El Colegio de la Frontera Sur

"Análisis de la variación y estructura genética de dos especies del género *Pterygoplichthys* en la Cuenca Grijalva – Usumacinta"

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ECOSUR

Villahermosa, Tabasco, 22 de noviembre del 2021.

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"Análisis de la variación y estructura genética de dos especies del género *Pterygoplichthys* en la cuenca Grijalva – Usumacinta"

para obtener el grado de **Maestro en Ciencias en Recursos Naturales y Desarrollo Rural**

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Dedicatoria

La ciencia y la vida cotidiana no pueden y no deben ser separados

Rosalind Franklin

Dedico este trabajo a toda aquella persona que sea de su interés el tema y que invierta su tiempo leyendo este trabajo.

Con agradecimiento y amor, dedico este proyecto a mis padres, quienes han sido los pilares y motivación de mi vida.

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Resumen

La invasión biológica del bagre armado (*Pterygoplichthys* spp.) representa una de las problemáticas ambientales, económicas y sociales más importantes en la región sureste del país y que se extiende a nivel mundial. El objetivo del estudio fue caracterizar la diversidad y la estructura genética de las poblaciones del género *Pterygoplichthys* en las cuencas de los ríos Grijalva y Usumacinta a través de un análisis de dos regiones del ADN mitocondrial. A partir de esta información, junto con datos morfológicos y ambientales, se esperaba identificar la fuente y el número de eventos de introducción, así como realizar la identificación taxonómica molecular e identificar las características morfológicas que diferencian a las especies. Se recolectaron 124 individuos en seis localidades ubicadas en las cuencas de los ríos Grijalva y Usumacinta. Se realizaron análisis descriptivos de la variación de parámetros fisicoquímicos del agua en las localidades y de la variación morfológica de los ejemplares capturados. En la cuenca del rio Usumacinta existe diferenciación ambiental entre las localidades, contrario al río Grijalva con condiciones homogéneas. Las medidas morfométricas consideradas, no mostraron diferencias significativas entre morfotipos: *P. pardalis*, *P. disjunctivus* y *Pterygoplichthys* sp. Por otra parte, se observaron diferencias significativas en las tallas de los peces de las cuencas de los ríos Grijalva y Usumacinta. Finalmente, se analizó la diversidad genética y no encontramos variación ni estructura genética a nivel de ADN mitocondrial entre los sitios muestreados. Todos los ejemplares de bagre armado analizados pertenecen al linaje *P. pardalis* o son híbridos de origen. El haplotipo hallado en las cuencas de los ríos Grijalva y Usumacinta es el más abundante a nivel mundial. En conclusión, podemos inferir que las poblaciones de bagre armado estudiadas fueron introducidas en un solo evento seguido de una rápida expansión a lo largo del territorio considerado en el presente estudio.

Palabras claves: bagre armado, delimitación taxonómica, especie invasora, genética de poblaciones, pez diablo.

CAPÍTULO I

Introducción

Actualmente, estamos atravesando un periodo de pérdida de biodiversidad, y una de las mayores amenazas para la supervivencia de animales y plantas son las invasiones biológicas (McGeoch et al. 2010; Pyŝek and Richardson 2010; Dirzo et al. 2014). La inserción de individuos de especies invasoras en ecosistemas ajenos propicia el desplazamiento de las especies nativas y daña el funcionamiento de los ecosistemas naturales. Este es un problema a escala global que se extiende a través de fronteras, hábitats y grupos taxonómicos (Hulme 2009; Geller et al. 2010; Torchin y Ruiz 2014; Alonso y Castro-Díez 2015).

Se conoce como especie invasora a aquella especie no nativa (en ocasiones, también llamada exótica), con poblaciones capaces de sobrevivir, reproducirse y establecerse en hábitats y ecosistemas naturales, fuera de su área de distribución natural. Estas actúan como agente de cambio y representan una amenaza para la biodiversidad nativa, la economía o la salud pública (Comité Asesor Nacional sobre Especies Invasoras 2010; Barret 2015).

Los ecosistemas acuáticos son susceptibles a las invasiones biológicas y en los últimos años se está dando a un ritmo acelerado, esto porque no existen barreras contra la dispersión, porque el flujo de materia y energía suele ser más rápido que en los ecosistemas terrestres (Torchin y Ruiz 2014; Tepolt 2015), y porque existen condiciones que hacen más difícil de controlar la inserción de los organismos invasores. Las invasiones en ecosistemas acuáticos pueden ocurrir por procesos naturales, aunque en su mayoría están relacionadas con el desarrollo de actividades antropogénicas, como la transferencia de organismos por buques, el comercio internacional, la acuicultura, la pesca, tráfico de especies, entre otras (Giller et al. 2004; Torchin y Ruiz 2014).

El establecimiento de estas especies es un fenómeno ecológico y evolutivo interesante, y a través de la información genética de los invasores se pueden conocer a fondo sus características, procesos evolutivos y cambios a nivel genético (Bock et al. 2015). De esta manera, se pueden realizar inferencias sobre el éxito del proceso de adaptación y distribución, develar la diversidad críptica, rastrear el origen de los colonizadores y las

posibles rutas de introducción. Algunos autores llaman a esta disciplina "genética de la invasión" (Estoup y Guillemaud 2010; Bock et al. 2015; Rius et al. 2015; Bariche et al. 2017).

Las herramientas moleculares permiten un mejor entendimiento de los procesos de invasiones acuáticas, así como integrar la historia evolutiva a los datos ecológicos, a fin de desarrollar mejores planes de manejo (Rocha y Gasca 2007; Frankham 2010; Sherman et al. 2016). En este sentido, los estudios genéticos sobre especies invasoras acuáticas han sido útiles para conocer el proceso biológico de la invasión, identificarlas taxonómicamente, determinar número de eventos de introducción, rastrear rutas de introducción, identificar la variación adaptativa, así como proponer alternativas para el monitoreo y control de las especies. Tal es el caso de: el caracol trompeta de Malasia (*Melanoides tuberculata*) (Facon et al. 2003), la estrella de mar japonesa (*Asterias amurensis*), algas marinas (*Caulerpa taxifolia*), el cangrejo verde europeo (*Carcinus maenas*), cangrejo de Shanghai (*Eriocheir sinensis*) (Sherman et al. 2016), los góbidos de Ponto-Caspian (*Proterorhinus sp.*) (Janáč et al. 2017), y del pez león (*Pterois sp.*) (Bariche et al. 2017), por mencionar algunos ejemplos.

Las especies invasoras normalmente encuentran condiciones bióticas y abióticas que difieren de sus hábitats nativos, por lo tanto, la selección natural y su potencial de adaptación son factores determinantes durante las primeras etapas de colonización (Hargrove et al. 2017). Los niveles de variación genética presentes en las poblaciones de especies invasoras y su habilidad para adaptarse a ambientes nuevos están determinados por una serie de factores cómo el número de eventos de introducción, sus sitios de origen y el número de Individuos liberados durante los eventos de invasión (Dlugosch et al. 2015). Aquellas poblaciones establecidas a partir de un solo evento de introducción, con pocos individuos, suelen mostrar una reducción significativa en su diversidad genética en comparación con aquellas poblaciones establecidas por varias fuentes y eventos de introducción (Hargrove et al. 2017).

En el caso de las invasiones biológicas, se ha observado un aumento en la tasa de hibridación entre las poblaciones, invasoras y nativas (si las hay), del mismo género que están presentes en una región. Esto trae consecuencias negativas para la diversidad

biológica, puesto que los híbridos pueden tener mayor éxito de supervivencia (vigor híbrido), incrementando su éxito para invadir nuevos ambientes y desplazar a las especies nativas (Leprieur 2006; Gonzáles Zuarth y Vallarino 2014).

Una especie invasora modelo es el bagre armado, también llamado pez diablo (México), o plecos (Sudamérica). Estos peces dulceacuícolas pertenecen al género *Pterygoplichthys*, el cual está conformado de 16 especies (Orfinger y Goodding 2018; Anjos et al. 2019). Son originarios de zonas templadas y tropicales de Sudamérica: la cuenca alta del Amazonas (Brasil y Perú), del río Madeira (Brasil y Bolivia) y el río Orinoco (Venezuela). El uso en acuarios de las especies *Pterygoplichthys* spp., como peces de ornato y "limpia-peceras", ha propiciado su distribución en ecosistemas de todo el mundo. (Wakida–Kusunoki y Amador-del-Ángel 2008; Nico et al. 2012; Emiroğlu et al. 2016, Orfinger y Goodding 2018). Las especies *P. disjunctivus* y *P. pardalis* se han introducido exitosamente en México, Estados Unidos, Hawái, Indonesia, Malasia, Taiwán, Singapur, Filipinas, Japón, Puerto Rico e India (Orfinger y Goodding 2018).

El bagre armado posee un conjunto de características biológicas y fisiológicas que permiten su rápida adaptación y colonización de nuevos ambientes, condiciones como la falta de depredadores naturales, amplia tolerancia a diferentes ambientes acuáticos, comportamiento generalista, alta tasa reproductiva, cuerpo acorazado, resistencia a enfermedades, aletas con espinas y sus hábitos han contribuido a su proliferación en diferentes cuerpos de agua dulce del mundo (Mendoza Alfaro et al. 2009; Capps et al. 2011; Nico et al. 2012; Velázquez-Velázquez et al. 2013; Ríos-Muñoz 2015; Kumar et al. 2018; Orfinger y Goodding 2018; Lai et al. 2020; Aida et al. 2021).

La invasión del bagre armado tiene diversos impactos a nivel ecológico, económico y social, desafortunadamente las estrategias de control han resultado poco efectivas para la atención del problema (Greene and Lee 2009; Hoover et al. 2014; Orfinger y Goodding 2018). Entre las complicaciones está que los organismos del género *Pterygoplichthys* son difíciles de identificar, y algunos autores han sugerido que estos taxa en realidad constituyen a una sola especie con amplia variación fenotípica (Wu et al. 2011; Jumawan et al. 2011; Bijukumar et al. 2015; Sánchez et al. 2015). Algunos autores han sugerido eventos de hibridación entre dos especies (por ejemplo, *P. pardalis* x *P. disjunctivus* y *P.*

pardalis x *P. multiradiatus*), debido a la presencia de organismos con características intermedias en distintos sitios invadidos. Por lo tanto, se ha propuesto que esto juega un papel importante en el éxito invasor de este género (Wu et al. 2011; Jumawan et al. 2011; Bijukumar et al. 2015; Sánchez et al. 2015; Orfinger y Goodding 2018; Lai et al. 2020).

En México, las especies del género *Pterygoplichthys* representan un problema ambiental en diferentes cuerpos acuáticos, pues se ha expandido de manera alarmante en poco tiempo en ríos, lagos, lagunas y esteros (Wakida–Kusunoki y Amador-del-Ángel 2008; Sánchez et al. 2015). Se sabe que *Pterygoplichthys* spp. tiene poblaciones establecidas a lo largo del territorio nacional desde ~1995, que es una especie predominante y con amplia distribución (Wakida-Kusunoki et al. 2007; Barba y Cano-Salgado 2014; Sánchez et al. 2015). Se ha reportado su presencia en Campeche, Chiapas, Guerrero, Jalisco, Michoacán, Morelos, Sinaloa, Sonora, Tabasco, Tamaulipas y Veracruz (Amador del Ángel y Wakida-Kusunoki 2014).

Entre los sitios que se han visto afectados por la invasión biológica del bagre armado son las cuencas de los ríos Grijalva y Usumacinta, unos de los sistemas acuáticos de mayor extensión territorial en el país y que alberga el 64 % de la diversidad nacional (Toledo 2003; Comisión Nacional del Agua 2012). Además, contiene el 28 % de los recursos hídricos del país, teniendo la máxima disponibilidad de agua superficial del país (Sánchez et al. 2008). Estas cuencas se ubican en el sureste del país, y parte del alto Usumacinta se encuentra en Guatemala. En México, administrativamente, comprende los estados de Tabasco, Chiapas y pequeñas partes de Campeche (Toledo 2003).

Los ecosistemas de las cuencas de los ríos Grijalva y Usumacinta proveen servicios como la regulación de ciclos biogeoquímicos, mantenimiento de los flujos hidrológicos y recarga de los acuíferos, conservación de la productividad biológica y biodiversidad de sus ecosistemas. Además, tiene diferentes funciones ecológicas, tales como regulación climática, capacidad de recuperación frente a las perturbaciones, el control de flujos, la oferta de agua dulce, control de erosión, retención de sedimentos y formación de suelos, reciclaje de nutrientes, el tratamiento y control biológico de desechos, la creación de áreas de refugio para la fauna silvestre, el establecimiento de zonas de producción de alimentos y la conservación de bancos genéticos (Toledo 2003). En consecuencia, este

sistema propicia un área óptima para actividades como la pesca y acuacultura que generen un desarrollo sustentable y equitativo (Sánchez et al. 2008; Cano Salgado 2011).

Es importante mencionar que el sistema del río Grijalva cuenta con cuatro presas: Dr. Belisario Domínguez o La Angostura (la más grande del país), Manuel Moreno Torres o Chicoasén, Malpaso o Netzahualcóyotl (la tercera más grande) y Ángel Albino Corzo o Peñitas. Estas construcciones afectaron negativamente el potencial de acarreo de sedimentos y formación de suelos del río Grijalva (Toledo 2003; Comisión Nacional del Agua 2012). También el impacto ocasionado por las descargas de contaminantes domésticos e industriales ha ocasionado una reducción en los niveles de calidad de agua del sistema, afectando la diversidad de la vida acuática y proliferando el establecimiento de especies oportunistas (Marin Contreras 2014). En contraste, la cuenca del Río Usumacinta se considera una cuenca en mejor estado de conservación, dónde no se han reportado daños en la calidad del agua ni sobre los organismos asociados al sistema (PROFEPA 2015). Además, según reportes oficiales, las aguas de la cuenca del rio Usumacinta se encuentran dentro de los parámetros de calidad del agua y no se han observado efectos por contaminantes de origen industrial (PROFEPA 2015; Comisión Nacional del Agua 2020).

Se ha señalado que los bagres armados fueron introducidos a la región con fines ornamentales y para el control de algas (Ramírez Suárez 2012; Amador-del-Ángel y Wakida–Kusunoki 2014), aunque se desconocen el número de eventos de introducción y el origen de las poblaciones. Además, las inundaciones propias de los meses de crecida en el estado han sido un factor que contribuyó sustancialmente a su dispersión, en especial las de 1999, 2007 y 2009. Su proliferación se debe en parte al mal manejo de la especie en criaderos acuícolas, desde donde eran distribuidos para su venta en acuarios (Barba Macías et al. 2014).

A pesar del grave problema que representa la invasión de las especies *Pterygoplichthys* en las cuencas de los ríos Grijalva y Usumacinta aún no está bien resuelta la identidad taxonómica de las poblaciones establecidas en la región. En otras áreas de distribución (Filipinas, India, Taiwán y Vietnam) ya se han realizado análisis genéticos de las especies y los resultados sugieren que, en efecto, los organismos con patrones ventrales mixtos

de *P. pardalis* y *P. disjunctivus* son posibles híbridos (Wu et al. 2011; Jumawan et al. 2011; Bijukumar et al. 2015; Stolbunov et al. 2021).

De acuerdo con lo anterior, el objetivo de este trabajo es caracterizar la diversidad y la estructura genética de las poblaciones de bagre armado (*Pterygoplichthys* spp.) de las cuencas de los ríos Grijalva y Usumacinta a través de un análisis de dos regiones de ADN mitocondrial (citocromo b y citocromo oxidasa subunidad I). Esta información permitirá realizar la identificación molecular de las especies y delimitar las relaciones genéticas entre diferentes poblaciones de la región, así como profundizar en nuestra comprensión de la historia de esta invasión.

Se espera encontrar: (1) altos niveles de diversidad genética y diferenciación genética significativa entre las localidades muestreadas y entre las cuencas de los ríos Grijalva y Usumacinta, debido a la variación morfológica reportada y la distancia entre sitios de colecta; (2) linajes mitocondriales de al menos dos especies (*P. pardalis* y *P. disjunctivus*), lo cual sugeriría al menos dos eventos de introducción; (3) la presencia de casos sin correspondencia entre la caracterización morfológica y el linaje mitocondrial, sugerirá la presencia de híbridos *P. pardalis* x *P. disjunctivus.* Alternativamente, si existe de baja a intermedia variación genética y baja estructura genética, entonces, se puede inferir que hubo pocos eventos de introducción y que la amplia distribución de la especie en las cuencas de los ríos Grijalva y Usumacinta se debe a eventos de expansión demográfica. Finalmente, comparar las secuencias de la región con las reportadas para otros países permitirá identificar la posible población fuente.

Esta tesis contribuye a complementar el conocimiento existente de la taxonomía, ecología y evolución de este género, así como, promover el manejo adecuado del bagre armado y generar estrategias de monitoreo y control más eficientes. El presente trabajo está conformado de tres capítulos, en el primer capítulo se presenta una introducción general y el marco de referencia del estudio. En el segundo capítulo, se incluye el manuscrito de artículo científico titulado "Putative identity of the exotic sailfin catfish (*Pterygoplichthys* spp.) from the Grijalva and Usumacinta river basins" en el cual se exponen y discuten los principales resultados de este estudio. En el tercer capítulo, se enlistan las principales conclusiones y perspectivas derivadas de este trabajo. Posteriormente, se presenta la

lista de referencias citadas a lo largo de los capítulos uno y tres. Finalmente, se incluye como anexo un artículo de divulgación publicado que se titula "¡El diablo anda suelto! La invasión biológica del bagre armado (*Pterygoplichthys* spp.)", y es producto de esta tesis.

CAPÍTULO II.

Artículo sometido a la revista *Biological Invasions*, índice *Journal Citation Reports* con factor de impacto 3.13.

Putative identity of the exotic suckermouth armored catfish (*Pterygoplichthys* spp.) in the Grijalva and Usumacinta River basins, Mexico.

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Abstract: South American suckermouth armored catfish (*Pterygoplichthys* spp.) are invasive species that cause severe environmental and socioeconomic impacts. In the Grijalva and Usumacinta Rivers basin the species *Pterygoplichthys pardalis, Pterygoplichthys disjunctivus* and possible hybrids have been identified based on ventral spots pattern. In this study we aimed at solving the taxonomic uncertainty regarding the *Pterygoplichthys* spp. individuals that inhabit this area. We used genetic data to make inferences about the number of invasion events and the possible origin of the invasive population. We sampled three zones of each of the river basins. We analyzed the environmental variation in the sampling sites based on physico-chemical properties, and we observed that in the Usumacinta River there is environmental differentiation between sampling sites while in the Grijalva River the environment is homogeneous. We analyzed the morphological variation between the morphotypes based on three morphological characteristics. Our results suggest that there are no differences between the morphotypes, in addition to the variation in the ventral patterns, and we observed size differences between basins. We amplified the *CYTB* and *COI* mitochondrial DNA regions, and we found that the fish in the Grijalva and Usumacinta River basins share a unique haplotype. Accordingly, all the specimens of the suckermouth armored catfish in both basins are *P. pardalis* or of hybrid origin, and the lack of diversity and genetic structure in the mitochondrial DNA suggests that they have a common origin and that there were one or few introduction events, followed by rapid spread and population growth.

Keywords: Genetic diversity; invasive species; Loricariidae; mitochondrial markers; morphological variation.

Conflict of interest/Competing interest

The authors declare no conflicts of interest/competing interests.

Availability of data and material

Molecular data are available with GenBank accession numbers MZ313560 and MZ313561.

Morphological data are in Supplementary Table S1.

Author's contributions

Alan G. Vargas-Rivas, Gabriela Castellanos-Morales and Everardo Barba contributed to the study design and conducted field work; Alan G. Vargas-Rivas 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.

Ethics 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.

Introduction

Biological invasions represent complex agents of change because they modify communities (Pyŝek 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 (Pyŝek and Richardson 2010; Harvey-Samuel et al., 2017). Current approaches and strategies to manage the expansion of some invasive populations have resulted 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 and obtaining information about the demographic history and population structure of invasive species, and at the same time, they allow assessing the impact of invasive species and delineating control measures (Rocha and Gasca 2007; Richardson and Pyŝek 2008; Frankham 2010; Barret 2015; Sherman et al. 2016). More importantly, genetic analyses allow identifying the events and routes of introduction of invasive taxa, as well as inferring the interactions between different invasive populations and the mechanism underlying successful invasion events (Barret 2015; Bock et al. 2015; Sherman et al. 2016). Therefore, population genetics should play a key role in the study of invasive species.

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 complexity of the group 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). Thus, clarifying taxonomic uncertainties is key for adequately controlling and managing this biological invasion because it enables the number and origin of invasive populations and the role of hybridization in invasion success to be determined (Bock et al. 2015).

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). However, they have shown wide tolerance to new environments. For instance, it has been reported that they can withstand minimum temperatures ranging from 8.8 to 11 °C (Mendoza Alfaro et al. 2009). 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, and some species show resistance to saline conditions (Capps et al.

2011; Cano-Salgado and Barba 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: 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). Furthermore, they have shown resistance to diseases and the ability to adapt easily, and 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. Accordingly, these studies have shown that individuals with intermediate morphological characteristics might be *P. disjunctivus x 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 for these taxa (Wu et al. 2011; Bock et al. 2015).

In southeastern Mexico, individuals of *Pterygoplichthys* spp. have been present since early 2000 (Wakida-Kusunoki and Amador del Ángel, 2008). In particular, 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 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 both *P. disjunctivus* and *P. pardalis* coexist in aquatic environments in this region and 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).

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), based on two mitochondrial DNA regions (cytochrome b and cytochrome oxidase subunit I), and considering morphological differentiation between three morphotypes and the environmental differentiation 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. The number of lineages and the relationship between them can be used to infer the possible number of introduction events for invasive species. Therefore, finding more than one lineage could indicate that there were two or more introduction events in the Grijalva and Usumacinta River basins. Finally, by comparing the identities of the mitochondrial sequences found in the present study to sequences deposited in the NCBI and BOLD database, we expect to identify the putative origin of the invasive population in the region.

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). Moreover, the study area covers 102, 465 km^2. 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 (Comisión Nacional del Agua 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 productive regions in terms of ecosystem services (Tapia-Silva et al. 2015.). The Usumacinta River has a total length of approximately 1,100 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 (Comisión Nacional del Agua 2012). As a result, seasonal changes in water volume and environmental parameters are different in each river (Ramos-Herrera et al. 2012).
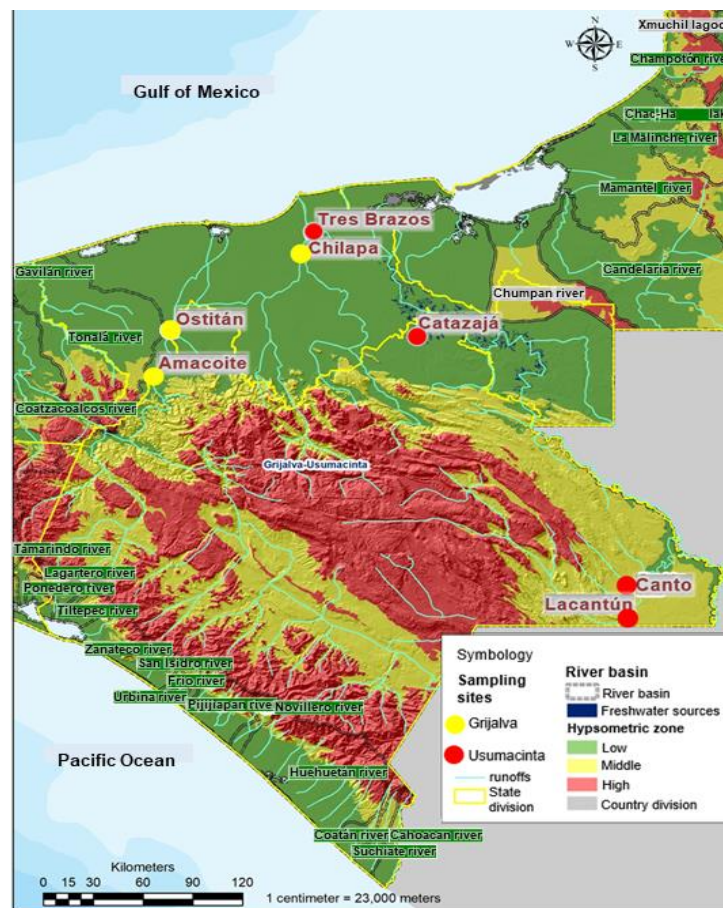
Fig. 1 Sampling sites in the Grijalva and Usumacinta River basins. The sites in the Grijalva River are Chilapa, Amacoite and Ostitan (yellow dots). The sites in the Usumacinta River are Canto and Lacantún, Catazajá and Tres Brazos (red dots). Sampling was performed from April to August 2018. Graphic was made with QGIS v.3.16 software

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, and 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).

We conducted an exploratory analysis of environmental differentiation between rivers and among sampled locations, first 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 2019). 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. Thus, we removed DO and salinity for the environmental analyses. We used the estimated mean of each variable to perform an ANOVA and a principal component analysis (PCA). Analyzes were conducted in XLSTAT 2021 (Addinsoft 2020, USA).

Morphotype classification and morphometric analysis

Suckermouth armored catfish specimens were captured using 50 m by 3.5 m weighted gillnets overnight. The sampling effort was the same among the areas. 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). 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 cm^2 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, in the PCA used to analyze size differences between basins, we standardized the data using the unbiased normalization (n-1) (Gal and Rubinfeld 2019), 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).
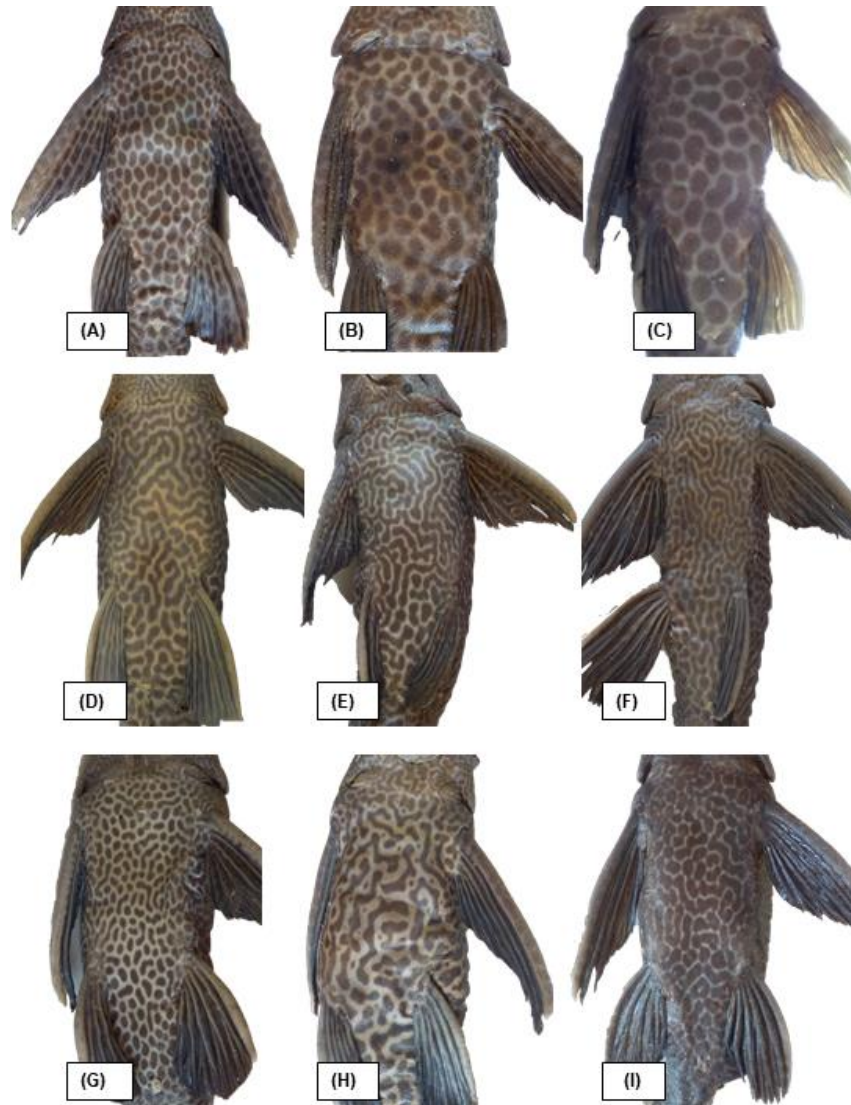
Fig. 2 Variations in ventral spots of the Amazon sailfin catfish (*Pterygoplichthys* spp.) in the Grijalva and Usumacinta River basin. Photos A to C represent the *P. pardalis* morphotype with discrete ventral spots; D to F are individuals identified as the *P. disjunctivus* morphotype with ventral vermiculations; and G to I are specimens from *Pterygoplichthys* sp. morphotype with mixed patterns of spots, classified as intermediate forms between the former two groups

Molecular data collection

The regions of the cytochrome b (*CYTB)* gene and cytochrome oxidase subunit I (*COI*) have been widely used for molecular identification, species delimitation, and the analysis of phylogenetic relationships (Rosero-Galindo et al. 2016; Scheinsohn et al. 2016). Mitochondria, being maternally inherited and not recombining, are especially useful for uncovering lineage-related phylogeographic histories and genetic structure; in addition, mitochondria allow making inferences of demographic changes and dispersal patterns (Avise et al. 1987; Rentaría Alcántara 2007; Hickerson et al. 2010).

DNA extraction was carried out based on the phenol:chloroform:isoamyl alcohol method, and DNA integrity was visualized by gel electrophoresis in 1X 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 AAA AT 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 $(NH_4)_2 SO_4$ 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 minutes followed by 35 cycles at 94 °C for 30 seconds, 55 °C for 40 seconds and 72 °C for 90 seconds with a final extension step at 72 °C for 10 minutes (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 $(NH_4)_2 SO_4$ 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 minutes, followed by 40 cycles at 95 °C for 30 seconds, 50 °C for 40 seconds, and 72 °C for 1 minute with a final extension step at 72 °C for 7 minutes (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).

Genetic identity

To conduct the molecular identification and to determinethe possible population of 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). I 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).

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

Site	pH	Temperature (°C)	Total dissolved solids (mg L^{-1})	Dissolved oxygen (mg L^{-1})	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
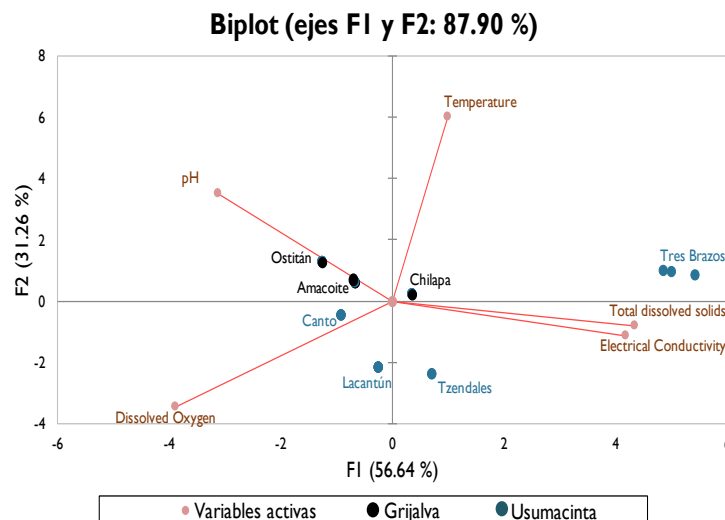
Fig. 3 Principal component analysis (PCA) of environmental parameters for sites of the suckermouth armored catfish (*Pterygoplichthys* spp.) collected in the Grijalva and Usumacinta River basins during the dry season. The sites in the Grijalva River basin are Chilapa, Amacoite and Ostitan (black dots), 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 from XLSTAT 2021

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 standardize data between morphotypes ($p > 0.05$, Kruskal Wallis test) (Supplementary data file S2).

Table 2 Morphometric measures (average ± standard deviation) of the three morphotypes of Amazon sailfin 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	*P. pardalis*	*P. disjunctivus*	*Pterygoplichthys* sp.
Standard length - SL (cm)	25.36 ± 0.8	24.21 ± 1.00	22.02 ± 0.61
Height - H (cm)	4.76 ± 0.16	4.51 ± 0.21	4.04 ± 0.12
Cleithral width - CW (cm)	5.82 ± 0.25	5.58 ± 0.24	5.20 ± 0.16
Ventral width - VW (cm)	4.76 ± 0.12	4.53 ± 0.21	4.29 ± 0.08
Weight - W (g)	329.23 ± 31.26	266.29 ± 3.30	207.15 ± 17.08

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.

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.
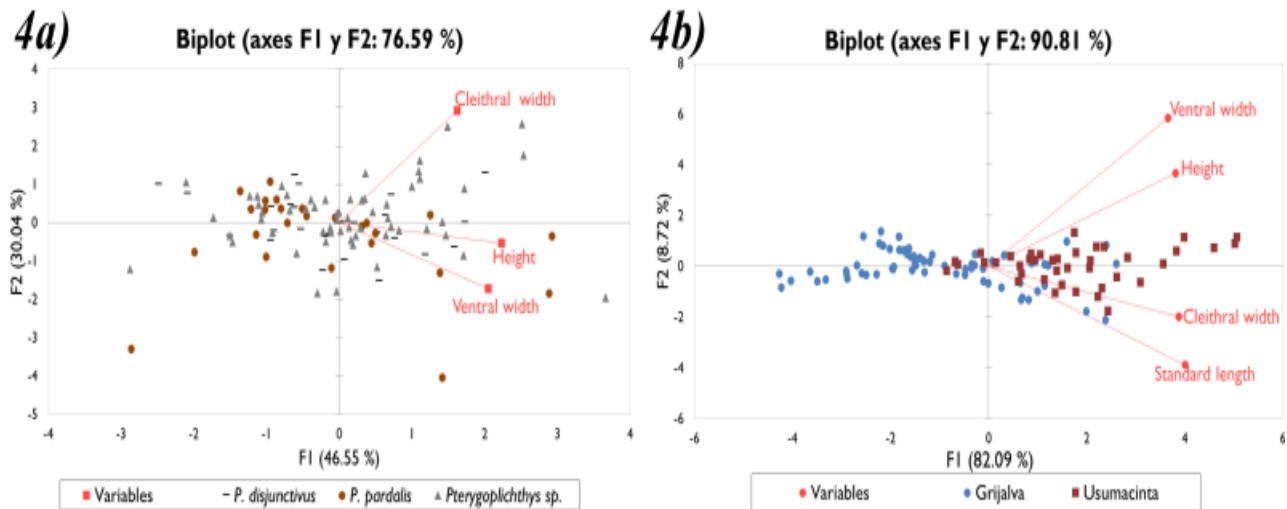
Fig. 4. Principal component analysis (PCA) of suckermouth armored catfish (*Pterygoplichthys* spp.) in the Grijalva and Usumacinta River basins: 4a) analysis of linear morphometric characteristic metrics of *Pterygoplichthys* sp. specimens, grouped by morphotype (ventral spots). 4b) analysis for *Pterygoplichthys* sp. morphometric characteristics, grouped by captured site (river basin). Graphic was obtained from XLSTAT 2021

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

 The analysis 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, 6 haplotypes have been reported: 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 (Fig. 5 and Fig. 6).
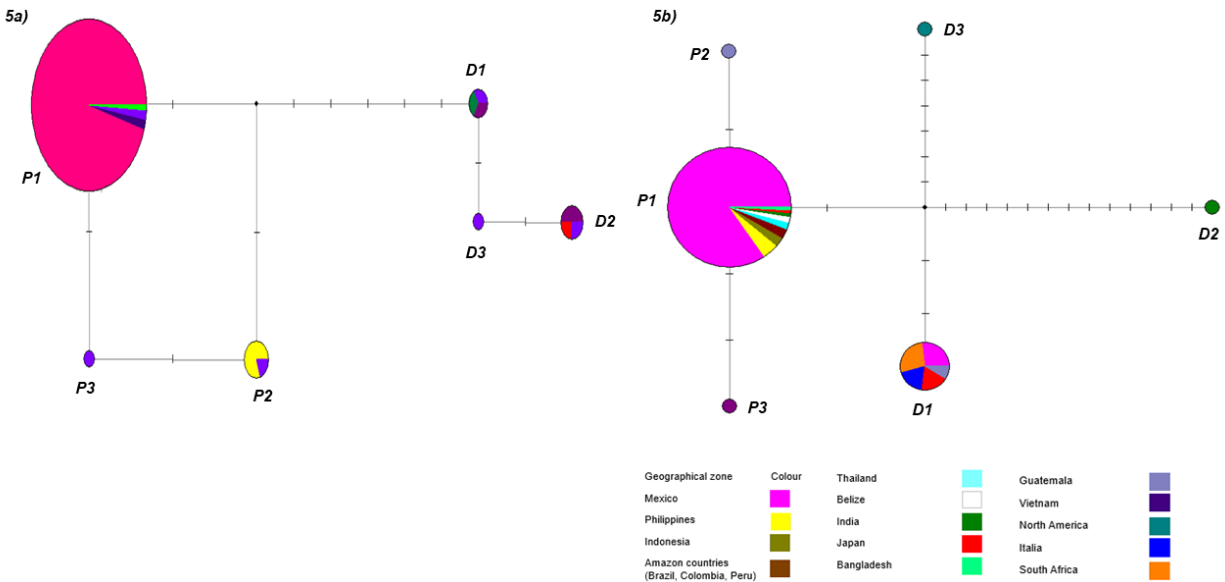
Fig. 5 Median-joining haplotype network of suckermouth armored catfish (*Pterygoplichthys* spp.) based on mtDNA *CYTB* (5a) and *COI* (5b) haplotypes. Sequences include the haplotypes obtained for the specimens sampled in the Grijalva and Usumacinta River basins in the present study as well as those 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

In the *CYTB* haplotype network (Fig. 5a), the most common haplotype P1 has also been reported in an individual native to Brazil and in invasive 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 invasive 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 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.
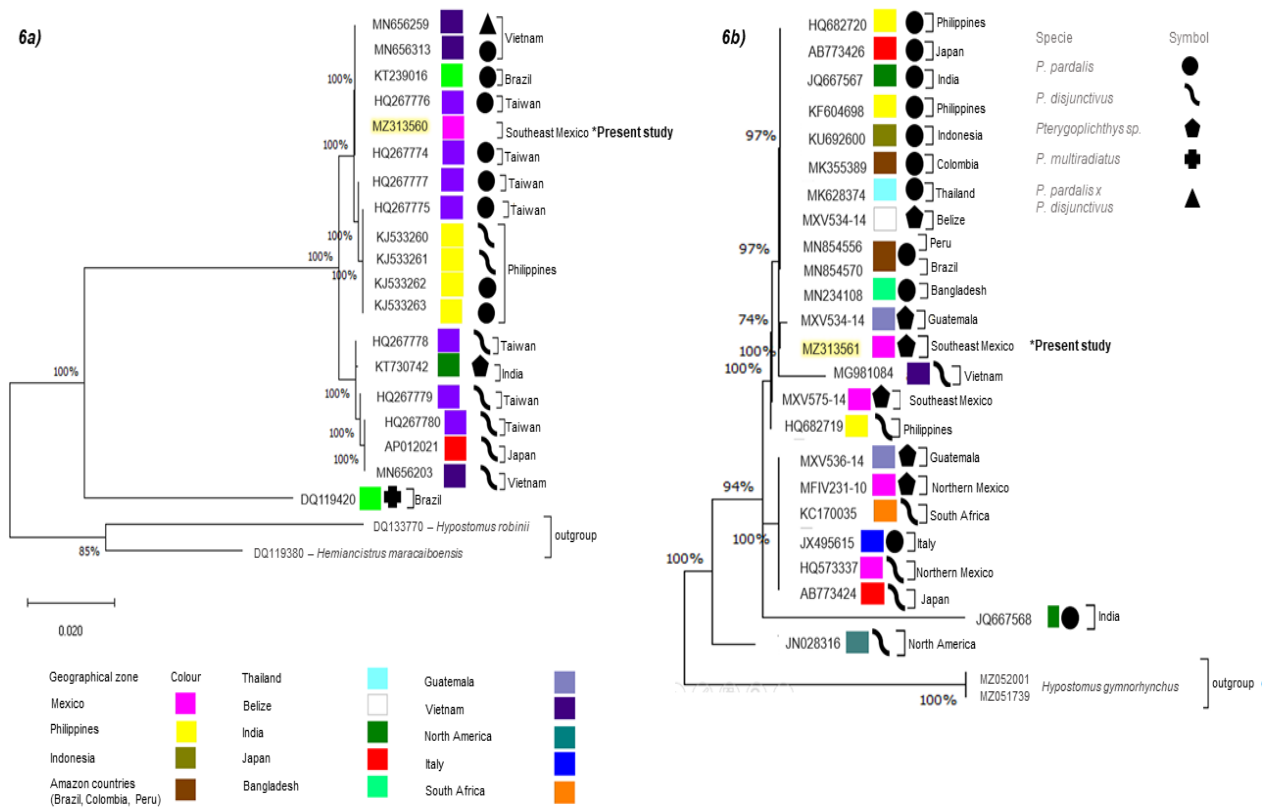
Fig. 6 Maximum probability trees for the suckermouth armored catfish (*Pterygoplichthys* spp.) based on mtDNA *CYTB* (6a) and *COI* (6b) haplotypes. Sequences include the haplotypes obtained in the present study for the Grijalva and Usumacinta River basins (highlighted), and sequences available in the 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

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. These differences could be due to the conditions of each river since the Grijalva River has four dams that have reduced the potential for sediment transport and soil formation (Toledo 2003; Comisión Nacional del Agua 2012). Ramos-

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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). Nevertheless, it is worth mentioning that our environmental analysis is exploratory and based on data for the dry season. Therefore, we suggest performing a wider study which includes a higher number of sampling sites along the environmental gradient and considers the temporal variation.

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; Marín Contreras 2014; Gómez-González et al. 2015; Sánchez et al. 2015b; Cruz-Ramírez et al. 2019a). 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. 2019b). 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).

Regarding the levels of EC and salinity (correlated), 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). There is no evidence of their presence in brackish waters, nor has their distribution been related to the salinity gradient in other countries (i.e., Vietnam), (Lai et al. 2020). In the present study, no direct association is apparent between the EC/salinity factor and the abundance of *Pterygoplichthys* spp.

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. 2009; 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 two years of life (Hoover et al. 2004).

Similarly, in other countries where these species are invasive (i.e., India, Malaysia, Sri Lanka, Turkey, and Vietnam), differences between the morphometric and meristic characteristics that allow identifying the morphotypes have been

observed. 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*. In contraste to our findings, 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 invasive specimens into three groups: *P. pardalis*, *P. disjunctivus* and *P. disjunctivus* x *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, more likely, 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 found in the present study might be related to the low number of characteristics analyzed and to possible yhybridization (Nico et al. 2012, Wu et al. 2012; Godwin et al. 2016).

 Taxonomic delimitation within the genus *Pterygoplichthys* is 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 *P. pardalis*, *P. disjunctivus* and other species of the genus could represent a single species with high morphological variation (Jumawan et al. 2011; Wu et al. 2011; Zworykin and Budaev 2013). Therefore, it is necessary to perform phylogenetic and taxonomic studies within the genus based on samples from the native range of the species. Similarly, it is necessary to carry out a study that analyzes all meristic, morphological and morphometric measurements and correlates this information with high 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) (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).

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 is a lack of genetic diversity in the invasive 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, there is a lack of population genetics studies in their native site – Jumawan et al. (2011) also mentioned this lack of information. This 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, up to seven haplotypes have been found for the *CYTB* region (Wu et al. 2011; Stolbunov et al. 2021) and six in *COI* (Jumawan et al. 2011). High levels of genetic diversity were found in Vietnam (Stolbunov et al. 2021) and Taiwan (Wu et al. 2011) with haplotypes corresponding to the lineages *P. pardalis* and *P. disjunctivus*. In the Philippines, fewer haplotypes have been reported than in Vietnam and Taiwan.

The lack of genetic diversity in our results is presumably 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). In this sense, we can infer that the populations established in the Grijalva and Usumacinta River basins are 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, can also contribute to the lack of genetic variation between populations (Roman and Darling 2007; Dlugosch et al. 2015). In addition, it has been suggested that most invasive populations experience decreased genetic diversity, and it is very likely that founder populations experience periods of isolation (Dlugosch and Parker 2008). However, these populations can also experience large and rapid adaptive changes after their introduction (Dlugosch and Parker 2008).

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*. Although the Grijalva River is a dammed system –which may represent genetic barriers –, there seems to be no effect on the genetic differentiation of populations for mtDNA, although we did find differences in the size of the organisms. Baggio et al. (2018) evaluated the effect of dams on genetic diversity in neotropical fish populations, and they found that in most cases, no genetic differentiation has been found between populations.

To understand these results, it is important to consider the biology of suckermouth armored catfish. These fish are usually very active; they can swim vigorously upward and move between habitats (i.e., spring channels and rivers), with a high mobility and dispersal capacity (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.

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 incorporate molecular markers of biparental inheritance in the analyses to estimate the degree of introgression in the genomes of these invasive populations. With this information, it could also be determined whether the variation shared between species is related to the retention of ancestral traits, incomplete lineage sorting, or recent hybridization. The levels of gene flow between sites in a basin could also be determined. In addition, this type of data would allow us to obtain 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 invasive 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).

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 *P. pardalis*, *P. disjunctivus* and *P. multiradiatus* could be the same species (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). In addition, 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 areas of distribution is needed to determine the number of species that constitutes *Pterygoplichthys* and to identify with greater reliability the organisms 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) 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.

Conclusion

The environmental conditions of the Grijalva and Usumacinta River basins are adequate for the establishment of populations of suckermouth armored catfish (*Pterygoplichthys* spp.), and management, control and mitigation plans should consider factors associated with low water quality and pollution. We did not find morphological differentiation between the morphotypes of suckermouth armored catfish in the study area. Nevertheless, we did find 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 indicate that all our specimens belong to the species *P. pardalis,* while the morphological diversity and their ability to adapt to a heterogeneous environment suggests 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. It is necessary to conduct studies that 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 is a lack of 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 invasive populations.

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Appendix 1

Appendix 1. Molecular data (sequences) of *Pterygoplichthys* spp. used to perform molecular analysis.These sequences of the *Pterygoplichthys* genus and outgoups were obtained from Genbank–NIH and BOLDSystems v4 databases.

Taxon identification	Geographical zone	Status	Accession number	Reference
Cytochrome B (CYTB)				
Pterygoplichthys sp.	Southeastern Mexico	Invasive	MZ313560	This study
	India	Invasive	KT730742	Bijukumar et al. 2015 (Unpublished)
Pterygoplichthys pardalis	Amazon rainforest - Brazil	Native	KT239016	Moreira et al. 2019
	Filipinas	Invasive	KJ533262 KJ533263	Yu and Quilang 2014
	Taiwan	Invasive	HQ267774 HQ267775 HQ267776 HQ267777	Wu et al. 2010
Pterygoplichthys disjunctivus	Filipinas	Invasive	KJ533260 KJ533262	Yu and Quilang 2014
	Japan	Invasive	AP012021	Nakatani et al. 2011
	Taiwan	Invasive	HQ267779 HQ267780	Wu et al. 2010
	Vietnam	Invasive	MN656203	Stolbunov et al. 2021
P. pardalis x *P. disjunctivus*	Vietnam	Invasive	MN656259	Stolbunov et al. 2021
P. multiradiatus	Brazil	Native	DQ119420	Hardman 2005
H. robinii	South America	Outgroup	DQ133770	Evans et al. 2016 (Unpublished)
H. maracaiboensis	South America	Outgroup	DQ119380	Hardman 2005
Cytochrome oxidase subunit I (COI)				
Pterygoplichthys sp.	Southeastern Mexico	Invasive	MZ313561	This study
		Invasive	MXV575-14 (BOLD)	Schmitter-Soto 2014(Unpublished)
	Northern Mexico	Invasive	HQ573337	Contreras and Garcia 2010 (Unpublished)
		Invasive	MFIV231-10	Contreras and Garcia 2010 (Unpublished)
	Belize	Invasive	MXV533-14 MXV534-14	Schmitter – Soto 2013 (Unpublished)
	Guatemala	Invasive	MXV536-14	Schmitter – Soto 2013 (Unpublished)
P. pardalis	Bangladesh	Invasive	MN234108	Ahmed et al. 2019 (Unpublished)
	Brazil	Native	MN854570	Queiroz et al. 2020

	Colombia	Invasive	MK355389	Papamija et al. 2018 (Unpublished)
	India	Invasive	JQ667567 JQ667568	Khedkar et al. 2012 (Unpublished)
	Indonesia	Invasive	KU692600	Dahruddin et al. 2016
	Italy	Invasive	JX495615	Walter et al. 2012 (Unpublished)
	Japan	Invasive	AB773426	Mukai et al. 2014 (Unpublished)
	Peru	Native	MN854556	Queiroz and Montoya-Burgos 2020
	Philippines	Invasive	HQ682720; KF604698	Aquino et al. 2011; Quilang and Yu 2014 (Unpublished)
	Thailand	Invasive	MK628374	Panprommin et al. 2019
P. disjunctivus	Japan	Invasive	AB773424	Mukai and Yodo 2013
	North America	Invasive	JN028316	April et al. 2011
	Nothern Mexico	Invasive	HQ573337	Contreras-Arquieta and Garcia 2010
	Philippines	Invasive	HQ682719	Aquino et al. 2011
	South Africa	Invasive	KC170035	Jones et al. 2013 (Unpublished)
	Vietnam	Invasive	MG981084	Quyen et al. 2018
H. gymnorhynchus	French Guiana	Outgroup	MZ052001 MZ051739	Papa et al. 2021

Supplementary file S1 and S2

https://1drv.ms/x/s!AtjsTpgwf--6hYgkPtH3_s5KKUvlRA?e=iPz0Uh

CAPÍTULO III.

Conclusiones generales y perspectivas

- La cuenca del río Usumacinta presenta diferencias ambientales entre los sitios muestreados, en contraste con la cuenca del río Grijalva dónde las condiciones son más homogéneas en la temporada de secas.

- A nivel morfológico, no observamos diferenciación entre los morfotipos de bagre armado (*Pterygoplichthys* sp.), por lo que la separación está basada únicamente en el patrón ventral. Es importante considerar que existe discrepancia entre la identificación morfométrica y la identificación molecular.

- Se encontraron diferencias en las tallas entre los ejemplares capturados en las cuencas de los ríos Grijalva y Usumacinta, lo cual debe abordarse de manera detallada en futuros estudios.

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- Contrario a lo esperado, se encontró solo un haplotipo para las cuencas de los ríos Grijalva y Usumacinta. A partir de este resultado, inferimos que todos los bagres armados (*Pterygoplichthys* spp.) pertenecen a un mismo linaje mitocondrial: *P. pardalis,* o son de origen híbrido.

- El único haplotipo hallado coincide con el reportado para el sitio de origen (cuenca del río Amazonas) y es el más abundante en poblaciones invasoras a nivel mundial. Dicho haplotipo es diferente al reportado para ejemplares de bagre armado de las cuencas del río Bravo y el río Hondo, identificados como *P. disjunctivus*.

- La falta de diversidad genética a nivel mitocondrial sugiere que hubo un solo evento de introducción en las cuencas de los ríos Grijalva y Usumacinta.

- No encontramos estructura genética en las cuencas de los ríos Grijalva y Usumacinta, esto puede deberse a la alta movilidad del bagre armado.

- Los resultados apoyan la hipótesis alternativa, la cual sugiere que hubo pocos eventos de introducción y que la amplia distribución de la especie en las cuencas

de los ríos Grijalva y Usumacinta se debe a eventos de rápida adaptación, expansión demográfica y alta movilidad del organismo.

Perspectivas

- Sugerimos realizar investigación de tipo ecológico, dónde se estimen índices de abundancia y parámetros poblacionales para develar sí existe correlación entre las condiciones ambientales de las cuencas de los ríos Grijalva y Usumacinta y la abundancia del bagre armado.

- Recomendamos realizar muestreos que abarquen una mayor área de las cuencas y capturando mayor número de ejemplares: para analizar las relaciones entre tallas y las condiciones ambientales, para tener mejor representación del gradiente ambiental y para realizar análisis finos de estructura genética con base en otros marcadores moleculares.

- Proponemos realizar estudios para evaluar la adaptación del bagre armado en ambientes invasores, comparándola con la adaptación en su distribución nativa con el objetivo de estimar los niveles de tolerancia que presenta a diferentes parámetros del agua. Esta información, podría resultar útil para identificar las condiciones que explican la abundancia y dispersión de la especie en ambientes colonizados.

- Recomendamos realizar análisis genéticos con marcadores moleculares altamente variables y de herencia biparental (microsatélites nucleares y SNPs), a fin de distinguir el grado de introgresión en las poblaciones invasoras.

- Sugerimos realizar un estudio que recabe datos moleculares de individuos *P. pardalis* y *P. disjunctivus* provenientes del sitio de origen (la cuenca del Amazonas), con el fin de comprobar los niveles de diversidad en ese sitio y poder hacer comparaciones con poblaciones invasoras de México y otros países.

- Consideramos pertinente realizar análisis genéticos que incluyan ejemplares de las diferentes cuencas en México dónde se han reportado poblaciones de bagre armado. Incluso se debe considerar obtener muestras de acuarios y tiendas de

mascotas para profundizar en el conocimiento de la dinámica de invasión de estos taxa en nuestro país.

- Nos parece importante integrar información sobre la biología, ecología, morfología, ontogenia, taxonomía y genética del bagre armado en su distribución nativa y ambientes invadidos, con la finalidad de resolver dudas relacionadas a la delimitación de especies y a un mejor entendimiento de las relaciones filogenéticas entre taxones. Así como, integrar esta información al manejo y estrategias de control del bagre armado.

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Anexo 1.
¡El diablo anda suelto! La invasión biológica del bagre armado (*Pterygoplichthys* spp.)

Artículo de divulgación publicado a la revista Hypatia No. 67 del Consejo de Ciencia y Tecnología del Estado de Morelos parte del índice de revistas CONACYT. Disponible en: https://www.revistahypatia.org/el-diablo-anda-suelto-la-invasion-biologica-del-bagre-armado-pterygoplichthys-spp.html

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Archivo: Ciencias ambientales

Cuando escuchamos el término "especie invasora" podríamos pensar en seres extraterrestres capaces de conquistarnos y, francamente, los bagres armados o peces diablo (*Pterygoplichthys* spp.) parecerían no ser de este planeta. Estas especies originarias del Amazonas (Brasil, Colombia y Perú) se consideran invasoras, pues sus poblaciones han logrado sobrevivir, reproducirse y establecerse en hábitats naturales de todos los continentes (excepto en la Antártida).

También conocidos como plecos o "limpia–peceras", están en México desde la década de 1990, y se identificaron por primera vez en la presa del Infiernillo (de ahí el apodo de diablos) en Michoacán. Actualmente, los podemos encontrar de norte a sur. En el sureste del país, predominan dos especies, que se diferencian por las manchas oscuras de su vientre: *Pterygoplichthys disjunctivus* con vermiculaciones (marcas en forma de gusanitos) y *Pterygoplichthys pardalis* con puntos redondeados (figura 1).
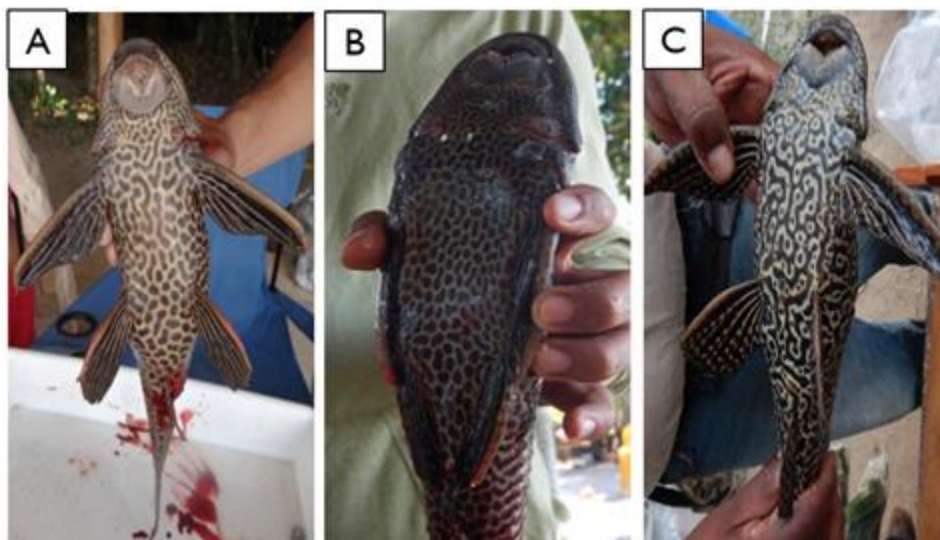
Figura 1. Bagres armados capturados en Tabasco: A) *Pterygoplichthys disjunctivus*; B) *Pterygoplichthys pardalis*; C) *Pterygoplichthys* sp (Barba, 2018).

Los bagres armados tienen características que los mantienen bien protegidos de los depredadores: su cuerpo está cubierto por una coraza de placas óseas como una armadura (de ahí que se le conozca como bagre armado) y sus aletas tienen forma de espinas. Pueden medir hasta 55 cm de adultos y viven alrededor de 5 años; su boca tiene forma de ventosas (que les permite adherirse a las riberas de los ríos o acuarios).

Los plecos cuentan con una tasa de reproducción muy alta, y anualmente llegan a desovar entre 500 y 3 mil huevos. Son organismos territoriales y muy resistentes, que pueden vivir en hábitats con distintos grados de acidez, sobreviven en aguas contaminadas, residuales, a bajas temperaturas (menores a 10 °C), condiciones con poco oxígeno (hipoxia) y pueden mantenerse vivos hasta 20 horas fuera del agua.

Podríamos pensar que unos peces que se adquieren en un acuario (figura 2) no representan riesgo, pero tristemente no es así. La presencia del bagre armado genera daños ambientales, pues al construir sus nidos en las riberas de los ríos causa problemas de sedimentación y turbidez; además, desplaza a las especies nativas por la ingesta de sus huevos y la competencia por recursos. Las aves acuáticas y mamíferos, como el manatí (figura 3), pueden resultar dañados al interactuar con estos peces.

Figura 2. Plecos de venta en acuario.

Figura 3. Bagres armados nadando junto a manatí en Florida (Berchem, 2019).

La invasión por plecos ocasiona daños económicos que ascienden a los $317 millones de pesos. Disminuyen la pesca, propicia la pérdida de empleos y daños a los motores de las embarcaciones, muelles y puertos (figura 4). Esto sin contar que pueden lastimar las manos de los pescadores por sus espinas. Por último, la presencia del pez diablo puede causar la pérdida de la diversidad biocultural, identidad y tradiciones relacionadas con las especies nativas.

Figura 4. Captura de plecos por pescadores tabasqueños (Barba, 2018).

Para reducir las poblaciones de pez diablo se ha recomendado consumir su carne, emplearlos en la elaboración de alimento para ganado, abono, biogás y artesanías. No obstante, el desagrado por su apariencia y la creencia de que almacenan metales pesados ha frenado el éxito de estas medidas; aunque son muy consumidos en Sudamérica y las investigaciones apuntan que su carne tiene un alto valor nutricional (alta en proteínas, ácidos grasos omega 3 y 6), y que no sobrepasan los niveles de mercurio, plomo o cadmio autorizados por la norma mexicana.

El bagre armado se adapta con facilidad y, desde el punto de vista evolutivo, resulta fascinante. Se han estudiado desde su llegada al país, pero aún existen dudas sobre cuántas especies hay presentes en México y si existe hibridación entre especies. Además, no se ha estudiado su diversidad y potencial adaptativo; asimismo, se desconoce de dónde provienen los individuos que se han establecido en México.

En el departamento de Conservación de la Biodiversidad de ECOSUR-Villahermosa actualmente trabajamos en un proyecto a nivel genético sobre estas especies, que permitirá llenar algunos vacíos de información y sumará para lograr un manejo adecuado de la invasión del bagre armado.