



Lack of mtDNA genetic diversity despite phenotypic variation and environmental heterogeneity in the exotic suckermouth armored catfish (*Pterygoplichthys pardalis*)

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Received: 25 November 2021 / Accepted: 29 October 2022 / Published online: 13 November 2022
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Abstract Molecular data is useful to determine the taxonomic identity and origin of invasive species. A reliable identification and a complete reference database are key for the adequate management of invasive species. South American suckermouth armored catfish (*Pterygoplichthys* spp.) are invasive species that cause severe environmental and socioeconomic

impacts. Although different species (*Pterygoplichthys pardalis* and *Pterygoplichthys disjunctivus*), and possibly hybrids, have been identified based on ventral spots' patterns, there remains taxonomic uncertainty regarding the *Pterygoplichthys* spp. individuals that are becoming invasive. We used genetic data to make inferences about the number of invasion events and found that there were one or few introduction events, followed by rapid spread and population growth. When we analyzed environmental variation of the sampling sites (based on physico-chemical properties), we observed both environmental differentiation between basins and environmental homogeneity within one of the studied river basins. We then analyzed the morphological variation between morphotypes and found that in addition to the variation in the ventral patterns, we observed size differences between individuals from different basins. We amplified the *CYTb* and *COI* mitochondrial DNA regions and found a unique haplotype which is shared across the sampled basins. Finally, we found that all the suckermouth armored catfish in the different basins were *P. pardalis* or of hybrid origin, and the lack of diversity in the mitochondrial DNA suggested a common origin. Our study highlights that combining genetic, morphological and ecological data provides complementary evidence to understand the introduction and invasion process.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10530-022-02961-w>.

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Resumen Los datos moleculares son útiles para determinar la identidad taxonómica y el origen de las

especies invasoras. Una identificación confiable y una base de datos de referencia completa son clave para el manejo adecuado de las especies invasoras. Aunque se han identificado diferentes especies (*Pterygoplichthys pardalis* y *Pterygoplichthys disjunctivus*), y posibles híbridos con base en los patrones de las manchas ventrales, aún permanece incertidumbre taxonómica en cuanto a los individuos de *Pterygoplichthys* spp. que se han vuelto invasores. Utilizamos datos genéticos para realizar inferencias respecto al número de eventos de invasión y encontramos que hubo solo uno o unos pocos eventos de introducción, seguidos de rápida difusión y crecimiento poblacional. Cuando analizamos la variación ambiental en los sitios de muestreo (con base en propiedades físico-químicas), observamos diferenciación ambiental entre las cuencas y cierta homogeneidad en una de las cuencas. Posteriormente analizamos la variación morfológica entre morfotipos y encontramos que además de la variación en los patrones ventrales, existen diferencias en el tamaño de los individuos de las distintas cuencas. Amplificamos las regiones mitocondriales de *CYTB* y *COI* y encontramos un haplotipo único compartido entre las cuencas muestreadas. Finalmente, encontramos que todos los bagres armados en las diferentes cuencas son *P. pardalis* o de origen híbrido, y la falta de diversidad en el ADN mitocondrial sugiere un origen común. Nuestro estudio resalta que combinar datos genéticos, morfológicos y ecológicos permite profundizar en nuestro conocimiento del proceso de introducción e invasión.

Keywords Genetic diversity · Invasive species · Loricariidae · Mitochondrial markers · Morphological variation

Palabras claves Diversidad genética · Especies invasoras · Loricariidae · Marcadores mitocondriales · Variación morfológica

Introduction

Biological invasions represent complex agents of change because they modify communities (Pyšek and Richardson 2010; Harvey-Samuel et al. 2017). These changes can alter predatory, competitive or disturbance interactions, which can lead to the removal of individuals, populations, or entire native species

(Pyšek and Richardson 2010; Harvey-Samuel et al. 2017). Current approaches and strategies to manage the expansion of some invasive populations have resulted in inadequate (Harvey-Samuel et al. 2017). Genetic analyses of invasive species help in the development of proper species management and more efficient monitoring and control strategies (Bock et al. 2015). In this sense, this type of analysis allows solving taxonomic uncertainties, uncover cryptic diversity, inferring the possible number of invasion events and identifying hybridization and introgression in introduced populations (Rocha and Gasca 2007; Richardson and Pyšek 2008; Frankham 2010; Fitzpatrick et al. 2012; Barret 2015; Sherman et al. 2016; Darling et al. 2017; Rius and Turon 2020). More importantly, genetic analyses allow identifying the events and routes of introduction of invasive taxa (Birky 2001; Rollins et al. 2011; Cristescu 2015), as well as inferring the interactions between different introduced populations and some of the mechanisms underlying successful invasion events (Rollins et al. 2011; Barret 2015; Bock et al. 2015; Sherman et al. 2016). Moreover, a reliable taxonomic identification and a good reference database are key for adequate management of invasive species (Darling et al. 2017).

Species from the genus *Pterygoplichthys* (Loricariidae) are known as suckermouth armored catfish, with the genus comprising 16 species (Orfinger and Goodding 2018; Anjos et al. 2019; Torres-Pineda and Armbruster 2020), of which at least 6 species, in addition to possible hybrids, have been identified as invasive species (Orfinger and Goodding 2018) in tropical and warm freshwater around the world. The taxonomic status of the invasive populations in many areas around the world has not yet been resolved due to the taxonomic complexity of the group, lack of a comprehensive taxonomic review and possible hybridization events (Chavez et al. 2006; Wakida-Kusunoki and Amador-del-Ángel 2008; Wu et al. 2011; Nico et al. 2012; Golani and Snovski 2013; Bijukumar et al. 2015; Wei et al. 2017; Orfinger and Goodding 2018; Lardizabal et al. 2020). Particularly, identification of this taxa in invaded areas of the Neotropics are based mainly on morphological characteristics (Wakida-Kusunoki and Amador-del-Ángel 2008; Rueda-Jasso et al. 2013; García-González et al. 2016; Wakida-Kusunoki et al. 2016; Agudelo-Zamora et al. 2020; Gaitán et al. 2020; Hernández Gómez and Schmitter-Soto 2020; Torres-Pineda and

Armbruster 2020), and rarely with additional genetic barcoding (Schmitter-Soto et al. 2015; Hernández Gómez and Schmitter-Soto 2020). In addition, levels of genetic diversity, and whether the same or different invasive lineages have been introduced in these areas are still unknown. Clarifying taxonomic uncertainties is key for adequately controlling and managing biological invasion because it enables the number and origin of introduced populations and the role of hybridization in invasion success to be determined (Bock et al. 2015). Moreover, genetic barcode databases are needed to implement early detection protocols based on environmental DNA surveys (Comtet et al. 2015; Valdez-Moreno et al. 2019; Elías-Gutiérrez et al. 2021), and a better representation of genetic variation data in introduced populations from understudied areas, such as Latin America, is needed for a better understanding of the invasion process (Nuñez and Pauchard 2010; Nuñez et al. 2022).

Species of the genus *Pterygoplichthys* are algivores and detritivores, and occasionally, they can eat larvae and small bottom-dwelling animals (Nico et al. 2009, 2012; Mendoza Alfaro et al. 2009). These species are native to temperate and tropical areas of South America: the upper Amazon River basin, the Madeira River basin and the Orinoco River basin and they have been introduced to 21 countries (Weber 2003; Armbruster and Page 2006; Nico et al. 2012; Orfinger and Goodding 2018). They have shown wide tolerance to new environmental conditions. For instance, it has been reported that they can withstand minimum temperatures ranging from 8.8 to 11 °C (Mendoza Alfaro et al. 2009) and they can become established in acidic and alkaline habitats ranging in pH from 5.5 to 8.0. Additionally, they can survive in polluted water and wastewater, some species show resistance to saline conditions, and they can breathe air by using the stomach as accessory respiratory organs (Armbruster 1998; Capps et al. 2011; Barba and Cano-Salgado 2014; Sánchez et al. 2015a; Kumar et al. 2018a). These characteristics make *Pterygoplichthys* spp. an ideal model for studying invasions.

These species represent an environmental problem that occurs in different aquatic environments. They have shown rapid spread in short periods of time in rivers, lakes, lagoons, and estuaries (Wakida-Kusunoki and Amador-del-Ángel 2008; Wu et al. 2011; Bijukumar et al. 2015; Sánchez et al. 2015a; Álvarez-Pliego et al. 2015; Orfinger and Goodding 2018;

Stolbunov et al. 2021). In colonized environments, *Pterygoplichthys* spp. do not have natural predators, although they can be eaten by some birds and otters (Ríos-Muñoz 2015), and there are reports of predation by other fish such as Mexican snook and tarpons (Toro-Ramírez et al. 2014). Furthermore, they have shown resistance to diseases and the ability to survive in anoxic waters and to tolerate mesohaline and oligohaline conditions (Capps et al. 2011; Nico et al. 2012). They also possess morphological and physiological characteristics that make them formidable competitors, contributing to their rapid and successful spread (Nico et al. 2012; Torres-Pineda and Armbruster 2020).

In the Philippines, India, Taiwan, and Vietnam, genetic analyses based on mitochondrial DNA (mtDNA) cytochrome b (*CYTB*) gene and cytochrome oxidase subunit I (*COI*) have been used to determine the taxonomic identity of invasive *Pterygoplichthys* populations (Aquino et al. 2011; Jumawan et al. 2011; Wu et al. 2011; Mukai et al. 2013; Yu and Quilang 2014; Bijukumar et al. 2015; Dahuruddin et al. 2016; Quyen et al. 2018; Pamprommin et al. 2020; Stolbunov et al. 2021). Some studies have shown that individuals with intermediate morphological characteristics might be *P. disjunctivus* × *P. pardalis* hybrids (Jumawan et al. 2011; Wu et al. 2011; Bijukumar et al. 2015; Stolbunov et al. 2021), suggesting that hybridization may play a significant role in invasion success (Wu et al. 2011; Bock et al. 2015).

In southeastern Mexico, individuals of *Pterygoplichthys* spp. have been present since early 2000 (Wakida-Kusunoki et al. 2007; Wakida-Kusunoki and Amador-del-Ángel 2008). In the Grijalva and Usumacinta River basins, one of the most important freshwater systems in Mexico, they cause severe environmental, economic, and social impacts (Cano Salgado 2011). Despite the serious problem posed by the invasion of *Pterygoplichthys* sp., there is still taxonomic uncertainty about the species present in Mexico (Sánchez et al. 2015a). Based on morphological characteristics—ventral patterns—they have been identified as possible *P. disjunctivus* and *P. pardalis* (Wakida-Kusunoki and Amador-del-Ángel 2008). Moreover, given that there are reports of intermediate morphotypes between these species, possible hybrids have been reported in this area (Amador-del-Ángel and Wakida-Kusunoki 2014; Sánchez et al. 2015a), but formal genetic analyses are still lacking.

Although the suckermouth sailfin catfish (*Pterygoplichthys* spp.) are typically freshwater species (Orfinger and Goodding 2018; Anjos et al. 2019) and in Mexico, they have been captured in oligohaline and mesohaline estuarine habitats (Capps et al. 2011). In contrast, a survey in Vietnam found no evidence of the presence of these taxa in brackish waters (Lai et al. 2020). The latter raises additional questions regarding the identity of the invasive lineage(s) found in Mexico and Asia.

The present study aims at solving the taxonomic uncertainty of sampled *Pterygoplichthys* spp. individuals that inhabit the Grijalva and Usumacinta River basins (*P. pardalis*, *P. disjunctivus*, and possible hybrids), using morphological and genetic data and considering the role of environmental factors (including salinity) within and between basins. In accordance with previous reports based on morphological information, we expect to identify at least two genetic lineages representing each parental morphotype and signals of hybridization (Wakida-Kusunoki and Amador-del-Ángel 2008; Amador-del-Ángel and Wakida-Kusunoki 2014; Sánchez et al. 2015a). The number of lineages and the relationship between them can be used to infer the possible number of introduction events for invasive species (Birky 2001; Rollins et al. 2011; Cristescu 2015). Finally, by comparing the identities of the mitochondrial sequences generated in the present study to sequences deposited in DNA sequence databases, we expect to determine the relationships among invasive populations in the region and across the globe.

Methods

Sampling area

The study area is the Grijalva and Usumacinta River basins. The region is located from 18°39'N to 16°30'N and from 90°22'W to 94°38'W (Toledo 2003) and covers an area of 102,465 km². The Grijalva and Usumacinta River basins are one of the most important aquatic systems in Mexico because approximately 35% of the country's water flows through these basins (CONAGUA 2011). In addition, the region is considered a hotspot of tropical biodiversity (Hudson et al. 2005; Vaca et al. 2019) and represents one of the most important regions in terms

of ecosystem services (Tapia-Silva et al. 2015). The Usumacinta River has a total length of approximately 1100 km, while the Grijalva River has a total length of 640 km (Yañez-Arancibia et al. 2009); both run from Guatemala to the Gulf of Mexico. The Grijalva River has four dams, La Angostura, Manuel Moreno Torres/Chicoasen, Malpaso, and Peñitas (Toledo 2003), and it runs through the city of Villahermosa, which is one of the largest cities in southeastern Mexico. In contrast, the Usumacinta River runs free (CONAGUA 2012). As a result, seasonal changes in water volume and environmental parameters are different in each river (Ramos-Herrera et al. 2012).

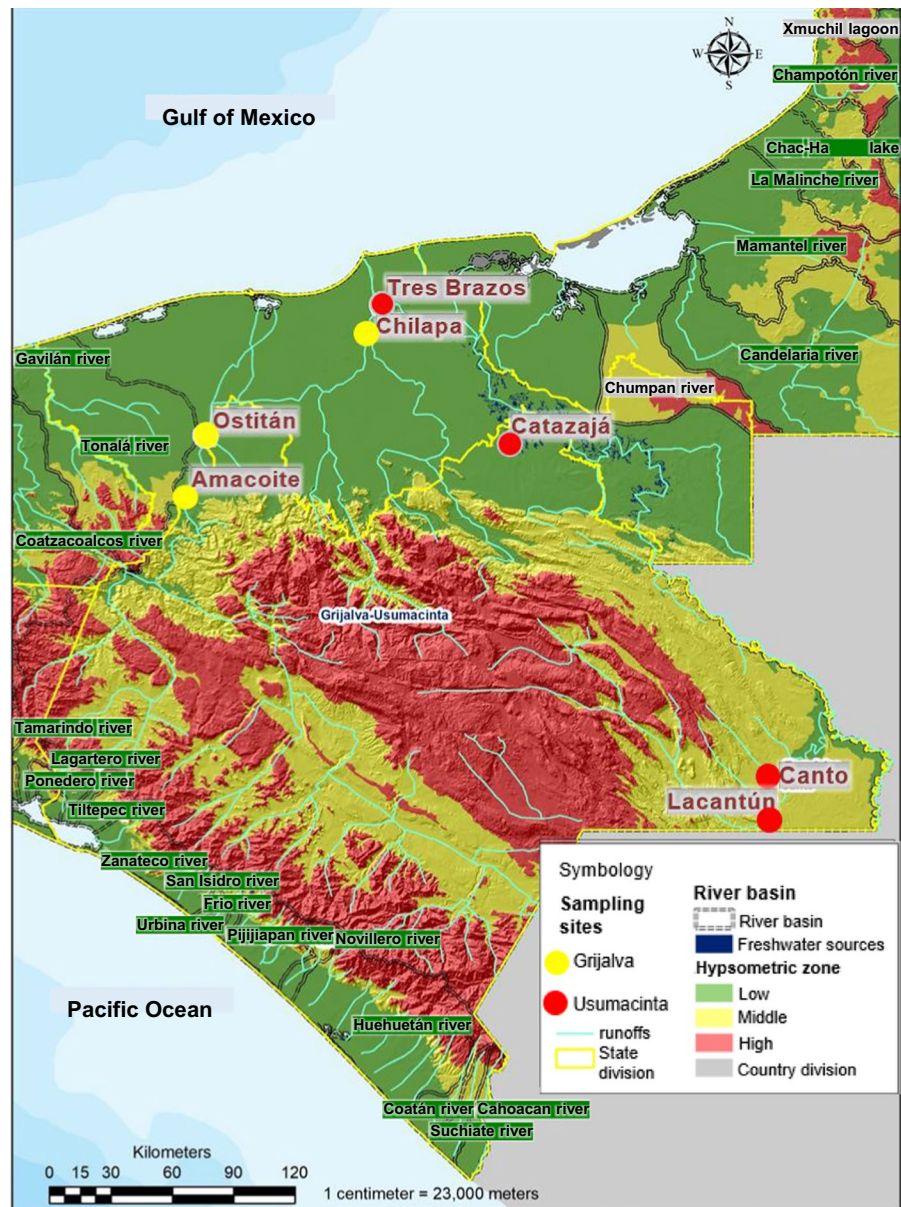
Environmental differentiation

The study was carried out in mid-April and mid-August 2018. Sampling was performed at 6 different locations in the Grijalva and Usumacinta River basins (Fig. 1), considering three points per site. Sampling sites were distributed in the floodplain and mountain sections of each basin. To document the environmental gradient occupied by *Pterygoplichthys* spp. between sampling sites and between basins, at each of these sites we measured pH, dissolved oxygen (DO), oxygen saturation, electrical conductivity (EC), total dissolved solids (TDSs), and salinity using an HI 9829 (HANNA Instruments, Hannapro S. A. de C. V., Mexico) multiparameter meter.

Environmental variables are useful as water quality indicators, and these variables provide an overall vision of the surroundings and set out a baseline to observe trends in river basins (Musálem-Castillejos et al. 2018). However, aquatic systems are experiencing a decline in their water quality worldwide (Lintern et al. 2018).

To assess environmental differentiation between sampling sites and between basin, we calculated the mean values for the three measurements taken at each site and for the dry season, then we standardized the data with an unbiased normalization ($n - 1$) (Gal and Rubinfeld 2009). We evaluated the correlation between six environmental variables with a Spearman correlation analysis. Accordingly, we retained variables with an $r < 0.85$ for further analyses. DO was strongly correlated with oxygen saturation ($r^2 > 0.99$) and salinity with EC ($r^2 = 0.99$); thus, we removed oxygen saturation and salinity for the environmental analyses. We used the estimated mean of

Fig. 1 Sampling sites in the Grijalva and Usumacinta River basins. The sites in the Grijalva River are Chilapa, Amacoite and Ostitan (yellow dots). The sites in the Usumacinta River are Canto and Lacantún, Catazajá and Tres Brazos (red dots). Sampling was performed from April to August 2018. Graphic was made with QGIS v.3.16 software



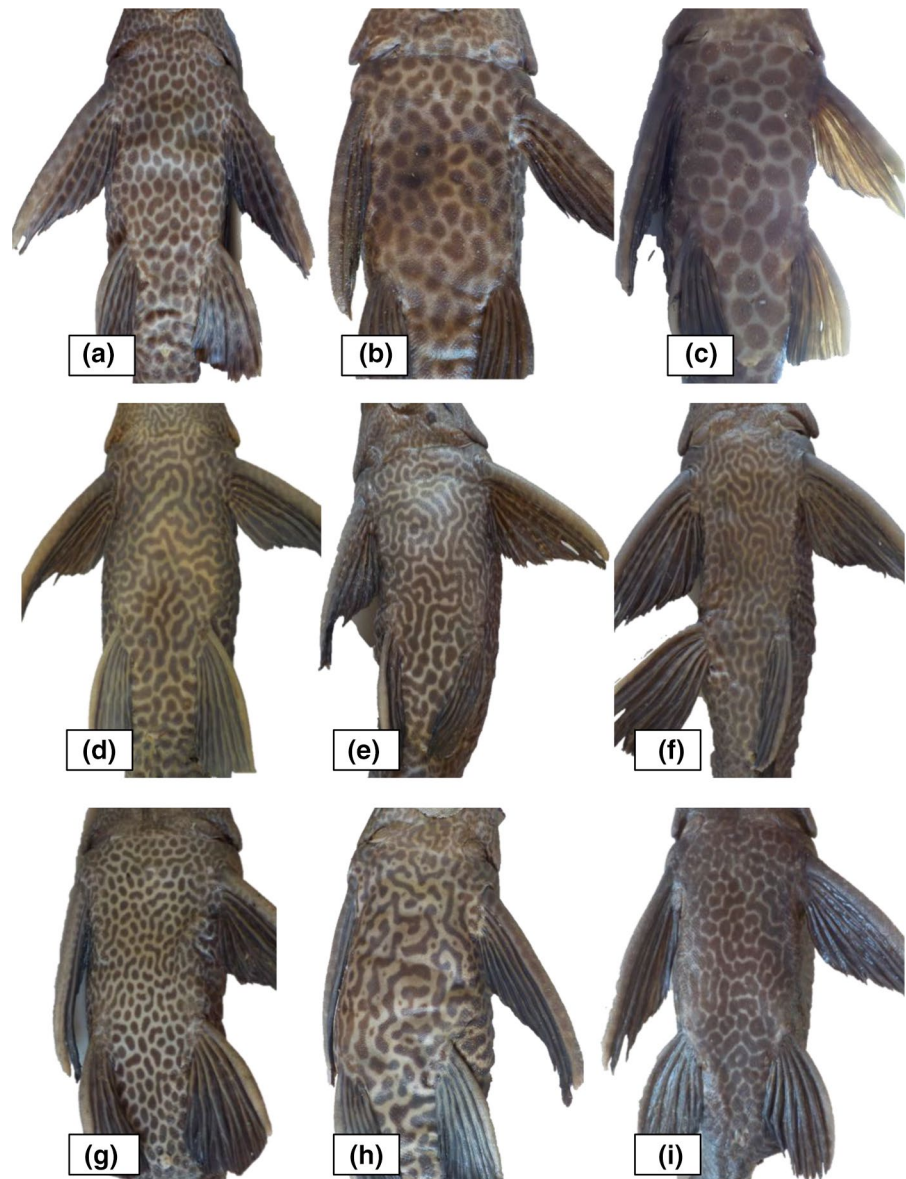
each variable to perform an ANOVA and a principal component analysis (PCA). Analyses were conducted in XLSTAT 2021 (Addinsoft 2020, USA). Graphics were obtained with R (R Core Team 2019).

Morphotype classification and morphometric analysis

Suckermouth armored catfish specimens were captured using 50 m by 3.5 m weighted gillnets overnight for one night. A total of 124 suckermouth armored catfish were captured and identified as

Pterygoplichthys sp. by having one dorsal fin ~10 soft rays (Armbruster and Page 2006; Page and Robins 2006; Covain and Fisch-Muller 2007). A total of 112 specimens were weighed, measured, and classified into morphotypes according to ventral spot patterns (Armbruster and Page 2006; Page and Robins 2006). Three morphotypes were described: *P. pardalis* (25 fishes) with small and discrete round spots, *P. disjunctivus* (27) with vermiculations, and *Pterygoplichthys* sp. (60) with a mixed pattern between those of the other two morphotypes

Fig. 2 Variations in ventral spots of the Suckermouth armored catfish (*Pterygoplichthys* spp.) in the Grijalva and Usumacinta River basin. Photos A to C represent the *P. pardalis* morphotype with discrete ventral spots; D to F are individuals identified as the *P. disjunctivus* morphotype with ventral vermiculations; and G to I are specimens from *Pterygoplichthys* sp. morphotype with mixed patterns of spots, classified as intermediate forms between the former two groups



(Fig. 2). In addition, we recorded the standard linear morphometric measurements for each specimen (standard length, height, cleithral width, and ventral width) according to Emiroğlu et al. (2016) (Supplementary data file S1). Muscle tissue biopsies of 1 cm² were collected and placed in 95% alcohol for DNA extraction. Tissue samples were stored at -20 °C until the DNA extraction. All individuals were deposited in the reference collection of aquatic fauna from southeastern Mexico: macroinvertebrates and fish, in the Laboratory of Aquatic Resources at ECOSUR-Villahermosa.

To test for differences regarding morphotype definition and sampling location (Grijalva River basin and Usumacinta River basin), we conducted an exploratory analysis through two PCAs based on the linear morphometric measurements. For the PCA used to analyze differences between morphotypes, to remove the possible effect of fish size we transformed data by considering the proportions of each measure to the standard length ([measure/ standard length] *100). We conducted a Kruskal–Wallis test to determine if differences between morphotypes were statistically significant. Then, for the PCA used to analyze

size differences between basins, we standardized the data using the unbiased normalization ($n-1$) (Gal and Rubinfeld 2009), because we considered that size could be affected by the environmental and ecological factors of each basin. In this case, we conducted a Mann–Whitney test to determine if differences between fish size of each basin were statistically significant. Every individual was photographed for reference (data available upon request to the authors). All statistical analyses were run in XLSTAT 2021 (Addinsoft 2020, USA).

Molecular data collection

The regions of the cytochrome b (*CYTB*) gene and cytochrome oxidase subunit I (*COI*) from mitochondrial DNA, being maternally inherited and not recombining, have been widely used for molecular identification, species delimitation, and the analysis of phylogenetic relationships (Rosero-Galindo et al. 2016; Scheinsohn et al. 2016). These molecular markers provide a baseline for the molecular identification of taxa because the *COI* gene is widely used as a barcode for vertebrates and *CYTB* gene is used for phylogenetic analyses (Avise et al. 1987; Rentara Alcantara 2007; Hickerson et al. 2010). Moreover, there is a wide basis of information for these mtDNA regions in international databases such as GenBank and BOLD database that will allow placing our sequences in a worldwide context.

DNA extraction was carried out based on the phenol:chloroform:isoamyl alcohol method, and DNA integrity was visualized by gel electrophoresis in 1× TAE using a 1% agarose gel stained with ethidium bromide ($C_{21}H_{20}BrN_3$). Furthermore, DNA concentration and purity were quantified using a NanoDrop™ 2000 spectrophotometer (Thermo Scientific, USA). For each sample, amplification of the *CYTB* region of the mtDNA was performed using the specific L1 (5′-AAA TAC GGC GCA GGA TTA GAA GCA AC-3′) and H2 (5′-GGG AGT TAA AAT CTC TCT TTT CTG GC-3′) primers reported by Wu et al. (2011). PCR was carried out at a final volume of 25 µl, containing 2.5 µl of $(NH_4)_2SO_4$ buffer, 2.8 mM $MgCl_2$, 0.2 mM dNTPs (Promega Corporation, USA), 0.4 µM forward (L1) and reverse (H2) primers, 1 µl of template DNA, 1 U/µl of *Taq* DNA polymerase (Thermo Scientific, USA) and nuclease-free water, with the following

amplification thermal cycler program: initial denaturation at 94 °C for 3 min followed by 35 cycles at 94 °C for 30 s, 55 °C for 40 s and 72 °C for 90 s with a final extension step at 72 °C for 10 min (Wu et al. 2011).

Additionally, the *COI* region of mtDNA was amplified using the specific primers Fish R1 (5′-TAG ACT TCT GGG TGG CCA AAG AAT CA-3′) and Fish F2 (5′-TCG ACT AAT CAT AAA GAT ATC GGC AC-3′) (Bijukumar et al. 2015). PCR was carried out at a final volume of 26 µl, containing 2.5 µl of $(NH_4)_2SO_4$ buffer, 3.3 mM $MgCl_2$, 0.14 mM dNTPs (Promega Corporation, USA), and 0.40 µM forward (Fish R1) and reverse (Fish F2) primers, 1 µl of template DNA, 1 U/µl *Taq* DNA polymerase (Thermo Scientific, USA) and nuclease-free water, with the following amplification thermal cycler program: initial denaturation at 95 °C for 5 min, followed by 40 cycles at 95 °C for 30 s, 50 °C for 40 s, and 72 °C for 1 min with a final extension step at 72 °C for 7 min (Bijukumar et al. 2015).

For both mtDNA regions, amplicon integrity was assessed by gel electrophoresis in TAE 1X using a 2% agarose gel stained with ethidium bromide. Both forward and reverse amplicon sequencing was carried out by capillary electrophoresis in an ABI 3730xl System (Applied Biosystems, USA) sequencer in MACROGEN, Seoul, North Korea (dna.macrogen.com), and Psomagen, Inc. Maryland, USA (psomagen.com).

Sequence assembly, alignment, and analysis

Electropherograms from the sequenced amplicons were visualized, processed, assembled, and aligned using Chromas v.2.6.6 software (Goodstadt and Ponting 2001; Technelysium Pty Ltd. 2003–2009, AUS). The consensus sequences were obtained using SeqTrace v.0.9.0 software (Stucky 2012). These sequences were compared with available data from GenBank of the National Center for Biotechnology Information (NCBI) and Barcode of Life Data (BOLD) System databases (Ratnasingham and Hebert 2007; www.boldsystems.org) using Basic Local Alignment Search Tool (BLASTn; Altschul et al. 1990).

Genetic diversity and structure

To assess the levels of genetic diversity in sailfin catfish present in the Grijalva and Usumacinta River basins, for each mtDNA region, we estimated the number of polymorphic sites (S), number of haplotypes (h), haplotype diversity (Hd) and nucleotide diversity (π) with DNAsp v.5.10.01 software (Librado and Rozas 2009). The genetic differentiation of the species was estimated through pairwise F_{ST} with DNAsp v.5.10.01 software (Librado and Rozas 2009). Although caution should be taken when interpreting results from genetic structure in invaded ranges as not enough time have passed since introduction for the populations to reach equilibrium (Fitzpatrick et al. 2012).

Genetic identity

To conduct the molecular identification and to determine the possible origin of the sailfin catfish population in the Grijalva and Usumacinta River basins, we downloaded sequences for *CYTb* and *COI* for *Pterygoplichthys* spp. available in the GenBank and BOLD System databases (Appendix 1), including all sequences reported from native and invasive populations. We generated a multiple sequence alignment for each mtDNA region using Clustal X v.1.83 software (Larkin et al. 2007). Finally, we obtained a haplotype network using the median-joining method (Kong et al. 2016) implemented in Network v.6 software (Fluxus Technology Ltd. 2020: <http://www.fluxus-engineering.com/index.htm>) for each region of the mtDNA.

To confirm the molecular identity of the sampled individuals, we obtained a maximum likelihood tree for each mtDNA region separately using MEGAX v.10.1.8 (Kumar et al. 2018b); we implemented the Kimura 2-parameter model as a substitution model and ran 1000 replications for bootstrapping. For this analysis, we included the sequences obtained in this study and those reported for other countries, as well sequences from other species of the genera *Pterygoplichthys* and *Hypostomus* (i.e., *H. robinii*) as outgroups.

Results

Environmental differentiation

The environmental PCA explained 87.90% of the variance in PC1 and PC2. This analysis showed that the environmental conditions among the three sampling sites in the Grijalva River basin are homogeneous, while those among the three sampling sites in the Usumacinta River basin show environmental differentiation (Table 1, Fig. 3). The parameters that had the greatest influence on the differentiation among the sites were TDS and EC (30.39 and 28.1%, respectively) (Fig. 3).

In the Grijalva River basin, the values of EC and TDS show a similar range in the three localities. On the other hand, in the Usumacinta River basin, a greater range of variation between locations was observed for TDSs, DO and EC (Table 1). It is worth mentioning that EC is highly correlated with salinity, and the sampling localities from the Usumacinta

Table 1 Physico-chemical properties of water at the sampling sites in the Grijalva and Usumacinta River basins for the dry season. Values represent the means and standard error of each parameter and the total number of individuals from each site

Site	pH	Temperature (°C)	Total dissolved solids (mg L ⁻¹)	Dissolved oxygen (mg L ⁻¹)	Electrical conductivity (mS cm ⁻¹)	No. individuals
Grijalva River basin						
Chilapa	9.72 ± 0	27.57 ± 0	183.60 ± 0	8.05 ± 0	367.60 ± 0	57
Amacoite	9.78 ± 0	28.05 ± 0	182.30 ± 0	8.52 ± 0	364.60 ± 0	21
Ostitán	11.63 ± 0	27.86 ± 0	183.60 ± 0	8.22 ± 0	367.60 ± 0	3
Usumacinta River basin						
Canto/ Lacantún	9.78 ± 0.34	25.76 ± 0.15	294.33 ± 16.57	10.12 ± 0.02	588.42 ± 33.18	15
Catazajá	NA	NA	NA	NA	NA	20
Tres Brazos	8.66 ± 0.05	28.48 ± 0.05	1091.33 ± 102.23	4.42 ± 0.01	2183.00 ± 204.68	8

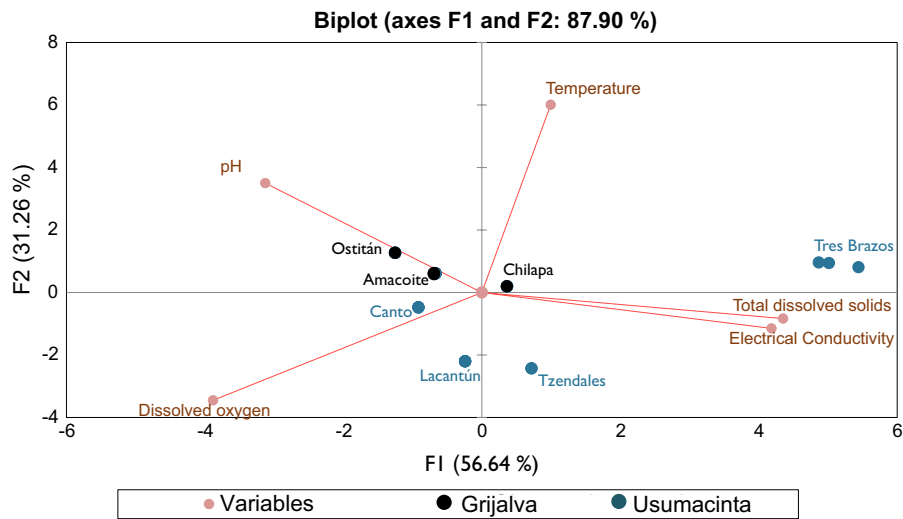


Fig. 3 Principal component analysis (PCA) of environmental parameters for sites of the suckermouth armored catfish (*Pterygoplichthys* spp.) collected in the Grijalva and Usumacinta River basins during the dry season. The sites in the Grijalva River basin are Chilapa, Amacoite and Ostitan

(black dots), and the sites in the Usumacinta River Basin are Canto-Lacantún and Tres Brazos (blue dots). The parameters included in the PCA are pH, temperature, total dissolved solids (TDS), dissolved oxygen (DO) and electrical conductivity (EC). Graphic was obtained with R (R Core Team 2019)

River basin showed EC values that were up to one order of magnitude higher than in the Grijalva River basin. In the Tres Brazos site, TDS showed the highest value and DO the lowest value (Table 1).

Morphotype classification and morphometric analysis

The group identified as the *P. pardalis* morphotype had the highest values for all the linear morphometric measures, while the group identified as the *P. disjunctivus* morphotype had the medium values. Specimens with intermediate morphotypes (called

Pterygoplichthys sp.) had the lowest value for each of the characteristics (Table 2). Nevertheless, we did not find significant differences for the standardized data between morphotypes ($p > 0.05$, Kruskal Wallis test) (Supplementary data file S2).

PC1 and PC2 (Fig. 4a) of the morphometric PCA explained 76.59% of the variance between morphotypes, being height and ventral width the variables with highest contribution to PC1 (46.55 and 30.04%, respectively), and cleithral width the variable with highest contribution to PC2 (72.30%). This result also shows a lack of differentiation between morphotypes.

Table 2 Morphometric measurements (average \pm standard deviation) of the three morphotypes of suckermouth armored catfish (*Pterygoplichthys* spp.) from the sampling sites in the

Grijalva and Usumacinta River basins. The morphotype for each individual was defined according to ventral spot patterns as shown in Fig. 2)

Characteristics	Morphotype		
Group	<i>P. pardalis</i>	<i>P. disjunctivus</i>	<i>Pterygoplichthys</i> sp.
Standard length—SL (cm)	25.36 \pm 0.8	24.21 \pm 1.00	22.02 \pm 0.61
Height—H (cm)	4.76 \pm 0.16	4.51 \pm 0.21	4.04 \pm 0.12
Cleithral width—CW (cm)	5.82 \pm 0.25	5.58 \pm 0.24	5.20 \pm 0.16
Ventral width—VW (cm)	4.76 \pm 0.12	4.53 \pm 0.21	4.29 \pm 0.08
Weight—W (g)	329.23 \pm 31.26	266.29 \pm 3.30	207.15 \pm 17.08

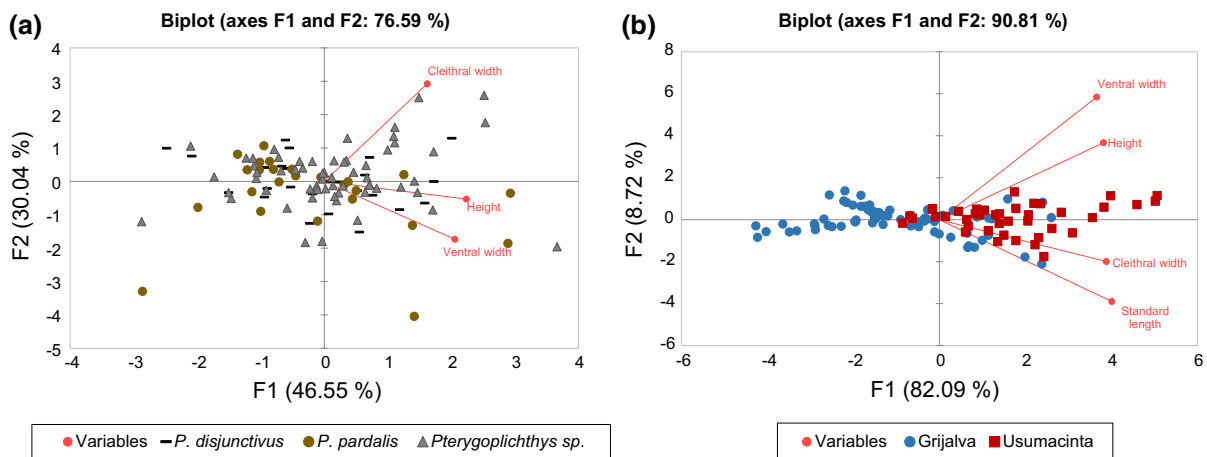


Fig. 4 Principal component analysis (PCA) of suckermouth armored catfish (*Pterygoplichthys* spp.) in the Grijalva and Usumacinta River basins: **a** Analysis of linear morphometric characteristic metrics of *Pterygoplichthys* sp. specimens,

grouped by morphotype (ventral spots). **b** Analysis for *Pterygoplichthys* sp. morphometric characteristics, grouped by captured site (river basin). Graphics were obtained with XLSTAT 2021

On the other hand, in the PCA that considered differences in size by river basin (Fig. 4b), we observed that the fish collected in the Usumacinta River basin were larger than those collected in the Grijalva River basin, with significant differences for all the characteristics ($p < 0.05$, Mann–Whitney test). The fish caught in the Grijalva River basin had an average standard length of 21.28 ± 0.53 cm and an average weight of 196.96 ± 15.79 g. The fish caught in the Usumacinta River basin had an average standard length of 26.79 ± 0.54 cm and an average weight of 349.09 ± 21.11 g.

Genetic diversity and structure

For each marker (*CYTB* and *COI*), a single haplotype was found considering the total number of samples collected in the Grijalva and Usumacinta River basins. Therefore, the measures of genetic diversity and genetic structure were 0 in all cases.

Genetic identity

In the analyses of the median-joining (MJ) haplotype network and the maximum likelihood (ML) tree, we observed a greater number of sequences available for the *COI* marker than for the *CYTB* marker (Appendix 1). For each marker, six haplotypes have been reported worldwide: P1, P2, and P3, which belong to

the *P. pardalis* lineage, and D1, D2, and D3, which correspond to the *P. disjunctivus* lineage. The haplotype obtained in the present analysis for each molecular marker corresponds to the P1 reported for different populations, both native and invasive (Figs. 5 and 6).

In the *CYTB* haplotype network (Fig. 5a), the most common haplotype P1 has also been reported in an individual native to Brazil and in introduced specimens from Taiwan and Vietnam. Haplotypes of the *P. disjunctivus* lineage have been reported for Japan, Taiwan, and Vietnam. In the *COI* haplotype network (Fig. 5b), the most frequent P1 haplotype was recorded in native populations in Brazil and Peru and in introduced populations in the Philippines, Indonesia, Colombia, Thailand, Belize, Japan, and Bangladesh. It should be noted that this haplotype has been reported also in the Hondo River basin, southeastern Mexico (Quintana Roo), and in the Bravo River basin in the state of Tamaulipas in northern Mexico. The *P. pardalis* lineage has also been recorded in Guatemala and Vietnam. Of the *P. disjunctivus* lineages, the D1 haplotype showed the highest frequency and has been found in northern Mexico, South Africa, Japan, Italy, and Guatemala. The other haplotypes have been found at low frequencies and have been reported in India and North America.

The ML trees showed branch support values $> 70\%$. The tree for *CYTB* (Fig. 6a) depicted two main groups or clades. The haplotype found in

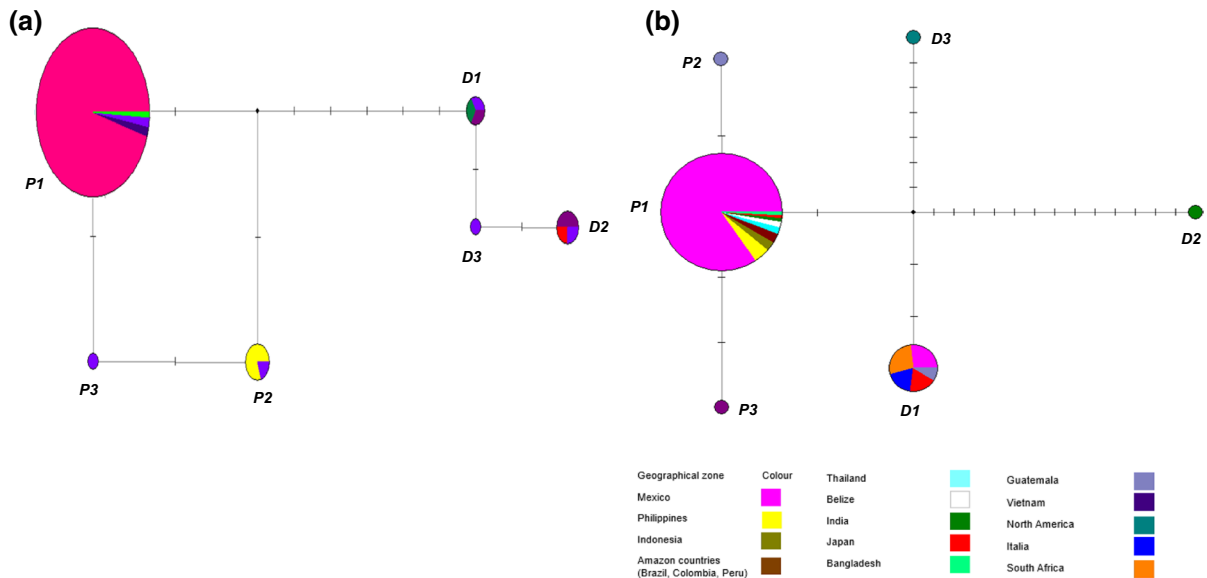


Fig. 5 Median-joining haplotype network of suckermouth armored catfish (*Pterygoplichthys* spp.) based on mtDNA CYTB (a) and COI (b) haplotypes. Sequences include the haplotypes obtained for the specimens sampled in the Grijalva and Usumacinta River basins in the present study as well as

those available in the GenBank and BOLD databases. The area of each circle is proportional to the haplotype frequency, and colors indicate the geographical origin of the sequences. The network was estimated with Network v.10.2.0.0. software

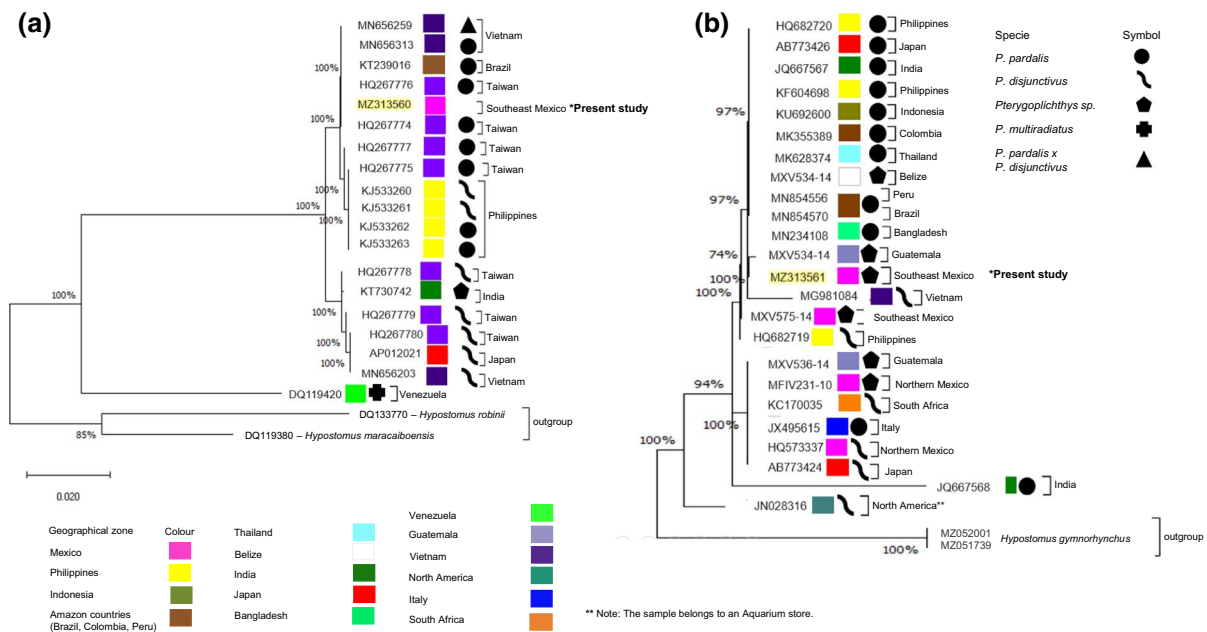


Fig. 6 Maximum probability trees for the suckermouth armored catfish (*Pterygoplichthys* spp.) based on mtDNA CYTB (a) and COI (b) haplotypes. Sequences include the haplotypes obtained in the present study for the Grijalva and Usumacinta River basins (highlighted), and sequences avail-

able in the GenBank and BOLD databases. Bootstrap values > 70% are shown. Colors indicate the geographical origin of the sequences, and symbols illustrate the species as identified in each database. Evolutionary analyses were conducted in MEGA X

the present study belongs to the first clade, which is composed mainly of *P. pardalis* sequences (Brazil, Taiwan, Vietnam and the Philippines). In this group, there were also specimens identified as *P. disjunctivus* (Philippines), and one specimen identified as *P. pardalis* x *P. disjunctivus* (Vietnam). In the second clade, *P. disjunctivus* sequences (Taiwan, Japan, Vietnam) were dominant, in addition to a specimen of *Pterygoplichthys* sp. (India). The closely related species *P. multiradiatus* (Brazil) remains an outgroup.

Regarding the *COI* (Fig. 6b), we observed that the first clade consisted mainly of *P. pardalis* sequences (Philippines, Japan, India, Indonesia, Colombia, Brazil, Peru, and Bangladesh), plus the haplotype found in the present study from the states of Tabasco and Chiapas (southeastern Mexico). In this clade, we also found sequences identified as *Pterygoplichthys* sp. (Belize and Guatemala), and a sequence of *P. disjunctivus* (Vietnam). The second clade was composed of sequences identified as *P. disjunctivus* (Bravo River basin in the state of Tamaulipas in northern Mexico, Philippines, Japan, and South Africa), a sequence of *P. pardalis* (Italy), and specimens of *Pterygoplichthys* sp. (Hondo River basin in southeastern Mexico in the states of Quintana Roo and Guatemala).

Discussion

Environmental differentiation

We observed greater environmental variability in the Usumacinta River basin than in the Grijalva River basin, thus we would expect to find higher levels of genetic diversity in the Usumacinta River basin than in the Grijalva River basin, as genetic variation constitutes the basis for adaptation. These differences are to be expected because each river shows different characteristics; the Grijalva River has four dams that may have reduced the potential for sediment transport and soil formation (Toledo 2003; CONAGUA 2012). Ramos-Herrera et al. (2012) reported that parameters such as pH and water temperature have remained stable over time (1978–2011) in the Grijalva and Usumacinta River basins. However, factors such as TSS and DO have shown fluctuations in some regions of the basin within the territory of Tabasco (Ramos-Herrera et al. 2012). It is worth mentioning that our

environmental analysis is exploratory and based on data for the dry season. Nevertheless, we found that the suckermouth sailfin catfish, particularly in the Usumacinta River basin, are exposed to conditions of higher salinity (correlated with EC) and higher TSS, and are adapting to heterogeneous environmental conditions despite the lack of genetic variation in mtDNA. Therefore, we suggest performing a wider study which includes a higher number of sampling sites along the environmental gradient and considers the temporal variation, along with type of submerged vegetation, angle of the riverbanks and type of substrate which could be important features to unravel the distribution of the suckermouth armored catfish.

The Grijalva River basin is affected by the discharges of domestic and industrial pollutants from activities such as livestock operations, agriculture, oil exploitation and sugar mill operations. Consequently, a decrease in the water quality of the system has been observed, affecting the diversity of native species and enhancing the establishment of opportunistic species (Ramos-Herrera et al. 2012; Marin Contreras 2014; Gómez-González et al. 2015; Sánchez et al. 2015b; Cruz-Ramírez et al. 2019b). For example, at the Amacoite site, it has been observed that most of the DO records are below 5 mg/L, which is the average level for the sustainability of aquatic life. Similarly, it has been reported that some species of suckermouth armored catfish are tolerant to pollution, low flow rates, and very low levels of DO (<2 mg/L) (Nico et al. 2012; Frederico et al. 2019; Aida et al. 2021), which allows population growth in the absence of competition (Aida et al. 2021).

In contrast, the Usumacinta River basin has been affected to a lesser extent by discharges of industrial and agricultural pollutants and governmental reports indicate low risk of reduction in water quality or for the organisms associated with the system (PROFEPA 2015; Cruz-Ramírez et al. 2019a). The National Water Commission (CONAGUA) reports that in the Usumacinta River basin water quality is ranked as acceptable and good quality. However, some effects of industrial pollutants have been observed (PROFEPA 2015; CONAGUA 2020). It is worth mentioning that we captured twice as many suckermouth armored catfishes in the Grijalva River basin ($N=81$) than in the Usumacinta River basin ($N=43$). Habitat degradation may be contributing to higher abundances of this

invasive species in one river basin over the other, but ecological studies that correlate relative abundance and habitat quality are needed to test this hypothesis.

Conductivity was directly correlated with salinity (see methods for environmental differentiation). Regarding the levels of EC and salinity in sites inhabited by the suckermouth sailfin catfish, values were similar and lower than those previously reported in a different study of suckermouth armored catfish in southeastern Mexico (Capps et al. 2011). The Grijalva and Usumacinta River basins are reported as the areas where populations of *Pterygoplichthys* spp. inhabit waters with higher saline concentrations (Capps et al. 2011; Lai et al. 2020), as we can see in the Tres Brazos site which showed values of conductivity that were one order of magnitude higher than the rest of the sites (Table 1). Sailfin catfish has been reported to withstand salinities of up to 12 gL⁻¹, but are usually found in sites with low salinity (Capps et al. 2011; Biju Kumar et al. 2018; Lai et al. 2020). In the present study, no direct association is apparent between the EC/salinity factor and the abundance of *Pterygoplichthys* spp., but genomic and transcriptomic analyses could be useful to help us understand how these invasive fish are adapting to higher salinities and degraded habitat in Mexico.

Morphological differentiation

The morphological variation in the suckermouth armored catfish (*Pterygoplichthys* spp.) from the Grijalva and Usumacinta River basins have been previously described (Amador-del-Ángel et al. 2014; Ayala-Pérez et al. 2014). These authors observed differences in the patterns of ventral spots and geometric designs of the head between two morphotypes, which they identified as *P. pardalis* and *P. disjunctivus*, similar to our observations. In addition, they also reported larger sizes of *P. pardalis* specimens (i.e., total length) than of the other *Pterygoplichthys* spp., and it has been noted that *P. pardalis* rapidly grows in its first 2 years of life (Hoover et al. 2004). In contrast, in the present study we did not find statistically significant differences in meristic measures between morphotypes.

The lack of morphological differentiation between morphotypes from the Usumacinta and Grijalva River basins contrast with analyses carried out in other countries where these species are invasive (i.e., India,

Malaysia, Sri Lanka, Turkey, and Vietnam). Those studies showed differences between the morphometric and meristic characteristics that allow identifying the morphotypes. The populations studied by Saba et al. (2020) showed significant differences in morphometric measurements (i.e., snout length) between two groups of *P. pardalis* (which they defined as type “A” and type “B”) and *P. disjunctivus*. Also, Emiroğlu et al. (2016) and Bijukumar et al. (2015) classified the specimens they captured into three groups: *P. pardalis*, *P. disjunctivus* and intermediates (or hybrids) based on ventral coloration and morphometric and meristic characteristics. Additionally, they observed lower values of the morphometric and meristic characteristics (i.e., height) in the intermediate or hybrid group than in *P. pardalis* and *P. disjunctivus* (Bijukumar et al. 2015). In addition, Stolbunov et al. (2021) indicated that there are eight qualitative and six meristic characteristics that contribute greatly to differentiating the introduced specimens into three groups: *P. pardalis*, *P. disjunctivus* and *P. disjunctivus* × *P. pardalis*. In another study, authors found significant differences between the morphometric characteristics of two of five groups (*P. pardalis*, *P. disjunctivus*, intermediate specimens, specimens close to *P. pardalis*, and specimens close to *P. disjunctivus*) (Wickramaratne et al. 2020). There is a disparity between the identities and number of morphotypes around the world, and these discrepancies may suggest that hybridization occurs in their native distribution or within aquariums and breeding farms before introduction to new environments (Nico et al. 2012; Godwin et al. 2016; Lai et al. 2020). The lack of morphological differentiation in the present study might be related to the low number of characteristics analyzed. This result was consistent with the lack of genetic variation we found in mtDNA that suggests that a single lineage or possible hybrids were introduced in the Grijalva and Usumacinta Rivers basins (Nico et al. 2012; Wu et al. 2011; Godwin et al. 2016).

Taxonomic delimitation within the genus *Pterygoplichthys* remains controversial. For example, the delimitation of species such as *P. anisitsi*, *P. multiradiatus*, *P. pardalis* and *P. disjunctivus* is based mainly on their ventral spot patterns (Armbruster and Page 2006; Page and Robins 2006; Nico et al. 2012). Other studies have even hypothesized that, at least in invaded areas, *P. pardalis*, *P. disjunctivus* and other species of the genus could represent a single taxon

with high morphological variation (Jumawan et al. 2011; Wu et al. 2011; Zworykin and Budaev 2013). Therefore, future phylogenetic and taxonomic studies within the genus based on samples from the native range of each species are needed. Similarly, it is necessary to carry out a study that analyzes all meristic, morphological and morphometric measurements and correlates this information with highly variable molecular markers for the specimens captured in the Grijalva and Usumacinta River basins.

In this study, we noted that size and weight were statistically different between the Grijalva River and Usumacinta River basins. The simplest hypothesis suggests that this variation could be due to the habitat condition of each ecosystem. It has been observed that during its development, the Amazon sailfin catfish tends to grow faster in size than in weight (allometric) (Wakida-Kusunoki and Amador-del-Ángel 2011; Rueda-Jasso et al. 2013; Lai et al. 2020). Similarly, the growth parameters of *Pterygoplichthys* spp. do not usually show variation related to seasonality or sex (Lai et al. 2020). However, it has been observed that there may be morphological differences (i.e., shape and size of the mandible) and differences in isotopic signature among loricariids (Loricariidae) based on their diet and resource availability (Lujan et al. 2011). It has been postulated that there is good availability of food in the Usumacinta River basin environment and that the populations of native species (i.e., *Eugerres mexicanus*) tend to be healthy, based on the analysis of the length–weight relationship of other species in the same basin (Valdez-Zenil et al. 2015). In addition, Wakida-Kusunoki and Amador-del-Ángel (2011) suggested that water temperature, depth and food supply are important factors affecting fish size and abundance. As previously mentioned, ecological studies are needed to understand the relationship between habitat quality and abundance of this invasive species, as well studies that focus on understanding their interactions with native species.

Our results invite further comparative studies on the morphology, taxonomy, ontogeny, physiology, and ecology of these invasive fish at sites where they have been recently introduced.

Genetic diversity and structure

Contrary to our expectations, there was a lack of genetic diversity in the *COI* and *CYTB* regions of

mtDNA from the introduced populations of the suckermouth armored catfish from the Grijalva and Usumacinta River basins (southeastern Mexico). Only one haplotype has been reported for native populations in Brazil; but, to our knowledge, no population genetics study of the native range has been conducted yet (Jumawan et al. 2011). The haplotype from Brazil corresponding to the *P. pardalis* lineage was reported by Wu et al. (2011), and it is the most frequent worldwide. In contrast, in other studies conducted with invasive populations, high genetic diversity has been reported with up to seven haplotypes for the *CYTB* region (Wu et al. 2011; Stolbunov et al. 2021) and six in *COI* (Jumawan et al. 2011). Moreover, in many invaded areas a mixture of haplotypes corresponding to the lineages *P. pardalis* and *P. disjunctivus* have been found (Jumawan et al. 2011; Wu et al. 2011; Stolbunov et al. 2021). The present study is the first population genetics analysis to report a complete lack of genetic variation for mtDNA for this species in an invaded area.

The lack of genetic diversity could be a consequence of propagule pressure, which describes the relationship between the number of introduced individuals and the number of introduction events (Roman and Darling 2007), and low genetic variation has been associated to introductions from aquarium release (Roman and Darling 2007). In this sense, we can infer that the populations established in the Grijalva and Usumacinta River basins were probably the result of a single introduction event and/or a small founder population (Roman and Darling 2007). Other effects, such as low diversity in the ancestral population and demographic bottlenecks, could also contribute to the lack of genetic variation between populations (Roman and Darling 2007; Dlugosch et al. 2015). Nevertheless, the lack of information about this species from their native ranges, and the lack of nuclear genomic data (both neutral and non-neutral), makes it difficult to reconstruct the history of invasion for these taxa, as well as understanding the role of hybridization in these invasions. In addition, there are contrasting patterns regarding the levels of genetic diversity in invasive populations, where low genetic diversity may be attributed to small founder populations and isolation (Dlugosch and Parker 2008). However, these populations can also experience large and rapid adaptive changes after their introduction (Dlugosch and Parker 2008). In other cases, invasive populations show high

levels of genetic diversity which could be explained by multiple introduction events and introgression that may be playing an important role in population expansion and adaptation (Roman and Darling 2007; Rius and Darling 2014). In this study we cannot rule out that hybridization occurred in the source population. Therefore, future studies should focus on analyzing nuclear genetic variation, to search for signals of introgression and candidate loci for adaptation.

In populations in Vietnam and the Philippines, the genetic structure was not explained by spatial distribution, which is consistent with our results. Stolbunov et al. (2021) did not find subdivision by basin and suggested that it was due to the small geographical differences between the rivers in the region (Vietnam), the small sample size, and the low polymorphism of the *CYTB*. It is important to also consider that the suckermouth armored catfish is usually very active; it can swim vigorously upward and move between habitats (i.e., spring channels and rivers), the stomach is used as respiratory organ and for buoyancy, thus giving it a high mobility and dispersal capacity (Armbruster 1998; Nico et al. 2012). In Florida, during floods, these fish likely can move between basins, which is also a frequent phenomenon occurring in the Grijalva and Usumacinta River basins. Additionally, other species of Loricariidae have been described as troglobites; that is, they can move through underground rivers and can disperse underground (Nico et al. 2012; Bijukumar et al. 2015). Thus, it is possible that suckermouth armored catfish can migrate between different sites in a basin and between basins despite geographical barriers, contributing to gene flow. Nevertheless, results from analyses of genetic structure in invaded areas should be taken with caution, because invasion processes are so recent that populations might have not reached equilibrium thus breaking the assumptions in which many population genetics analyses are based (Fitzpatrick et al. 2012; Rius and Turon 2020).

Genetic identity

As previously mentioned, based on molecular identification, the suckermouth armored catfish of the Grijalva and Usumacinta River basins should be identified as *P. pardalis* or an intermediate lineage (hybrid). The discrepancy between the level of morphological variation (ventral patterns) and molecular variation

leaves both possibilities open. It is necessary to use a genomic approach to estimate the degree of introgression in the genomes of these invasive populations, as intraspecific admixture has been cited as a possible mechanism for rapid adaptation in invasive species (Rius and Darling 2014). Nevertheless, detecting introgression might be challenging without available molecular data from native ranges (Rius and Darling 2014). In addition, a genomic approach would allow gaining a better understanding of how these organisms are adapting to the different environmental conditions throughout these basins.

It is important to note that inconsistency has been observed between morphological and genetic identifications in introduced populations in various countries (i.e., Vietnam, the Philippines, and Taiwan) (Jumawan et al. 2011; Wu et al. 2011; Stolbunov et al. 2021). In addition, minimal differences have been reported at the level of molecular sequences between morphotypes, and consequently, the presence of hybrids between different species has been suggested (Jumawan et al. 2011). Available information for these taxa in introduced regions come mainly from Asia, and from a few individuals from different countries that have been sequenced; therefore, there was a lack of information—at the population level—regarding the identity and origin of the lineages present in introduced areas of the Neotropics.

The *CYTB* and *COI* haplotype networks obtained from this study and other studies based on *COI* sequences have shown few variable sites between lineages (Jumawan et al. 2011; Schmitter-Soto et al. 2015). The high similarity between sequences may suggest that they belong to the same species (Ward et al. 2009). As previously mentioned, some authors have already suggested that in introduced areas *P. pardalis*, *P. disjunctivus* and *P. multiradiatus* could have been misidentified (Jumawan et al. 2011; Wu et al. 2011). Levels of genetic differentiation reported within the genus *Pterygoplichthys* (i.e., *P. pardalis*, *P. disjunctivus*, *P. etentaculatus* and *P. gibbiceps*) are similar to those reported for other fish species (Ward et al. 2005; Hubert et al. 2008). Invasive populations usually show less genetic divergence than their parental populations due to founder effect and bottlenecks (Dlugosch and Parker 2008). A review of the phylogenetic relationship between species within this genus based on variable molecular markers and morphological data, using large samples in their native range is

needed to determine the number of species that constitutes *Pterygoplichthys* and to identify with greater reliability the origin of the invasive populations.

Finally, it should be noted that two lineages of suckermouth armored catfish have been found for the *COI* marker, for all available *COI* sequences from Mexico. In this study conducted in the Grijalva and Usumacinta River basins, we found only one lineage belonging to *P. pardalis*, while *P. disjunctivus* is found in the Rio Grande (northern Mexico) (deposited in BOLD by Contreras and Garcia 2010, Appendix 1) and Río Hondo (Quintana Roo) (Schmitter-Soto et al. 2015) (Appendix 1). Thus, we can infer that independent introduction events have occurred in different areas of Mexico and probably from different source populations. Therefore, it is necessary to conduct a nationwide study, including individuals for sale in aquariums and fish farms, to estimate the diversity of the invasive group at the national level and to better identify the lineages present in the basins of the country.

Conclusions

The environmental conditions of the Grijalva and Usumacinta River basins are adequate for the establishment of populations of suckermouth armored catfish (*Pterygoplichthys* spp.), as these taxa have been reported in the region for the past 15 years. We did not find morphological differentiation between the morphotypes of suckermouth armored catfish in the study area. However, we found individuals' size differences between basins. In contrast to our expectations, the populations of the Grijalva and Usumacinta River basins share a single haplotype. Mitochondrial DNA data indicated that all our specimens belonged to *P. pardalis*, while the morphological diversity and their ability to adapt to a heterogeneous environment suggested that they could be of hybrid origin. The possible origin of *Pterygoplichthys* sp. in the Grijalva and Usumacinta River basins is from one or a few introduction events, followed by rapid dissemination and population growth resulting in its spread throughout this territory. Future studies could involve native populations of the species *P. pardalis* and *P. disjunctivus*; integrate biological, ecological, morphological, ontogenetic, taxonomic and genetic data; and incorporate nuclear markers of biparental inheritance to test the

hybrid origin hypothesis of these invasive populations. Our study highlights that there remains a lack of genetic information about *Pterygoplichthys* spp. in their native distribution, and that we need to better understand the phylogenetic relationships among taxa, including times of divergence, to adequately solve taxonomic uncertainties regarding introduced populations. Our study provides evidence that a combined genetic, morphological and ecological approach allows making inferences regarding the identity of an introduced fish and is needed for a better understanding about the invasive process.

Acknowledgements We thank Alejandra Bellizia Carrillo, Ana Cristina Carrillo Hernández, Inés Guadalupe García Cortes, Juan Carlos Martínez Juárez, José Francisco Miranda Vidal, Cinthia Trinidad-Ocaña, M.Sc., Juan Juárez Flores for their help during fieldwork. Biól. Maricela García Bautista and Laboratorio Institucional de Genética in ECOSUR for her help performing laboratory work and Dr. Lorena Ruíz Montoya. We are grateful to CONACYT, Mexico, for the master's degree fellowship, and the Maestría en Ciencias en Recursos Naturales y Desarrollo Rural—El Colegio de la Frontera Sur. We also thank Dr. Nicolas Álvarez Pliego, Dr. Alfonso González Díaz and Dr. Lorena Ruiz Montoya for their comments on an early version of the manuscript. We also thank anonymous reviewers and the associate editor for their comments, which helped us to greatly improve this manuscript.

Author's contributions AGV-R, GC-M and EB contributed to the study design and conducted field work; AGV-R conducted the laboratory work and analyzed the data; and all authors contributed to the discussion and preparation of the manuscript. All authors reviewed and approved the final version.

Funding Fondo de Investigación Científica y Desarrollo Tecnológico de El Colegio de la Frontera Sur (FID-784 project number 30013) "Invasion genomics: the suckermouth armored catfish (*Pterygoplichthys* sp.) in the Grijalva-Usumacinta". Operational funds from ECOSUR—Conservation of the Biodiversity to Gabriela Castellanos-Morales (project 3103711920). Research project—Caudal Ecológico del Río Usumacinta (WWF-ECOSUR 2017–2018) to Everardo Barba-Macias. Consejo Nacional de Ciencia y Tecnología (CONACyT) Master of Science degree scholarship to Alan G. Vargas-Rivas, Master's Thesis Support Program (PATM)—ECOSUR, Complementary Support Grant for Article Publication – ECOSUR to Alan G. Vargas-Rivas.

Availability of data and material Molecular data are available with GenBank accession numbers MZ313560 and MZ313561. Morphological data are in Supplementary Table S1.

Declarations

Conflict of interest The authors declare no conflicts of interest/competing interests.

Ethical approval The study complies with animal handling ethics approved by ECOSUR's ethics committee.

Consent to participate All authors provided consent to participate.

Consent for publication All authors provided consent to publish.

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