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# Unraveling the complex habitat use of white mullet *Mugil curema* of several environments from Neotropical Pacific and Atlantic waters

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**Abstract**

The white mullet *Mugil curema* is a widely distributed euryhaline species, whose migratory behavior is poorly understood. The objective of this work was to study large-scale habitat use of this species for the first time, considering several environments such as euryhaline and hypersaline lagoons, sea, and a river, distributed in the central Pacific (México) and Atlantic (Gulf of México, Caribbean Sea-Venezuela, and Northeast of Brazil). Otolith core-to-edge Sr/Ca ratios of 161 fish, determined by laser ablation inductively coupled plasma mass spectrometry, were used to study the salinity-habitat migration history. Fish from México (Tamiahua Lagoon, N=4; Alvarado Lagoon, N=2), Venezuela (N=1), and Brazil (N=10) (10.6% of the total) showed high Sr/Ca values at the beginning of the transects and were classified as marine migrants. Two specimens (Alvarado Lagoon and Balsas River, México) showed Sr/Ca values consistently below high salinity guide value (salinity<33.5). In the rest of the fish (88.1%), the Sr/Ca suggested a displacement from the estuary towards the sea or hypersaline environments, so they were classified as estuarine migrants. A change point analysis identified six individuals with a single stable Sr/Ca signature (SSS) through ontogeny (3 for Brazil, 1 for Venezuela, and 2 for Tamiahua Lagoon), suggesting limited displacement between environments with different salinity. The rest of the individuals showed between 2 and 10 SSSs (mean= 4.07±1.85). The highest number of SSS (4.87±1.1) was found in Laguna Madre Fish (México) and the lowest in Brazil (3.27±1.70) (H=19.8, p=0.002). Otolith Sr/Ca time-series suggested a highly plastic migration behavior for *M. curema*, where the marine and estuarine migratory were the most common ones. This work revealed that the sustainable use of *M. curema* depends on the conservation of the corridors between river, estuary, mangrove and sea.

**Keywords: catadromous, diadromous, LA-ICP-MS, life history, migration, mugilidae, otolith microchemistry,**

## 1. Introduction

The study of life history in diadromous fish is crucial for the understanding habitat use and migration behavior, so as to generate proper conservation and management regulations for species and used areas (Beck et al., 2001; Jenkins et al., 2010; Wynne, Wilson & Limburg, 2015). Different methods have been applied to study movements and habitat selection of fish such as mark-recapture, and the chemical composition of calcified structures like otolith, spines and scales (Avigliano et al., 2017; Clarke, Telmer & Mark Shrimpton, 2007; Clément et al., 2014; Raabe & Gardner, 2013). In particular, the study of features in otoliths has facilitated not only the study of fish movements and migrations but also the stock identification of important commercial species (Biolé et al., 2019; Lemos et al., 2017; Soeth et al., 2019). Elemental deposition in the otolith is influenced by physiological and environmental factors, most particularly by the concentration of elements in the surrounding water (Avigliano, et al., 2019; Thomas & Swearer, 2019). The chemicals deposited represent a permanent record of the environmental conditions experienced by the fish at a particular time; therefore, they can be used to reconstruct their environmental migratory patterns and habitat use (Campana, et al., 2000). Different elemental ratios have been used to study displacements between environments with different salinities, being Sr/Ca the most used (Avigliano et al., 2017; Avigliano, Miller & Volpedo, 2018; Elsdon & Gillanders, 2005). Specially in diadromous fishes, the Sr/Ca ratio in otolith and water has been shown to be positively correlated to the salinity, thus having a strong association to marine environments (Avigliano, & Volpedo, 2013; Kraus & Secor, 2004; Tabouret et al., 2010). As a result, otolith Sr/Ca ratio has been used in a large number of studies worldwide to reveal movements of diadromous species through salinity gradients (Arai & Chino, 2017; Avigliano et al., 2018; Brown, & Severin, 2009; Chang, Lin, et al., 2004).

The white mullet *Mugil curema* Valenciennes 1836, is a widely distributed species from the Mugilidae family that inhabits the Atlantic Ocean (from Nova Scotia to Argentina in the east, from Gambia to the Congo in the west coast of Africa), and the eastern Pacific Ocean (from the Gulf of

California to Northern Chile) (Crosetti et al. 2016; Froese and Pauly 2019). This euryhaline mugilidae species is thought to spawn offshore and its larvae to migrate from the sea to estuarine water, especially in mangrove habitat, until reaching sexual maturity (Barletta & Dantas, 2016; da Silva et al., 2018). Some authors have studied this species because of its important economic value as a commercial species and in aquaculture, from Brazil all through the Caribbean (Ibañez-Aguirre 1996; Marin et al. 2003; Ibáñez et al. 2012; Avigliano et al. 2015; Ibáñez et al. 2017; Mai *et al.*, 2018; Santana *et al.*, 2018). Santana *et al.* (2018) have found a positive relationship between otolith Sr/Ca and salinity for *M. curema* and have studied the life history of fish from a small estuary in northeast Brazil. Moreover, Ibañez et al. (2012) have revealed migratory patterns of *M. curema* in three sampling sites from the Mexican Atlantic coast using Sr/Ca, while Mai et al. (2018) have used Ba/Ca to study displacements in southeast Brazil. These studies reported some plasticity in the previously known life history migratory behavior of the species. However, they have focused on few specimens (Mai *et al.*, 2018, N=32; Ibáñez *et al.*, 2012, N=40; Santana *et al.*, 2018, N=23) and local estuarine systems, and there is no previous evidence of the habitat use through ontogeny in hypersaline, Pacific ocean or Caribbean sea environments; therefore, migratory patterns are not fully understood. This information is necessary because the first step to generate conservation and management strategies at the ecoregional-scale is to know the use of the habitat and identify the sites that must be managed (Beck & Odaya, 2001).

The objective of this study was to unravel for the first time the habitat use of *M. curema* from a wide range of environments and distribution in Pacific and Atlantic waters using otolith core-to-edge Sr/Ca time-series. For this purpose, otolith core-to-edge Sr/Ca time-series were analyzed in fish of euryaline and hypersaline lagoons, beaches, and a river from the Gulf of México (México), Caribbean Sea (Venezuela), neotropical Atlantic (Brazil) and neotropical Pacific (México) coasts.

## 2. Materials and methods

### 2.1. Sample collection and preparation

Adult *M. curema* (N=161, Table 1), were collected between November 2009 and July 2011 using trammel nets from the Gulf of México, Pacific coast, and Caribbean Sea, and gill nets from Southwestern Atlantic (Figure 1). Fish were caught from Mecoacan, Alvarado, Tamiahua and Laguna Madre lagoons (Gulf of México, México, Atlantic Ocean), Balsas River (México, Pacific Ocean), Nueva Esparta State (Margarita Island, Venezuela, Caribbean Sea), and Northeast coast of Brazil (Alagoas state, Atlantic Ocean) (Table 1). The Balsas River is the major river from south-central México and drains at an average height of 1,000 m.a.s.l. and covers a total area of 117,400 $km^2$. Laguna Madre is a long, shallow, and hypersaline lagoon (salinity up to 63.0), while Mecoacán and Alvarado are shallow coastal lagoon systems dominated by mangroves (Contreras & Castañeda, 2004). The Tamiahua Lagoon is a polyhaline water body surrounded by mangroves (Contreras & Castañeda, 2004). The Margarita Island and Brazil sampling sites correspond to sandy coastal beaches with great oceanic influence (Astor & Cárdenas, 1997). The features of the sampled environments are shown in Table 1.

The mullets were identified with the taxonomic keys of Harrison (2002) and Harrison et al. (2007), and using microsatellites markers (Pacheco-Almanzar, Loza-Estrada & Ibáñez, 2020). Fish were measured, and the *sagittae* otoliths were extracted. Right otoliths were weighted, decontaminated with 2% $HNO_3$, rinsed three times with ultrapure water (resistivity of 18 MΩ/cm), and embedded in crystal epoxy resin. Samples were sectioned transversely through the core using a Buehler Isomet low speed saw (Hong Kong, China). To reduce the effect of growth on the interpretations, samples were selected according to size and similar age (Table 1). Age was estimated using the annual growth ring count method, observing the sections of the otoliths immersed in ultrapure water. The age validation by the ring count in otoliths of *M. curema* from the Caribbean Sea was validated by Ibañez-Aguirre & Gallardo-Cabello (1996). The selected samples were fixed to glass slides with epoxy resin, individually polished using a decreasing gradient of sandpaper (from 9 to 3 µm-grit), rinsed with ultrapure water, and sonicated for 10 min (Avigliano, et al., 2019).

**2.2. Chemical analysis**

The elements $^{43}Ca$, and $^{88}Sr$ were quantified from core to edge in scan mode (Figure 2) by Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS) using a 193 nm ArF Excimer laser (Photon Machines Analyte G2, USA) coupled to an ICP-QMS Agilent 7700 (Japan).

Samples were measured during three analytical sessions using a laser-induced spot size of ∅40 µm at 5 µm/s, at a laser fluence of 3.75 $J/cm^2$ and a repetition rate of 10 Hz. Helium was used as carrier gas (0.8 l/min) in the ablation cell, and argon was also added (0.9 l/min) before entering the ICP which was operated at 1600 W. The $^{238}U/^{232}Th$ (~1.2) and $^{232}Th^{16}O/^{232}Th$ (<0.4 %) ratios were monitored on the reference material NIST 612 (trace elements in glass, National Institute of Standards and Technology, NIST, USA) to check plasma robustness and oxide production rates, respectively. The standard reference materials NIST612, NIST610 (trace elements in silicate glass) and MACS-3 (trace elements in synthetic calcium carbonate, USGS, USA), were run in triplicate at the beginning and at the end of the each analytical session (in triplicate) and also every 10 transects for drift monitoring. To convert elemental signals to concentrations, NIST612 and Ca (38.3% weight, Yoshinaga *et al*., 2000) were used as calibration and internal standards, respectively. Strontium recovery rates base on NIST610 and MACS-3 (Jochum et al., 2011; Pearce et al., 1997) ranged from 101 to 105%. The relative standard deviation percentage of quadruplicate analysis of NIST610 and MACS-3 was below 3.5%. Strontium concentrations were expressed in relation to Ca (mmol/mol).

**2.3. Data analysis and interpretation**

Migratory patterns were described according to the use of environments with different salinities using the otolith Sr/Ca as a salinity proxy, as suggested by Ibáñez *et al.* (2012) and Santana *et al.* (2018). The positive relationships among *M. curema* otolith Sr/Ca and salinity were previously validated by Santana *et al.* (2018). Due to the lack of relationship between Ba/Ca and salinity found in pilot analysis, only the Sr/Ca ratio was used as a salinity proxy.

To assess if the changes among Sr/Ca signatures through ontogeny were significant, Change-Point analyzes (CPA) were performed (Avigliano et al., 2017, 2018). This analysis uses a combination of cumulative sum charts and bootstrapping to identify significant changes in stable Sr/Ca signatures (SSS) across chemical time-series. The analyses were performed using 95% confidence and 95% confidence levels. To assess spatial differences in the number of stable signatures experienced throughout life, SSS was compared between sampling sites using Kruskal Wallis test. Because potential differences in growth between individuals could be associated with the number of SSS thus affecting Kruscal Wallis' results, Spearman's correlation tests were performed to assess the relationship of SSS with fish size and age.



Several authors have used transition Sr/Ca thresholds, based on experimental or field observations, to identify changes between freshwater, estuarine, and marine habitats (Avigliano et al., 2017; Fowler et al., 2016; Wang, 2014). Santana *et al.* (2018) have proposed transition thresholds for estuarine use based on the otolith Sr/Ca ratio of the early stages from wild adult *M. curema* ($5x10^{-3}$-$7.4x10^{-3}$ ppm/ppm, ~2.29-3.38 mmol/mol). However, the authors showed no direct evidence that assures the estuarine location in the early stage of these fish, and the estuarine salinities are not defined either. In this sense, it is not clear what the range of salinities represented by that threshold is. For this reason, these environmental transitional thresholds were not used. Instead, the mean Sr/Ca ± twice standard deviation (mean±2SD) of the otolith edge, which represents approximately the catch environment, from fish caught at Brazilian sea (salinity=33.5, N=32) was plotted with the core-to-edge Sr/Ca series as an approximate guide value for high salinity use (GHS). This approach was previously employed for several diadromous species such as *Genidens barbus* (Avigliano et al., 2017), *Anguilla anguilla* (Tabouret et al., 2010), *A. mossambica* (Lin et al., 2014), among others.

Fish were classified as marine migrant, estuarine migrant and estuarine resident according to Elliott *et al.* (2007). Use of the high salinity environments (salinity≥33.5, for example open sea and hypersaline lagoons) was considered as when the stable signatures of Sr/Ca were within or above the GHS. Therefore, marine migrants are fish that spawn at sea and often enter estuaries, estuarine migrant fish have larval stages in the estuary and often move to sea, and estuarine resident fish complete the entire life cycle within the estuarine environment (Elliott et al., 2007).

To know the position of the rings along the ablation transect, the otolith sections were immersed in water and photographed after ablation analysis to observe the ablation line. The position of the rings was determined on the images using the Image-Pro Plus 4.5 software.

Finally, core-to-edge Sr/Ca transects, GHS and CPA results were plotted together in order to facilitate the interpretation of fish movements through their life time.



## 3. Results

### 3.1. Otolith edge

The mean Sr/Ca±SD based on otolith edge from fish caught at sea (N=32) was 4.01±0.32 mmol/mol, then the GHS (mean±2SD) range was 3.46-4.75 mmol/mol. All Sr/Ca values of the otolith edge from fish caught at salinity 33.5 were included within that range.

Core-to-edge Sr/Ca ratio ranged from 1.37 to 8.40 mmol/mol, where lowest levels were observed in Alvarado and Balsas River (e.g. Figure 3a and c), while the highest in Laguna Madre (e.g. Figure 4i and j).

Only two specimens (Alvarado Lagoon and Balsas River) showed Sr/Ca values consistently below GHS (Figure 3a and b), representing the 5% of the total for these sampling sites. These individuals were considered estuarine resident (Figure 1).

Around 10.6% of all individuals (N=17) showed Sr/Ca values above GHS at the beginning of the transects, being after both below and within (or even above) the GHS (Figure 3c-h) and so classified as marine migrants. These specimens were caught from Tamiahua (N=4), Alvarado (N=2), Margarita Island (N=1), and Brazil (N=10), representing the 20.0%, 10.5%, 9.5%, 18.5%, respectively, of total of each site.

The rest of the specimens (N=141, 88.1% of the total) showed values below GHS at the beginning of the life (Figure 4), and after that, presented values within or above GHS range, suggesting a shift from relatively lower to higher salinities; therefore, they were classified as estuarine migrants. The spatial distribution of estuarine migrant individuals was 100% for Laguna Madre, 80% for Tamiahua, 84.5% for Alvarado, 100% for Mecoacán, 95% for Balsas River, 90.5% for Margarita Island, and 81.5% for Brazil (Figure 1). With these specimens, the individuals with relatively low chemical signatures in the otolith core reached 89.4% of the total sample (estuarine migrant plus estuarine resident).

Regarding age, it was observed that the first movement between high (GHS) and moderate (e.g. estuary) salinity environments of estuarine and marine migrant fish occurred within the first year of life (except for one specimen, Figure 4b), after which no apparent migration patterns were observed in relation to age.

According to the correlation analyzes, no significant relationship was found between the SSS (r=0.07, p=0.7) and age or total size (r=0.2, p=0.6). With a confidence interval of 95%, the CPA identified six individuals with a single stable Sr/Ca signature (e.g. Figure 3f) through ontogeny (N=3 from Brazil, N=1 from Margarita Island, and N=2 from Tamiahua Lagoon). The rest of the individuals showed between 2 and 10 Sr/Ca stable signatures (Figure 3 and 4), with a global mean of

4.07±1.85. According to the Kruskal Wallis test ($H=19.8$, $p=0.002$), the highest number of Sr/Ca stable signatures was found in Laguna Madre fish (4.87±1.1) and the lowest in Brazil (3.27±1.70) (Figure 5). Intermediate mean values were found in the rest of the catch stations (Figure 5).

## 4. Discussion

### 4.1. Otolith chemistry as a salinity proxy

Otolith edge Sr/Ca ratio showed an increase in relation to salinity, as reported by Santana *et al.* (2018) for *M. curema* from northeast Brazil, and by several studies based on other mugilids such as *M. cephalus* caught in Taiwan (Chang, Iizuka & Tzeng, 2004; Chang, Lin, et al., 2004; Wang et al., 2010) and Australia (Fowler et al., 2016), and *M. liza* from Argentina and Brazil (Callicó Fortunato et al., 2017).

On the other hand, Ba/Ca turned out to be a good indicator of salinity for some species (Elsdon & Gillanders, 2005), but this does not appear to be the case for mugilids in general, where the relationship between Ba/Ca and environment is not fully understood. Specifically, Wang (2014) and Wang et al. (2010) have reported high otolith Ba/Ca levels for freshwater *M. cephalus* from Taiwan (e.g. Tanshui River), suggesting that this ratio may be useful as a freshwater marker. In addition, Wang *et al.* (2011) and Fowler *et al.* (2016) have reported a weak relationship between otolith Ba/Ca and Sr/Ca in *M. cephalus*. Wang *et al.* (2011) have reported a poor linear relationship (regression analysis, $r^2 = 0.058$), while Fowler *et al.* (2016) have informed a better fit (exponential fit, $r<0.6$), but have used a sampling size of 8,662 points. These analyses were based on all core-to-edge transect values, then, the significant results probably can be explained by the high number of points included in the analysis, rather than by a real relationship between both ratios. For *M. curema*, the use of otolith Ba/Ca ratio as a salinity proxy has not been directly validated. Mai et al. (2018) have classified *M. curema* from a relatively small estuary of southeastern Brazil as a marine migrant species by using otolith Ba/Ca. These authors stated that they used Ba/Ca because the Sr/Ca ratio fluctuated among individuals and a directional trend throughout the otolith transect was not clear (Ba/Ca patterns also looked abnormally variable). Moreover, they suggested that, in species that experience salinities from 20 to 35, the Sr/Ca ratio has limited ability to distinguish movements among habitats. For *M. curema* (this study, Ibáñez *et al.*, 2012, and Santana *et al.,* 2018), *M. cephalus* (e.g. Wang *et al.*, 2010; Wang, 2014; Fowler *et al.*, 2016) and *M. liza* (e.g. Callicó Fortunato *et al.*, 2017), Sr/Ca did not behave as described by Mai *et al.* (2018), suggesting that these observations could be due to analytical issues rather than intrinsic patterns of the species.

Chang et al. (2004b) have suggested reference values for marine, freshwater and environmental use of *M. cephalus*, based on otolith Sr/Ca ranges ($3\times10^{-3}$ to $7\times10^{-3}$ ppm/ppm for estuarine water use, and those above or below corresponded to seawater and freshwater use, respectively). Some authors (Ibáñez et al., 2012; Mai et al., 2018) have assumed that these thresholds are the same for other mugilids species like *M. curema*, which could lead to an error in the classifications of habitat use because the incorporation rate of trace elements into the otolith is species-dependent. Even the incorporation rate can vary within the same species, responding to genetic factors (Clarke, Conover & Thorrold, 2011). To give some examples on other euryhaline fishes, Sr/Ca thresholds (estuarine use) between 3.3–6.4 mmol/mol have been estimated for *M. cephalus* (Fowler et al., 2016), 4.2–6.4 mmol/mol for *Zenarchopterus dunckeri* (Kanai et al., 2014), ~2.3–4.2 mmol/mol for *Osmerus mordax* (Bradbury, Campana & Bentzen, 2008), and 3.75–5.98 mmol/mol for *G. barbus* (Avigliano et al., 2017). To avoid adding confusion to the interpretations, a transition threshold was not used for *M. curema* because of the lack of validation in relation to the use of known salinities. Instead, a Sr/Ca guide value (3.46-4.75 mmol/mol) for high salinity environments (salinity=33.5) was used as an aid for the interpretations. The minimum Sr/Ca value found in the present study for use of the high salinity water (3.46 mmol/mol) was remarkably comparable to the maximum ratio (3.38 mmol/mol, relative difference of 2.3%) for estuarine use estimated by Santana *et al.* (2018), suggesting that both guide values are reliable. Finally, as it happened in previous studies (Ibáñez et al., 2012; Santana et al., 2018), here it was not possible to distinguish the use of environments with salinities greater than the marine ones, because the Sr/Ca signatures compatible with salinities higher than 33.5 were classified within the same category. This could confuse ocean incursions with the use of other environments with marine-like salinity (mangroves, lagoons, among others) or even higher like hypersaline lagoons.

### 4.2. Core Sr/Ca as a potential spawning area indicator

A typical concern in the interpretation of diadromous fish core-to-edge chemical time-series is to assume that the incorporation of elements into otolith only varies with salinity. However, this may not be the case for all species, especially in otolith core (Kalish, 1990; Liberoff et al., 2014; Volk et al., 2000), which would be reflected in a misinterpretation regarding the classification of spawning environments. In some species, the yolk-feeding could influence the Sr incorporation into the core, phenomenon known as "maternal effect" (Kalish, 1990). The maternal effect was observed mainly in salmonids (e.g. *Oncorhynchus mykiss* and *Salmo trutta*) (Kalish, 1990; Liberoff et al., 2014; Volk et al., 2000), which exhibit high egg diameter (>3 mm), long egg duration (30–170 days), and long yolk-feeding period (> 2 weeks) (Lowe et al., 2012). In those cases, the chemistry of the larval otolith core is influenced by the environment where the mother hydrated the eggs, and not by spawning site. Nevertheless, unlike salmonids, *M. curema* has smaller egg diameter (0.46-0.9 mm, Marin *et al.*, 2000), short incubation period prior to hatching (40 hs, Willam, 1957), and a short yolk-feeding periods of 3.5 days (Houde et al., 1976), which represent an otolith diameter of ~60 µm (Radtke, 1984). In this regard, it was assumed that in this species there is no significant maternal effect at the binning of the Sr/Ca time-series, and if it exists could be imperceptible due to the size of the laser ablation spot used (40 µm).

Historically, it was assumed that *M. curema* had a catadromous reproductive behavior, where generally spawns at sea, and the eggs and larvae are carried by the currents to coastal environments (Moore, 1974). In the last two decades, it was reported that the white mullet spawns in mangles and coastal lagoons, and could use brackish environments most of its life (Ibáñez et al., 2012; Marin et al., 2000, 2003; Santana et al., 2018). Here, when the beginning of the transects was analyzed, the 10.6% of the fish showed a Sr/Ca signatures that overlapped with the GHS range, while the remaining specimens showed values were below GHS (89.4%; total sampling size, Nt=161), suggesting that the spawning occurs mainly in relatively low or moderate salinity waters. These results suggest that the expected catadromous behavior is less frequent. This observation agreed with those reported by Ibáñez *et al.* (2012) and Santana *et al.* (2018), who found high proportions of core chemical signatures compatible with estuarine hatching for Tamiahua Lagoon (México) (80%, Nt=20) and Northeast Brazil (70%, Nt=23), respectively. On the contrary, Ibáñez *et al.* (2012) have found a high proportion (60%, Nt=10) of individuals from the Cazones Estuary (México) with relatively high chemical signatures in the primordium, suggesting hatching in seawater. However, these estimates were based on a low number of samples, which added to the use of Sr/Ca thresholds of another species could have produced an overestimation of the proportions. In summary, the findings of this work suggest that low or intermediate salinity environments are essential for *M. curema* spawning and growth; therefore, they need special attention when generating conservation and management policies.

### 4.3. Core-to-edge Sr/Ca time-series

Three other studies have assessed the ontogenetic migration of *M. curema* using chemical time series in otoliths (Ibáñez et al., 2012; Mai et al., 2018; Santana et al., 2018); nevertheless, the present work has been the most exhaustive in relation to the samples size and study areas so far.

The results presented in this study showed a high variability in the Sr/Ca patterns throughout the ontogeny, evidencing a complex habitat use. Interestingly, despite one exception, all fish classified as migratory showed changes between signatures consistent with estuarine and marine (or high salinity) use within the first year of life. This suggests that there is high mobility in the early stages, perhaps associated with the search for nursery areas such those with mangroves or coastal lagoons. Considering all core-to-edge Sr/Ca time-series, the results obtained recorded a wide variation in otolith chemistry in the different locations, being estuarine and marine migrant the most common patterns, as showed by Ibáñez *et al.* (2012). The Sr/Ca patterns suggested that a few fish spent their entire life in low or intermediate salinity environments (estuarine resident). Some specimens even recorded Sr/Ca values below 2 mmol/mol (Figure 3a, c and g), which could be associated with the use of freshwater. Santana *et al.* (2018) have suggested that values below 2.29 mmol/mol could be associated with the use of freshwater; however, they have not caught specimens in freshwater to test this value. The freshwater environment use is supported by previous observations, which reported migrations 700 km upstream in rivers from the Gulf of México (Rodiles-Hernández, González-Diaz & Chan-Sala, 2005). In addition, six fish from Brazil, Margarita Island, and Tamiahua Lagoon showed a single stable Sr/Ca signature through ontogeny, which suggests a relatively low mobility between environments with different salinity, highlighting plasticity of the species. Finally, several fish showed relatively high chemical signatures (>7 mmol/mol), suggesting the use of hypersaline environments. These specimens mainly correspond to the hypersaline lagoon Laguna Madre (Figure 4i and j), which can reach salinities greater than 60 (Table 1). The use of this environments have also been reported for other sites such the Saloum Delta (Senegal), whose salinities reach 55 (Le Loc'h et al., 2015).

The number of changes in Sr/Ca stable signatures was highly variable for all sites (Figure 5). Nevertheless, Laguna Madre fish showed the highest values, suggesting that they experienced more salinity changes. Laguna Madre has the widest salinity range of all the sampled sites (Table 1), which allows exposure to extreme salinities. On the contrary, Brazilian fish, which were caught at the sea, seem to have been exposed to fewer changes in salinity, being consistent with a more homogeneous environment in relation to the estuaries or lagoons allocated to the ocean.

## 5. Final remarks, conservation and management

This work assessed for the first time the habitat use of *M. curema* in a wide range of distribution in the Neotropical Pacific and Atlantic waters. Core-to-edge Sr/Ca time-series suggested a marine and estuarine migratory behavior, rather than catadromous. The apparent number of changes in salinity was highly variable between specimens and studied environments. Finally, high migratory plasticity was observed in most of the studied sites, with the estuary being the most used environment. Due to the complexity in the migration patterns, the conservation and management of this important fishing and cultural resource will also need comprehensive and complex management strategies (Jenkins et al., 2010). This finding suggests that resource management and conservation strategies should focus on various coastal environments, but mainly on those with intermediate and low salinity, such as estuaries and mangroves, which are largely used as spawning, nursery and growth areas. In this sense, the maintenance of corridors between river, estuary, mangrove and sea is needed to preserve this migratory fish.

## 6. Acknowledgments

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## 7. References


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Table 1. Characterization of sampling locations.

| Location | Coast | N | Total length mean±std (cm) | Age (year) | Salinity range (ppt) | Depth mean (m) | Temperature range (°C) | pH range | Habitat type | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Laguna Madre, México | Gulf of México | 20 | 30.2±1.5 | 2-4 | 33.5-63.0 | 1.1 | 14.6-28.0 | 7.9-9.4 | Hypersaline lagoon | Contreras & Castañeda, 2004 |
| Tamiahua, México | Gulf of México | 19 | 29.9±2.1 | 2-4 | 14.4-37.5 | 2.5 | 23.0-34.0 | 7.5-9.4 | Polyhaline lagoon surrounded by mangrove | Contreras & Castañeda, 2004 |
| Alvarado, México | Gulf of México | 19 | 29.4±1.6 | 2-4 | 0.1-39.0 | 2.0 | 22.5-33.0 | 7.0-9.0 | Coastal lagoon system dominated by mangrove | Contreras & Castañeda, 2004 |
| Mecoacán, México | Gulf of México | 17 | 29.7±2.4 | 2-3 | 0.5-29.0 | 1.2 | 26.2-29.0 | - | Coastal lagoon system dominated by mangrove | Contreras & Castañeda, 2004 |
| Balsas, México | Pacific | 19 | 32.7± 2.15 | 2-4 | 0.0-34.5 | 5 | 24.0-26.0 | - | Freshwater river | CNA, 2000 |
| Margarita Island, Venezuela | Caribbean Sea | 11 | 26.7±2.1 | 2-3 | 35.8-36.6 | <5 | 23.5-24.5 | - | Beach | Astor & Cárdenas, 1997 |
| North Alagoas, Brasil | Atlantic Sea | 56 | 29.1±2.0 | 2-4 | 29-35 | 20 | 28.03±0.38 | - | Costal sea and low estuary | Passos et al., 2016 |

Figure 1: *Mugil curema* sampling sites. Charts show the classification of the fish based on otolith Sr/Ca ontogenetic profiles.

Figure 2: *Mugil curema* otolith sectioned at the core level showing the core-to-edge-laser ablation transects. The red line represents the Sr/Ca ratio and the arrows indicate the *annuli* position.

Figure 3: Otolith core-to-edge Sr/Ca profiles of *Mugil curema*. Solid horizontal lines illustrate stable signatures identified using change-point analysis. The light blue horizontal bar suggests high salinity environment use (~33.5). TL= total length (cm).

Figure 4: Otolith core-to-edge Sr/Ca profiles of *Mugil curema*. Solid horizontal lines illustrate stable signatures identified using change-point analysis. The light blue horizontal bar suggests high salinity environment use (~33.5). TL= total length (cm).

Figure 5: Box plot based on the number of significant changes in the Sr/Ca signatures through ontogeny. Different letters show significant differences between sampling sites (Kruskal Wallis test, $p<0.05$).

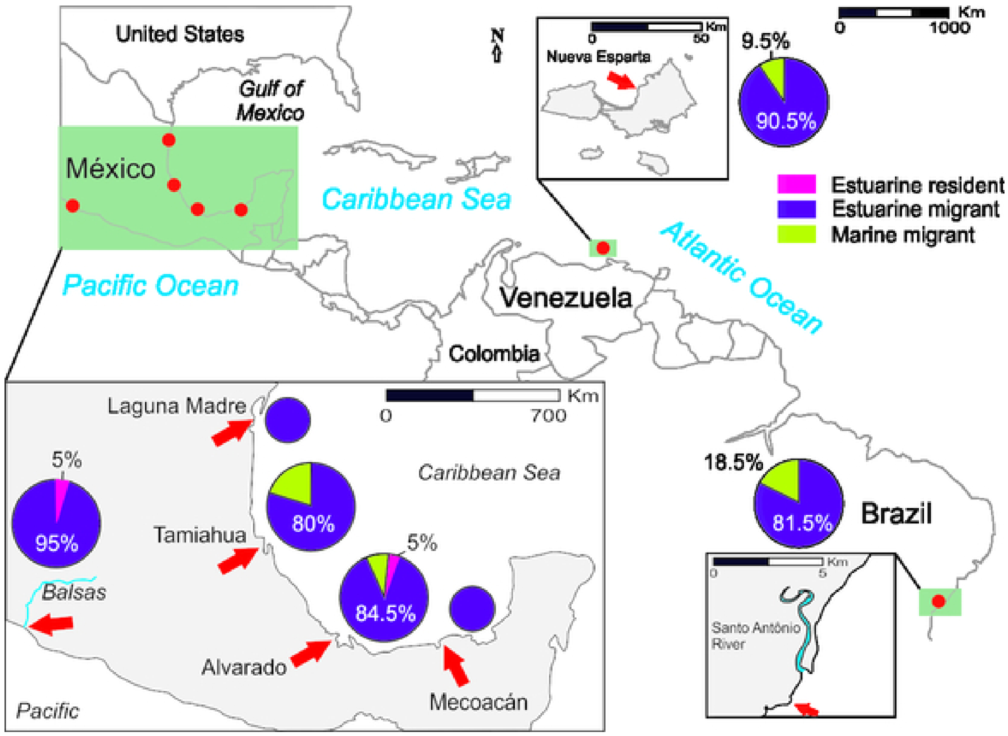


Figure 1: Mugil curema sampling sites. Charts show the classification of the fish based on otolith Sr/Ca ontogenetic profiles.

49x35mm (300 x 300 DPI)

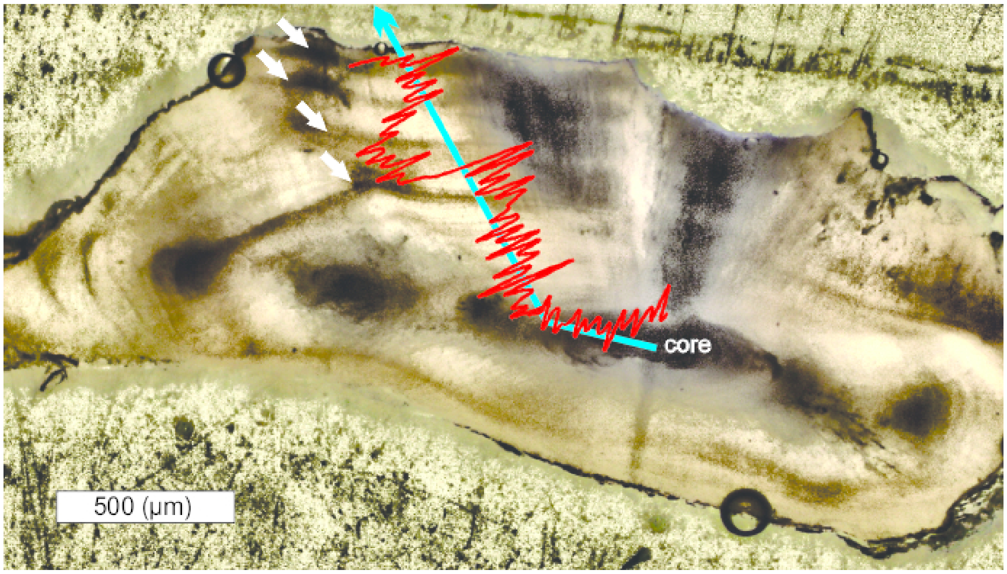


Figure 2: Mugil curema otolith sectioned at the core level showing the core-to-edge-laser ablation transects. The red line represents the Sr/Ca ratio and the arrows indicate the annuli position.

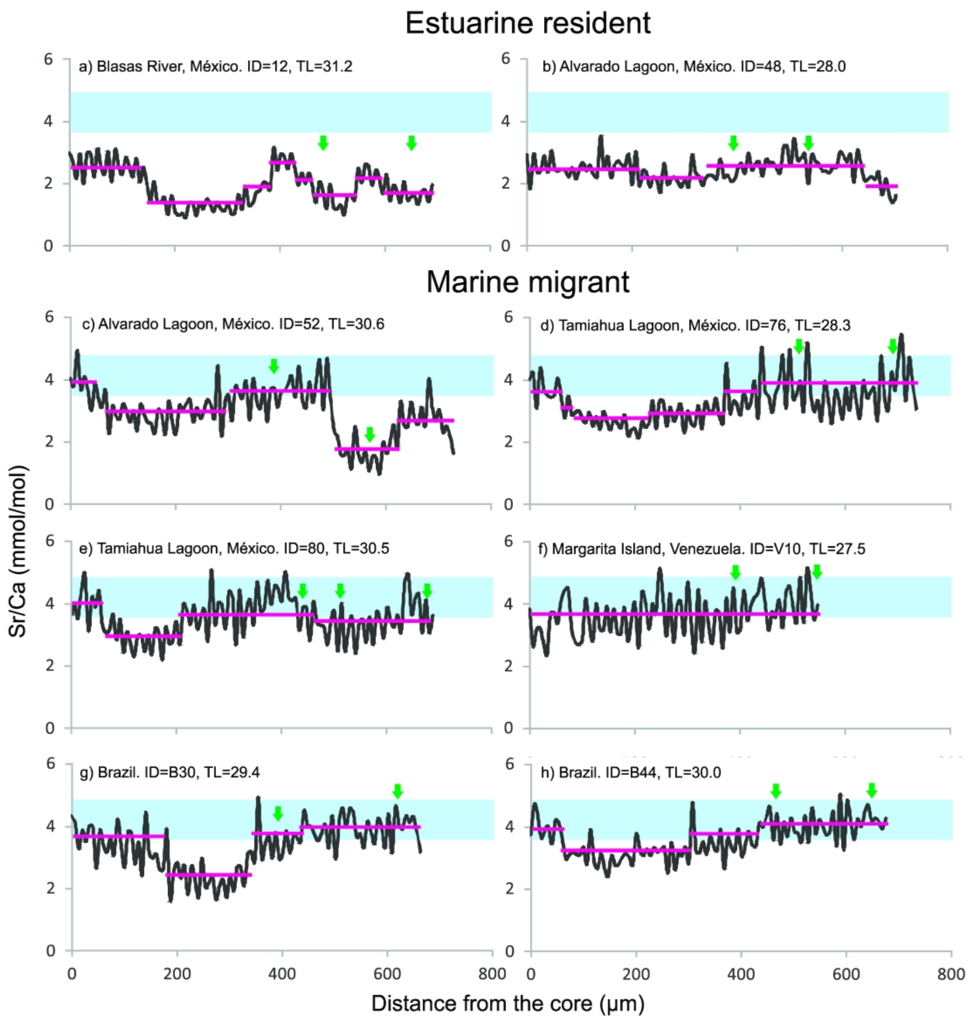


Figure 3: Otolith core-to-edge Sr/Ca profiles of Mugil curema. Solid horizontal lines illustrate stable signatures identified using change-point analysis. The light blue horizontal bar suggests high salinity environment use (~33.5). TL= total length (cm).


Figure 4: Otolith core-to-edge Sr/Ca profiles of Mugil curema. Solid horizontal lines illustrate stable signatures identified using change-point analysis. The light blue horizontal bar suggests high salinity environment use (~33.5). TL= total length (cm).

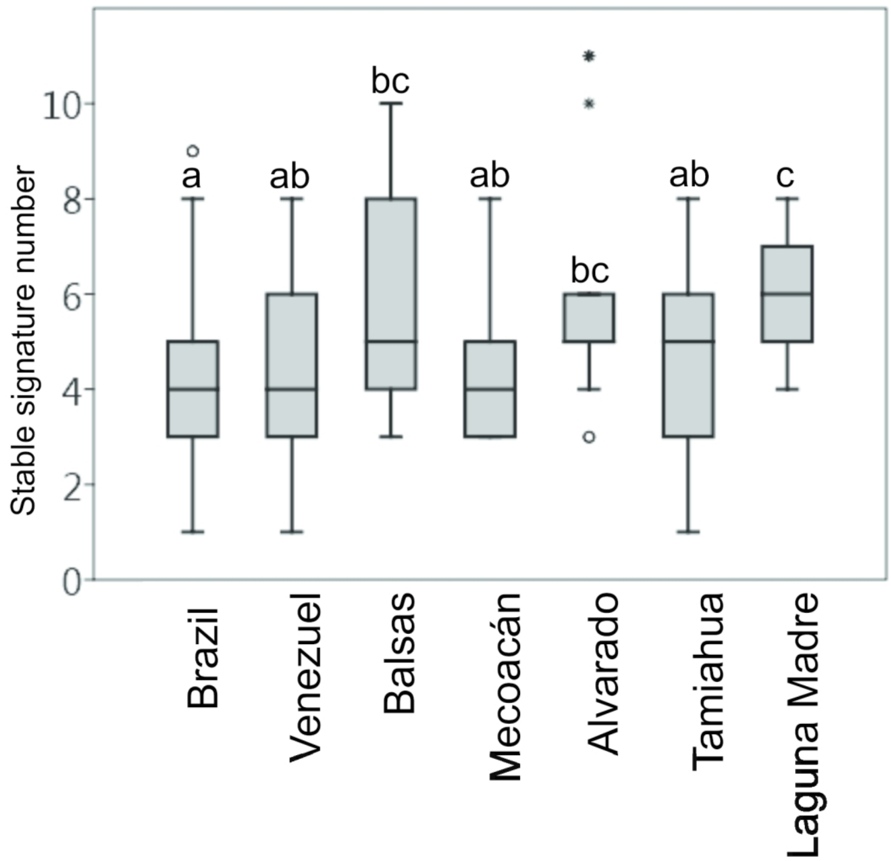


Figure 5: Box plot based on the number of significant changes in the Sr/Ca signatures through ontogeny. Different letters show significant differences between sampling sites (Kruskal Wallis test, $p<0.05$).