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Artículo

Invasive Mozambique tilapia (*Oreochromis mossambicus*), dominates Southeastern Caribbean Sea island estuary

Eliaira Rodríguez, Ernesto Ron, Iván Mikolji, José L. Fuentes and Oscar M. Lasso-Alcalá

Abstract. Some structural and population aspects of the fish community of Laguna de Los Mártires, a small positive estuary (1.9 - 25 PSU), located on Isla de Margarita, in the Southeast Caribbean Sea, were studied. During a year of monthly sampling at five stations, only 10 fish species were recorded. Of these, *Oreochromis mossambicus* (Peters 1852), was the only one caught in all seasons throughout the year, with higher abundance (39.8%) and relative biomass (54.3%), frequency of occurrence (100%) and Importance Valuation Index (194.1). The invasive success of this species was also evidenced by a high abundance of juveniles (65%), continuous reproduction and rapid growth. Its effects on the native fish community was also observed in the ecological indices, with low values of Species Richness (S: 1 - 6 species), Diversity (H: 0 - 0.94) and Equity (J: 0.13 – 0.54), and high Community Dominance Index (CDI: 0.4 - 0.9). A high anthropogenic impact was also observed in the Laguna de Los Mártires, due to the contamination of the waters and physical modification of the habitat. This characterizes a highly deteriorated ecosystem, with a poor fish community, product of the synergy between the dominance of *O. mossambicus* over the native fish community, as well as the alteration of the habitat (invasive meltdown). Systematic extraction of the population of this invader in the lagoon is recommended to improve the environmental conditions of this ecosystem and the recovery of the biota.

Keywords: Introduced species; biological invasions; habitat alteration; invasive meltdown; coastal marine lagoons; fish communities; Venezuela.

La invasiva tilapia de mozambique *Oreochromis mossambicus,* domina un estuario insular en el sureste del Mar Caribe.

Resumen. Se estudiaron algunos aspectos estructurales y poblacionales de la comunidad de peces de la Laguna de Los Mártires, un pequeño estuario de tipo positivo (1.9 - 25 PSU), ubicado en la Isla de Margarita, al Sureste del Mar Caribe. Durante un año de muestreos mensuales en cinco estaciones, se registraron tan solo 10 especies de peces. De estas, *Oreochromis mossambicus* (Peters 1852), fue la única capturada en todas las estaciones durante todo el año, con la abundancia (39,8%), biomasa relativa (54,3%), frecuencia de aparición (100%) e Índice de Valoración de Importancia (194,1), más altos. El éxito invasivo de esta especie, también se evidenció por una alta abundancia de juveniles (65%), reproducción continua y crecimiento rápido. Su influencia en la comunidad íctica autóctona, también se observó en los índices ecológicos, con valores bajos de Riqueza (S: 1 – 6 especies), Diversidad (H: 0 – 0,94) y Equidad (J: 0,13 – 0,54), y altos de Dominancia (IDC: 0,4 – 0,9). También se observó un alto impacto antropogénico en la Laguna de Los Mártires, por la contaminación de las aguas y modificación física del hábitat. Esto lo caracteriza como un ecosistema altamente deteriorado, con una comunidad de peces pobre, producto de la sinergia entre la dominancia de *O. mossambicus* sobre la comunidad de peces nativa, así como la alteración del hábitat (fusión invasiva). Se recomienda la extracción sistemática de la población de este invasor en la laguna así como realizar obras de saneamiento y mejorar las condiciones ambientales de este ecosistema y la recuperación de la biota.

Palabras clave: Especies introducidas; invasiones biológicas; alteración del hábitat; fusión invasiva; lagunas marino costeras, comunidades de peces, Venezuela.

Introduction

The introduction of non-native exotic and/or translocate species in natural ecosystems has been indicated as a serious problem and threat to the conservation of biodiversity, causing degradation of ecosystems as well as indirect (*e.g.*, loss of economic activities) and direct (*e.g.*, disease transmission) impacts on humans (Lasso-Alcalá 2001; Ojasti *et al.* 2001, Lasso-Alcalá 2003, Canonico *et al.* 2005, Pimentel *et al*. 2005, Casal 2006; Gutiérrez *et al.* 2012; Katsanevakis *et al.* 2016, Cassemiro *et al.* 2018, Vitule *et al.* 2019, Chinchio *et al*. 2020, Pysek *et al.* 2020, Doria *et al.* 2021). In the long term, the worst scenario that can be expected with the introduction of non-native species is the invasion and the homogenization of the biota (Baiser *et al*. 2012, Vitule and Pozenato 2012, Daga *et al.* 2020). However, negative impacts can also occur in the short term, as the non-native species does not need to be established or become invasive to cause such impacts. This is the case, for example, of large fish piscivores (top predators), which once introduced will certainly cause negative impacts on native fish assemblages, even before they become established/invasive in the new environment (Blackburn *et al.* 2011, Cunico and Vitule 2014, Vitule *et al.* 2019, Doria *et al*. 2020).

Different authors (*e.g.*, Wonham *et al*. 2000, Blackburn *et al*. 2011, Olden *et al.* 2021) mention that the invasion process of an non-native exotic species in a new environment includes at least three phases: 1) transport from a native biota to a non-native, through a pathway or dispersion mode; 2) introduction of the non-native species in a new biota and its subsequent survival (establishment stage) through reproduction and adaptation, 3) colonization and accelerated dispersal for the ecosystems adjacent to its introduction (invasion stage). Finally, the accumulation of these invasion processes concludes with great changes in the invaded ecosystems. The main change is the replacement of local biota with non-native species, which occurs when a disturbance promotes the geographic expansion of some "winning" (non-native) species and the geographic reduction or death of other "losing" (native) species (McKinney and Lockwood 1999). This process is what is known as biotic homogenization, in which the similarity between two or more areas, in terms of biological entities, increases over time (Vitule and Pozenato 2012).

Regarding the coastal marine ecosystems of the southeastern Caribbean Sea, in Venezuela, to date at least 29 non-native exotic species have been recorded as established: six algae, one seagrass, two corals, four mollusks, nine crustaceans, one sea squirt and six fishes (Ramírez-Villarroel 2001, Ojasti *et al.* 2001, Barrios 2005, Lasso-Alcalá *et al.* 2011, Ruiz-Allais 2012, Vera *et al.* 2014, Lasso-Alcalá *et al.* 2019, Ruiz-Allais *et al.* 2021). Of the fish species, four have been recorded in estuarine ecosystems, two in marine ecosystems and at least one of freshwater origin, but with strong eurihaline habits, has been documented in estuarine and marine ecosystems (Carvajal 1965, Springer and Gomon 1975, Aguilera and Carvajal 1976, Cervigón 1966, Chung 1990, Nirchio and Pérez 2002, Pezold and Cage 2002, Lasso *et al.* 2004, Lasso-Alcalá *et al.* 2005a,b, 2008a, Lasso-Alcalá and Posada 2010, Lasso-Alcalá *et al.* 2011, 2019, Salazar *et al.* 2019, Cabezas *et al.* 2020). The latter species corresponds to the Mozambique tilapia, *Oreochromis mossambicus* (Peters 1852), which stands out for its capacity and adaptation to colonize coastal marine ecosystems, due to its extraordinary adaptive plasticity (Costa-Pierce *et al.* 2003, Pérez *et al.* 2006).

Native to Southeastern Africa, *Oreochromis mossambicus* has been introduced mainly for aquaculture purposes, but also for aquarism, in about 112 countries, of which, in at least 101 countries (13 from Africa, one from Europe, 25 from Asia, 23 from Oceania and 32 from America including Venezuela), this species has become established with great success (Trewavas 1982, 1983, Welcomme 1988, Canonico *et al.* 2005, Bills 2019, Brosse *et al.* 2021). However, due to its negative effects on native fauna and ecosystems, such as predation, competition, displacement and extinction of native species, changes in the specific composition and trophic structure of communities, generalized loss of biodiversity in the ecosystem, destruction and habitat alteration, hybridization with species of the same or relative genus (only in Africa) and transfer of parasites and diseases (Canonico *et al.* 2005, Cassemiro *et al.* 2018, Wilson 2019), it has been listed as one of the 100 worst invasive alien species in the world (Lowe *et al.* 2004).

In the Caribbean Sea region, the Mozambique tilapia, *Oreochromis mossambicus*, has been formally identified as an non-native introduced and invasive species in continental coastal lagoon systems of the southeast, such as Los Patos, Punta Delgada and Campoma, as well as in the mouths of the Manzanares and Los Bordones rivers, and the coastal waters of the Golfo de Cariaco, in northeastern Venezuela (Aguilera and Carvajal 1976, Chung 1990, Chung and Méndez 1993, Solórzano *et al.* 2001, Nirchio and Pérez 2002, Marín *et al.* 2003, Ruiz *et al.* 2005, Gaspar 2008, Bonilla *et al.* 2010, Salazar *et al.* 2019). Likewise, this species has been recorded in coastal and interior lagoons of some islands in the southern Caribbean Sea, such as Aruba and Curaçao (Debrot 2003; Hulsman *et al.* 2008).

However, in coastal lagoon systems of this Caribbean Sea region, no detailed biological and ecological studies have been carried out to diagnose the consequences of this invasive species on native fish communities and the island estuarine ecosystems. In this context, in order to analyze the negative effects of the invasive species *Oreochromis mossambicus*, on the biota and the ecosystem, and its relationship with the alteration of the habitat, the following objectives were set: 1) to physically (physico-chemically) characterize the ecosystem studied, 2) to assess community parameters such as relative abundance and biomass, frequency of occurrence, Importance Valuation Index, permanence in the ecosystem (ecological residence), habitat use, feeding habits and trophic categorization, 3) to calculate and analyze the variation of ecological indices such as Species richness (S), Diversity (H), Equity (J) and Community Dominance Index (CDI), 4) to analyze the invasion of *O. mossambicus* and its relationship with the conservation status of the fish community and the ecosystem, and 5) to propose recovery measures for the fish community and the estuarine ecosystem.

Material and Methods

Study area

This study was carried out in the coastal marine lagoon adjacent to the City of Juan Griego and the town of Altagracia, called Laguna de Los Mártires, located in the northeast of Isla de Margarita (Venezuela), in the Southeast Caribbean Sea, between 11º 05 '20.45 "/ 11º 05' 36.33" N and 63º 58'21.47 "/63º 57 '41.49" W (Figure 1). It occupies 177 hectares in the lower or estuary sector of the El Toro river micro-basin, with an average depth of 1.5 m (Ramos, 2003). It was declared as a protected figure or Area Under Special Administration Regime (Protective Zone), according to Decreto Presidencial Nº 2.535 of 1.988, due to its importance as a natural resource of high scenic value (República de Venezuela, 1988).

Sampling

For the capture of the organisms and the measurement of the physicochemical parameters, in five stations, monthly diurnal samplings were carried out, from January to December 2006 (Figure 1). The fishing gear used was a cast net, with a radius of two meters and a mesh opening of 2.5 centimeters, with which 10 sets were made per station in each of the months. The captured organisms were stored in properly labeled plastic bags, in portable cellars with ice, and transferred to the Laboratorio de Ictiología, Escuela de Ciencias Aplicadas al Mar (ECAM) of the Universidad de Oriente (UDO), where they were processed. The physicochemical parameters were measured *in situ* at each of the sampling stations, using a YSI model 33 (salinity) and YSI model 57 (dissolved oxygen) probe, as well as a HANNA model HI 9024 pH meter (temperature and pH).

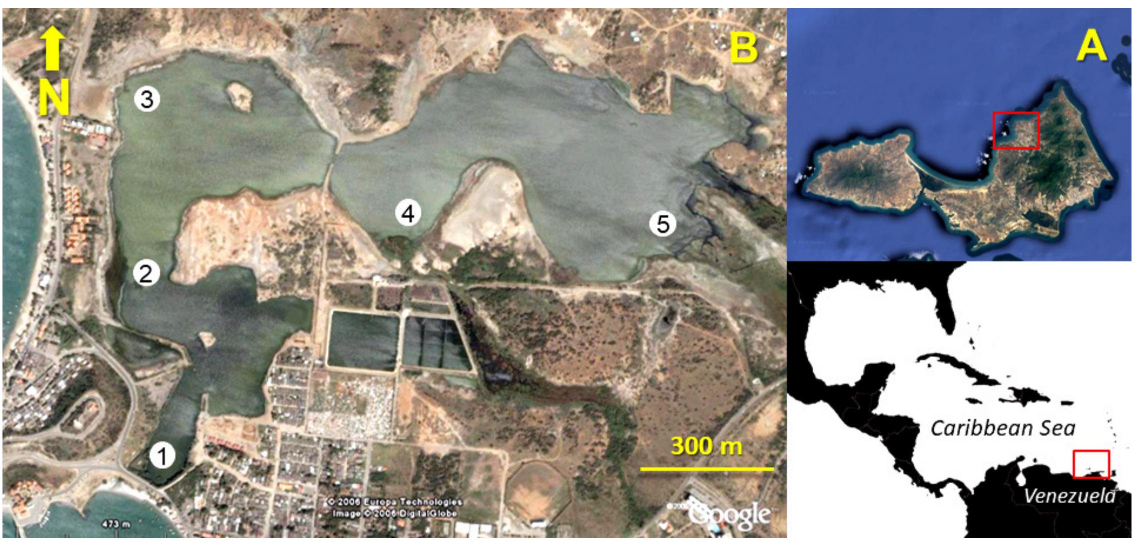

Figure 1. Map of the Southeastern Caribbean Sea (Northeast Venezuela), showing: A) Isla de Margarita, B) Laguna de Los Mártires. The circles (1-5) indicate the locations of samplings. Source: Modified from Google Earth 2006 base map.

Data Analysis

The specimens were identified up to the taxonomic level of the species, through specialized references (Luengo 1970, Román 1978, Trewavas 1982, 1983; Cervigón 1991, 1993, 1994, 1996, Cervigón *et al.* 1992, Skelton 1993, Lasso and Machado-Allison 2000, Lamboj 2004, Lasso-Alcalá and Lasso 2008, Lasso and Sánchez-Duarte 2011), as well as counted, measured and weighed. A reference collection of each of the captured species was fixed and preserved in a 10% formalin solution and deposited in the Fish Collection of the Laboratorio de Ictiología of ECAM-UDO. The classification and systematic order of the species follows Van der Laan *et al*. (2021).

Community parameters such as Relative Abundance (RA: number of specimens), Relative Biomass (RB: weight in grams) and Frequency of Occurrence (FO: Amezcua-Linares and Yánez-Arancibia 1980) were calculated. An Importance Valuation Index (IVI) was calculated, for which the percentage values of RA, RB and FO were added (Lasso *et al.* 2004, 2008, Lasso-Alcalá *et al.* 2008b). Based on the FO of the species in the samplings, the permanence of the species in the studied ecosystem was estimated, following three categories proposed for tropical lagoon estuarine systems: a) permanent residents (FO: > 71%), b) regular visitors (FO: between 31% and 70%) and c) occasional visitors or accidental species (FO: < 31%) (Amezcua-Linares and Yánez-Arancibia 1980). Likewise, ecological indices were determined, such as Species richness (number of species (S) Margalef 1980), Shannon -Wiener Diversity (H) and Equitability or Equity (J) (Browen and Zar 1977, Krebs 1989), as well as the Community Dominance Index (CDI: McNaughton 1968), with the help of the PAST application, version 1.43 (Hammer *et al.* 2001). To determine the existence of significant variation at the spatial and temporal level of the community parameters, at the ecological indices, and of the physicochemical variables, a Kruskall-Wallis contrast analysis was used (Sokal and Rohlf 1995).

The feeding habits of the species were obtained from specialized references (Munro 1967, Randall 1967, Bell-Cross 1976, Infante 1985, Bell-Cross and Minshull 1988, Cervigón 1991, 1993, 1994, 1996, Watson 1996, Allen *et al.* 2002, Lamboj 2004, Weliange and Amarasinghe 2007, Lasso-Alcalá and Lasso 2008, Lasso and Lasso-Alcalá 2011a,b, Lasso and Sánchez-Duarte 2011). The classification into trophic categories follows Yáñez-Arancibia (1978): 1) Primary consumers: this includes planktonphage fish (phyto and zooplankton), detritivores and omnivores that consume detritus, plants and small fauna; 2) Secondary consumers: this includes fish, predominantly carnivores, even though they may include some vegetal material and detritus in their diet, but with little quantitative significance; and 3) Consumers of the third order: includes exclusively carnivorous fish, where plants and detritus are accidental foods.

Some population parameters of the *Oreochromis mossambicus* species were calculated, such as the size structure, the type of growth through a length - weight relationship, and the physiological condition factor. For each individual, the Standard Length (cm), the Total Weight (g), and the sex were determined. The Standard Length and Total Weight of the specimens by sex was related through the relative growth curve $TW = a \times SL^b$ and its logarithmic expression:

Log TW = Log *a* + *b* x Log SL; where the coefficients *a* and *b* are the regression constants.

A Student's t-test analysis was applied to compare the slope "b" according to Sokal and Rohlf (1995) and determine isometry ($b \approx 3$), allometric major ($b > 3$) or minor ($b < 3$) (Ricker 1975). The physiological condition factor (Kr) was calculated by the formula: Kr = TW / W, where TW is the total weight and W the estimated weight (Le Cren 1951). The statistical analysis to establish the relationship between the variables, as well as to detect evidence of significant differences between the sexes, were carried out with the help of the statistical package PAST version 1.43 (Hammer *et al.* 2001).

Results

Physicochemical parameters of the Laguna de Los Mártires

In estuarine ecosystems, salinity is considered the most important physical parameter for its ecological characterization. The general average value of salinity in this ecosystem was 8.55 ± 4.20 PSU. Spatially, an increase of this parameter was observed as the stations got closer to the mouth of the lagoon on the beach of the city of Juan Griego. Due to this, on average, the highest value was found in station 1 (11.55 ± 5.50 PSU), near to the mouth, and the lowest in stations 4 (6.81 ± 2.91 PSU) and 5 (7.10 ± 3.15 PSU), respectively, in the most internal stations of the lagoon. These maximum and minimum values coincided with the temporal variations of September (maximums of 16.53 to 25.00 PSU, stations 2 and 1) and January (minimums of 1.9 to 2.00 PSU, stations 3 and 4) (Figure 2).

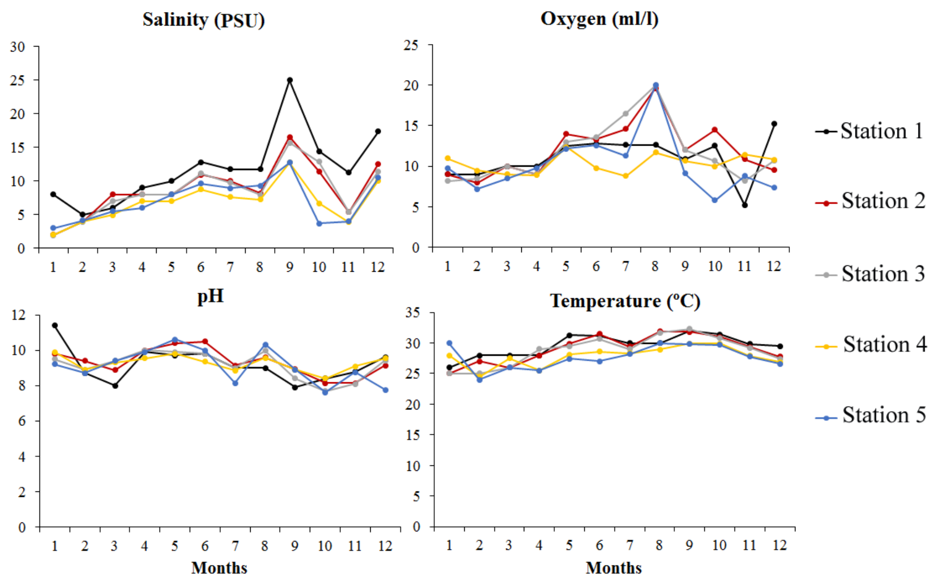

Figure 2. Monthly variation of the physicochemical parameters in the Laguna de Los Mártires, Isla de Margarita, Southeast Caribbean Sea, during January to December 2006.

Regarding dissolved oxygen, the general average was 7.84 ± 2.19 ml/l, ranging between 7.27 ± 0.83 ml/l in station 4 and 8.61 ± 2.34 ml/l in station 2. The lowest values of dissolved oxygen were found during the first months of the year and the highest value (12.08 ± 2.48 ml/l) during the month of August (Figure 2).

The pH of the lagoon was alkaline with a general average value of 9.23 ± 0.79, varying between 9.11 ± 1.13 in station 5 and 9.33 ± 1.13 in station 2. This parameter range from 8.05 ± 0.38 in the month of October, to 10.08 ± 0.40 in the month of May (Figure 2).

Finally, the general average of the water surface temperature was 28.59 ± 2.12 ºC. Between stations it presented a decreasing from station 1 (30.38 ± 1.23 ºC) to station 5 (27.99 ± 1.55 ºC), recording the lowest values during the first quarter of the year, while the highest temperatures occurred during the months of August, September and October (Figure 2).

Species composition and community structure

The effectiveness of the sampling is presented in Figure 3, where the absolute and accumulated frequency of the species captured per month in the Laguna de Los Mártires. According to the 12 standardized samplings carried out in five stations, over a year, the recording of 70% of the species captured in the first three months of 2006 is observed. Then, during six continuous months a period of stability is observed (asymptote of the accumulated curve), where no additional species were captured. However, during the months of October and November, three additional species were captured, for a total of 10 species, stabilizing the curve again as of December. This allows evidence of the inclusion of most of the species present in the study area during that particular year. These species belong to the Class Actinopterygii, with seven orders, nine families and genera respectively (Table 1).

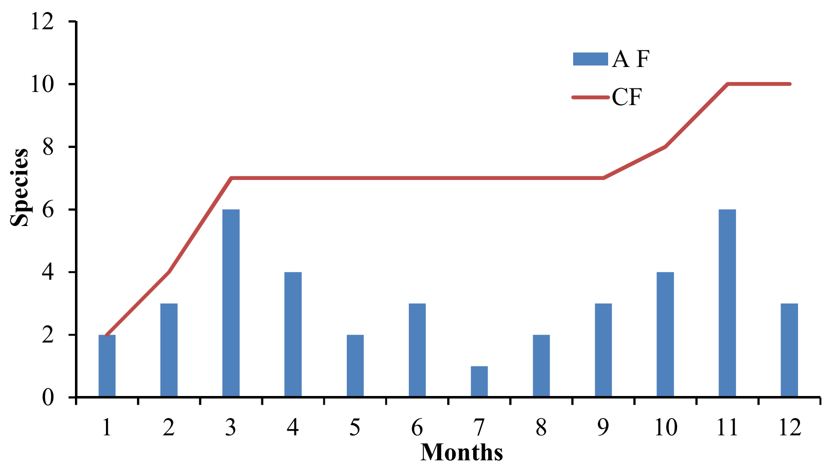

Figure 3. Absolute Frequency (AF) and Cumulative Frequency (CF) of the species captured in the Laguna de Los Mártires, Isla de Margarita, Southeast Caribbean Sea, during January to December 2006.

Table 1. Taxonomic categories, community parameters and ecological aspects of the ichthyofauna in the Laguna de Los Mártires, Isla de Margarita, Southeast Caribbean Sea. The classification and systematic order follows Van der Laan *et al.* (2021). RA: Relative Abundance (%), RB, Relative Biomass (%), FO: Frequency of Occurrence (%). Importance Valuation Index (IVI: RA + RB + FO = 1-300%). Residence Category: PR = Permanent Resident (FO > 71%), OV = Occasional Visitor (FO < 31%). Habitat Use: B = benthic species, P = pelagic species. Feeding Habits: OMN = Omnivore, CAR = Carnivore, HER = Hevibore, DET = Detritivore. Trophic Category: FOC = First Order Consumer, SOC = Second Order Consumer, TOC = Third Order Consumer.

Taxonomic Category	Nº Specimens	RA (%)	Absolute weight (g)	RB (%)	Nº samples	FO (%)	IVI	Residence Category	Habitat Use	Feeding Habits	Trophic Category
Class Actinopterygii											
Order Elopiformes											
Family Elopidae											
Elops saurus Linnaeus 1766	2	0.37	150.7	0.32	1	8.33	9.02	OV	B/P	CAR	TOC
Family Megalopidae											
Megalops atlanticus Valenciennes 1847	30	5.62	11143.28	23.63	9	75	104.25	PR	P	CAR	TOC
Order Aulopiformes											
Family Synodontidae											
Synodus foetens (Linnaeus 1766)	1	0.19	42.6	0.09	1	8.33	8.61	OV	B	CAR	TOC
Order Gobiiformes											
Family Gobiidae											
Awaous banana (Valenciennes 1837)	1	0.19	81.5	0.17	1	8.33	8.69	OV	B	OMN	FOC
Order Carangiformes											
Family Centropomidae											
Centropomus undecimalis (Bloch 1792)	3	0.56	709.9	1.51	2	16.66	18.73	OV	B	CAR	TOC
Centropomus pectinatus Poey 1860	1	0.19	37	0.08	1	8.33	8.6	OV	B	CAR	TOC
Family Achiridae											
Achirus lineatus (Linnaeus 1758)	1	0.19	1.4	0.003	1	8.33	8.52	OV	B	CAR	TOC
Order Cichliformes											
Family Cichlidae											
Oreochromis mossambicus (Peters 1852)	290	39.8	18764.1	54.3	12	100	194.1	PR	B	OMN	FOC
Order Mugiliformes											
Family Mugilidae											
Mugil liza Valenciennes 1836	204	38.2	16215.52	34.39	9	75	147.59	PR	P	HER/DET	FOC
Order Perciformes											
Family Gerreidae											
Eugerres plumieri (Cuvier 1830)	1	0.19	3.7	0.008	1	8.33	8.53	OV	B	CAR/HER	SOC

A total of 535 specimens were captured, which contributed a total of 47,149.78 g of biomass. According to the community parameters of Relative Abundance (39.8%), Relative Biomass (54.3%), and Frequency of Occurrence (100%), the Mozambique tilapia *Oreochromis mossambicus*, was the dominant species in the ichthyofauna of this estuary (Table 1), occupying the first place in terms of the Importance Valuation Index (IVI: 194.1%) of all registered species (Table 1, Figure 4). It is followed in order of importance by the native species *Mugil liza* and *Megalops atlanticus* (IVI: 147.59 and 104.25%), with Relative Abundance (38.2 and 5.62%), Relative Biomass (34.39 and 23.63%), Frequency of Occurrence (75% both cases), always below the *O. mossambicus* (Table 1, Figure 4).

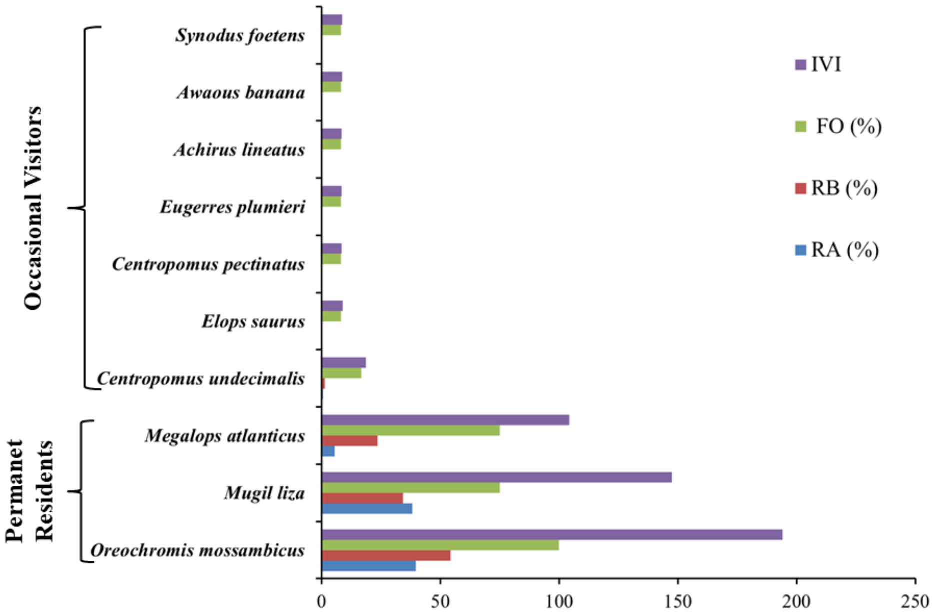

Figure 4. Community parameters of the ichthyofauna in the Laguna de Los Mártires, Isla de Margarita, Southeast of the Caribbean Sea. RA: Relative Abundance (%), RB: Relative Biomass (%), FO: Frequency of Occurrence (%), IVI: Importance Valuation Index (IVI = RA + RB + FO).

Variation of community parameters

Both the Relative Abundance (RA) from the number of captured individuals and the Relative Biomass (RB) did not present statistically significant differences in spatial terms (RA / KW = 7.40; $p > 0.05$; RB / KW = 8.19, $p > 0.05$). However, of these parameters the abundance did present statistically significant temporal differences (RA / KW = 22.85; $p < 0.05$). Despite the dominance throughout the year of *Oreochormis mossambicus* in terms of the community parameters of relative abundance and biomass, the native species *Mugil liza* and *Megalops atlanticus* punctually presented higher abundance values in terms of the number of specimens and biomass, also weight in grams, in April and August respectively (Figure 5). This is mainly due to the differences in the sizes observed between these three species, being lower for *O. mossambicus* (6.9 - 20.8 cm SL), intermediate for *M. liza* (10.5 - 26 cm SL) and higher for *M. altlanticus* (14.5 - 88 cm SL).

Ecological aspects

The Frequency of Occurrence of the species in the samples shows only *Oreochromis mossambicus* as permanent residents, present in all the samples (FO 100%), followed by *Mugil liza* and *Megalops atlanticus*, with percentages of 75%. The latter is due to the fact that these two species were absent during the May (*M. liza*) and July (*M. atlanticus*) samplings respectively (Figure 5). It is worth noting the extremely low values of this parameter in the rest of the species (8.3 to 16.6%), as a result of the capture of just one to three specimens in a whole year of sampling, classifying these species as occasional visitors (OV) or accidental species (Table 1, Figure 4).

Regarding the use of habitat (niche utilization) in Laguna de Los Mártires, 80% of the species were benthic, and only two species were pelagic (Table 1). This composition, as well as the low abundance of native benthic species, confers some interesting implications to this community of fishes (see Discussion section).

On the other hand, species belonging to the three trophic categories indicated for fish communities in lagoon ecosystems were found (Table 1). This was due to the variety of feeding habits of the species, despite the low species richness.

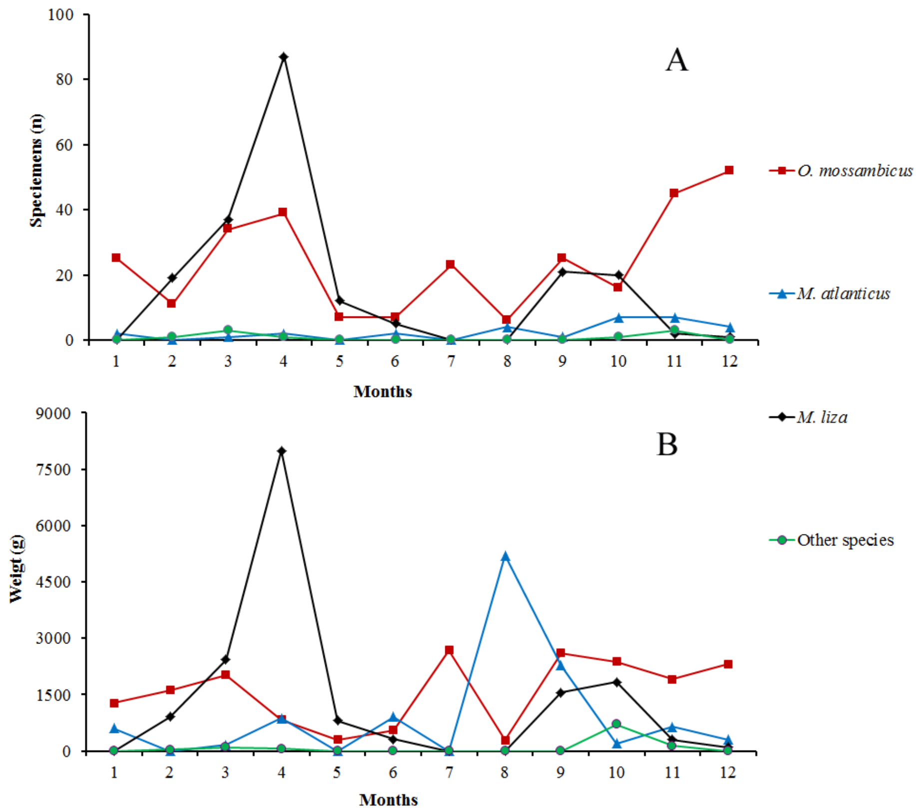

Figure 5. Number of specimens (A) and absolute weight (B), of the species captured in the Laguna de Los Mártires, Isla de Margarita, Southeast Caribbean Sea, during January to December 2006.

In this way, carnivorous species dominated (60%), with extensive consumption on animal organisms, from invertebrates to fish, which classified them as Third Order Consumers. Only two species were classified as First Order Consumers, due to their omnivorous (*Oreochromis mossambicus*) and herbivore / detritivore (*Mugil liza*) feeding habits.

The dominance and influence of *Oreochromis mossambicus* in the fish community of Laguna de Los Mártires is also observed in the behavior of the calculated ecological indices. In general, a significant variation of these indices was only found on a temporal scale, since no significant statistical differences were found on a spatial scale.

The richness (S: number of species) did not present statistically significant differences on a spatial scale (KW = 7.13; p> 0.05). By contrast, on a temporal scale, the variation was of one species in July (*Oreochromis mossambicus*), up to six species in March and November, finding statistically significant differences (KW = 21.99; p < 0.05) (Figure 6).

The monthly average diversity index (H) ranged from 0 bits/ind in July (when 100% of the catch corresponded to *Oreochromis mossambicus*) to 0.94 bits/ind. in September, detecting significant differences only at this time scale (KW = 25.87; p <0.05). The equitability index (J) varied from 0.13 in the month of August to 0.54 in January, the lowest values correspond to those months in which *O. mossambicus* was found as the dominant species. This index varied significantly between months (KW = 25.47; p <0.05). On a spatial scale, no significant differences were found in the diversity indices (H / KW = 4.61; p> 0.05;) and equitability (J / KW = 2.45; p> 0.05) (Figure 6).

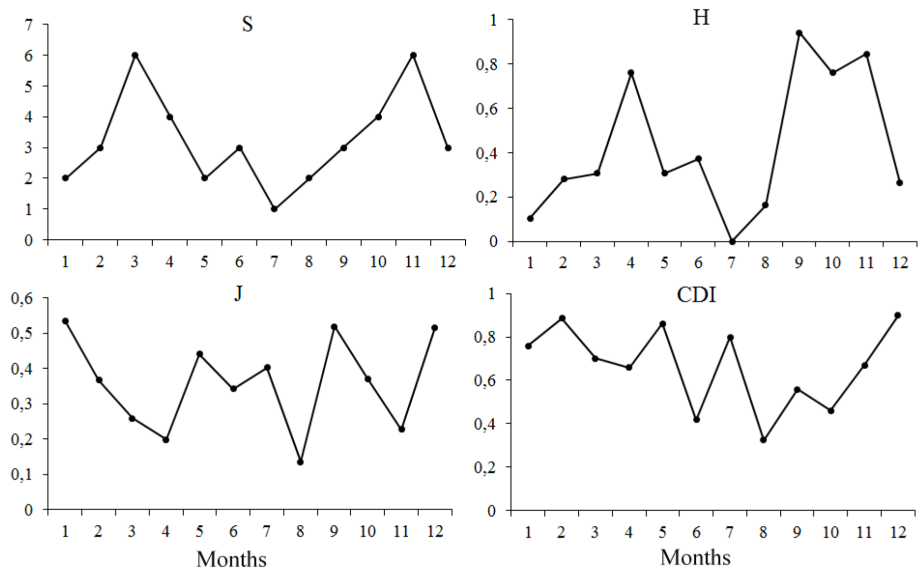

Figure 6. Temporal variation of the ecological indices calculated for the fish community of Laguna de Los Mártires, Isla de Margarita, Southeast Caribbean Sea, during January to December 2006. S: Species richness, H: Diversity, J: Equitability, CDI: Community Dominance Index.

Regarding the average values of the Community Dominance Index (CDI), this had its minimum (0.3), only in the month of August and a maximum (0.9) in December when 91.23% of the total catch in number consisted of specimens of *Oreochromis mossambicus*. As can be seen in Figure 6, this index did not vary significantly between seasons (KW = 2.11; $p > 0.05$), while it did vary between months (KW = 21.1; $p < 0.05$). However, during most of the year (11 months), the CDI presented average values above 0.4, indicators of true community dominance (Goulding *et al.* 1988), exerted by the invasive species *O. mossambicus*.

Population aspects of *Oreochromis mossambicus*

Due to the dominance of *Oreochromis mossambicus* in Laguna de Los Mártires, it is important to show some of its population aspects. Of the 273 individuals captured, 102 were females, 95 males and 76 juveniles or indeterminate, resulting in a sex ratio of 1:1. The Standard Length of the organisms ranged from 6.9 to 20.8 cm, with an average of 11.39 cm. Eight categories or length were established in the population studied. Most outstanding is that 65% of the population (177 specimens), were found within the first three categories of sizes (6 - 12 cm SL). This represents an interesting finding, the implications of which are explained in the Discussion section. Regarding the variation of the sizes during the sampling period (Figure 7), the previous situation became more evident, where it was found that 66% of the specimens captured in the first and second quarter (January to June), and 81% of the specimens in the fourth quarter (October to December) also corresponded to individuals of the first three size classes. A more "normal" distribution of the sizes was found only during the third quarter (July to September), with 70% of the specimens registered between the fourth and seventh category (12 to 20 cm SL) (Figure 7).

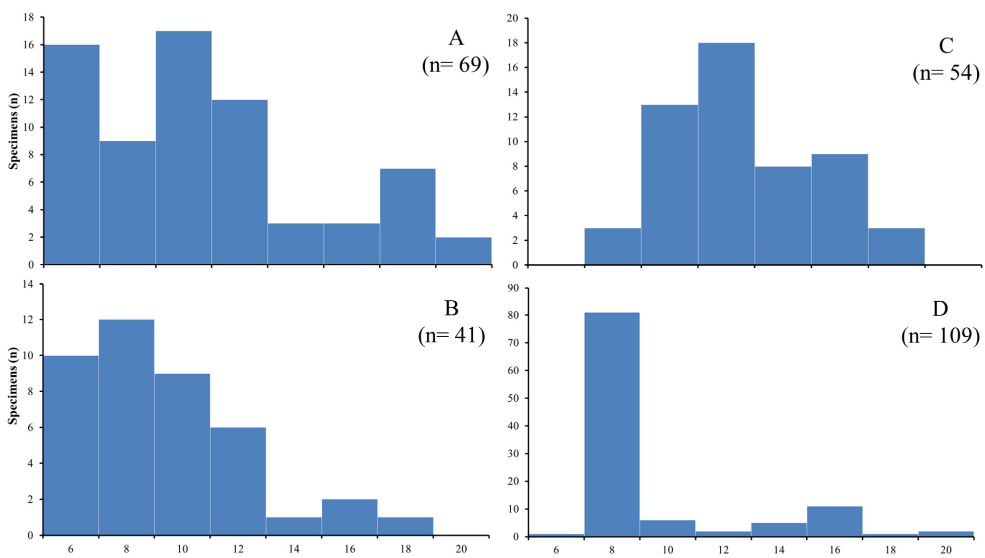

Figure 7. Comparative length frequency distribution of *Oreochromis mossambicus*, in Laguna de Los Mártires, Isla de Margarita, Southeast Caribbean Sea, during 2006. A) January - March, B) April - June, C) July - September, D) October - December

In addition to the description and variation of the sizes described above, the weight of the studied specimens varied between 11.5 and 354.6 g, with an average of 66.11 g. The Student's t-test allowed the detection of statistically significant differences ($p < 0.0001$) in Total Weight and Standard Length between the sexes, with males being larger and heavier than females. Despite this, there was no statistically significant difference between the parameters of the length - weight relationship estimated for each sex separately ($p > 0.05$), so it was possible to establish a common regression equation for both sexes using the equation:
Log TW= -1.2148 + 2.7856 x Log SL ; which corresponds to the model $TW = 0.061 \times SL^{2.7856}$, with a value of $R^2 = 0.9643$ ($P<0.0001$), evidencing a diminishing allometric growth (Figure 8).

Finally, no statistically significant differences were found between the Physiological Condition Factor (Kr) between the sexes ($P > 0.05$), which presented an average value of 100.09% ± 0.04 (Figure 9), which suggests a good physiological condition of the species in the Laguna de Los Mártires.

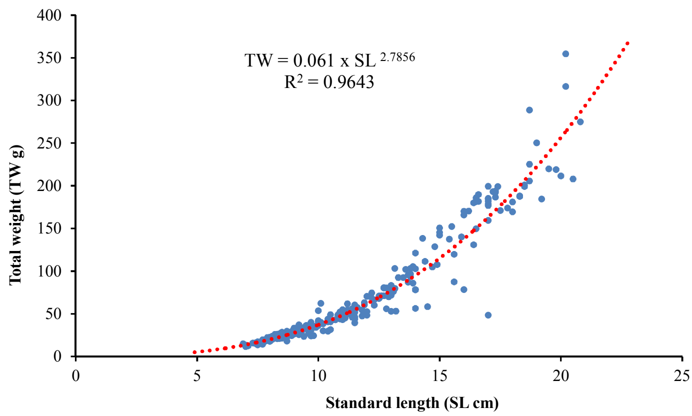

Figure 8. Length-weight relationship of *Oreochromis mossambicus*, in Laguna de Los Mártires, Isla de Margarita, Southeast Caribbean Sea, during January to December 2006.

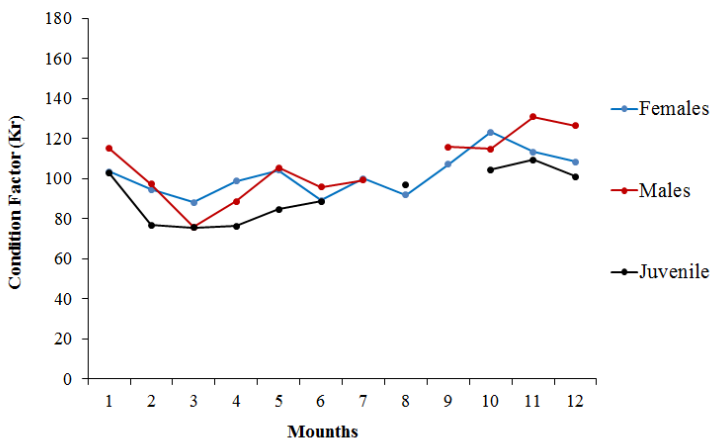

Figure 9. Condition factor (Kr) of *Oreochromis mossambicus*, in Laguna de Los Mártires, Isla de Margarita, Southeast Caribbean Sea, during January to December 2006.

DISCUSSION

There is no doubt that the introduction, establishment and invasion of *Oreochromis mossambicus*, in the Laguna de Los Mártires have a series of implications and consequences, given the biological and ecological characteristics of this species of Cichlidae. Among these are its omnivorous habits that include predation of animal organisms from invertebrates to fish, moderate fecundity but with strong parental care of eggs and young (territorialism), and rapid population growth, among others (Bell-Cross 1976, Trewavas 1982, 1983, Lamboj 2004, Bills 2019); therefore, the ecological consequences that the introduced fish species of this family may have are unpredictable (Lasso-Alcalá *et al*. 2014). However, one of these first consequences found in the present study is the generalized loss of biodiversity in the estuarine ecosystem, due to the displacement and extinction of native species.

The record of only 10 species in the Laguna de Los Mártires corresponds to around 14% of what is expected in similar ecosystems in this region. In the coastal marine lagoons of Isla de Margarita, between 55 and 92 species have been recorded (Cervigón 1966, Salaya 1968, Padrón 1976, Salazar 1978, Gómez 1981, Boadas 1985, Cervigón and Gómez 1986, Jory 1988, Ramírez-Villarroel 1991, 1993, 1994a,b,c, 1996), and 25 species in particular habitats of these lagoons (González and Velázquez 1994) or 12 species in some groups of fish larvae (Esteve *et al.* 2010). This extremely low species richness found in Laguna de Los Mártires, can be compared with another similar ecosystems where *Oreochromis mossambicus* has been introduced. In 1964, 800 specimens were introduced in the coastal system adjacent to the mouth of the Manzanares River, known as Laguna de Los Patos (coast of the Cumaná city, Eastern continental region of Venezuela), with the aim of experimental crops by the Universidad de Oriente (Kahndker 1964; Carvajal 1965; Luengo 1970). Twelve years after this introduction, the displacement or disappearance of 74% of the species of fish and benthic macro-invertebrates previously known for said littoral ecosystem was noted, registering at that time only six species of fish (Aguilera and Carvajal 1976, Jiménez 1977). This low species richness is similar to that found in this study for Laguna de Los Mártires.

Another consequence of the introduction and invasion of *Oreochromis mossambicus*, highlighted in the different studies (*e.g.*, Solórzano *et al*. 2001, Canonico *et al.* 2005, Gutiérrez *et al*. 2012, Cassemiro *et al.* 2018), are the changes in the specific composition and the native community structure, as well as the reduction of the abundance, biomass and frequency of the species. This is clearly observed in the present study, where *O. mossambicus*, presented the highest values of abundance and biomass integrated in the Importance Valuation Index (IVI), of the fish community of the Laguna de Los Mártires. Except for the *Mugil liza* and *Megalops atlanticus* species, 70% of the remaining native species as a whole presented extremely low values of abundance (<2%) and biomass (<3%), clearly indicative of this displacement.

This consequence or displacement of the species is likewise observed if we consider the use of the habitat by the species of this community. In the Laguna de

Los Mártires as in other estuarine ecosystems (*e.g.*, Orinoco River Delta: Lasso *et al.* 2004, 2008, 2009), around 80% of the species have benthic habits (see Table 1). Precisely, the use of the benthic habitat is shared by the invasive species *Oreochromis mossambicus* and the rest of the 70% displaced native species, whose abundance and biomass were extremely low. Only the two native species that managed to obtain the highest abundance and biomass (*Mugil liza* and *Megalops atlanticus*), presented a different habitat use than the invasive species, exploiting the upper sectors of the water column (Table 1: pelagic species). In this way, the competition between these species turned out to be less, with only these two native species being favored or less affected. However, in the Hawaiian Islands, Randall (1987) indicates the reduction of the native species *Mugil cephalus*, due to direct competition with *O. mossambicus* for the same type of food (algae and detritus).

Likewise, the low Frequency of Occurrence of the displaced native species found in the present study (FO: 8.3 to 16.6%), indicates that all the native benthic species were occasional visitors or rare species (Table 1, Figure 4). It is precisely these occasional species that show an increase in the accumulated curve or species saturation (Figure 3). However, under normal conditions, without the effect or dominance of introduced and invasive species, other studies mention the native species found in the present study as permanent residents. Such is the case of *Awaous banana*, resident species of positive or coastal estuaries and rivers (Lasso-Alcalá and Lasso 2008), *Elops saurus, Achirus lineatus* and *Eugerres plumieri*, resident species of positive or negative estuaries of coastal marine lagoons (Mago 1965, Cervigón and Gómez 1986, Jory 1988, Ramírez-Villarroel 1993, 1994a, b, c, 1996, Rodenas and López-Rojas 1993, Esteve *et al.* 2010, Salazar *et al.* 2019), as well as large positive estuaries (Rodríguez 1973, Lasso *et al*. 2004, 2008, 2009, Lasso and Lasso-Alcalá 2011a, Lasso-Alcalá *et al*. 2008b, Sánchez-Duarte and Lasso 2011a, b).

The alterations in the "typical or normal" values of the ecological indices found for the fish community of Laguna de Los Mártires is also clear evidence of the negative effect of the introduction and invasion of *Oreochromis mossambicus*. Margalef (1974), indicates that the diversity of fish communities is usually between 1 and 3.5, while Krebs (1989), indicates that low values of diversity and equitability, such as those found in our study (H: 0 - 0.94; J: 0.13 - 0.54), are clear indicative of disturbances in the ecological conditions of the communities (Cognetti *et al*. 2001). For example, in different coastal lagoons of Isla de Margarita, higher values of diversity and equitability have been found (H: 1.97 - 3.51; J: 0.45 - 1.04), a sign of greater stability and less disturbance due to anthropic activities in those ecosystems, in which introduced and invasive species have not been detected up to now (Ramírez-Villarroel 1991, 1993, 1994a, b, c, 1996). Similarly, the high values found in the Community Dominance Index (CDI: 0.4 - 0.9) of Laguna de Los Mártires during 92% of the sampling year, is a clear indication of the greater influence and dominance of *O. mossambicus* over the native fish community. Average CDI values above 0.4 are indicators of true community dominance (Goulding *et al*. 1988). In other lagoons of Isla de Margarita, high CDI values (0.5 - 0.9) have also been recorded, but in this case, as a result of the dominance of native estuarine species such as *Eucinostomus gula, E. argenteus, Diapterus rhombeus, Eugerres plumieri, Gerres cinereus, Anchoa hepsetus, A. parva, A. trinitatis, Anchovia cluepoides, Cetengraulis edentulus, Lile piquitinga, Archosargus rhomboidalis, Sciades herzbergii, Xenomelaniris brasiliensis, Poecilia vivipara, Strongylura marina* and *Mugil curema* (Gómez 1981, Ramírez-Villarroel 1991, 1993, 1994a, b, c, 1996), all of them absent from the Laguna de Los Mártires fish community.

The success of the invasion of *Oreochromis mossambicus* in the Laguna de Los Mártires is also due to its biological and population characteristics. For example, in this study, we found that 65% of the captured specimens belonged to the first three size categories, between 6 and 12 cm SL. This entire population belongs to juvenile and pre-adult specimens, because the minimum size at sexual maturity for this species ranges between 12 and 15 cm SL (Lévêque 1997, Allen *et al.* 2002). As can be seen in Figure 7, these numerous populations of juveniles and pre-adults (66 to 81%) were recorded during most of the year (January to June and October to December), which shows numerous recruitments due to continuous reproduction. This type of reproduction is well known in this species, which makes the most of the conditions of the environment where it lives (Trewavas 1982, 1983, Lamboj 2004, Canonico *et al.* 2005, Bills 2019). The frequency of spawning varies considerably depending on environmental factors, ranging from five to eight a year, with an ideal temperature between 24 to 34 ºC (Canonico *et al*. 2005, Gutiérrez *et al*. 2012).

Likewise, due to the extraordinary adaptive plasticity of *Oreochromis mossambicus* (Costa-Pierce *et al.* 2003, Pérez *et al*. 2006), their feeding habits vary greatly depending on the type of habitat and food availability, consuming phyto and zooplankton items in juvenile phase, changing its diet to detritus, algae, aquatic plants, invertebrates and small fish items in adult phase (Munro 1967, Bell-Cross 1976, Infante 1985, Bell-Cross and Minshull 1988, Allen *et al.* 2002, Weliange and Amarasinghe 2007). This classifies this species, as a Consumer of the First Order in the Laguna de Los Mártires, only together with the native species *Mugil liza* (Randall 1967, Cervigón 1991), excluding other competitors in the fish community of this ecosystem. In the same way, the availability of plankton, as well as organic detritus is very high in this lagoon, due to a massive enrichment of nutrients in its waters due to the continuous contributions of the wastewater treatment plant of the city and town of Juan Griego and Altagracia. Therefore, the Laguna de Los Mártires has been classified as a mesotrophic ecosystem, with a tendency to generalized eutrophication (Fontanive *et al.* 2010).

The effects of this high availability of food are shown in a high factor of physiological condition (Kr: Figure 9), and a diminishing allometric type rapid growth (Figure 8). The behavior of the condition factor constitutes a valid indicator of the reproductive activity of the species (Le Cren 1951, Prieto *et al.* 2016). Even though this parameter did not show a considerable variation, and taking into account that the population of *Oreocrhomis mossambicus* was composed of 65% juvenile individuals, it is significant that in the month of March, when a high number of individuals of these sizes (60%) was obtained, the condition factor presented the minimum value (Kr: 76% in males and Kr: 88% in females). This trend could be interpreted as the period of sexual conditioning of the population, prior to the beginning of maturity. The speed with which this reproductive process occurs depends on physiological and environmental factors such as temperature and abundance of food (Ayoade and Ukulala 2007), which were high in the Laguna de Los Mártires.

On the other hand, due to its tolerance to large variations in environmental parameters (*e.g.*: temperature, salinity, dissolved oxygen, pH, turbidity, etc.), the Mozambique tilapia has successfully colonized and invaded freshwater lakes, rivers, swamps, estuaries, brackish coastal lagoons, coral atolls, hypersaline desert lakes, and hot springs where it has been introduced worldwide (Trewavas 1983). Likewise, the great capacity and adaptation to colonize coastal marine ecosystems, due to its extraordinary adaptive plasticity (Costa-Pierce *et al.* 2003, Pérez *et al.* 2006), make it very successful as an invasive species. In this way, due to its freshwater origin, it has been classified as a highly euryhaline species (tolerance of 0 to 36 PSU) (Whitfield and Blaber 1979, Trewavas 1983).

The tolerance range to salinity of *Oreochromis mossambicus* described above, coincides with that registered in this study for Laguna de Los Mártires (1.9 to 25 PSU). In our opinion, this is the most important physical characteristic of this coastal lagoon ecosystem, which draws attention powerfully, since the salinity values are below those registered in the adjacent sea (about 36 PSU), therefore the coastal lagoon of Los Mártires would be classified as a positive estuary (Cervigón and Gómez 1986), similar to the mouth of a river in the sea. However, these salinity values radically contrast with those registered in all the coastal marine lagoons of Isla de Margarita (Cervigón and Gómez 1986, Ramírez-Villarroel 1991, 1993, 1994a, b, c, 1996), where the values exceed the salinity of the adjacent sea (36 PSU), and can even reach 56 PSU or higher values. In this way, they are classified as negative or hypersaline estuaries (Cervigón and Gómez 1986). This is due to the fact that the region's climate is characterized by strong aridity, due to the joint action of a very marked dry season (March-June, and August-November), when the oceanographic phenomenon of coastal upwelling, low rainfall (100 - 300 mm), high ambient temperatures (25 - 35 ºC) and relative humidity (75 - 77%), as well as the strong action of the trade winds in a northeast direction (4.0 m/s - 5.0 m/s during drought and 2.0 m / s - 3.0 m/s during rains), which result in high evaporation throughout the year (3,430 mm), exceeding more than 10 times the precipitation (Cervigón and Gómez 1986, Ramírez-Villarroel 1994b, López-Monroy and Troccoli-Ghinaglia 2014; Quintero and Terejova 2016).

However, it is important to note that the classification as a positive estuary of the Laguna de Los Mártires is due to its great anthropic modification or ecological disturbance. During the sampling year (2006), the Laguna de Los Mártires received constant and permanent contributions of freshwater from the adjacent treatment plant, which collects the effluents or sewage from the city of Juan Griego and the town of Altagracia. Likewise, this lagoon also receives freshwater discharges from its hydrographic micro-basin (El Toro river), during two short periods of rain (December - February and July - August) and due to poor communication with the sea, due to a small diurnal tide (+/- 1 m) of a very narrow mouth, sedimented by the coastline of Juan Griego Bay, which also constitutes a temporary water supply. These physical conditions, as well as the sampling method (taking samples or morning measurements in the surface layer of the water), made some physicochemical parameters of this lagoon markedly different from those of the rest of the lagoons of Isla de Margarita. Just to cite one example of this, in the Laguna de Los Mártires, much higher values of dissolved oxygen were obtained (7.27 - 12.08 mg/l), than those registered in the rest of the lagoons of this island, whose normal values are between 2.11 and 4.25 mg/l (Cervigón and Gómez 1986, Ramírez-Villarroel 1993, 1994b, González and Velázquez 1994). In fact, some authors were able to detect higher point values (17.10 mg/l) of dissolved oxygen for the Laguna de Los Mártires (Fuentes *et al.* 2009). This is due to the high biomass or density of phytoplankton organisms present in this lagoon, which provide oxygen to the water body through the photosynthetic process, observed in the field phase of this study and also pointed out by several authors (Brito and Martínez 2008, Fuentes *et al.* 2009, Fontanive *et al.* 2010, Natera *et al.* 2020). However, Natera *et al*. (2020), found oxygen values of 0.21 ml/l, in the area of the mouth of the lagoon, indicative of an anoxic environment, due to the high bacterial decomposition, product of the large accumulation of organic matter in that area.

It is important to mention here that in addition to the influence and dominance of *Oreochromis mossambicus* on the native fish community, there is a synergy between the invasion of this species and the ecological conditions caused by other anthropic impacts in the estuary ecosystem studied. As already mentioned, the Laguna de Los Mártires is the receiver of the water from the treatment plant of the neighboring city of Juan Griego, as well as from the town of Altagracia, and directly from the homes of the city that border most of the perimeter of the lagoon. In turn, it also receives the temporary discharges of the polluted waters of the El Toro river, which crosses other smaller human populations to the city of Juan Griego. This generates conditions of contamination of its waters as reported by some studies, where the values of nutrients such as Nitrite (0.084 mg/l), Nitrate (0.369 mg/l), Ammonium (3.403 mg/l), Phosphate (1.080 mg/l) are very high, and in the same way, Dissolved Solids (39,525 mg/l), pathogenic bacteria such as Total Coliforms (1,100 MPN/100 ml) and Fecal Coliforms (460 MPN/100 ml) and Biochemical Oxygen Demand (67; 71 mg/l). The Laguna de Los Mártires at the time of the samplings of this study (2006), presented strong signs of contamination, which is why it was classified as mesotrophic, and in some sectors eutrophic, with a tendency to generalized eutrophication (Brito and Martínez 2008, Fuentes *et al.* 2009, Fontanive *et al.* 2010, Natera *et al.* 2020).

Anthropic alteration and environmental degradation of ecosystems make them more vulnerable and create ideal conditions for the establishment and invasion of introduced species (Kolar and Lodge 2000, Rahel and Olden 2008, Lozon and MacIsaac 2011, Früh *et al.* 2012, Sorte *et al*. 2013, Havel *et al.* 2015). This is called invasive meltdown, which can be defined as a community-level phenomenon, in which the net effect of ecosystem alterations facilitates an increasing rate of establishment of introduced species, as well as their accelerated impact (Simberloff 2006), and has been well studied in aquatic organisms (Braga 2018, 2020).

In addition to the case recorded in the present study, some other examples exist of the relationship between the alteration of ecosystems and invasive species that we can cite in the southern region of the Caribbean Sea and nearby regions. A well-known and previously detailed case is that of the introduction and invasion of *Oreochromis mossambicus* in the Laguna de Los Patos, in Venezuela (Kahndker 1964; Carvajal 1965; Luengo 1970 Aguilera and Carvajal 1976, Jiménez 1977). This ecosystem, being currently located within the urban area of the Cumaná city, receives several sources of contamination from its sewage, as well as its habitat has been strongly altered or modified during the last decades (Toledo *et al.* 2000, Pérez *et al.* 2003, Senior *et al.* 2004, 2005, Torcatt 2015, Salazar *et al.* 2018, 2019). This created the favorable conditions for the establishment of new species of introduced fish, such as the translocated Cichlidae *Caquetaia kraussii* and *Crenicichla geayi* (Senior *et al.* 2004, Salazar *et al.* 2007, 2018), both predatory and piscivorous species (Royero and Lasso 1992, Señaris and Lasso 1993, Lasso and Machado-Allison 2000).

In another estuary off the coast of Venezuela, the muzzled blenny *Omobranchus punctatus*, a native species of the Indian and western Pacific oceans, was recorded as introduced (Springer and Gomon 1975, Lasso-Alcalá *et al.* 2008a, 2011, Cabezas *et al.* 2020). This species was registered as invasive on a rocky beach in the Orinoco River Delta, affected by a natural oil flow (permanent oil discharges), as well as wastewater discharges of Pedernales village (Lasso *et al* 2004, Lasso-Alcalá and Lasso 2011). Later, two other introduced species, originating from the Indo Pacific and Gulf of Mexico, were also recorded in the same region, the mud sleeper *Butis koilomatodon* and the naked goby *Gobiosoma bosc* (Lasso-Alcalá *et al.* 2005a, b, Lasso and Lasso-Alcalá 2011c, d).

We must not forget that the consequences of the introduction and invasion of *Oreochromis mossambicus* on biodiversity and native ecosystems include the transmission of parasites and other diseases. In one of the latest reviews made on this topic, Wilson (2019) detected the presence of at least 38 species or morphotypes of parasites in native and exotic populations, in 14 countries where *O. mossambicus* has been introduced, suggesting transmission and co-evolution of parasite species. Some of these groups belong to the protozoan (Oligohymenophorea), of the genus *Trichodina*, with species from Africa, Taiwan, the Philippines, Israel, Vietnam and Australia. Specimens of this genus, along with metacercariae of a flatworm from the *Ascocotyle* complex, were recorded in specimens of *O. mossambicus* from Laguna de Los Mártires (Moreno 2006), and the question remains whether these populations of parasites are of native or exotic origin. The biological cycle of *Trichodina* and *Ascocotyle* includes higher organisms such as mammals (Ebert *et al.* 2021). This can have serious implications (zoonosis) for human health, since *O. mossambicus* is captured and consumed locally by the inhabitants of the neighboring city communities of Laguna de Los Mártires. On the other hand, protozoa of the genus *Trichodina* are indicators of poor quality or low health status of aquatic ecosystems, proliferating in eutrophic ecosystems with high bacterial loads (as in the Laguna de Los Mártires), causing an increase in levels of infestation and pathogenesis in fish and other organisms (Zanolo and Yamamura 2006, Fernandes *et al.* 2011).

Finally, we recommend a series of actions to reverse the impact of *Oreochromis mossambicus* on the Laguna de Los Mártires ichthyofauna. These are the monitoring and systematic extraction campaigns of the population of this invasive species in the lagoon and its hydrographic basin (El Toro River). Sanitation works, such as the dredging of the mouth of the lagoon, rechanneling of the sewage to it and the tributary river, as well as improvements in the operation of the wastewater treatment plant of the city adjacent to the lagoon, must be carried out in order to improve the environmental conditions of this ecosystem and the consequent recovery of the native fish community.

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Eliaira Rodríguez [1], Ernesto Ron [2], Iván Mikolji [3], José L. Fuentes [4]

Oscar M. Lasso-Alcalá [3*]

[1] Dirección de Energía y Ambiente, Fundación de Estudios Avanzados IDEA, Valle de Sartenejas, Estado Miranda, Venezuela.

[2] Laboratorio de Ictiología, Escuela de Ciencias Aplicadas del Mar, Universidad de Oriente, Boca del Río, Estado Nueva Esparta, Venezuela.

[3] Museo de Historia Natural La Salle, Fundación La Salle de Ciencias Naturales, Caracas, Venezuela.

[4] Centro Regional de Investigaciones Ambientales, Universidad de Oriente, Guatamare. Estado Nueva Esparta. Venezuela.

* Corresponding author: oscar.lasso@gmail.com oscar.lasso1@fundacionlasalle.org.ve