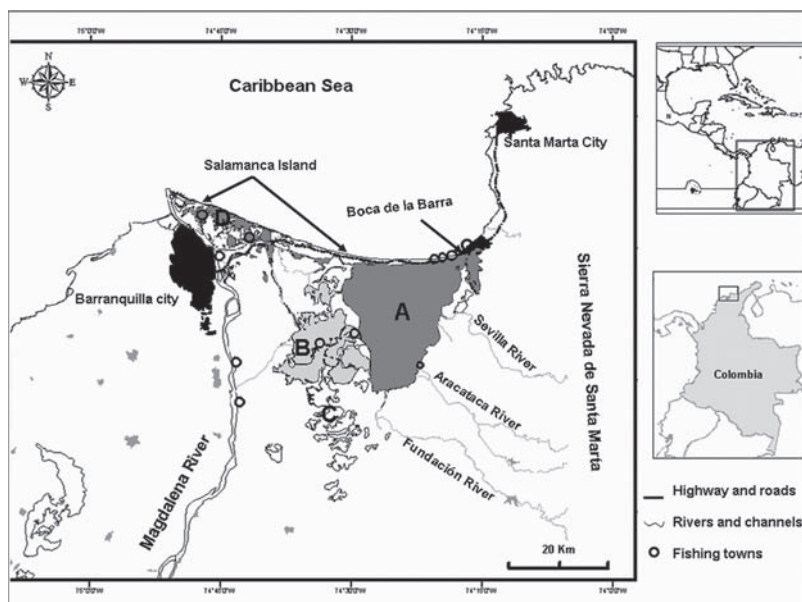


Figure 1. Location of Ciénaga Grande de Santa Marta Estuary and study zones A–D along the north coast of Colombia.

salinity ranges between 0 and 40 and the tidal amplitude between 20 and 30 cm (Polanía et al., 2001). The climate in the area is particularly dry (arid) with a mean air temperature of 28 °C and a mean hydrological deficit that ranges between -211.6 and -1146.8 mm yr⁻¹ resulting from the difference between mean local rainfall and mean evaporation (Botero and Salzwedel, 1999; Blanco et al., 2006). Therefore, riverine water input is vital for the system's water budget (Kauffman and Hevert, 1973). A dry season extends from December to March and a rainy season from April to November (Blanco et al., 2006). Of the 122 teleost fish species that have been recorded in the CGSM, 81 are commercially exploited (Polanía et al., 2001). Historically important native estuarine species include *Mugil incilis* Hancock, 1830, *Cathorops mapale* Betancur-R. and Acero-P., 2005, *Eugerres plumieri* Valenciennes, 1830, *Ariopsis bonillai* Miles, 1945, *Megalops atlanticus* Valenciennes, 1846, and *Elops saurus* Linnaeus, 1766 (Santos-Martinez and Acero, 1991; Sanchez and Rueda, 1999).

DATA COLLECTION.—The data used for this study were collected by the Institute for Marine and Coastal Research (INVEMAR) in Santa Marta, Colombia. Since 1994, monthly fishery information was collected within the framework of an ecosystem monitoring program. Data collected included weight of catch (kg), species composition of catch, effort (number of fishing trips) by gear type and location, as well as environmental information such as salinity, dissolved oxygen (mg L⁻¹), and pH. We also used local rainfall (mm) and river discharge (m³ s⁻¹) data provided by the National Institute for Meteorology, Hydrology and Environmental Studies (IDEAM). Catch per unit effort (CPUE) was calculated and used as a relative measure of fish abundance in the system—the term abundance shall be used throughout this study instead of CPUE. For the analyses we used fish abundance (CPUE) data from cast nets. This gear was the most consistently used over the eight-year study period and collected the widest spectrum of species when compared to all the other gear types.

DATA ANALYSIS.—Our study area was divided into four zones: ZA, the main lagoon; ZB, the lagoon complex of Pajarales; ZC, the lagoon complex in the south-western protected area; and ZD, the western side of Salamanca Island (Fig. 1). Moving east to west through these zones (A–D) represents a gradient of decreasing salinity (Giraldo et al., 1995). The change in abundance of *O. niloticus* was used as a criterion to divide the set of monthly data into four periods: PI = 1994–1995 (few or no *O. niloticus* in catches; N = 58); PII = 1996 (*O. niloticus*

Table 1. The 21 commercial species that account at least for 1% of the total catch per unit effort (CPUE—kg fishing trip⁻¹) in at least one of the 8 yrs (1994–1996, 1999–2003) considered for this study. Taxonomical classification after Froese and Pauly (2006) and Nelson (2006).

Family	Scientific name	Abbrev.	Total catch (ton)	CPUE (kg fishing trip ⁻¹)
Mugilidae	<i>Mugil incilis</i> Hancock, 1830 ^a	Mug_in	900.9	15.1
Ariidae	<i>Cathorops mapale</i> Betancur-R. and Acero-P., 2005 ^a	Cat_9	537.0	5.7
Cichlidae	<i>Oreochromis niloticus</i> Linnaeus, 1757	Ore_ni	235.8	15.6
Gerreidae	<i>Eugerres plumieri</i> Valenciennes, 1830 ^a	Eug_pl	197.1	2.3
Ariidae	<i>Ariopsis bonillai</i> Miles, 1945 ^a	Ari_bo	87.1	1.8
Scianidae	<i>Bairdiella ronchus</i> Cuvier, 1830	Bar_ro	51.2	0.5
Elopidae	<i>Elops saurus</i> Linnaeus, 1766 ^a	Elo_sa	39.1	0.8
Megalopidae	<i>Megalops atlanticus</i> Valenciennes, 1846 ^a	Meg_at	38.0	1.9
Scianidae	<i>Micropogonias furnieri</i> Desmarest, 1822	Mic_fu	31.8	0.5
Mugilidae	<i>Mugil liza</i> Valenciennes, 1836	Mug_li	26.8	0.8
Prochilodontidae	<i>Prochilodus magdalenae</i> Steindachner, 1879	Pro_ma	15.6	0.8
Engraulidae	<i>Anchovia clupeioides</i> Swainson, 1839	Bna ^b	14.9	0.6
Engraulidae	<i>Cetengraulis edentulus</i> Cuvier, 1829	Bna ^b	14.9	0.6
Cichlidae	<i>Caquetaia kraussi</i> Steindachner, 1878	Caq_kr	10.6	0.6
Characidae	<i>Triportheus magdalenae</i> Steindachner, 1878	Tri_ma	9.9	0.7
Centropomidae	<i>Centropomus undecimalis</i> Bloch, 1792	Cen_un	9.9	0.2
Gerreidae	<i>Diapterus auratus</i> Ranzani, 1840	MBI ^b	9.8	0.2
Gerreidae	<i>Diapterus rhombeus</i> Cuvier, 1829	MBI ^b	9.8	0.2
Gerreidae	<i>Gerres cinereus</i> Walbaum, 1792	MBI ^b	9.8	0.2
Erythrinidae	<i>Hoplias malabaricus</i> Bloch, 1794	Hop_ma	6.5	0.8
Mugilidae	<i>Mugil curema</i> Valenciennes, 1836	Mug_cu	3.8	0.2
Characidae	<i>Leporinus muyscorum</i> Steindachner, 1900	Lep_mu	1.7	0.3
Characidae	<i>Astyanax fasciatus</i> Cuvier, 1819	Vie ^b	1.2	0.2
Characidae	<i>Cyphocharax magdalenae</i> Steindachner, 1878	Vie ^b	1.2	0.2
Characidae	<i>Hemibrycon</i> sp.	Vie ^b	1.2	0.2
Osphronemidae	<i>Trichogaster pectoralis</i> Regan, 1910	Tri_pe	1.1	0.2

^a The six (6) most abundant and commercially important native fish species

^b Several species were recorded with the same code due to the difficulty fishermen had distinguishing among species

present but occurring in < 5% of the total catches; N = 25); PIII = 1999–2001 (after reestablishment of freshwater and salt water connections and marked *O. niloticus* increase; N = 34); and PIV = 2002–2003 (subsequent *O. niloticus* decrease; N = 36).

Species Composition and Fish Abundance.—Kruskal-Wallis tests were performed to compare differences in abundance of *O. niloticus*, species richness (R, number of fish species), fish diversity (expressed as Shannon-Weaver Index—H'; Shannon and Weaver, 1949), and environmental parameters among the four periods of study (Sokal and Rohlf, 1995). Multiple comparisons (Kruskal-Wallis routine in Statistica v. 8) were used to test differences between all pairs of periods compared. Due to the lack of environmental data of PIII in ZD, this zone was excluded from these analyses.

A two way analysis of similarities (ANOSIM) was performed to test if species composition and multispecific fish abundance significantly differed among periods and zones (factors; Clarke, 1993). A Similarity Percentage (SIMPER) analysis was used to identify the species accounting for most of the similarity in abundance and species composition within periods and

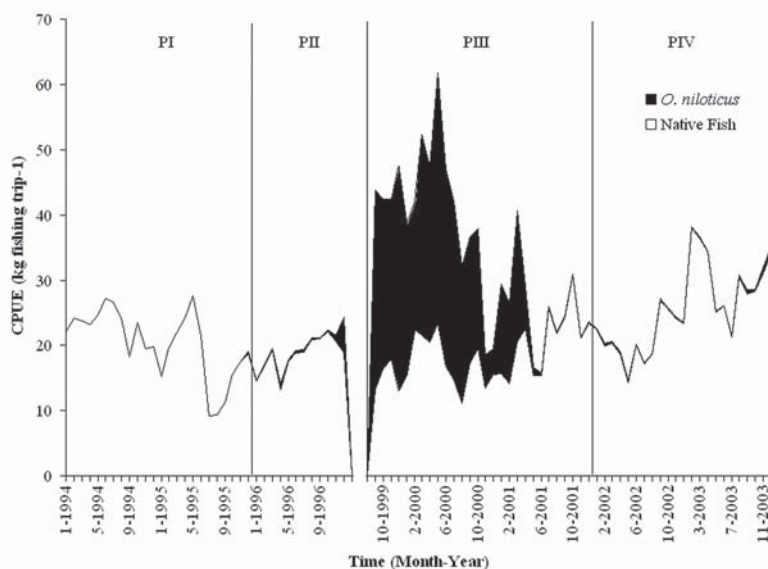


Figure 2. Changes in relative abundance measured as CPUE (kg fishing trip⁻¹) of non-native and native fishes in the estuary during the time period of study. Fishes were caught using cast nets. PI = 1994–1995; PII = 1996; PIII = 1999–2001; PIV = 2002–2003

zones. It also was used to determine the species that discriminate best between these grouping factors (Clarke, 1993). For these analyses, all fish species accounting for more than 1% of the total abundance in at least one of the 8 yrs of the study were selected (21 species; Table 1). PRIMER for Windows v. 5.2.2 (Plymouth Marine Laboratory) was used for these analyses.

Relationship Between Fish Abundance and Environmental Variables.—Forward stepwise Multiple Regression Analysis (MRA; Zar, 1996) was conducted to determine the extent that *O. niloticus* abundance and environmental factors explained the monthly variations in fish abundance for the six most abundant and commercially important native fish species. Due to high correlation between salinity and abundance of *O. niloticus* (Spearman Rank Order Correlation = -0.60 , $P < 0.05$), these two variables were used separately as independent variables. All data were Log+1 transformed to normalize the residuals and 0.025 was used as significance level (Bonferroni adjustment). In all cases the statistical criterion (F) to enter variables into the model was $F > 1$. In the first MRA, the abundances of the native species were used as dependant variables and that of *O. niloticus* as an independent variable, while in a second MRA the abundances of all fishes including *O. niloticus* were used as dependent variables, and salinity, pH, and DO as independent variables. Using ZA as a reference, dummy variables were created for ZB and ZD to determine the effect of zone differences in the variables in these two MRAs. Zone C was excluded from these analyses due to lack of environmental data. Given the difficulty of establishing geographical limits to the influence of local rainfall and river input, their regional monthly average values were used in a third MRA as independent variables and the regional monthly mean abundance of native fishes and *O. niloticus* as dependent variables.

RESULTS

SPECIES COMPOSITION AND FISH ABUNDANCE.—The abundance of *O. niloticus* differed significantly among all four periods ($H = 195.83$, $df = 3$, $N = 327$, $P < 0.05$;

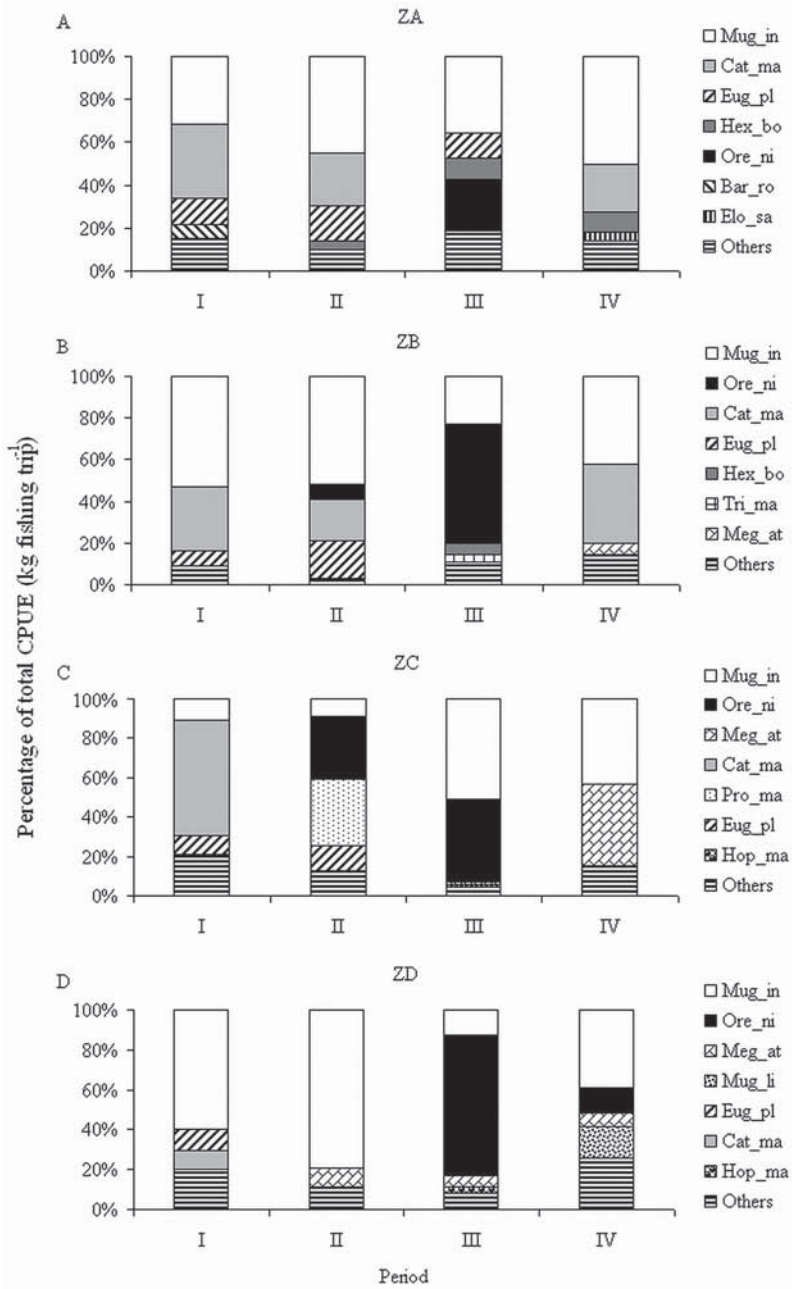


Figure 3. Changes in fish abundance and species composition in the four zones of the Ciénaga Grande de Santa Marta estuary (A, B, C, D) during the four different periods considered in this study (PI = 1994–1995; PII = 1996; PIII = 1999–2001; PIV = 2002–2003). See abbreviations of fish names in Table 1.

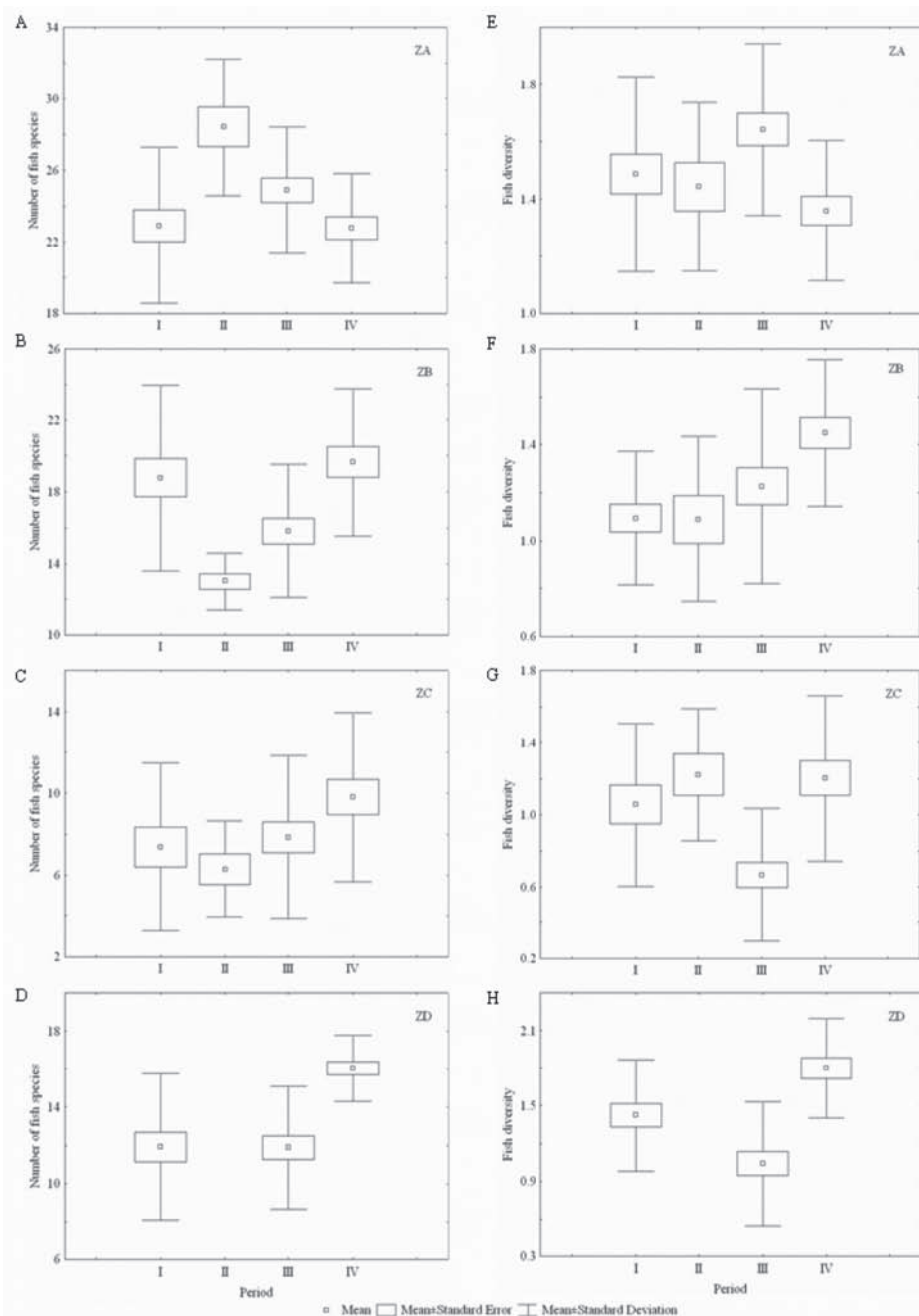


Figure 4. Changes in species richness (R, number of fish species) and fish diversity (expressed as Shannon-Weaver Index-H'; Shannon and Weaver, 1949) in the four zones of the Ciénaga Grande de Santa Marta estuary (ZA, ZB, ZC, and ZD) during the four different periods considered in this study (PI = 1994–1995; PII = 1996; PIII = 1999–2001; PIV = 2002–2003)

all post-hoc, $P < 0.05$) from complete absence in PI and very low abundance in PII to very high in PIII when it dominated the catches in the estuary and back to very low in PIV (Fig. 2). In contrast, the group of native fish maintained a very similar abundance over the entire study period. A variable group of very few species (2–4) represented between 70 and 95% of the total abundance (Fig. 3). The native estuarine fish *M. incilis* was the only species consistently ranking among the most abundant over all zones and periods. The non-native fish *O. niloticus* became the most abundant species (total CPUE > 50%) during PIII in all zones except in ZA, where *M. incilis* was the most abundant. *Oreochromis niloticus* drastically decreased during PIV in all zones. The abundance of the native *C. mapale* decreased during the periods when *O. niloticus* was the most abundant fish in all zones. *Eugerres plumieri* varied considerably from period to period, but with no apparent relation to any other species. Native freshwater fishes like *Triporthesus magdalenae* Steindachner, 1878, *Prochilodus magdalenae* Steindachner, 1879, and *Hoplias malabaricus* Bloch, 1794 appeared only in PII or PIII in ZB, ZC, and ZD. Piscivorous fishes such as *A. bonillai*, *M. atlanticus*, and *E. saurus* increased in some zones during PIII and PIV.

The small differences in richness (number of fish species) and fish diversity (H') (Fig. 4) were not significant ($P < 0.008$) during the period of greatest abundance of *O. niloticus* (PIII) relative to the earlier periods. However, during the following period (PIV) with a low abundance of *O. niloticus*, a few differences were significant ($P < 0.008$) in some zones relative to PIII. Fish diversity (H') decreased in ZA ($H_{3,N=87} =$

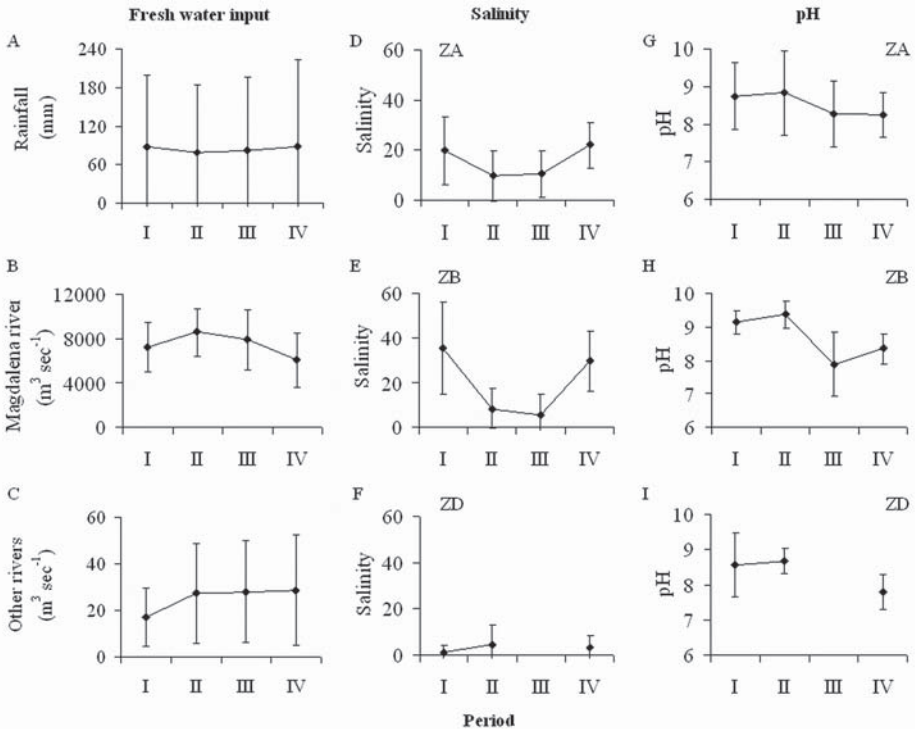


Figure 5. Variation in mean values (\pm standard deviation) of the main environmental parameters in CGSM during the four periods (PI: 1994–1995; PII: 1996; PIII: 1999–2001; PIV: 2002–2003) of study: (A–C) Freshwater input in the whole region; (D–F) Salinity and (G–I) pH in three of the zones of study (ZA, ZB, ZD). Zone C is not included due to lack of environmental data.

11.31; Fig. 4E) but increased in ZC (H' : $H_{3,N=79} = 20.33$; Fig. 4G) and ZD ($H_{2,N=74} = 26.48$; Fig. 4H). In this last zone, richness also increased during PIV ($H_{2,N=74} = 24.25$; Fig. 4D).

The two way crossed Analysis of Similarities (ANOSIM) revealed significant differences in species composition and abundance among periods ($R = 0.601$, $P < 0.001$) and zones ($R = 0.49$; $P < 0.001$), as well as significant differences ($R > 0.3$; $P < 0.001$) between all pairwise comparisons. Furthermore, the SIMPER analysis revealed that *M. incilis* was the species that best accounted for the similarity in species composition and abundance in all zones (% Similarity > 16) and periods (% Similarity > 22), except in PIII when *O. niloticus* accounted for the largest similarity (22%). *Oreochromis niloticus* was the species that best discriminated between most pairs of compared periods (% Dissimilarity > 12) and zones (% Dissimilarity > 10), followed by the native fish *C. mapale* (% Dissimilarity ~9 between periods and ~10 between zones).

RELATIONSHIP BETWEEN FISH ABUNDANCE AND ENVIRONMENTAL VARIABLES.—Salinity and river discharge were the variables exhibiting the greatest variation over the study periods (Fig. 5). Salinity fluctuations were significantly different among study periods except in ZD (ZA: $H_{3,N=71} = 14.48$; ZB: $H_{3,N=69} = 38.65$; ZD: $P < 0.05$, $H_{2,N=33} = 0.13$; $P > 0.05$) while water discharge differed significantly among periods in the whole region (Magdalena: $H_{3,N=89} = 8.15$; other rivers: $H_{3,N=91} = 13.85$; $P < 0.05$). Changes in salinity (Fig. 5D–E) reflected (opposite) patterns of water discharge of the Magdalena River (Fig. 4B), which is the main input of freshwater into the estuary. Zones A and B had similar patterns of salinity fluctuation (Fig. 5D,E), varying from high (20 ± 14 to 35 ± 21) in PI and PIV to low values (6 ± 9 to 10 ± 9) in PII and PIII. pH differed significantly among all zones (ZA: $H_{3,N=71} = 21.25$; ZB: $H_{3,N=68} = 52.32$; ZD: $H_{2,N=33} = 13.84$; $P < 0.05$; Fig. 5G–H). This parameter tended to decrease slightly over the four periods at ZA, and more abruptly at ZB. No environmental data are available for PIII in zone D (Fig. 5F–I), therefore data from this zone must be interpreted with caution. However, overall, the salinity range in this zone is much lower (0–5) than at the other zones, whereas pH is similar to that of the other zones.

Multiple regression analyses revealed that the environmental variables (salinity, pH, and river discharge) and the abundance of *O. niloticus* contributed to variation in the abundance of native fishes. The abundance of *O. niloticus* best explained (Table 2, $P < 0.025$) variation in abundance of *C. mapale* ($r = -0.45$) and *M. atlanticus* ($r = 0.19$). When salinity, pH, and DO were treated as independent variables (Table 3, $P < 0.025$), salinity best explained the variation in abundance of *M. incilis* ($r = -0.32$),

Table 2. Forward stepwise multiple regression analysis with native fish abundances as dependent variables (Y) and the abundance of *Oreochromis niloticus* as independent variable (X). Only significant results reported ($P < 0.025$). N = 141. NS: not significant, NE: variable not in the equation, r = standardized regression coefficients.

Y	r			Multiple R ²	Std. Error estimate	P
	ZB	ZD	<i>Oreochromis niloticus</i>			
<i>Ariopsis bonillai</i>	-0.61	-0.51	NS	0.41	0.43	0.000
<i>Mugil incilis</i>	NS	-0.15	NE	0.06	0.69	0.014
<i>Elops saurus</i>	-0.26	-0.39	NE	0.15	0.35	0.000
<i>Cathorops mapale</i>	-0.16	-0.51	-0.45	0.43	0.84	0.000
<i>Eugerres plumieri</i>	-0.46	-0.48	NE	0.29	0.66	0.000
<i>Megalops atlanticus</i>	NS	NS	0.19	0.60	0.45	0.027

Table 3. Forward stepwise multiple regression analysis with native and non-native fish abundances as dependent variables (Y) and salinity (SAL), pH (units), and dissolved oxygen (DO, mg L⁻¹) as independent variables (X). Only significant results reported ($P < 0.025$). $N = 136$. NS: not significant, NE: variable not in the equation, r = standardized regression coefficients.

Y	r					Multiple R ²	Std. Error estimate	P
	ZB	ZD	SAL	pH	DO			
<i>Ariopsis bonillai</i>	-0.56	-0.44	0.28	-0.50	NS	0.58	0.37	0.000
<i>Mugil incilis</i>	NS	NS	-0.32	NS	NE	0.12	0.68	0.002
<i>Elops saurus</i>	-0.22	-0.31	0.36	-0.44	0.19	0.30	0.33	0.000
<i>Cathorops mapale</i>	-0.27	-0.22	0.45	NS	NS	0.45	0.82	0.000
<i>Eugerres plumieri</i>	-0.50	-0.56	-0.35	0.32	NS	0.43	0.59	0.000
<i>Megalops atlanticus</i>	0.19	NE	NE	-0.51	NS	0.27	0.34	0.000
<i>Oreochromis niloticus</i>	0.17	-0.37	-0.43	-0.32	0.30	0.50	0.92	0.000

C. mapale ($r = 0.45$), *E. plumieri* ($r = -0.35$), and *O. niloticus* ($r = -0.43$). pH best explained variation in abundance of *A. bonillai* ($r = -0.50$), *E. saurus* ($r = -0.44$), and *M. atlanticus* ($r = -0.51$). When river discharge and local rainfall were treated as independent variables (Table 4, $P < 0.05$), river discharge best explained variation in abundance of *E. plumieri* ($r = 0.39$) and *E. saurus* ($r = -0.29$).

DISCUSSION

The hypothesis of *O. niloticus* being solely responsible for fluctuations in the abundance of native ichthyofauna should be rejected since fluctuations in environmental variables (salinity, pH, and river discharge) explained much of the variation in abundance of most fish species including *O. niloticus*. However, our findings indicate that although the duration of low salinity conditions was relatively short, this non-native fish could have affected the native ichthyofauna.

On the largest spatial scale (all zones combined) the overall native fish abundance remained quite constant over the four study periods. However, when the specific composition was analyzed for each period and zone, changes in relative abundance on the species level became evident. This relative constancy of the overall native fish component could be indicative of a high resilience due to a high species redundancy, meaning that this component has several fish species with similar functions and they

Table 4. Forward stepwise multiple regression analysis with native and non-native fish abundances as dependent variables (Y) and local rainfall (mm) and river discharge (m³ s⁻¹) as independent variables (X). Only significant results reported ($P < 0.05$). $N = 67$. NS: not significant, NE: variable not in the equation, r = standardized regression coefficients.

Y	r		Multiple R ²	Std. Error estimate	P
	Rainfall	River discharge			
<i>Ariopsis bonillai</i>	NE	NS	0.04	0.40	0.057
<i>Mugil incilis</i>	NE	NE	-----	-----	-----
<i>Elops saurus</i>	NE	-0.29	0.08	0.34	0.007
<i>Cathorops mapale</i>	NE	NE	-----	-----	-----
<i>Eugerres plumieri</i>	NS	0.39	0.15	0.57	0.001
<i>Megalops atlanticus</i>	NS	NE	0.01	0.61	0.290
<i>Oreochromis niloticus</i>	NS	NS	0.05	1.38	0.126

react in different ways to the same environmental fluctuations (Walker, 1995; Gunderson, 2000; Hooper et al., 2005). Such a differential response to the environment (as seen in the MRA results) may explain the observed variations in species abundance and composition at smaller spatial and temporal scales (zones and periods), and therefore the changes in fish diversity and richness.

During the periods of low salinity, the inflow of unusual amounts of freshwater may increase the variety and size of available habitats for freshwater and euryhaline species in the estuary. In contrast, species not well adapted to low salinity may migrate to areas with more favorable conditions or experience a decrease in their populations. This is evidenced by the increase in the number and abundance of native freshwater fishes (e.g., *P. magdalенаe*, *H. malabaricus*, *T. magdalенаe*) during PIII, and the decrease in abundance of native estuarine fishes (e.g., *M. incilis*, *C. mapale*) over the same period. The increase of piscivorous fishes during PIII and PIV in some zones might be a response to an increase of prey represented by non-native and native freshwater fishes. This may explain the positive relationship between the predator *M. atlanticus* and the potential prey *O. niloticus*.

The great adaptability of *O. niloticus* to new environmental conditions is evidenced by its high growth rate, variable maturation size, and opportunistic feeding (Trewavas, 1983; Balirwa, 1998; Beveridge and McAndrew, 2000). In strongly altered and stressed ecosystems, *O. niloticus* could be a superior competitor, debilitating or completely out-competing native species (Ogutu-Ohwayo, 1990; Ogutu-Ohwayo and Hecky, 1991; Léveque, 2002; Canonico et al., 2005). For example, the negative relationship between the abundances of *O. niloticus* and the native fish *C. mapale* could be indicative of interspecific competition. Both species utilize soft bottoms, *O. niloticus* for spawning and *C. mapale* for feeding (Carpenter, 2002; Froese and Pauly, 2006). The abundance of both fishes, however, was related to the variation in salinity, so they could be responding instead in opposite ways to the same environmental variable. Thus, although the SIMPER analysis revealed a shift in the dominant species within the fish community during the period of greatest abundance of *O. niloticus*, this does not necessarily imply that the non-native fish displaced native species. Further research is needed to investigate the likelihood of competition between native and non-native fishes in the ecosystem.

The salinity tolerance of tilapias is highly variable, as evidenced by the different tolerance limits reported in different populations of *O. niloticus*. In laboratory experiments, Watanabe et al. (1985) reported a salinity tolerance limit of 19, Villegas (1990) of 10 and Schofield et al. (2007) > 40 after weekly increments. Peterson et al. (2004) reported the existence of actively reproductive populations of *O. niloticus* in coastal environments with salinities that range at about 25 in Mississippi, USA. *Oreochromis niloticus* also has established wild populations in a coastal lagoon in eastern Italy with salinities between 22 and 33 (Scordella et al., 2003). In CGSM, *O. niloticus* seems to be less euryhaline since its abundance dramatically decreased when salinities increased above 15 (Blanco et al., 2007). This variable environmental tolerance indicates a high adaptability of the species. Therefore, it should not be discarded that the arrival of a more tolerant strain of this fish or its adaptation to the variable environment, could favor a long term establishment of *O. niloticus* in the estuary.

Negative impacts of tilapias have been reported in several ecosystems around the world (Costa-Pierce, 2003; Canonico et al., 2005). *Oreochromis niloticus* has

out-competed several native tilapiine species in the African Lake Victoria (Ogutu-Ohwayo, 1990; Ogutu-Ohwayo and Hecky, 1991). Tilapias, including *O. niloticus*, have impacted the native fish communities in several lakes of Nicaragua, where they eliminated the habitat of some native fish by feeding on native aquatic plants. Tilapias also compete with native fish for spawning sites in the same lakes and seem to be responsible for an outbreak of a trematode parasite that has probably caused blindness among native cichlids (McKaye et al., 1995; McCrary et al., 2007). The rapid proliferation of *O. niloticus* and its high potential to compete for spawning grounds with native fish (e.g., centrarchids) is considered as a threat to the US coastal areas of Mississippi (Peterson et al., 2004, 2005, 2006).

Other studies in tropical and sub tropical estuaries and coastal lagoons have also found that abiotic factors such as salinity are the primary factors determining the fish species richness, distribution, and abundance. Such is the case of the Shellharbour lagoon in southeast Australia (Griffiths, 2001), the Caeté estuary in northern Brazil (Barletta et al., 2005), St. Lucia estuary in South Africa (Whitfield et al., 2006), and Terminos lagoon in the southern Gulf of Mexico (Sosa-López et al., 2007). Based on their research experience in California streams, Moyle and Light (1996) suggested that “if abiotic factors are appropriate for a non-native species, then that species is likely to successfully invade, regardless of the biota already present”. In our study of *O. niloticus* in CGSM, its establishment was likely restricted by the lack of appropriate abiotic factors. Changes in the recipient ecosystem can foster adequate biological, ecological, and environmental conditions creating an “invasion window” for the successful establishment of new species (Johnstone, 1986; Carlton, 1996); the timing of arrival of these new species often coincides with favorable environmental conditions (Crawley, 1989). Thus, if favorable conditions occur in the CGSM estuary for longer periods, *O. niloticus* may be able to establish self-sustaining populations.

Being one of the most popular cultured fish worldwide, *O. niloticus* has been introduced in many tropical countries (FAO, 2006). However, the impacts of this non-native fish in natural waters are not yet well studied (Canonico et al., 2003; Costa-Pierce, 2003). The present study is, to our knowledge, the first to investigate the impact of this fish on the native ichthyofauna of a Caribbean estuary. Our findings indicate that environmental fluctuations constrain the long-term establishment of *O. niloticus* in the estuary and may therefore reduce its possible effects in the abundance and species composition of the native ichthyofauna. However, it is feasible that the arrival of a more tolerant strain of this species or its future adaptation to the variable environment or a longer duration of freshwater conditions, could favor a long-term proliferation of *O. niloticus*. Considering the biological features of this species, in such a case, the occurrence of negative impacts on the native fishes can not be discounted.

ACKNOWLEDGMENTS

The authors express their gratitude to the Institute of Marine and Coastal Research “José Benito Vives de Andreis”—INVEMAR in Santa Marta (Colombia) and the Center for Marine Tropical Ecology—ZMT in Bremen (Germany) and their staff for their logistical and academic support. Thanks also to T. Alpermann, I. Freytag, J. Blanco, B. Grote, C. Roder, and two anonymous reviewers for the useful comments and suggestions. This study has been financed by INVEMAR. The first author was funded by the scholarship program COLFUTURO-DAAD (Colombia-Germany) and this study is part of her PhD Dissertation.

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DATE SUBMITTED: 24 July, 2007.

DATE ACCEPTED: 30 April, 2008.

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