Zoological Studies **57:** 7 (2018)
doi:10.6620/ZS.2018.57-07

Zoological Studies

Open Access

The Global Invasion of the Suckermouth Armored Catfish Genus *Pterygoplichthys* (Siluriformes: Loricariidae): Annotated List of Species, Distributional Summary, and Assessment of Impacts

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(Received 1 November 2017; Accepted 25 January 2018; Published 14 February 2018; Communicated by Hin-Kiu Mok)

Citation: Orfinger AB, Goodding DD. 2018. The global invasion of the suckermouth armored catfish genus *Pterygoplichthys* (Siluriformes: Loricariidae): annotated list of species, distributional summary, and assessment of impacts. Zool Stud **57:**7. doi:10.6620/ZS.2018.57-07.

Alexander Benjamin Orfinger and Daniel Douglas Goodding (2018) The suckermouth armored catfish genus *Pterygoplichthys* (Siluriformes: Loricariidae) includes popular aquarium fishes and constitutes one of the most successful freshwater invasive taxa, having achieved global distribution. To date, however, no comprehensive distributional record nor impact assessment exist for the spread of the genus, precluding informed management strategies. To provide these tools, our study aims to (1) provide an annotated checklist of species for this taxonomically confusing genus, (2) survey all available literature on the spread of the genus and summarize and map its invasive distribution, and (3) assess the overall socioeconomic and environmental impact of the genus on a global scale using the Generic Impact Scoring System (GISS). First, we provide an updated annotated species list. We then summarize seventy-one unique invasion records along with twenty-one instances of demonstrated impacts. Species of the genus *Pterygoplichthys* have now invaded five continents and twenty-one countries, and show an extended range in their native South America. Impact analysis yielded a GISS score of 18 to 19, indicating low to moderate levels of socioeconomic and environmental threats. However, to bolster the confidence in this analysis in future iterations, more research should aim to move beyond just "first records" and instead empirically evaluate species' effects on native ecosystems.

Key words: Generic Impact Scoring System, Armored sailfin catfish, Distribution, Aquarium trade, Fisheries.

BACKGROUND

The genus *Pterygoplichthys* (Siluriformes: Loricariidae) includes several popular aquarium species that have become invasive in tropical, subtropical, and warm-watered regions around the world (*e.g.* Hoover et al. 2004). Commonly called armored sailfin catfish, janitor fish, peces diablos (devil fish), or "plecos," species of the genus exhibit most of the characteristics that predispose certain fishes to successful invasion (Marchetti et al. 2004; Ruesink 2005; García-Berthou 2007). This suite of biological traits include: (1) high fecundity (Hoover et al. 2004; Gibbs et al. 2008), (2) broad physiological tolerance (*i.e.* salinity (Capps et al. 2011; Brion et al. 2013), pH (Harter et al. 2014), pollution (Liang et al. 2005), and hypoxia (*i.e.* enlarged, hypervascularized stomachs allow for air-breathing and survival for up to 30 hours out of water (Armbruster 1998; Gibbs and Groff 2014)), (3) rapid growth of 10 cm/year (Liang et al. 2005; Gibbs et al. 2013), (4) an armored exterior with powerful pectoral spines (Ebenstein et al. 2015), (5) life span of more than 5 years (Gibbs et al. 2013), and (6) high aquarium-vectored propagule pressure. Human-mediated factors also foster

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the spread of *Pterygoplichthys* spp., namely the popularity of members of the genus in aquariums and subsequently aquaculture, contributing to high propagule pressure (*e.g.* Hoover et al. 2014). Once established, these fishes are extremely difficult to remove (Hill and Sowards 2015).

Also common to the genus is a complicated taxonomic history, including numerous generic and specific synonymies (*e.g.* Armbruster 2004). Such taxonomic confusion can make sifting through literature for past invasion records difficult and lead to uninformed management decisions. Further complicating management strategies is the diffuse nature of invasion records for *Pterygoplichthys* spp. There is no database that tracks the genus' spread comprehensively. Online distribution databases such as the Global Biodiversity Information Facility (GBIF) and the Global Invasive Species Database (GISD) are incomplete, providing fragmented records and excluding non-established invasion records that can be valuable for predicting and thwarting future invasions (Kulhanek et al. 2011; GISD 2017, respectively). Further complicating potential management efforts is the lack of any quantitative or comprehensive framework for threats to colonized areas that these fishes may impose. A quantitative, flexible, and generic framework for analyzing impacts can be useful for prioritizing control and eradication efforts (Nentwig et al. 2010; van der Veer and Nentwig 2014).

In an effort to fill these knowledge gaps and provide tools to aid in future management efforts, our study has three objectives: to (1) provide an annotated checklist of species for this taxonomically confusing genus, (2) survey all available literature on the spread of the genus and summarize and map its invasive distribution, and (3) assess the overall socioeconomic and environmental impact of the genus on a global scale using the Generic Impact Scoring System (GISS). We then discuss some common themes and knowledge gaps in the literature. Finally, we conclude by making suggestions for future studies of this highly invasive genus.

MATERIALS AND METHODS

Literature Survey

We conducted an exhaustive literature search using Web of Science^{TM} (Reuters 2017), Google Scholar (2017), and online government databases (*e.g.* USGS Nonindigenous Aquatic Species Database (2017)). Literature was surveyed through October 1, 2017. We considered peer-reviewed scientific publications, technical reports, theses and dissertations, and governmental records. To ensure accurate reporting of records, we only included studies with deposited voucher material and/or high-resolution photographs of specimens, along with identification remarks for the specimens, excluding any records not conforming to these criteria, such as personal communications. Such practices are recommended to avoid erroneous records of introduced taxa (Bello et al. 2014). In cases of redundant records such as those reporting on the same species in the same locality, we included the more comprehensive record and excluded the other(s). Keywords we used to find relevant literature were '*Pterygoplichthys*', '*Liposarcus*', '*Glyptoperichthys*', 'armored catfish', 'invasive', 'record', and combinations thereof. We read each work, extracted relevant data, and catalogued the data into a summary table of all unique records. We also used the literature survey to compile an annotated list of species.

Distribution Mapping

All exotic occurrences of the genus were mapped. We generated the map using Esri's ArcGIS version 10.4 software based on all records available in Appendix 1. To show finer-scale distributions, we split some countries into second-level geopolitical subdivisions. We represented the global distribution of *Pterygoplichthys* spp. with solid geopolitical polygons for established populations, solid circles for potentially isolated detections, and an open circle with a red X for eradications. We designated each species using a unique color. Geopolitical areas with multiple species established are displayed with a multicolor pattern using the relevant species' colors. The Gulf Coast/Caribbean region and central Indo-Pacific region were represented in higher resolution map insets with red and yellow borders, respectively.

Quantifying Impacts

To assess the degree to which introduced *Pterygoplichthys* spp. impart socioeconomic and environmental impacts, we used the Generic Impact Scoring System (GISS). The GISS was developed by Nentwig et al. (2010) and refined by Nentwig et al. (2016) and Rumlerová et al. (2016). This scoring system is robust to gaps in data, not taxon-specific, and can be customized per case of interest (Lavoie 2017; Nentwig et al. 2016). The system uses a six-level scale ranging from 0 (no detectable impact) to 5 (the highest possible impact) (Table 1).

Normally these criteria are applied to six environmental and six socioeconomic categories to assess overall impact. Categories may be excluded (or otherwise receive a score of 0) for taxa for which the categories do not apply (Lavoie 2017). For our study, terrestrial-specific categories (*n* = 2) were excluded to include only those categories for which *Pterygoplichthys* spp. potentially have an impact. Given the lack of evidence of interspecific differences in impacts (Table 2) and the difficulty in species-level identification of members of *Pterygoplichthys*, we pooled species in order to increase the power of the data set and assess the overall impact of this genus of ecologically and physiologically similar species following the treatment of the genus by the Global Invasive Species Database (GISD 2017). All categories followed Nentwig et al. (2016). The environmental categories we used were effects on (1) plants or vegetation, (2) animals, (3) native species through competition, (4) native species through the transmission of diseases or parasites, (5) native species through hybridization, and (6) ecosystems. The four socioeconomic categories we used were effects on (1) animal production, (2) human infrastructure and administration, (3) human health, and (4) human social life. We used in our analysis all demonstrable impacts relevant to any of the abovementioned categories encountered in the literature review. We followed the GISS scoring rubric as closely as possible per the instructions provided by Nentwig et al. (2016) in assigning scores to achieve a summed impact score.

RESULTS

Annotated List of Species

The last annotated list of species in the genus *Pterygoplichthys* was published in Ferraris (2007). A new species has since been described and another redescribed, bringing the total number of valid species to 15. Presented below is an updated annotated species list including taxonomic history and type material of the genus, taxonomic history and type material of each species, native distributions, and relevant comments.

Pterygoplichthys Gill, 1858

Pterygoplichthys Gill, 1858: 408. Type species: *Hypostomus duodecimalis* Valenciennes 1840. Type by subsequent designation in Bleeker (1862-63:2) with genus spelled *Pterygophlichtys*. Gender: Masculine.

Liposarcus Günther, 1864:238. Type species: *Hypostomus multiradiatus* Hancock 1828. Type by subsequent designation by Jordan (1919b:332). Gender: Masculine

Glyptoperichthys Weber, 1991: 639. Type species: *Ancistrus lituratus* Kner, 1854. Type by original designation. Gender: Masculine.

Remarks: Revised by Weber (1992), with *Liposarcus* and *Glyptoperichthys* also treated as valid. Generic synonymy herein based on Armbruster (2004).

Pterygoplichthys ambrosettii (Holmberg, 1893)

Liposarcus ambrosettii Holmberg, 1893b: 354. Type locality: Río Paraguay, in front of Formosa. No types known.

Pterygoplichthys anisitsi Eigenmann and

Table 1. Definition of the impact levels used for the generic impact scoring system (GISS). Reproduced from Nentwig et al. (2016)

Impact Level	Impact Description
0	No data available, no impacts known, not detectable, or not applicable
1	Minor impacts, only locally, only on common species, negligible economic loss
2	Minor impacts, more widespread, also on rarer species, minor economic loss
3	Medium impacts, large-scale, several species concerned, relevant decline, relevant ecosystem modifications, medium economic loss
4	Major impact with high damage, major changes in ecosystem functions, decrease of species, major economic loss
5	Major large-scale impact with high damage and complete destruction, threat to species including local extinctions, high economic costs

Table 2. Reported socioeconomic and environmental threats posed by invasive *Pterygoplichthys* spp.

Species	Country	Socioeconomic Threats	Environmental Threats	References
P. disjunctivus	Phillipines	Damaging fisheries equipment	Declining native fish populations	Chavez et al. 2006a
	Phillipines	Bioaccumulation of heavy metals and coliform bacteria		Chavez et al. 2006b
	Phillipines	Decreased yield of desirable food fishes; Damaging fisheries equipment	Food competition with native fishes; Increased turbidity caused from burrowing males	Hubilla et al. 2008
	USA		Induced behavioral modifications in threatened *Trichechus manatus latirostris* (Florida Manatee)	Gibbs et al. 2010
	USA		Drastic modification of nutrient regimes and biogeochemical cycling	Rubio et al. 2016
	Japan		Vector for nonnative parasites	Nitta and Nagasawa 2016
	Mexico		Vector for nonnative parasites	Rodríguez-Santiago et al. 2016
P. multiradiatus	Mexico	Damaging fisheries equipment		Wakida-Kusunoki et al. 2007
	India	Damaging fisheries equipment	Displacement of native fishes	Krishnakumar et al. 2009
	USA (Puerto Rico)		Bird mortality due to asphyxiation	Bunkley-Williams et al. 1994
	USA (Puerto Rico)		Displacement of native fishes	Bunkley-Williams et al. 1994
P. pardalis	Phillipines	Damaging fisheries equipment	Declining native fish populations	Chavez et al. 2006a
	Phillipines	Bioaccumulation of heavy metals and coliform bacteria		Chavez et al. 2006b
	Mexico	Damaging fisheries equipment		Wakida-Kusunoki et al. 2007
	Mexico		Act as egg predators of native fishes	Chaichana and Jongphadungkiet 2012
	Mexico		Vector for nonnative parasites	Rodríguez-Santiago et al. 2016
	Thailand		Displacement of native fishes (up to 100% decline of native fishes)	Chaichana et al. 2011
Pterygoplichthys spp.	Mexico		Drastic modification of nutrient regimes and biogeochemical cycling	Capps and Flecker 2013a; Capps and Flecker 2013b
	All populations		Siltation and erosion caused by burrowing males	Hoover et al. 2004; Nico et al. 2009; Hoover et al. 2014
	All populations		Reduction in fish food resources (e.g. aquatic insects, aquatic vegetation)	Hossain et al. 2008; Mendoza-Alfaro et al. 2009
	USA		Displacement of native fishes, including the Vulnerable River minnow (*Dionda diaboli*)	Cohen 2008, Mendoza-Alfaro et al. 2009
	USA		Ingesting eggs of Vulnerable *Etheostoma fonticola*	Cook-Hildreth 2009
	USA	Reduced Catch Per Unit Effort (CPUE) in recreational fisheries		Mendoza-Alfaro et al. 2009
	China	Decreased yield of desirable food fishes and shrimp		Wei et al. 2017

Kennedy, 1903:503. Type locality: Laguna of the Rio Paraguay at Asuncion. Holotype: IU 9873; whereabouts unknown.

Pterygoplichthys juvens Eigenmann and Kennedy, 1903:504. Type locality: Asuncion, Río Paraguay, Paraguay. Holotype: CAS 59784.

Ancistrus multiradiatus alternans Regan, 1904b: 229. Type locality: Paraguay and Southern Bolivia [restricted by Weber (1992:28) to: Paraguyan Chaco [...] région Vila Concepción (= Concepción) - Caraya Vuelta -2/3 Piste Pozo Colorado, probablement Waikthlatingmayalwa (= ? Mission Inglesia)]. Lectotype: BMNH 1898.7.4.5, designated by Weber (1992:28). Originally proposed as *A. multiradiatus* var*. alternans*.

Distribution: Paraguay, middle Paraná, Bermejo, and Uruguay River basins (Weber 2003).

Remarks: Weber (1992 2003) treated *Liposarcus ambrosettii* Holmberg, 1893, as a *nomen oblitum*, but its use in several publications negate that status. Redescribed as *Liposarcus anisitsi* in Weber (1992:13).

Pterygoplichthys disjunctivus (Weber 1991)

Liposarcus disjunctivus Weber 1991: 638. Type locality: Rio Madeira, système de l'Amazonas, Restauracão, Amazonas, Brésil. Holotype: MZUSP 28360; illustrated in Weber (1992: pl. 9).

Native Distribution: Madeira River basin, Bolivia and Brazil (Weber 2003).

Pterygoplichthys etentaculatus (Spix and von Agassiz 1829)

Hypostoma etentaculatum Spix and von Agassiz 1829: 7, pl. 4 (fig. 1). Type locality: in Brasilae septentrioralis fluviis [now: São Francisco River at Januaria, Minas Gerais State, Brazil, by neotype designation]. Neotype: MZUSP 35821, designated by Weber (1992:25).

Hypostomus duodecimalis Valenciennes in Cuvier and Valenciennes 1840b: 498 (367 in Strasbourg deluxe edition), pl. 454. Type locality: dans la rivière Saint-François au Brésil. Holotype: MNHN a-9446.

Hypostomus brevitentaculatus Ranzani 1841: 63. Type locality: nelle aqua dolci della Provinciadi S. Paulo nel Brasile. Holotype: at MZUB. Described in more detail in Ranzani (1842:329).

Ancistrus longimanus Kner 1854: 283, pl. 5 (fig. 1). Type locality: [Not stated]. Syntypes (2): at NMW. Originally proposed as *Anc. longimanus.*

Native Distribution: São Francisco River basin, Brazil (Weber 2003).

Pterygoplichthys gibbiceps (Kner 1854)

Ancistrus gibbiceps Kner 1854: 284, pl. 5 (fig. 2). Type locality: aus dem Rio Negro bei Marabitanos [Brazil]. Holotype: at NMW. Originally proposed as *Anc. gibbiceps*.

Liposarcus altipinnis Günther 1864: 239. Type locality: Rio Cupai [Brazil]. Holotype: BMNH 1853.3.19.34.

Native Distribution: Middle and upper Amazon and Orinoco basins (Weber 2003).

Remarks: Redescribed in Weber (1992:17), with type locality of *Liposarcus altipinnis* as: Cupari River, Tapajós River basin, Amazon drainage, Amazonas State, Brazil.

Pterygoplichthys joselimaianus (Weber 1991)

Glyptoperichthys joselimaianus Weber 1991: 640, illustrated in Weber (1992:20, pl. 15b). Type locality: Rio Araguaya, affl. du Tocantins, système de l'Amazone, Aruanã, Goiàs, Brésil. Holotype: MZUSP 4873.

Native Distribution: Tocantins River basin, Brazil (Weber 2003).

Pterygoplichthys lituratus (Kner 1854)

Ancistrus lituratus Kner, 1854: 285, pl. 5 (fig. 3). Type locality: aus dem Rio Guaporé bei cidade do Matogrosso [Amazon system, Brazil]. Lectotype: NMW 16416; designated by Weber (1992: 28). Originally as *Anc. lituratus*.

Native Distribution: Madeira River basin, Bolivia and Brazil (Weber 2003).

Remarks: Redescribed in Weber (1992:28).

Pterygoplichthys multiradiatus (Hancock 1828)

Hypostomus multiradiatus Hancock, 1828: 246. Type locality: Demerara [in title] [...] Lakes [...] on the slime. Holotype: BMNH 1857.6.13.162.

Native Distribution: Orinoco River basin, possibly also in Guyana (Weber 2003).

Remarks: Redescription and type locality interpretation in Weber (1992:9, 27).

Pterygoplichthys pardalis (Castelnau 1855)

Hypostomus pardalis Castelnau 1855: 42, pl. 20 (fig. 3). Type locality: l'Amazone. Holotype: MNHN a-9574.

Liposarcus varius Cope 1872a: 284. Type locality: The Ambyiacu river, which empties into the Amazon near to Pebas, in Eastern Equador, some distance east of the Napo [Peru]. Lectotype: ANSP 21931, designated by Fowler (1915:233).

Liposarcus jeanesianus Cope, 1874b: 135. Type locality: Nauta, Peru [= Marañon River, Amazon basin]. Lectotype: ANSP 8241, designated by Weber (1992:27).

Native Distribution: Lower, middle and upper Amazon River basin (Weber 2003).

Remarks: Redescribed in Weber (1992:10).

Pterygoplichthys parnaibae (Weber 1991)

Glyptoperichthys parnaibae Weber 1991: 641. Type locality: Lac de Parnaguá, Rio Paraim, bassin de Parnaíba, sys. côtier brésilien; Maranhão, Brésil. Holotype: NMW 48034, illustrated in Weber (1992:21, pl. 16b).

Native Distribution: Parnaíba River basin, Brazil (Weber 2003).

Pterygoplichthys punctatus (Kner 1854)

Loricaria punctata Kner, 1854: 281. Type locality: S. Vincente [...] aus einer Lache [Brazil]. Holotype: NMW 76587.

Native Distribution: Madeira, Purus, Jurua and Marañon River basins (Weber 2003).

Remarks: Redescribed in Weber (1992:22). Redescribed again in Armbruster and Page (2006: 403).

Pterygoplichthys scrophus (Cope 1874)

Liposarcus scrophus Cope 1874b: 136. Type locality: Nauta [Peru]. Syntypes: USNM 132587 (2).

Native Distribution: Marañon and Ucayali River basins, Peru (Weber 2003).

Remarks: Redescribed in Page et al. (1996: 186).

Pterygoplichthys undecimalis (Steindachner 1878)

Chaetostomus undecimalis Steindachner 1878: 90. Type locality: Cienaga Grande de Santa Marta, Magdalena basin, 40 km east of Barranquilla, Colombia. Lectotype: NMW 47224, designated in Weber (1992:26); illustrated in Steindachner (1879d:43, pl. 8).

Native Distribution: Magdalena River basin, Colombia (Weber 2003); also Cauca and Catatumbo River basins (Maldonado-Ocampo et al. 2005).

Pterygoplichthys weberi Armbruster and Page 2006

Pterygoplichthys weberi Armbruster and Page 2006: 406. Type locality: Colombia, Caquetá, Florencia, Río Caqueta drainage, Laguna El Vaticano. Holotype: ICNMHN 13455.

Native Distribution: Río Marañon, Río Ucayali, Río Caquetá, and upper Río Amazonas drainages of Colombia, Ecuador, and Peru (Armbruster and Page 2006)

Pterygoplichthys xinguensis (Weber, 1991)

Glyptoperichthys xinguensis Weber 1991: 640. Type locality: Rio Fresco, affl. du Rio Xingu, système de l'Amazone; Aldeio Gorotire, municipe de São Felix do Xingu, Pará, Brésil. Holotype: MZUSP 35961, illustrated in Weber (1992:pl. 14, fig. b).

Native Distribution: Xingu River basin, Brazil (Weber 2003).

Pterygoplichthys zuliaensis Weber 1991

Pterygoplichthys zuliaensis Weber 1991: 638. Type locality: Río Santa Ana, bassin du Maracaibo, Hacienda Río Grande, 9°36'20"N, 72°07'00"W, état de Zulia, Venezuela. Holotype: MBUCV V-14653; holotype illustrated in Weber (1992:pl. 4b).

Native Distribution: Lake Maracaibo basin, Venezuela (Weber 2003).

Distributional Summary

The summary table of all records for introduced *Pterygoplichthys* spp. through June 1, 2017 along with relevant remarks is provided in Appendix 1. We included seventy-one unique records. Seven introduced species or hybrids of the genus *Pterygoplichthys* have been reported from five continents, plus an extended range in their native South America, and twenty-one countries (Fig. 1).

Of these, fifteen records involve detections (*i.e.* species present but whose establishment status is unknown) and fifty-five instances are established (*i.e.* reproducing) populations. A single successful eradication of a previously established population of *P. disjunctivus* is reported from the Rainbow River, Florida, USA (Hill and Sowards 2015). The most abundant established populations are those of *P. disjunctivus* and *P. pardalis* (*n* = 22 each), followed by *P. multiradiatus* (*n* = 5), *P. ambrosetti* (*n* = 4), and likely hybrids of *P. disjunctivus x pardalis* (*n* = 2) (Table 3).

The first established population was reported from Florida, USA in the late 1950s (Fuller et al.

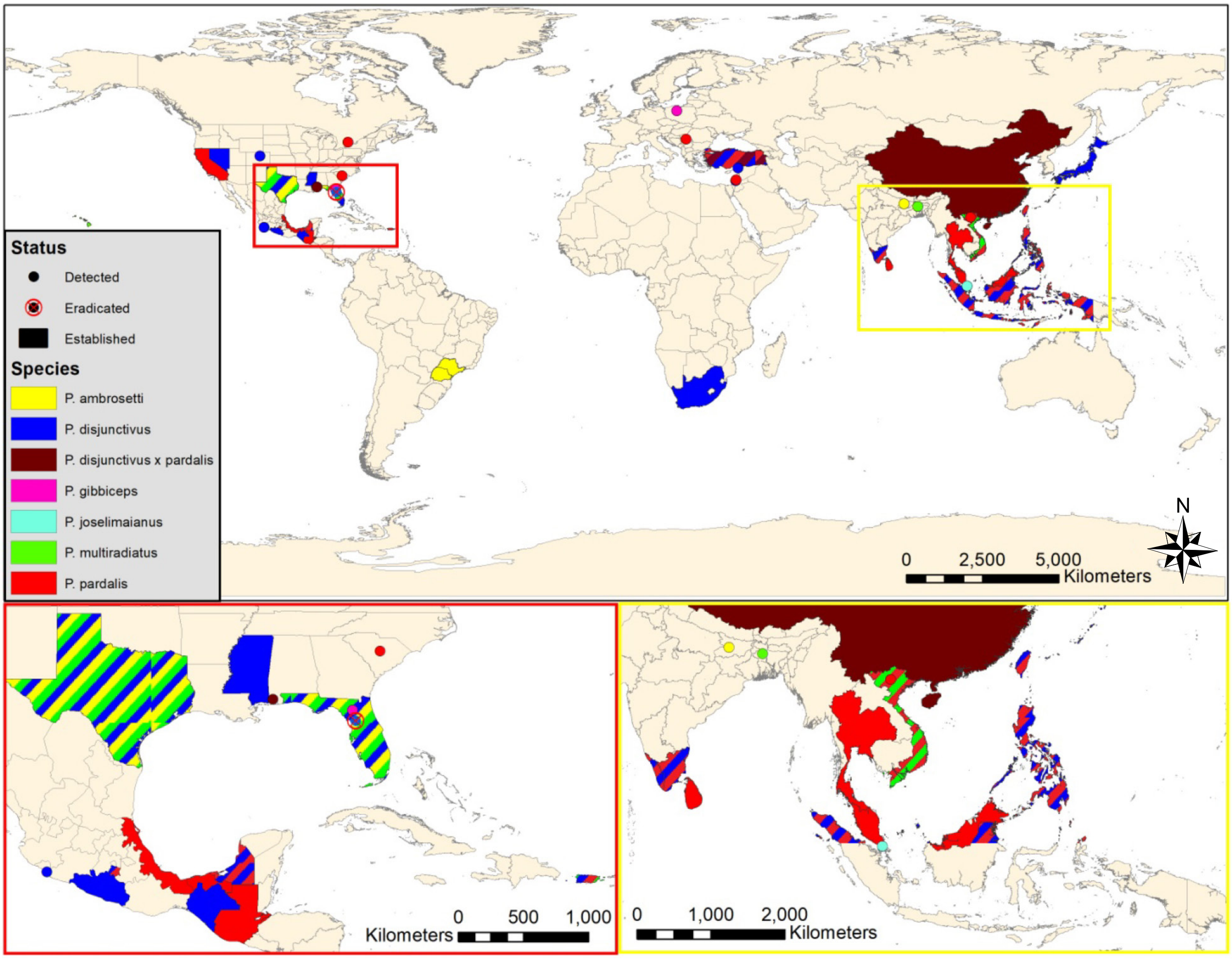

Fig. 1. Global distribution of nonnative *Pterygoplichthys* spp. represented with filled-in geopolitical polygons for established populations, filled-in circles for potentially isolated detections, and a circle with a red X over it for the single eradication. Each species is represented by a different color. Geopolitical areas with multiple established species are displayed with a multicolor pattern using the relevant species' colors. The Gulf Coast/Caribbean region and central Indo-Pacific region are represented in higher resolution map insets with red and yellow borders, respectively. Color-filled polygons (*e.g.* states) indicate establishment in, but not necessarily throughout, an area.

Table 3. The number of established populations of all *Pterygoplichthys* species (or hybrids) detected outside of their native ranges

Species	Established Exotic Populations
P. ambrosetti	4
P. disjunctivus	22
P. disjunctivus x pardalis	2
P. gibbiceps	0
P. joselimaianus	0
P. multiradiatus	5
P. pardalis	22

1999). Since 1985, the number of both detected and established reports in the literature has rapidly risen (Fig. 2). The summarized data will be deposited online through GBIF.

Generic Impact Scoring System (GISS)

Our literature survey produced twenty-one papers providing evidence on the impacts of *Pterygoplichthys* spp. in their nonnative ranges. In table 4, we provide detailed justifications for scores along with references used to calculate the GISS. The six environmental categories yielded a score of 11-12 (of a possible 30), while the four socioeconomic categories evaluated yielded a score of 7 (of a possible 20), resulting in a cumulative GISS of 18-19 (of a possible 50) for the genus.

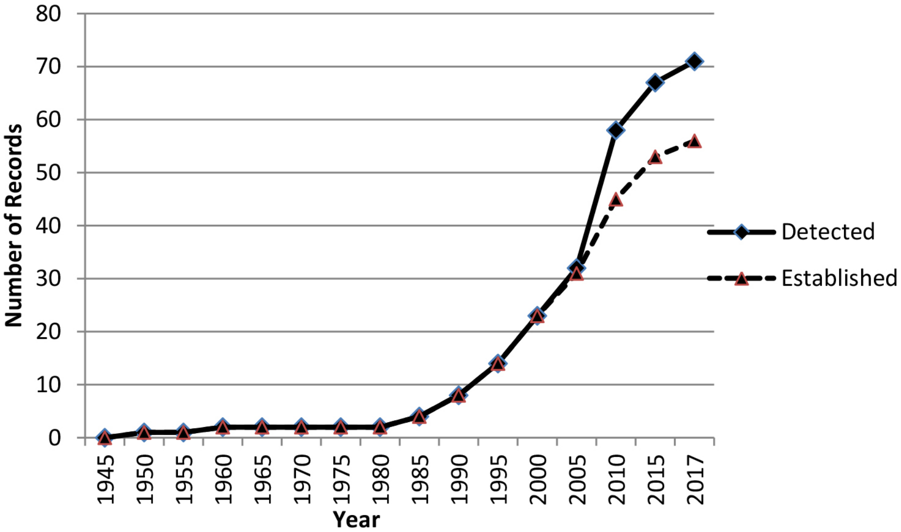

Fig. 2. Number of exotic records of *Pterygoplichthys* spp. by year recorded in the literature. Records with missing dates were treated using the publication date and the single record of "late 1950s" was treated as 1960. A total of 71 records of exotic *Pterygoplichthys* spp., either individuals or populations, were reported through October, 2017; 55 of these records represented established populations.

Table 4. Scores attributed, using the Generic impact scoring system (GISS), to *Pterygoplichthys* spp. for different categories of environmental and socioeconomic impacts. GISS categories for which *Pterygoplichthys* spp. do not apply (*i.e.* terrestrial-specific categories) are excluded

Category	Score and Justification	Reference(s)
Environmental Impacts		
1.1. Impacts on plants or vegetation through mechanisms other than competition	2 (minor impacts, more widespread): Many studies in different localities have demonstrated drastic changes in local biogeochemical cycling that promote algal growth and may result in altered aquatic flora; additionally, siltation caused by burrowing males obscures light penetration wherever populations are established	Hoover et al. 2004; Hubilla et al. 2008; Mendoza-Alfaro et al. 2009; Nico et al. 2009; Capps and Flecker 2013a; Capps and Flecker 2013b; Hoover et al. 2014; Rubio et al. 2016
1.2. Impacts on animals	2 (minor impacts, more widespread): Noted incidences of bird mortality due to asphyxiation via erected pectoral spines, fish-egg predation (including threatened taxa), and feeding on algal growth on skin of the threatened *Trichechus manatus latirostris* (Florida Manatee) leading to stress and behavioral medications	Bunkley-Williams et al. 1994; Cook-Hildreth 2009; Gibbs et al. 2010; Chaichana and Jongphadungkiet 2012

Table 4. (continued)

Category	Score and Justification	Reference(s)
1.3. Impacts on species through resource competition	3 (Medium impacts, large-scale, several species concerned, relevant decline): Many demonstrated cases of displacement of native fishes through indirect food competition (*i.e.* reduced food resources such as aquatic insects and vegetation) and direct habitat competition due to high biomass of populations	Bunkley-Williams et al. 1994; Chavez et al. 2006a; Hubilla et al. 2008; Cohen 2008; Hossain et al. 2008; Krishnakumar et al. 2009; Mendoza-Alfaro et al. 2009; Chaichana et al. 2011
1.4. Impacts through transmission of diseases or parasites to native species	1 (minor impacts): Two studies have detected co-introduced parasites but have not indicated transmission to native fauna	Nitta and Nagasawa 2016; Rodríguez-Santiago et al. 2016
1.5. Impacts through hybridization	0 (no known impact): While *Pterygoplichthys* spp. are known to hybridize with their congeners, perhaps facilitating invasion, there are no demonstrated cases of hybridization with native fauns	N/A
1.6. Impacts on ecosystems	3 or 4 (major small-scale effects, geographically widespread, and multi-faceted): Significant changes in biogeochemical cycling and nutrient load, as well as siltation and bank erosion caused by burrowing males, have altered ecosystem quality and function where populations are established. Difficult to precisely evaluate given current evidence	Hoover et al. 2004; Hubilla et al. 2008; Mendoza-Alfaro et al. 2009; Nico et al. 2009; Capps and Flecker 2013a; Capps and Flecker 2013b; Hoover et al. 2014; Rubio et al. 2016
Socioeconomic Impacts		
2.2. Impacts on animal production	4 significant widespread economic loss): Numerous studies have reported damaged and loss of fisheries gear as well as decreased yield of desirable food fishes and shrimp in many geographic areas, resulting in loss of capital and livelihood	Chavez et al. 2006a; Hubilla et al. 2008; Wakida-Kusunoki et al. 2007; Krishnakumar et al. 2009; Mendoza-Alfaro et al. 2009; Wei et al. 2017
2.4. Impacts on human infrastructure and administration	1 (poorly demonstrated impacts and negligible economic loss): Dense populations of males of the genus excavate burrows in bank walls for egg guarding. Concern exists that this may lead to damage to banks, impaired shoreline stability, and exacerbated erosion. These concerns have only been modestly documented and not yet empirically evaluated	Hoover et al. 2004, Nico et al. 2009; Van den Ende 2014; Hoover et al. 2014
2.5. Impacts on human health	1 (minor, local impacts): Bioaccumulation of heavy metals and coliform bacteria have been demonstrated. People have occasionally been known eat these fishes in introduced ranges, leading to potential contamination	Chavez et al. 2006b
2.6. Impacts on human social life	1 (minor, local impact): Reduced Catch Per Unit Effort (CPUE) of popular recreational fishes in presence of *Pterygoplichthys* spp. Demonstrated in Florida, USA (correlative)	Mendoza-Alfaro et al. 2009
Total score	18-19	

DISCUSSION

Distribution and Potential Hybridization

Four species and at least one hybrid form in the genus *Pterygoplichthys* have successfully established themselves outside of their native ranges, and this subgroup - dominated by *P. disjunctivus* and *P. pardalis* - has proved incredibly successful in invading novel localities worldwide. These consistent invasions by a select few species likely reflect the ubiquity of those species in the aquarium trade (ABO personal observation). The rise in popularity of these species in aquaria coupled with increased sampling effort is likely responsible for the steep uptick in detections and the disparity between detections versus establishments observed since 2005 (Fig. 2). While reproductive success following aquarium dumping is not a guarantee, increased propagule pressure results in more frequent detections, a higher rate of failed establishment, and a higher rate of successful establishment (Lockwood et al. 2005). However, to our knowledge, no comprehensive, geographically widespread survey of genus composition in the aquarium trade has been performed and species availability likely fluctuates temporally and geographically.

Such a survey, when complemented with molecular analysis, may also help to elucidate the nature of the morphologically intermediate forms that have been noted in many places around the world, particularly between *P. disjunctivus* and *P. pardalis*. One hypothesis posits that these intermediate forms represent hybrids (Capps et al. 2011; Wu et al. 2011; Nico et al. 2012). Nico et al. (2012) suggests these cases may be best described as “hybrid swarms”.

Alternatively, it has been suggested that *P. disjunctivus* and *P. pardalis* are synonymous, actually representing extremes of variation in pigmentation (Wu et al. 2011; Jumawan et al. 2011). This is not unreasonable considering that, unlike other species of *Pterygoplichthys* that exhibit allopatric native distributions, *P. pardalis* and *P. disjunctivus* occur in sympatry in their native range. They are also the most commonly reported “species” to be hybridizing in invaded waters. *P. disjunctivus* is noted as occurring in the Upper Madeira River Basin as well as the main channel of the upper Amazon River, while *P. pardalis* occurs in the lower and middle stretches of the Amazon River (Weber 1991 1992). Overlap occurs over a wide section of the middle Amazon River Basin (Weber 1991 1992; J.W. Armbruster, personal communication). Original descriptions of these species diagnosed them by lateral and abdominal pigmentation alone - primarily the density of ventral mottling (Weber 1991 1992; Armbruster and Page 2006).

These perplexing forms may provide a unique opportunity to study the prevalence and consequences of hybridization among multiple invasive species or, at the very least, suggest the need to revisit the alpha-taxonomy of the genus.

Threats and Eradication

Pterygoplichthys spp. impose threats to their invaded ranges. The most well-documented of these impacts were the displacement of native fishes (Bunkley-Williams et al. 1994; Chavez et al. 2006a; Hubilla et al. 2008; Cohen 2008; Krishnakumar et al. 2009; Mendoza-Alfaro et al. 2009; Chaichana et al. 2011; Wei et al. 2017), bioturbation and increased turbidity (Hoover et al. 2004; Hubilla et al. 2008; Nico et al. 2009), and damage to fisheries gear and subsequently fishermen livelihood (Chavez et al. 2006a; Wakida-Kusunoki et al. 2007; Krishnakumar et al. 2009).

This impact evaluation is comparable to the one done by Hoover et al. (2014), which also analysed the genus’ environmental effects. Hoover et al. (2014) based their analysis on expert opinion in which researchers studying the genus ranked its environmental impacts as Low, Medium, or High. The analysis was restricted to the United States. Three experts ranked the impacts as Low, three as Medium, and seven as High. These results suggest a moderate to high level of environmental impact in the United States, which is higher than the 18-19 GISS score that the present study recovered. Unlike the study by Hoover et al. (2014), we evaluated both socioeconomic and environmental impacts and did so on a global scale using many more data. Future studies may shed further light on the true nature of the threats that species of *Pterygoplichthys* pose.

Based on the current GISS score, impacts of the genus are present but somewhat low. Still, depending on locality and local densities, these fishes may merit eradication efforts by managers. One previous successful eradication occurred via hand- and spear-removal in a Florida, USA river (Hill and Sowards 2015). However, such physical removal is intractable for large or widespread populations. Fortification of bank walls to prevent burrowing males from allowing egg deposition is another avenue. While possible, this strategy can be expensive and has been utilized very little; for example, in some south Florida, USA communities (GISD 2017; K. Gestring, personal communication). Other options for removal include incentivizing the development of food fisheries for these high-biomass species and/or the collections of their eggs from male-guarded burrows to sell in the aquarium trade. Both of these options lend socioeconomic benefits while removing wild *Pterygoplichthys*. For example, successful commercial and recreational fisheries of invasive red lionfish (*Pterois volitans*) (Linnaeus 1758) are underway in the United States and have been shown to help inhibit local lionfish population growth (Barbour et al. 2011). Unlike the predatory lionfish, however, a food fishery for members of the genus should be cautioned in certain localities where polluted waters have led to potentially dangerous bioaccumulation of heavy metals and coliform bacteria of resident *Pterygoplichthys* detritivores (Chavez et al. 2006b). Rotenone may also be used as a piscicide but its application should be limited and follow appropriate guidelines (*e.g.* Britton et al. 2011).

Eradication is not typically feasible (Hill and Sowards 2015). Removal of these fishes is difficult and potentially time consuming and expensive per the reasons discussed earlier (see Introduction). Where resources are limited, managers may wish to focus efforts on containing the current established populations and preventing future introductions (Hill et al. 2017; Lawson et al. 2015). The best means of accomplishing this is by educating the public on the importance of not releasing unwanted aquarium fishes into local waterways. Educational campaigns have been found to be successful, inexpensive options in minimizing the release of unwanted fishes (Maceda-Veiga et al. 2016).

CONCLUSIONS

Our study highlights the paucity of data in many areas relevant to informing management schemes. The present GISS assessment should be evaluated with caution in light of the empirically robust data. For example, the means by which invasive *Pterygoplichthys* spp. displace native fishes is largely unknown but may be food competition (Hubilla et al. 2008) or space (Mendoza-Alfaro et al. 2009). Also unknown are the effects of the siltation produced by burrowing males on aquatic flora. In fact, the vast majority of studies surveyed focus on fauna and socioeconomic impacts. Finally, most studies are local and almost none are regional or national.

In general, the scope of research remains modest and more data are needed. Future research should focus on empirically evaluating impacts rather than reporting simple “first records” or anecdotal evidence. Once additional data are available, they should be subjected to the GISS and compared to this analysis to maintain the best available evidence-based resources for managers.

Our paper also provides the first comprehensive list of records and impacts and aims to inform managers as best as currently possible, while also highlighting research areas in need of more attention. We conclude by offering the following recommendations for collecting future data. Researchers should (1) collect voucher specimens and tissue sample for identification purposes and genetic studies, (2) publish explicit collection and identification remarks in methodology to better compare across studies and demonstrate study limitations, (3) employ empirical evaluations of local impacts through observational and/or manipulative experiments to establish causal rather than anecdotal relationships, (4) use the GISS to roughly quantify and track impacts as new data are available, and (5) deposit collection material, including high-resolution photographs and voucher accession codes, to online databases such as GBIF.

Acknowledgments: The authors wish to thank Pamela J Schofield, Jonathan Armbruster, and anonymous reviewers for providing helpful feedback that helped to improve the manuscript. Kelly Gestring also provided insight into the invasions in Florida, USA which was helpful in appreciating community responses to Florida invasions.

Authors’ contributions: ABO conducted the literature review, analysis, and taxonomic review, and drafted the manuscript. DDG generated the map and revised the manuscript. Both authors read and approved of the final manuscript.

Competing interests: The authors declare that they have no competing interests.

Availability of data and materials: Additional data is provided in Appendix 1.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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Supplementary material

Appendix 1. All detected, established, or extirpated records of *Pterygoplichthys* spp. through June, 2017. Redundant records, personal communications, and records missing voucher specimens and/or photographs are excluded. (download)