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Original Research Article

## Conservation and trade of the endangered *Hypancistrus zebra* (Siluriformes, Loricariidae), one of the most trafficked Brazilian fish

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## ABSTRACT

*Hypancistrus zebra*, also known as the zebra pleco, is a small sucker-mouth catfish endemic to the Xingu River in Brazil where its survival in the wild is threatened by habitat modification and overfishing for the ornamental fish industry. It is a highly sought-after freshwater ornamental species and one of the most commonly trafficked from Brazil. To date, little is known about its global legal and illicit supply chains within the ornamental fish trade. Through a mixed methods approach (i.e., online survey, key informant interviews and web scraping), we examined the trade and trafficking of this species as well as the awareness of the international aquarist community and local and international stakeholders regarding its conservation. We also establish the historical timeline of zebra pleco keeping and breeding in captivity and assess whether commercial captive breeding can play an important role in the conservation of this species. The retail price of the zebra pleco increased worldwide after an export ban in 2004 but have since decreased to an average of \$US 155 (+/- \$US 23 based on geographical location) per fish. Fishermen have been consistently paid relatively little (\$US 7–60) for each specimen compared to the average wholesale price of \$US 100 (+/- \$US 94 over time). We conservatively estimate ~100,000 specimens are trafficked out of Brazil annually, of which half or more die in transport, and only a small fraction is seized by law enforcement in Brazil or internationally. The fishes are primarily smuggled from Brazil to Peru and Colombia and then exported internationally with the majority sent to China. The majority of aquarists surveyed (representing 35 countries) were aware the zebra pleco is both endangered and highly endemic. There was less awareness that buying wild caught specimens shipped from Peru, Colombia or elsewhere implies supporting wildlife trafficking. Nevertheless, nearly three quarters of respondents preferred aquarium bred specimens, if available. The zebra pleco is being bred in captivity in high numbers in several countries, yet in Brazil it remains illegal to keep in private aquaria or to commercially breed them. Given the large success of hobby and commercial breeders around the world, *H. zebra* is well suited for indoor breeding facilities. We argue that implementing regulated local breeding facilities in Brazil to increase the already large numbers reproduced in captivity worldwide, could decrease the demand for trafficked specimens, one of the primary factors threatening its

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survival. Given its iconic status among freshwater fishes it should be recognized as a flagship species of the Xingu River's conservation.

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## 1. Introduction

Freshwater ecosystems are recognized among the most threatened in the world (Dudgeon et al., 2006; IPBES, 2019; Nogueira et al., 2010). Nevertheless, they have received comparatively less conservation attention than their marine or terrestrial counterparts (Maitland, 1995; Stiassny, 1996; Strayer and Dudgeon, 2010). The freshwater fishes of South America are the most diverse on Earth, comprising approximately one third of known species with many new species being described every year. It is estimated there may be up to 9000 species of freshwater fish in South American waters (Reis et al., 2016). Due to extensive changes in land use, hydroelectric dam induced water impoundment, water quality degradation and overfishing, up to 10% of fishes in South America face mounting pressure towards extinction (Reis et al., 2016; Revenga et al., 2005). In Brazil, overfishing has been identified as a primary cause of population decline of several endangered species (Andrews, 1990; Reis et al., 2016).

The biodiversity hotspot of the Brazilian Shield rivers has one of the largest concentrations of narrowly distributed species (Dagosta et al., 2020). In particular, the lower and middle sectors of the Xingu River, in the State of Pará, Brazil, with its clear water and complex geomorphology (Bogotá-Gregory et al., 2020; Sawakuchi et al., 2015) has led to a unique ichthyofaunal assemblage (Fitzgerald et al., 2018). Due to the immense diversity of body shapes, behavior and color patterns (Lujan et al., 2012), the catfish of the Locariidae family have become some of the most popular exported ornamental fishes from Brazil, contributing to the multi-billion dollar ornamental fish industry (Biondo and Burki, 2020). Ninety percent of the worldwide trade volume consists of tropical freshwater fishes, of which 10% are wild-caught species (Evers et al., 2019; Olivier, 2001). Ornamental fisheries, especially for freshwater fish, are driven by consumer interest in diversity (e.g., rare species), rather than volume as seen with food fish (Engelhard et al., 2019).

In Brazil, wild caught ornamental fish are primarily captured in the Amazon region (Moreau and Coomes, 2007; Pelicice and Agostinho, 2005). The ornamental fishery in the Brazilian Amazon has been estimated to employ over 360,000 fishermen (Isaac et al., 2015). Historically, three quarters of the legal exports from Brazil were sent to Germany, the United States, Japan, the Netherlands and Taiwan (dos Anjos et al., 2009). Over the last decade, China, including Taiwan, has become one of the primary destinations for exported ornamental fish. Over the 2015–2019 period, Germany, Japan and China combined represented 58% of the reported market value of legally exported Brazilian freshwater fish (UNSD Department of Economic and Social Affairs, 2020). In the state of Pará, unemployed gold prospectors turned to ornamental fishing in the mid-1980 s, and since then, the local industry has grown such that the majority of fishermen depend primarily on ornamental fish for their livelihoods (Carvalho Junior et al., 2009). In the Xingu region alone, approximately 3000 fishermen are involved in the trade; equal to 1 in 100 as opposed to the national Brazilian average of 0.23 per 100 inhabitants (Isaac et al., 2015). In the city of Altamira on the banks of the Xingu River, over 200 ornamental species are traded, many of which are endemic to the region (Camargo et al., 2015).

Among the Xingu's endemic ornamental fishes, *Hypancistrus zebra* Isbrücker and Nijssen (1991) is perhaps the most iconic, referred to by its common names as acari-zebra and cascudo-zebra-imperial (in Portuguese) or zebra pleco in English. Its recognizable color pattern of a white base with horizontal black lines on the body and a characteristic transversely arranged capital letter E in black pigment on the snout (Fig. 1) is not known to occur in any other freshwater fish (Isbrücker and Nijssen, 1991). It is highly sought-after in the commercial ornamental fish trade and is one of the few ornamental fish with an entire forum dedicated solely to information on its husbandry and breeding (www.zebraleco.com) as well as numerous social media pages, groups and posts on many platforms from hobby aquarists worldwide.

The high pressure of fishing for this highly endemic species for the ornamental industry was analysed in a biodiversity assessment by Brazilian environmental authorities and *H. zebra* was categorized as 'critically endangered' (Ministerio do Estado do Meio Ambiente (MAPA), 2004). Instrução Normativa MMA No 05, de 21 de Maio de 2004. Brasília, Brazil. Until then, it had been declared as *Peckoltia* spp. for export, which were allowed on Brazil's limited positive (export) list. Once recognized as *H. zebra*, in 2004, it was no longer allowed to be exported from Brazil. The zebra pleco remains listed as critically endangered in the most recent revision of the Red List (Instituto Chico Mendes de Conservação da Biodiversidade, 2018) and cannot be legally caught or exported (Zuanon and Py-Daniel, 2008). Additionally, in 2008 the State of Pará listed *H. zebra* in the regional list of endangered species as "Vulnerable" (Secretaria de Meio Ambiente e Sustentabilidade, 2008). On January 3, 2017, its inclusion in Appendix III of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) took effect further restricting its international trade (CITES, 2016; UNEP, 2020). The zebra pleco is by consequence also listed in Annex C of the European Union Wildlife Trade Regulations. Its status in the wild, however, has not yet been evaluated by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. Despite all these regulations and regular seizures of trafficked wildlife by the Brazilian Environmental Protection Agency (IBAMA), and Brazilian Federal Police, *H. zebra* is consistently among the most common fishes trafficked out of Brazil (Charity and Ferreira, 2020) contributing to the illegal global wildlife trade.



**Fig. 1.** Adult live specimen of *Hypancistrus zebra*, 8.3 cm TL, in lateral (upper) and frontal (lower) view. Photographs by L. Sousa.

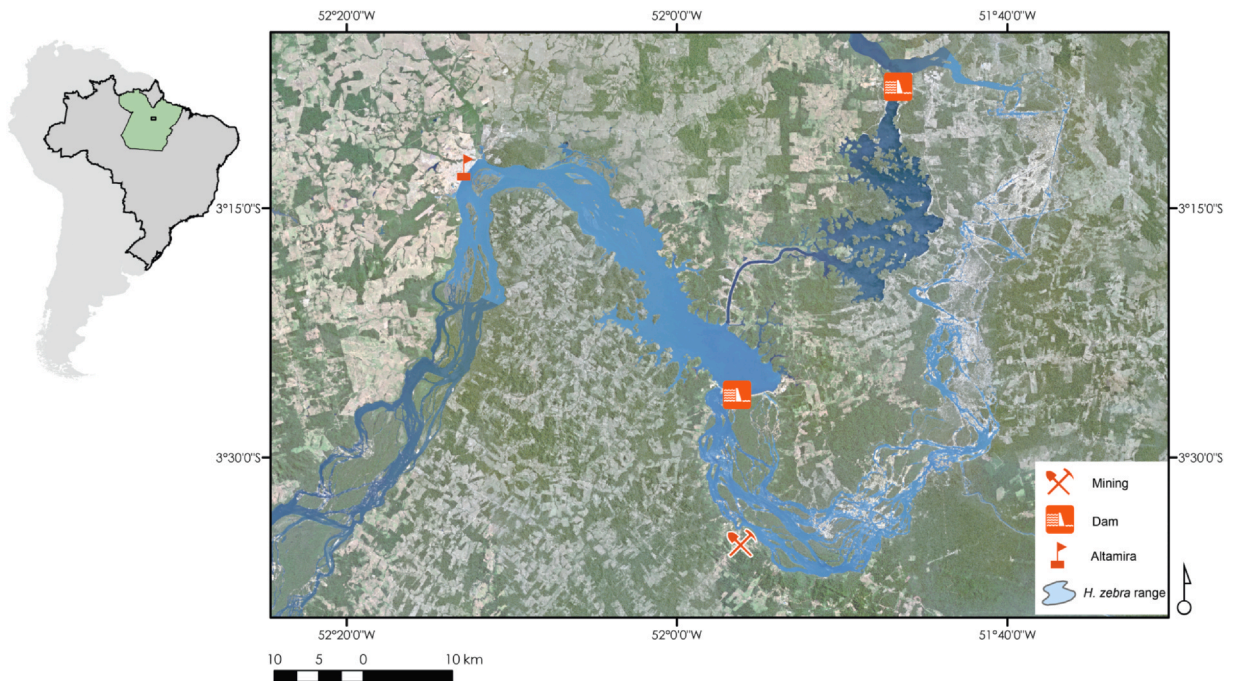
The global illegal wildlife trade is estimated to be worth ~\$US 19B per year and is the 4th largest illegal trade after narcotics, counterfeit goods, and human trafficking (Fedotov and Scanlon, 2013; WWF et al., 2012; Wylter et al., 2008). Wildlife trafficking is a crime that involves the illegal trade, smuggling, poaching, capture or collection of endangered species, protected wildlife or their derivatives (UNODC, 2016; Wylter et al., 2008). Bony fishes comprised nearly 5% of all CITES seizures up to 2019 (UNODC, 2020). The internet has exacerbated the pace at which specimens can be sold, providing a true globalized market, in which nearly every country in the world participates (UNODC, 2020). Since 2011 there has been an upturn of wildlife trafficking via the internet on legitimate platforms (i.e., auctions, forums, etc.) and in particular, over social media (Demeau et al., 2019). The demand for trafficked *H. zebra* specifically, is primarily driven by aquarists who want to keep wild specimens (Bourscheit, 2019).

In this comprehensive mixed-methods study we establish the baseline for conservation of the zebra pleco by determining its history in the ornamental fish trade, from discovery to current worldwide popularity as an ornamental fish. In addition, through an online survey of aquarium hobbyists, key informant interviews and web scraping, we gauge their awareness of the zebra pleco's conservation and trade and assess whether commercial captive breeding can play an important role in the conservation of this species. Furthermore, because little is known about the overall legal and illicit global trade of *H. zebra*, especially its potential impact on both *in-situ* and *ex-situ* conservation, we investigate the market demand for *H. zebra* over time. To date there are no reports or actions in Conservation Evidence about *H. zebra*. Therefore, our study provides an overall assessment of the status of *H. zebra in-situ* and within the aquarium hobby worldwide for informing decision and policy makers on the conservation of the wild population within Brazil.

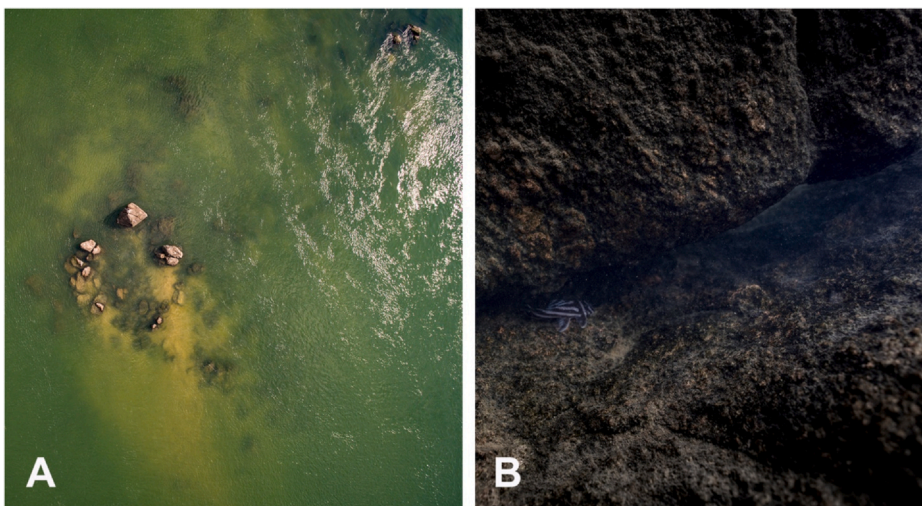
## 2. Methods

### 2.1. Habitat description and threats

The zebra pleco is a small fish (total length up to 9 cm) endemic to a 150 km stretch of the Xingu River, Pará, Brazil (Fig. 2) (Lees et al., 2016), which is a 2700 km long north-flowing clear water tributary of the Amazon River known for its extraordinary aquatic biodiversity and high rates of endemism (Sabaj-Perez, 2015a, 2015b). The zebra pleco is usually found inhabiting fissures or gaps between large gneiss boulders in moderate to low current in the main channel of the river (Fig. 3, Supplemental Video 1) feeding mainly on freshwater sponges and the associate invertebrate fauna that thrive in between the rocks in the current. The depth range of this species is from < 1–10 m, approximately coinciding with the photic zone. In nature, *H. zebra* breeds throughout the whole year but has two peaks of higher intensity reproduction, one at the beginning of the Middle Xingu's high-water season (November–December) and the other at the end of the high-water season (May–June) (Roman, 2011). The fecundity of the species is low when compared to other fishes, averaging between 10 and 15 eggs per spawn and they reach maturity at approximately 2.5 years old, measuring 3.5 cm in total length. The zebra pleco is considered vulnerable to the impacts of climate change due to its low dispersal ability, water quality needs and sensitivity to hydrological drought regimes (Frederico et al., 2016).



**Fig. 2.** Map of the Volta Grande and a 150 km stretch of the middle and lower Xingu River encompassing the entire known habitat range (light blue) of the zebra pleco. The background satellite imagery is from a cloud free mosaic from August 2020 acquired by the Planet Dove constellation. The location of Altamira as the primary city from where this species is exported is shown along with the location of the Belo Monte dam complex, including the reservoirs. The location for the planned Belo Sun gold mine is also shown. River layer was extracted from Kalacska et al. (2019, 2020). Inset shows the location of the study area within the State of Pará (green) in Brazil (gray). (For interpretation of the references to color in this figure, the reader is referred to the web version of this article)



**Fig. 3.** *Hypancistrus zebra* requires a very specific underwater habitat consisting of giant gneiss boulders and warm water (>28 °C) with low to moderate current. Contrary to what is commonly believed, it is not a rheophilic species, and therefore is not found in the rapids. A) Aerial photograph of a collection of gneiss boulders from a known zebra pleco habitat in relatively shallow water. B) *Hypancistrus zebra* habitat underwater, the species prefers deep horizontal crevices caused by fractured boulders stacked atop each other, a unique feature that is not seen throughout the river. Photographs by O. Lucanus.

The large number of undescribed Loricariidae prompted DATZ (Deutsche Aquarien und Terrarien Zeitschrift), the German fish keeping magazine to implement a system of “L-numbers” giving consecutive ‘L codes’ to photos of unidentified species published in the magazine (Camargo et al., 2013). When introduced to the hobby, *H. zebra* received the code L46 (or L046) and it is still often referred to with this code within the aquarium community.

The zebra pleco’s habitat is undergoing rapid changes due to synergistic river impoundment and mining projects (Tófoli et al., 2017). In particular, the Belo Monte dam complex in the Volta Grande sector of the river, which became operational



**Video S1.** A video clip is available online. Supplementary material related to this article can be found online at [doi:10.1016/j.gecco.2021.e01570](https://doi.org/10.1016/j.gecco.2021.e01570).

in November 2015, represents the most significant threat to its habitat (Bratman, 2015; Norte Energia, 2019; Sabaj-Perez, 2015b) (Fig. 2). Furthermore, permits for an open pit mine on the largest undeveloped gold deposit in Brazil along the southern sector of the dewatered section of the Volta Grande are also underway (Tófoli et al., 2017). The zebra pleco's entire known range falls within the impact zone (reservoirs and dewatered section) of the operational Belo Monte dam, and the planned Belo Sun mining project (if final permits are approved).

## 2.2. Field observations

The presence/absence of the zebra pleco in known boulder formations throughout its habitat range has been monitored (ad-hoc sampling) on a yearly basis by the first author (LS), accompanied by an experienced fisherman since 2011 using Scuba gear. Field observations were made during the low water season (July - November) covering its entire known range, visiting the same locations where its presence was recorded before the construction of the Belo Monte dam. The presence/absence of *H. zebra* was noted in each video recorded dive.

## 2.3. Historical documents

The timeline of the zebra pleco and Loricariid catfish in general in the ornamental fish hobby were established from historical documents, including price lists of early importers and books mentioning catfish in the early years of the modern aquarium (pre 1950s). Popular fish hobby magazines printed at the time *H. zebra* was discovered were searched for the first mention of the species imported to Japan, Germany, the UK, Taiwan, and the United States.

## 2.4. Online survey

We carried out an anonymous online survey of 21 structured questions through LimeSurvey (LimeSurvey GmbH, Hamburg, Germany). No identifying information including IP address, name or email was collected. We specifically targeted aquarium hobbyists and commercial breeders who keep or have kept zebra plecos in the past. The survey consisted of questions about the purchase or sales prices of their fish, their opinions and knowledge about the number of zebra plecos kept by the respondents, purchase or sales prices of their fish, their opinions and knowledge about the provenance of their fish and the current threats to the wild populations.

An initial pilot survey ( $n = 11$  respondents) allowed us to improve the clarity in the wording of questions. For the main survey we aimed for at least 300 respondents who were recruited through advertisements in Facebook groups, online forums and specialized fish keeping magazines. The online survey was available for 12 months in Chinese, English, French, German, Indonesian, Japanese, Korean, Portuguese, Spanish, Thai and Vietnamese. The largest internet catfish forum, planetcatfish.com (> 18,000 members) had 497 registered hobbyists keeping *H. zebra* at the time the survey was launched in December 2018 (J. Dignall pers. comm. October 3, 2020). Because respondents could enter prices in the currency of their choice, all entries were standardized to \$US as the benchmark currency using the historical yearly average conversion rates from <https://poundsterlinglive.com>. Prices were further corrected to 2020 prices using an online inflation calculator (<https://smartasset.com/investing/inflation-calculator>).

## 2.5. Interviews

To complement the survey responses, 16 semi-structured key informant interviews with commercial ornamental fish importers from China, Germany, Japan, the Netherlands, Singapore, Taiwan, the UK and the United States, and commercial exporters from Brazil, Colombia, Indonesia, Peru and the United States were carried out. All the major large volume importers and exporters in the respective countries were contacted. The interview guide focused on the history of *H. zebra* in the ornamental fish trade as well as on wholesale prices from the early days of importing and exporting the species (i.e., 1990s to the present) and geographic popularity of this species. A semi-structured interview was carried out with Yoshio Ogawa, one of the individuals who discovered *H. zebra* in the late 1980's. The interview guide focused on the discovery and the introduction of the zebra pleco to the international ornamental fish trade. In addition, 12 unstructured interviews were carried out with local fishermen and three consolidators based in Altamira using key informant sampling (Newing, 2010). The focus was to gather information about the natural history of *H. zebra* and the history of its collection and export. A semi-structured phone interview was also carried out with a customs official in a European Union country focusing on *H. zebra* trafficked into the EU.

All interviewees' names with the exception of YO (with consent) have been kept confidential. Their responses are identified throughout the text as: I/E/F/C# where I is an importer, E is an exporter, F is a fisherman and C is a commercial breeder and # is their unique numerical identifier. Three decades of commercial ornamental fish import and export experience (OL) and more than ten years of field observations (LS) support the qualitative data and statistics gathered through the interviews. Interviewee responses were coded manually through inductive coding (Skjott Linneberg and Korsgaard, 2019). Words that represent summative attributes of segments of the responses were used as descriptive codes (Saldaña, 2015).

## 2.6. Trade data

Queries of trade databases such as the UN Comtrade database (UNSD Department of Economic and Social Affairs, 2020), and those specific to many countries are limited by the resolution of the harmonized commodity codes (i.e. code 0301.11 represents all live ornamental freshwater fish without a breakdown by genus or species (King, 2018). Also, it is well known that sources reporting trafficking statistics represent a fraction of illegally trafficked animals (Nijman, 2015). Therefore, in addition to the online survey and interviews described above, two additional methods were applied to gather data related to historical prices and the supply chains from unconventional sources, web scraping and Freedom of Information Act requests and access to trafficking and trade bases as described below.

### 2.6.1. Web scraping

Both manual searches and automated web scraping were used to complement the firsthand data described above. Online aquarist forums, auctions, Facebook groups and discussion board postings about *H. zebra*, its trade and conservation were searched. The Octoparse 8.1 (Octopus Datas Inc., Diamond Bar, CA) web scraping tool was used to automatically scrape Google's search engine for mentions of *H. zebra*. Automated web scraping involves the use of templates to scan web pages and simulate user clicks in order to extract relevant information (Berry and Linoff, 2001; Liu, 2007). Templates in English, German, Portuguese, Spanish and Japanese were used, and public online comments related to zebra pleco history, trade and conservation were extracted from the output. The templates searched for *Hypancistrus zebra*, zebra pleco (and language specific common names), and L046. For webpages in China, only manually searches were conducted via Baidu and WeChat and Facebook groups because Google search engine access was blocked in 2014 (Zheng and Wang, 2020). Both manual and automated searches were also carried out to look for web pages mentioning seizures of illegal fish in or from Brazil (in Portuguese, English and Spanish) because the media in Brazil and Peru often announces seizures of wildlife carried out by IBAMA or the Brazilian Federal Police.

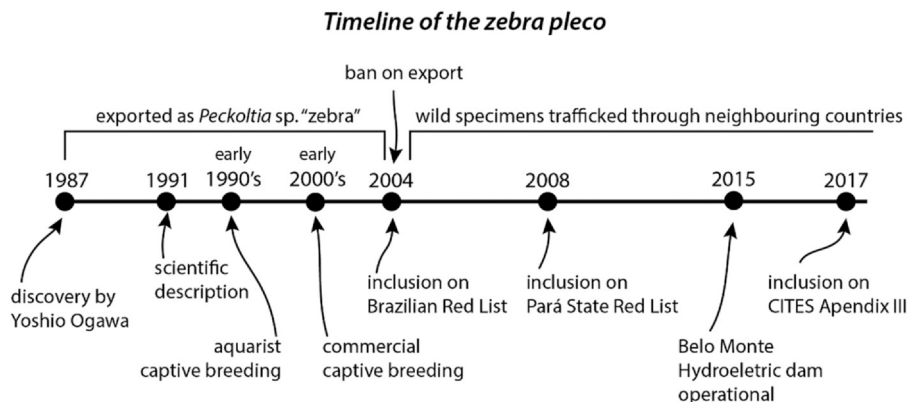
### 2.6.2. Databases

To supplement the data described above, Freedom of Information Act requests were submitted to US Fish and Wildlife (USFW), to the Canadian Food Inspection Agency (CFIA) and Environment and Climate Change Canada (ECCC) for information on legally declared *H. zebra* imports and seizures of trafficked *H. zebra* at ports of entry in North America. Access to the same data from the European Union's TWIX database, the United Nations Office on Drugs and Crime (UNODC) World WISE database and the TRAFFIC Wildlife Trade Portal was also requested. CITES declared cross tabulated trade records were downloaded from the CITES Trade Database for the 2017–2019 period (CITES, 2020). Each record in this database provides details about one permitted shipment (import, export or re-export). For records with a discrepancy in import and export quantities, both records were retained because while the records correlate in terms of purpose and year, they are for different quantities (CITES et al., 2013).

## 3. Results and discussion

### 3.1. Introduction of *Hypancistrus zebra* to the aquarium hobby

The earliest mention of a Loricariid catfish kept in an aquarium references *Hypostomus commersoni* (then named *Plecostomus commersoni*) imported to Berlin, Germany in 1893 (Dürigen, 1893; Teletchea, 2016). While Loricariidae have been a mainstay in the aquarium hobby for over 100 years, *H. zebra* was introduced relatively recently, in 1987, after Yoshio Ogawa and Minoru Matsuzaka discovered it in the Xingu River's main channel, near Altamira, by coincidence (Fig. 4). In the 1980's, main river



**Fig. 4.** A timeline of the main events in the history of *Hypancistrus zebra* as an ornamental asset, including restrictions on capture and export and subsequent trafficking.



**Fig. 5.** The hookah diving equipment used by the “acarizeiros”. A) A homemade air-compressor; B) Fisherman adjusting his dive mask and air-hose. The bottles are attached to his belt. He also carries a wooden stick (called “vaqueta”) to coax the fish from the crevices; C) Soda bottle being prepared to hold the fishes captured during the dive; D) Acarizeiro ready to go fishing. Photographs by L. Sousa.

economic activity around Altamira was mining for sand and gold using homemade hookah diving equipment (Fig. 5) with which a miner could spend several hours dredging at various depths. While searching for new fish to export, Ogawa and Matsuzaka discovered not only the zebra pleco but many previously unknown loricariids in the remote and hard to access sectors of the Xingu near Altamira. They contracted the dredge miners to start hookah diving to capture plecos. These newly specialized divers become the first “acarizeiros” (acari is the local word for pleco).

The fishing technological breakthrough from the dredge-dive miners who adapted their techniques to dive for plecos was applied to other Brazilian Shield rivers, allowing for the collection of new plecos at every locality visited by the acarizeiros.

Pictures of the zebra pleco were first published in a Japanese hobby magazine, *Aqualife Magazine* (March 1988 issue). The caption of the first *H. zebra* photograph stated [translated]:

“This imperial zebra pleco is the most beautiful plecostomus (still undescribed, Matsuzaka & Ogawa). Most of the specialists have never seen this fish before. It has a beautiful shape, pure white and contrasting pattern with clean stripes unlike any other. This time only one fish was imported and it is a really important record. It is just 6 cm long.”

Photographs of the first imported specimens were also published on the cover of the American *Tropical Fish Hobbyist* magazine (April 1988 issue), in the German magazine *Deutsche Aquarien- und Terrarien-Zeitschrift* (DATZ) (September 1989 issue) and *Fish Magazine* (October 1989 issue) in Taiwan. The zebra pleco was on the cover of *Tropical Fish Hobbyist* for a second time in September 1993 with a full-length article about its care in the aquarium (Carletti, 1993). The news of its discovery (and of sucker-mouth catfishes in general) in the Xingu, rapidly spread across the aquarium magazines and online message boards setting off a new craze, referred to as ‘the pleco fever’, that moved Loricariid catfish from generally being regarded as cleaner fish (many species eat algae), to the focal species of the aquarium, with hobbyists dedicating aquariums exclusively to their care (interview, YO, I2, E4). Among the PlanetCatfish forum members it has consistently been the most wished for species since such records began in 2016 (planetcatfish.com, 2020a).



### 3.2. Reproduction in captivity

Soon after the first regular imports of *H. zebra* to Asia, Europe and the United States, aquarium hobbyists began successfully breeding it in captivity. The first description of its reproduction in captivity for aquarists was published in DATZ in 1996 (Seidel, 1996). Currently, it has the third most captive reproductions documented online dating back to 1999 (planetcatfish.com, 2020b). Additional spawning records logged on zebrapeco.com indicate an additional 4322 fry produced prior to 2011 (zebrapeco.com, 2020). And, as one of the most sought-after “pleco” (planetcatfish.com, 2020a) it is one of the species responsible for what is today a thriving community of thousands of people worldwide dedicated to armoured sucker-mouth catfishes.

Small Loricariidae, such as *H. zebra*, readily breed in small aquaria (~100 cm in length) as long as the water conditions are suitable, and appropriate caves and the right diet are offered (Girardet, 2002; Korotev, 2002; Ramos et al., 2013). *Hypancistrus zebra* have very few eggs compared to other Loricariidae, averaging 5–15 eggs per brood from one female (under ideal conditions, this number may increase to ~30 for generations raised in captivity) with 6–10 spawns per year in the aquarium (interview, C1). Typically, the male will guard the offspring for 15–20 days after the eggs are laid. The juveniles absorb the yolk sac until the 13–15th day and start eating exogenous food when they leave the father to colonize the outer world, making the cave available again to another female ready to lay eggs. The young reach sexual maturity in approximately 2.5 years (interview, C1). In the wild, the generation time has been estimated to be 2.5 years (Zuanon and Py-Daniel, 2008). There are currently only a few large-scale commercial zebra pleco breeders worldwide. The largest one in Indonesia produces on average 10,000 young per year from approximately 5300 breeding adults (interview, C1).

### 3.3. Interview themes

Comparison of word clouds (DePaolo and Wilkinson, 2014) representing codes from the interviews with the fishermen (Supplementary Fig. 1a), exporters and consolidators (Supplementary Fig. 1b), and importers (Supplementary Fig. 1c) reveals differences in the themes important to the three groups. The fishermen, at the base of the supply chain, are fully aware that the capture of illegal species bears risks. A primary theme that emerged was the risk involved with their illegal activities with the codes *IBAMA* and *fear of jail* frequently occurring in the interviews. Another important theme was their justification of their activity by believing statements the zebra pleco is endangered are an overreaction, rather it is more affected by the *Belo Monte* dam. In contrast, they acknowledge that the zebra pleco population is decreasing (i.e., *fewer*). The population decline is an important theme because it makes it increasingly more difficult to fulfill orders for zebra plecos given to them by the consolidators. If they do not fish for zebra plecos, they believe someone else will (i.e., *everybody does it*). Lastly, the economic aspect is also important (i.e., *price*) to the fishermen because they usually receive more money for zebra plecos than for many other species.

For the consolidators and exporters (Supplementary Fig. 1b) the theme of zebra pleco trafficking is of primary importance. While they also discussed all the concerns addressed by fishermen, the business aspect also emerged as an important theme. Specifically, the fact that *trafficking* allows illegal *competition to transport* zebra plecos across the border in *Tabatinga to Peru* (and Colombia) via *Manaus* is viewed as *unfair* to the legal exporters. They would like to see *quotas* to allow the export of at least some zebra plecos annually. Despite the high price of the zebra pleco, the Altamira and Belem based suppliers face heavy fines levied by IBAMA and other regulatory agencies make trafficking too risky from their standpoint. The impact of the *Belo Monte* dam and how it will affect not only the zebra pleco, but their business with all other fishes as well was also an important theme.

Shipping (i.e., *airline, shipping, transport*, geographic locations) and financial considerations (i.e., *discount, price, volume, competition*) were among the primary themes that emerged from the importers (Supplementary Fig. 1c). Of note, another loricariid, *Baryancistrus xanthellus* Rapp Py-Daniel, Zuanon & de Oliveira, 2011, the *gold-nugget* pleco, was often referred to by the importers. Because of the consistently low price, large number of individuals in nature and nearly year-round availability, this species is one of the main exports from the Xingu today. Trafficking was not a common theme from the importers, because the large companies that we interviewed generally avoid trafficked fish and rely on *volume* with other species. In Europe and elsewhere the increased competition makes wholesale companies increasingly reliant on their overall volume and discounts from suppliers, as well as year-round availability of a wide variety of species. The wild zebra pleco exports for all of the import companies interviewed were from at least 15 years ago. If zebra plecos are sold by the larger companies, they are either purchased in bulk from local breeders or imported from the commercial breeders. The sale of trafficked zebra plecos seems to be largely done online by smaller importers.

### 3.4. Survey respondents

The survey was completed by respondents from five continents (Asia, Oceania, Europe, North America and South America) represented by 35 countries (Supplementary Fig. 2) resulting in 317 valid responses (from a total of 894 ‘views’ of the survey). Responses were considered invalid if the participants did not agree to the consent dialog or viewed the survey but did not answer the questions. The frequency of responses follows the general trend in reported value of imported Brazilian ornamental fish with the exception of Japan, South Korea and China that are among the largest consumers of ornamental fishes (UNSD Department of Economic and Social Affairs, 2020) but from where comparatively fewer responses were received. In particular, respondents from China reported technical challenges such as described by (Chen and Yang, 2019) accessing the survey website.

The majority of respondents (47%) purchased or received their first zebra pleco after 2004 when the species was classified as critically endangered by Brazilian agencies. In contrast, their most recent zebra pleco was predominantly (57%) purchased or received after the species was listed in CITES Appendix III in 2017 (Supplementary Fig. 3).

### 3.5. Wild caught versus captive bred preference and awareness of trade restrictions

Ten percent of the fish accounted for by the respondents were indicated to be known wild caught specimens. Thirty-five respondents, predominantly hobbyists intending to breed their fish from Europe and North America, indicated their entire colony of *H. zebra* (up to 30 fish in a tank) are wild caught. In contrast, 58% of respondents indicated all of their fish are captive bred. Asked about the importance of the provenance when deciding to purchase a fish, the largest number of respondents indicated they would either only purchase captive bred zebra plecos (44%) or prefer captive bred ones if available (27%) (Fig. 6). Only 2% responded they will exclusively purchase wild caught fish while 9.5% prefer wild caught specimens if available. An example of a justification from a forum post from a user preferring wild caught zebra plecos is to "give locals an income" while others justified their opinion by stating it "will [soon] be extinct" in the wild. While web scraping results showed there is an outspoken portion of aquarists supporting trafficking, such comments were also countered with those advocating for the purchase of captive bred specimens.

From our survey, we found that 70% of the hobbyists keeping *H. zebra* in their tanks do so with the intent of breeding them. The reported 2687 specimens (plus 693 not intended for breeding) is an underestimation of the total number being kept outside of Brazil. Our survey captured approximately 53% of the total current number registered zebra pleco keepers on planetcatfish.com. Accounting for low responses received from Asia (Supplementary Fig. 2), and the volume of trafficked fish (90%) regularly shipped there (see Section 3.8), we conservatively estimate 60,000–75,000 zebra pleco are being kept in hobby aquariums worldwide, but likely the number is higher.

Overall, respondents' awareness about the geographic origin and legal constraints on catching and exporting *H. zebra* was high (Fig. 7). Ninety-seven percent responded they are aware that *H. zebra* is endemic to the Xingu River and 88% and 89% responded they are aware that this species has been illegal to catch and export since 2004, respectively. Nevertheless, only 74% indicated they are aware that wild caught specimens purchased since 2004 from Peru, Colombia or other countries have been smuggled out of Brazil and sold illegally. Overall, 61% indicated they are aware that many *H. zebra* die in transport when they are smuggled out of Brazil.

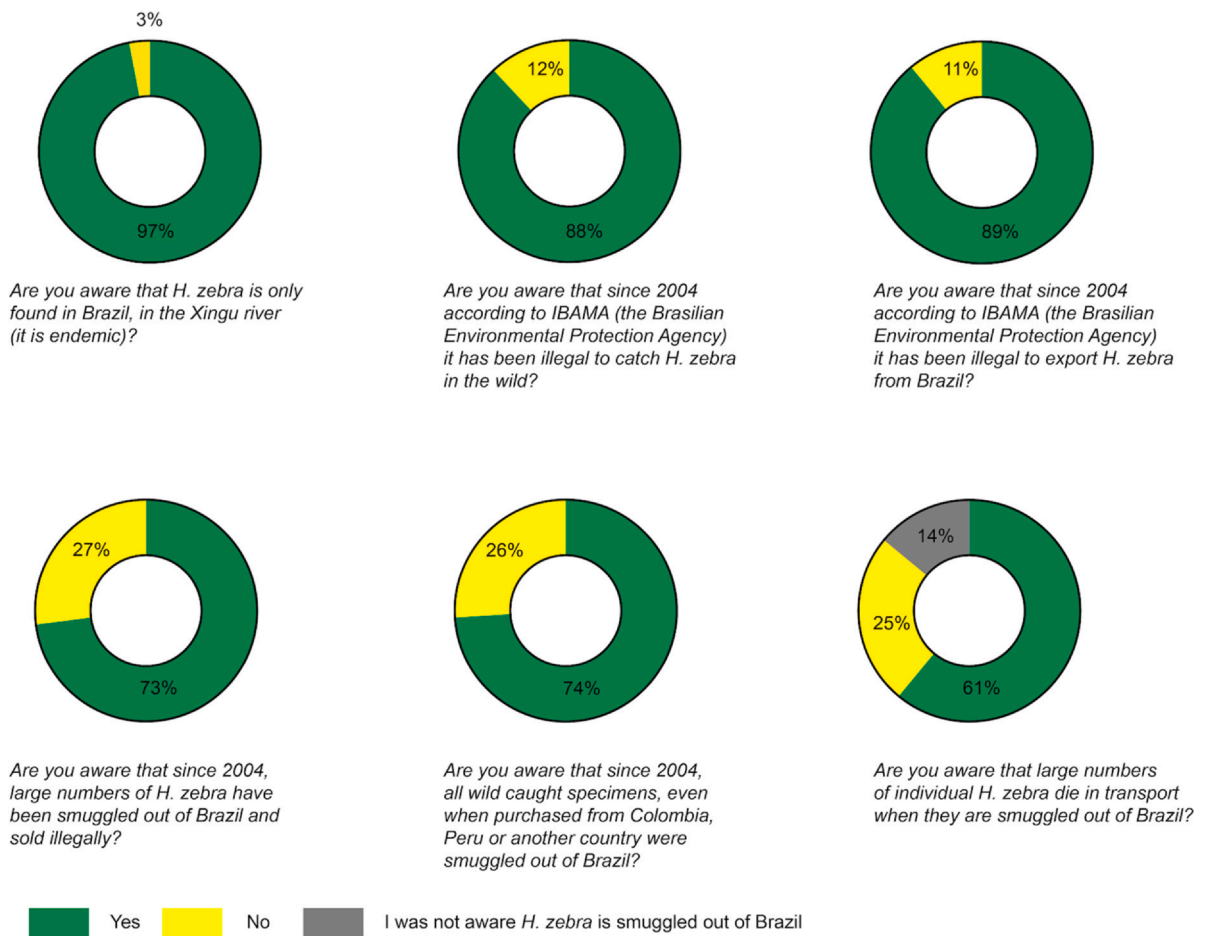
### 3.6. Threats to the zebra pleco and its conservation in nature

When asked about the impacts on the conservation of *H. zebra* in the wild, 78% of respondents indicated they believe the Belo Monte Hydropower dam will have a negative impact on its habitat (Fig. 8). In comparison, only 38% indicated they believe fishing will negatively impact the species. Comparing the two factors, 60% indicated that the Belo Monte dam alone puts the greatest pressure on this species, which is more than fishing (6%) or the dam and fishing combined (33%). Sixty-seven percent responded that combined, the dam and fishing will result in *H. zebra* becoming extinct in the wild. Opinions about the impact of listing *H. zebra* on CITES were mixed, with only 26% believing it would lead to an improvement in the conservation of the species, while 41% disagreed. Web scraping results showed considerable misinformation repeated online through forums and social media confusing the CITES listing with the 2004 Brazilian red list. For example, a forum poster in 2016 wrote "[the zebra pleco] is off [the banned list], then it will be banned starting March 2017...as I was told by my importer friend." Often such posts were corrected by other users, but the clarifications were not always accepted.

Similar to the opinions shown in Fig. 8, the Belo Monte dam was often identified and discussed by the online community of aquarists as the primary factor threatening the zebra pleco. Online opinions such as "If they are going to destroy [the river] why is it so bad to ... get [the zebra pleco] out?" were common among postings from several different countries across Europe, North America and Oceania. The low percentage of survey respondents identifying fishing as a major ongoing threat to the zebra pleco (Fig. 8), was also corroborated by comments in forums and social media such as "it not is the aquatics trade that is threatening the fish", "the illegal trade in fish is the biggest problem? That's ridiculous". In contrast, the yearly scuba facilitated field observations do not entirely corroborate the popular opinion. Recent (i.e., 2019, 2020) presence/absence surveys revealed that



Fig. 6. Preference of respondents to purchase captive bred or wild caught *H. zebra*. Each circle represents 1% (total of 100% shown).



**Fig. 7.** Percentage of respondents indicating awareness regarding the geographic origin and the legal constraints regarding the catching and export of zebra plecos from Brazil.

specimens of *H. zebra*, including juveniles likely younger than a year old, are still present at several locations within both flooded and dewatered sectors of the impacted area, indicating that the natural cycle of this species is ongoing in nature. However, there is strong evidence based on the ad-hoc sampling of a decline in the population since.

While field observations revealed a decline in the wild population since 2015, we argue that the decreasing trend in the number of individuals observed is due not only to the local negative impact of Belo Monte dam in some areas, but also to overfishing to fill greater consumer demands for trafficked fish. Prior to the construction of the Belo Monte dam, because of the large seasonal flood pulse (Sabaj-Perez, 2015a), fishing for zebra plecos was limited to approximately 6 months per year coinciding with low water season and in some years during the transition seasons. Therefore, fewer fish were removed from the habitat on a yearly basis. Due to the nearly negated flood pulse following operationalization of the dam resulting in consistently lower water level throughout the dewatered sector of the Volta Grande, access to the *H. zebra* habitats is now available nearly year-round. The habitat alterations caused by the Belo Monte dam did impact the populations of *H. zebra* but not sufficiently to cause the extinction of the species. The remaining populations are struggling to find their new equilibrium in the hydrological regime imposed in their habitat range after the operationalization of Belo Monte. The additional fishing pressure on an already vulnerable population could be the final stressor that results in the extinction of *H. zebra* in the wild. Paradoxically, the aquarists' attempts to save the species by purchasing wild specimens is what might be leading to its extinction in the wild given the current environmental conditions.

### 3.7. Supply chains and market prices

#### 3.7.1. Supply chain structures

The structures of the zebra pleco supply chains are shown in Fig. 9. Notably, the path taken by wild fish from capture by fishermen and arriving at an international wholesale import facility changed in 2004 when it was listed critically endangered (interview, I1–4, E1,2). Also noteworthy is that the species was never offered domestically, in Brazilian aquarium shops, and was targeted only for export. Web scraping revealed a social media post from 2013 referencing the single known instance *H. zebra*

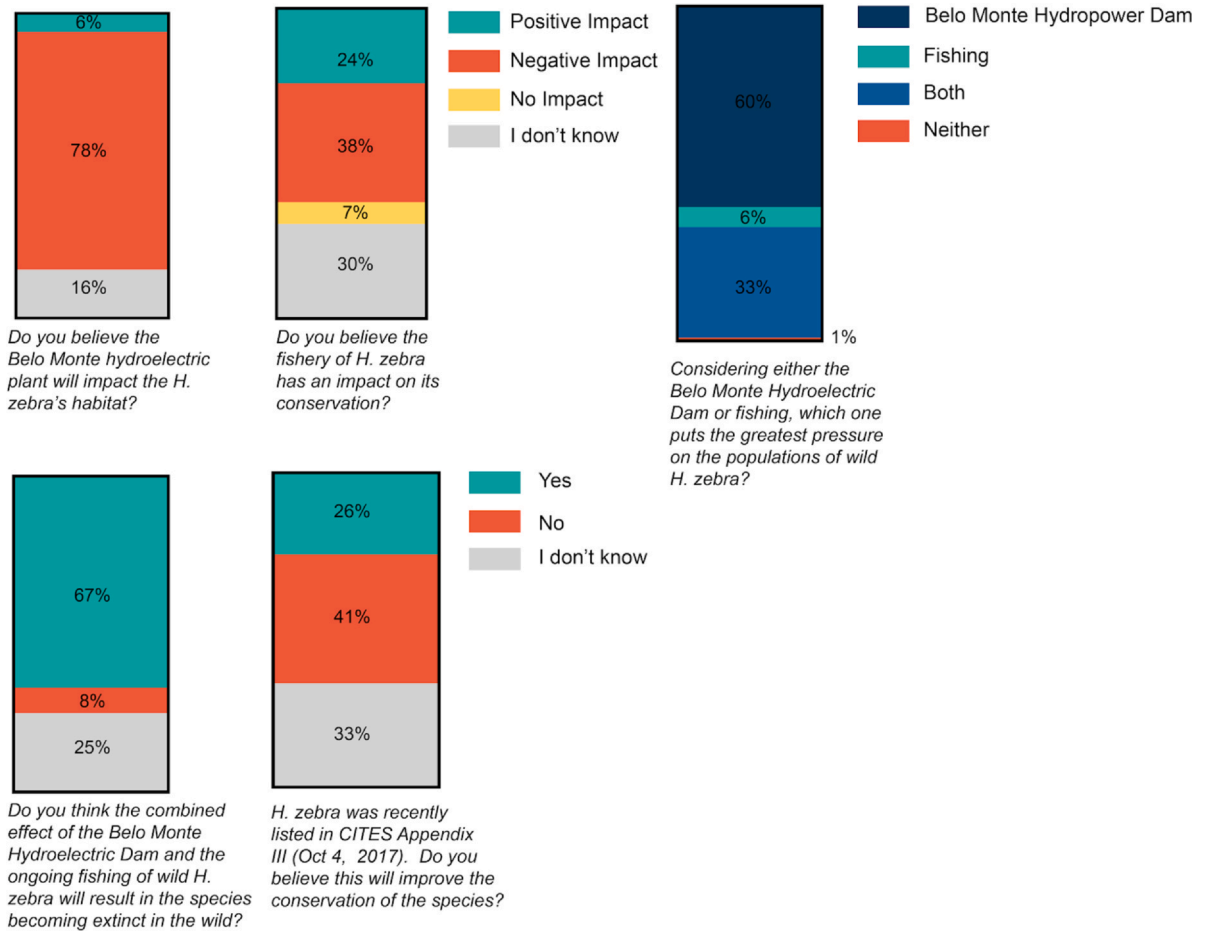


Fig. 8. Survey respondents' opinions about the relative impacts of threats to the conservation of *H. zebra* in the wild.

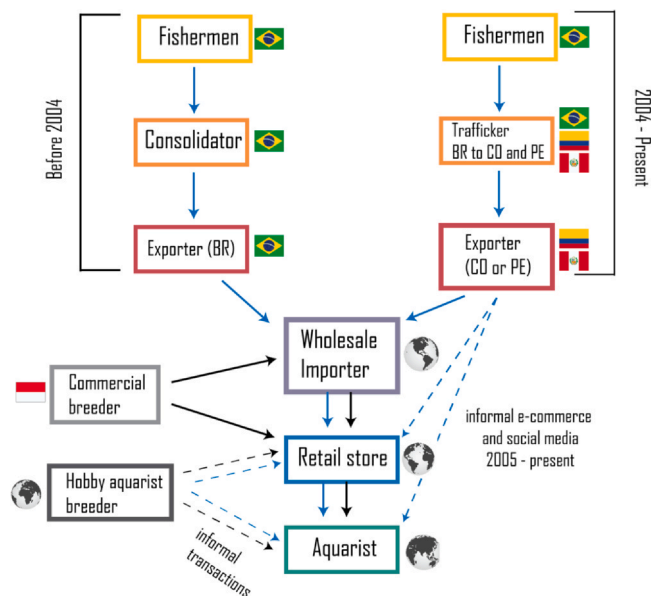


Fig. 9. Overview of the supply chains for the zebra pleco trade from Brazil before and after the 2004 export ban. Blue arrows represent wild caught fish and black arrows represent captive bred fish. Dashed lines indicate a predominance of informal transactions, solid lines indicate conventional transactions.

was allowed to be reimported into Brazil for sale by an aquarium store in Rio de Janeiro at a high cost of R\$ 950 per specimen (~\$US 494, inflation corrected) (Maxims Fish Tijuca, 2013). According to the exporter and consolidator interviewees, prior to 2004, consolidators located in transit cities such as Altamira with facilities to hold fish temporarily before shipping to a large volume Brazilian exporter played an important role in the trade of zebra plecos. Exporters in Brazil located in Belém, Manaus and São Paulo with the logistical and labor capacity to ship large volumes of fishes internationally profited from the sales and were the primary link to the international market. However, laws prohibiting the shipping of endemic species across state borders resulted in legal and financial difficulties for companies profiting from Xingu pleco sales outside of Pará (e.g., see Midia News, 2009). The law greatly benefits Belém-based suppliers, exporting from Pará state, and put suppliers in Manaus (in Amazonas state) at a disadvantage. After 2004, the role of the consolidators was taken over by traffickers who transport the zebra plecos from Brazil to Peru and Colombia for export (interview, E1, E2, E4). The illicit supply chain of wild specimens (post 2004) illustrates a loss of profit within Brazil as the majority of the exported revenue is gained in Peru and Colombia (see Section 3.8).

Since 2002, zebra plecos from large-scale commercial breeding facilities (primarily located in Indonesia) have become affordable alternatives to trafficked wild specimens (interview, C1). In the last decade, with the popularization of social media, aquarists are able to reach out to exporters and even fishermen directly, bypassing importers to get lower prices, at times with limited success due to the complex logistics and permits needed to import fish into many countries (interviews, I2,3). The popularity of the zebra pleco and success by hobbyists in breeding the fish in home aquaria led to an informal market where they sell, donate or trade fish through social media, personal connections, aquarium clubs, online forums and auctions (interview, I4, 5). Web scraping results showed that in some countries such as Australia, which have very restrictive import policies, these informal transactions are the primary means through which hobbyists acquire new zebra plecos. In most countries few brick and mortar retail stores have zebra plecos in stock. Therefore, hobbyists wanting to acquire zebra plecos often use the informal markets on social media, electronic retailers or auctions to purchase their fish (Fig. 9).

In recent years, there has been an increasing shift towards aquaculture specimens in the ornamental fishing industry and the most popular species are reproduced in large numbers at dedicated captive breeding facilities (Evers et al., 2019). Similarly, in the international wildlife trade, specimens marketed as 'captive bred' have gained popularity (van Schingen et al., 2016). In many regions around the World, and in South America especially, the high volume and/or value of several species (e.g., *Paracheirodon axelrodi*, *Potamotrygon leopoldi*) provided temporary incentives to protect natural habitats. With the expansion of large-scale commercial breeding operations in South East Asia, income and poverty alleviation from these species shifted from South American countries to Asia (Evers et al., 2019; King, 2018). While many aquarists prefer captive bred specimens due to their hardier nature, habituation to prepared food, generally parasite and disease-free health, and brighter color (e.g., farmed Asian arowana *Sclerophagus formosus* (Charity and Ferreira, 2020)), many consumer motivations remain for purchasing wild caught specimens, even if a species is illegal to export. Within the freshwater ornamental fish industry novelty, rarity, financial gain and enhancement of social relationships (Thomas-Walters et al., 2020) are strong motivators for aquarists to purchase wild caught specimens. In addition, as seen here, some may be driven by a sense of conservation to 'save' a species they perceive to be under threat of extinction, while for others the wild caught fish also support income and protect habitats.

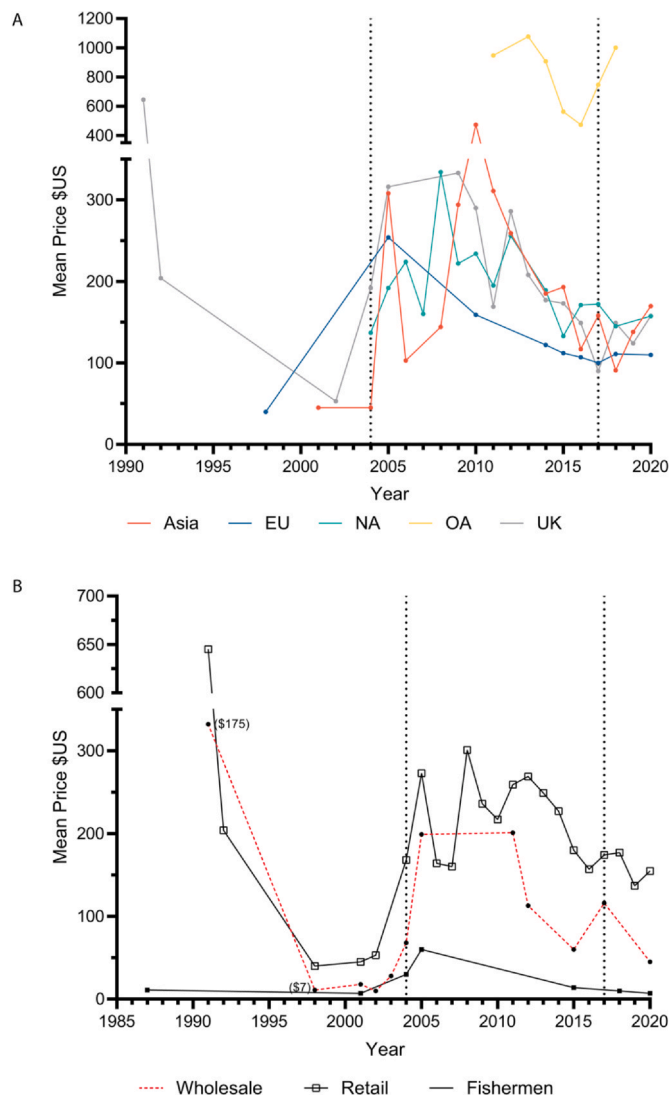
### 3.7.2. Market prices

Web scraping results from the earliest imports into the UK revealed high prices for the zebra pleco (> \$US 400, inflation corrected) during this time (Fig. 10a). The major wholesale companies in the trade consistently purchased "a handful of zebra plecos" in the early days of export (1989–1992), at wholesale prices of around \$US 100–250 (\$190–475 inflation corrected) before shipping from Brazil (interview, I1–3), reselling fish in the \$US 200–350 (\$380–664, inflation corrected) range (interview, I1, 2, 4) (Fig. 10b). According to Importers 1 and 2 (interview, October 2020) retail prices to the aquarists reached as high as \$US 500 in the early 1990s in Europe, North America and Asia. The high prices resulted in the exact collection points kept secret by fishermen who intentionally mislead others asking about the localities (interview, F1), which likely led to the presumed occurrence of *H. zebra* in the Iriri river, 75 km south of its southernmost known extent without a single specimen of the genus caught in more than two decades of intense scientific sampling in that river.

The high prices did not last long, as the new boom of fishes from the Xingu quickly resulted in new exporters starting businesses in Belém. This competition dropped the prices of the fish. In 1998–1999 the price of *H. zebra* dropped as low as \$US 5–10 wholesale (\$US 8–16, inflation corrected) (Fig. 10b), requiring minimum purchases of 5–7 boxes (50–60 fish per box), before gradually rising again until the 2004 export ban (interviews, I1–4, E1, 2). For example, a wholesale sales record from the United States from 1993 lists a sale price of \$US 12/fish (\$US 21, inflation corrected). The inclusion of the zebra pleco in CITES Appendix III led to an increase in demand and increased the price of trafficked fish from a wholesale price from \$US 45 (\$US 48, inflation corrected) to an average \$US 90–120 (\$US 95–127, inflation corrected) per individual (interview, E3–5).

Several social media and forum posts also make reference to the linkage between export regulations and the increased price of zebra plecos from 2004 onwards (Figs. 4, 10). As stated by one forum poster from Asia in 2014 [translated] "the price of L46 is 9500 TWD [\$US 300], this is ridiculous!" to which another user replied "I purchased two for 650 TWD [\$US 19] each in 2003 in a store and sold them [in 2005] at 6000 TWD [\$US 188] each. At the time the store price was 9000 TWD [\$US 281]. People were saying the price increase is due to restrictions from the country where it is from".

Compared to other countries, prices of zebra plecos in Australia are much higher, varying from \$US 437 in 2016 to \$US 990 in 2018 (yearly averages, inflation corrected) (Fig. 10a). Following the initial increase in retail and wholesale prices after the 2004 export ban, a gradual decrease in prices is observed. This same trend is also seen in the prices paid to fishermen for collecting zebra plecos (Fig. 10b). A small overall increase in retail prices following the CITES listing can be seen, but this is primarily



**Fig. 10.** A) Average retail price per specimen of *H. zebra* determined from web scraping for the five regions separately. Horizontal dotted line (A) highlights the year of the export ban (2004) and dotted line (B) the year the CITES listing came into effect (2017). B) Average retail price per specimen of *H. zebra* determined from web scraping for all regions (except Oceania), wholesale price per fish and price received by fishermen per specimen as reported by the interviewees. Vertical dotted lines highlight the year of the export ban (2004) and the year the CITES listing came into effect (2017). All prices shown are inflation corrected to 2020. The highest and lowest nominal price (i.e., not inflation corrected) of the wholesale fish are shown in brackets in BEU = European Union, NA = North America, OA=Oceania, UK = United Kingdom.

driven by prices in Asia, North America and the UK. Retail prices in Europe seem to have been less impacted (Fig. 10a). While not included in the overall average, an increase post 2017 is also observed for retail prices in Oceania. The increase in retail and wholesale price after 2017 is not passed on as higher profits to the fishermen (for the trafficked fish) as the price paid to them is nearly as low (\$US 7 nominal, \$US 11 inflation corrected) per specimen as the minimum (\$US 5 nominal, \$US 7 inflation corrected) they received prior to 2004 (Fig. 10b). Post 2017, the wholesale price continued to decline. Prevalence of social media leading to increased communication between breeders, exporters and hobbyists (Fig. 9) has gradually led to a decrease in the wholesale price of the zebra pleco resulting in lower profits for the commercial breeders (interview, I4, 5).

The sharp increase in the late 2000s (Fig. 10) is likely due to the increase in demand and access of customers through the popularity of social media platforms (Demeau et al., 2019; Ortiz-Ospina, 2019). The success of the internet in establishing a global communication network (Wellman et al., 1996), both facilitated trafficking (Demeau et al., 2019) as well as promoted the development of the informal and e-commerce networks (Fig. 9). Ironically, this same increased access of consumers to exporters or even fishermen directly, is likely also partially the reason for the subsequent decrease in prices over time. From the fishermen's point of view, the price of the zebra pleco is higher than most other sympatric fish, although it is not the most valuable (e.g., stingrays and other species of loriciariids such as *Pseudacanthicus* spp. and *Scobinancistrus* spp. often have higher prices). Fishing for wild *H. zebra* is not necessarily their main goal, they only fish for species ordered by the traffickers or

consolidators. These orders essentially reflect the needs of the exporters to satisfy the market demand from the final customers. If a more profitable request is made in a given season, for a different species, for example a rare variant of *Ancistrus ranunculus*, they will focus on fulfilling this new order rather than the one for the zebra pleco.

The retail market prices pre- and post-2004 described by the interviewees are substantiated by both the survey results and web scraping data (Supplementary Fig. 4). However, large variability in the retail price of zebra plecos is reported by survey respondents across all regions (Supplementary Fig. 4). The increase in retail price worldwide after the export ban in 2004 seen in the web scraping data is also reported by the survey respondents for both wild caught specimens and also for the captive bred fish. The increase is most pronounced in the web scraping (sales) data from Asia and Europe (Fig. 10a, Supplementary 4c). Interestingly, the interviewees' reported increase in price of wild caught trafficked specimens following the CITES listing was only partially corroborated by the survey respondents and web scraping results indicating that the increased wholesale price was not passed on to the consumers evenly in all countries. However, the price of captive bred fishes was significantly lower than wild caught specimens in the period after the CITES listing in all regions except those in the 'Other' category (Supplementary Fig. 4a,b).

Recently, zebra pleco color morphs such as aberrant patterned specimens or hybrids between *H. zebra* and closely related species have gained in popularity, especially in online sales. These color morphs are often selectively bred from odd colored wild specimens to increase the amount of white or unusual patterns (interview, I3). Color morphs and hybrids may occur randomly within the wild populations or be chance results of cross breeding between the different species of *Hypancistrus* occurring in the same habitat in nature. Like many reptile species, aberrant color morph fish are much sought after by aquarium hobbyists, especially in Asia. Web scraping results indicated that *Hypancistrus* polymorphs typically sell for 3–6 times higher prices than normal zebra plecos, especially in Japan and China. There are albino and axanthic morphs available, but the most sought-after ones are oddly patterned specimens. Web scraping results from Chinese and Japanese websites indicated that these specimens are currently being sold at or above \$US 500 per fish. As line breeding for polymorph aquarium fish continues to gain popularity it will reduce pressure on the wild population where such specimens are extremely rare (less than 1 in 5000 fish) (interview, E1,2, F1–3). Rarity fueled demand and the predisposition to place increased value on rare species or individuals has been well documented across taxa (Courchamp et al., 2006; Hall et al., 2008). Similar to the zebra pleco, aberrant color morph and albino specimens are also a trend in other fish species. For example, aberrant morph clown fish (*Premnas biaculeatus*) have been documented to cost 5–30 times the value of regular color individuals exported from Papua New Guinea (Militz et al., 2018). Similarly, albino specimens of high value South American freshwater fish such as the silver Arowana (*Osteoglossum bicirrhosum*) are regularly sold at 20–30 times the cost of regular specimens while albino Bosemani rays (*Potamotrygon boesemani*) can cost up to 50 times the price of regular specimens (unpub. export data).

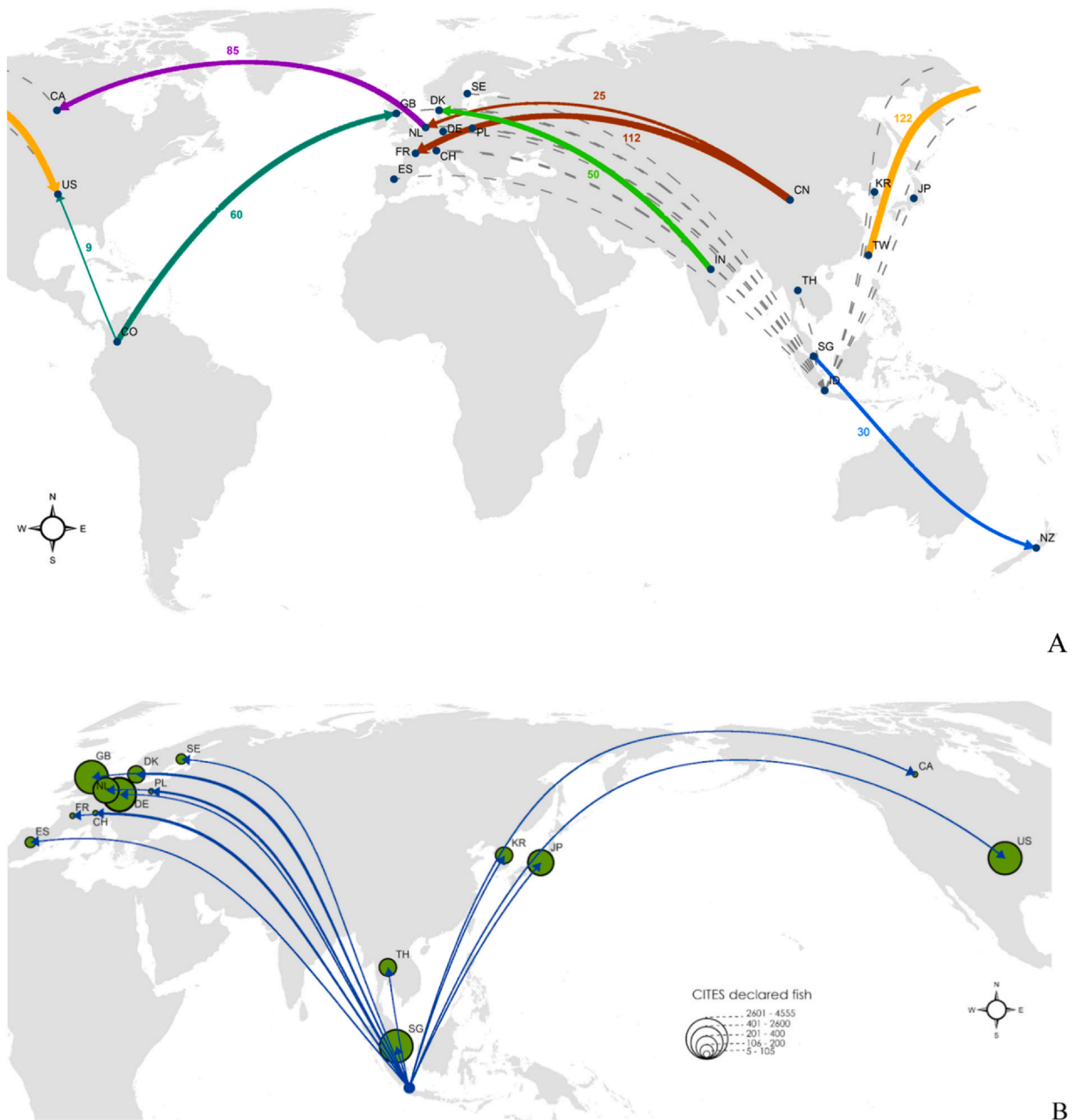
The CITES declared cross tabulated trade records indicate 20,815 zebra plecos were shipped worldwide in the 2017–2019 period (Fig. 11) representing a wholesale cost of approximately \$US 1.5 M and a retail value of approximately \$US 3.1 M. The greatest proportion (97.6%) of these captive bred fish were shipped from Indonesia to the redistribution point of Singapore (21.9%), as well as Germany (12.5%), Great Britain (19.6%) and the United States (20.8%). Of note are the two reported shipments originating in Colombia, with 9 and 60 fish shipped to the United States and Great Britain respectively (Fig. 11a) given that it is a well-known collection and export hub for trafficked zebra plecos.

### 3.8. *Hypancistrus zebra* trafficking

Trafficking of wild caught *H. zebra* has been common since the export ban in 2004 (Bourscheit, 2019; Tapullima, 2019). The most common trafficking route delivers fish from Altamira to Manaus and on to the export centers of Bogotá, Colombia and Iquitos, Peru (interview, E1, 2, 5) (Fig. 12). The three-country triangle of Colombia, Brazil and Peru where the cities of Tabatinga, Letícia and Santa Rosa are all directly adjacent is one of the primary routes along which the fishes are trafficked out of Brazil (Bourscheit, 2019; Charity and Ferreira, 2020; Tapullima, 2019).

As described by Exporter 1 (interview, October 2020), zebra plecos are regularly seized on boats from Manaus to Letícia, Colombia and Iquitos, Peru hidden in luggage or among other aquarium fish. The fish are also smuggled to the neighboring countries by small or commercial aircraft and then hidden among exports of other native fishes from the exporting countries. Informal estimates from suppliers of those countries indicate that approximately 5000 to 10,000 zebra plecos are exported this way monthly during the peak season. The long land journey from the Xingu also means that half or more of the fishes die in transport (interview, E2). The more than 6800 specimens of zebra plecos reported seized by IBAMA and the Federal Police over the last decade (Bourscheit, 2019) represent a very small fraction of the animals trafficked out of Brazil. The years with the largest number of *H. zebra* seizures include 2014, and 2015 with nearly 1000 specimens each, although the number is increasing over time and was likely surpassed in 2019 (Charity and Ferreira, 2020). Trafficked specimens are often in poor health due to malnourishment, low water quality and overcrowded shipping conditions (Fig. 13a). Accounting for the approximate 50% loss in transit of the trafficked fishes, the annual wholesale value is conservatively estimated to be \$US 3–7.2 M with a retail value of \$US 5.3–10.5 M.

Web scraping returned local media articles on seizures from 2004 through 2020 in Tabatinga, Santarém, São Paulo, Manaus and Altamira. In most instances the seizures reported hundreds of specimens and in some cases, zebra plecos were only one of the species found with the traffickers. For example, in 2017, Folha de São Paulo reported a seizure of 672 fish at the airport in Manaus of which 302 were *H. zebra* (Maisonnavé, 2017). In 2014, reports one month apart stated individuals were caught trafficking 161 and 268 *H. zebra* respectively at the airport in Manaus on route to Colombia (Albuquerque, 2014a, 2014b). In

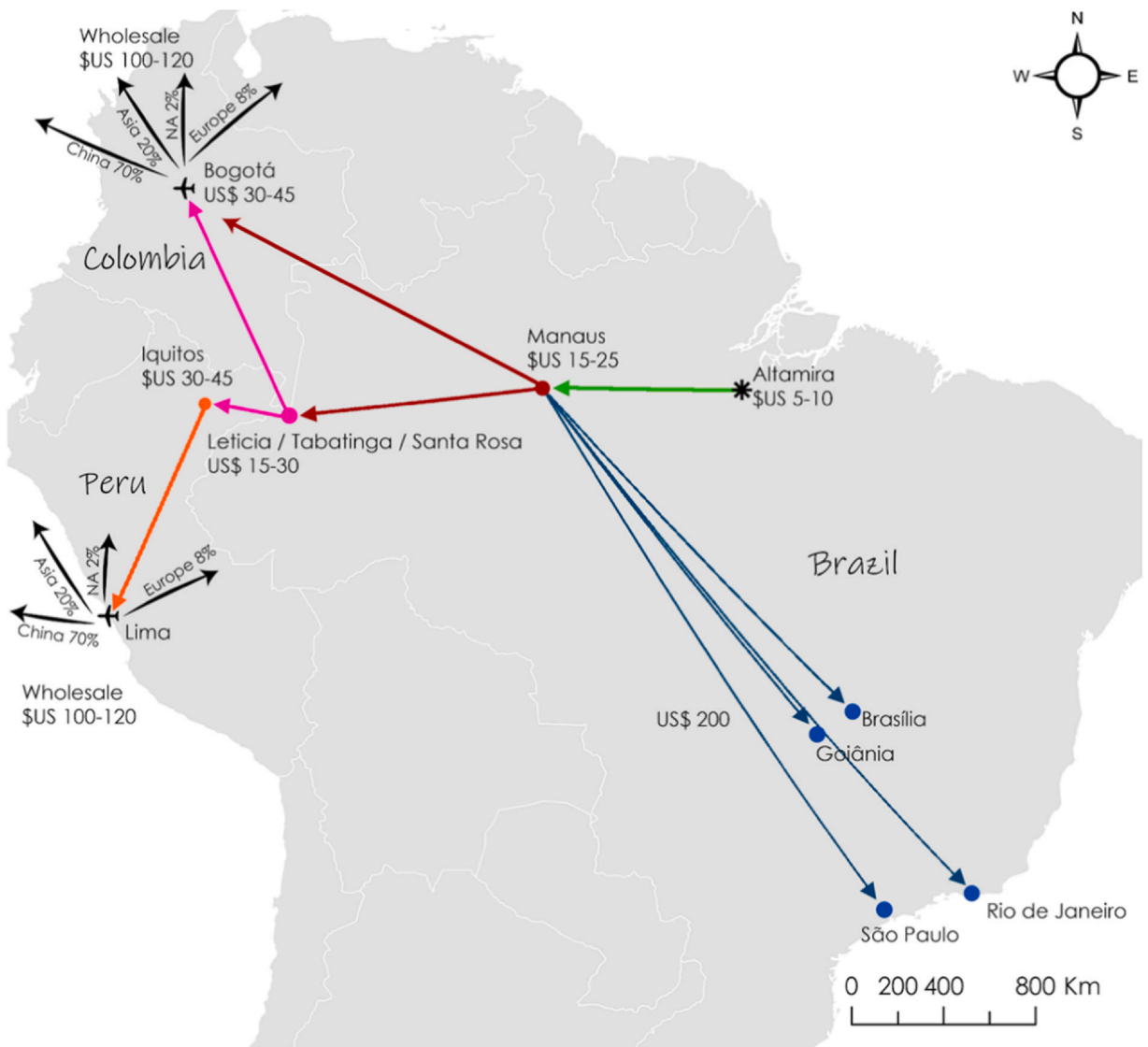


**Fig. 11.** A) Pathways of CITES permitted shipments of *H. zebra* for the 2017–2019 period. Due to the large number of exports from Indonesia (dashed lines), those are shown in detail in B. The thickness of the arrows is relative to the number of fish in the shipments indicated by the number in corresponding color. B) Detailed view of the pathways of CITES permitted exports of *H. zebra* from Indonesia for the 2017–2019 period. The size of the circles in the destination countries indicate the number of fish in the shipments.

2019, G1, an online news portal, reported 487 *H. zebra* seized at the Altamira airport (G1, 2019) and recently a shipment of 630 *H. zebra* were seized in Tabatinga during a routine inspection of a speedboat (Portal do Holanda, 2020).

Officials in Peru and Colombia also seize ornamental fishes through inspections of exporter facilities and in transit. Colombian officials, for example, stated having seized 70,000 illegal ornamental fishes, but do not have information at the species level (Bourscheit, 2019). Similarly, in Iquitos, Peru, officials regularly visit exporters with a known history of trafficking illegal species. Over 2000 illegal ornamental fish were seized in 2018–2019, including zebra plecos (Tapullima, 2019). Similar to the statement by Brazilian exporters (Section 3.3), a Peruvian exporter caught with illegal fish mislabeled as legal species was quoted as saying it is not a crime, rather it is a mistake and that as far as he knows, he is not the only exporter having committed such mistakes (Tapullima, 2019). In another incident, in 2015, Tapullima (2019) reports zebra plecos discovered in Iquitos were



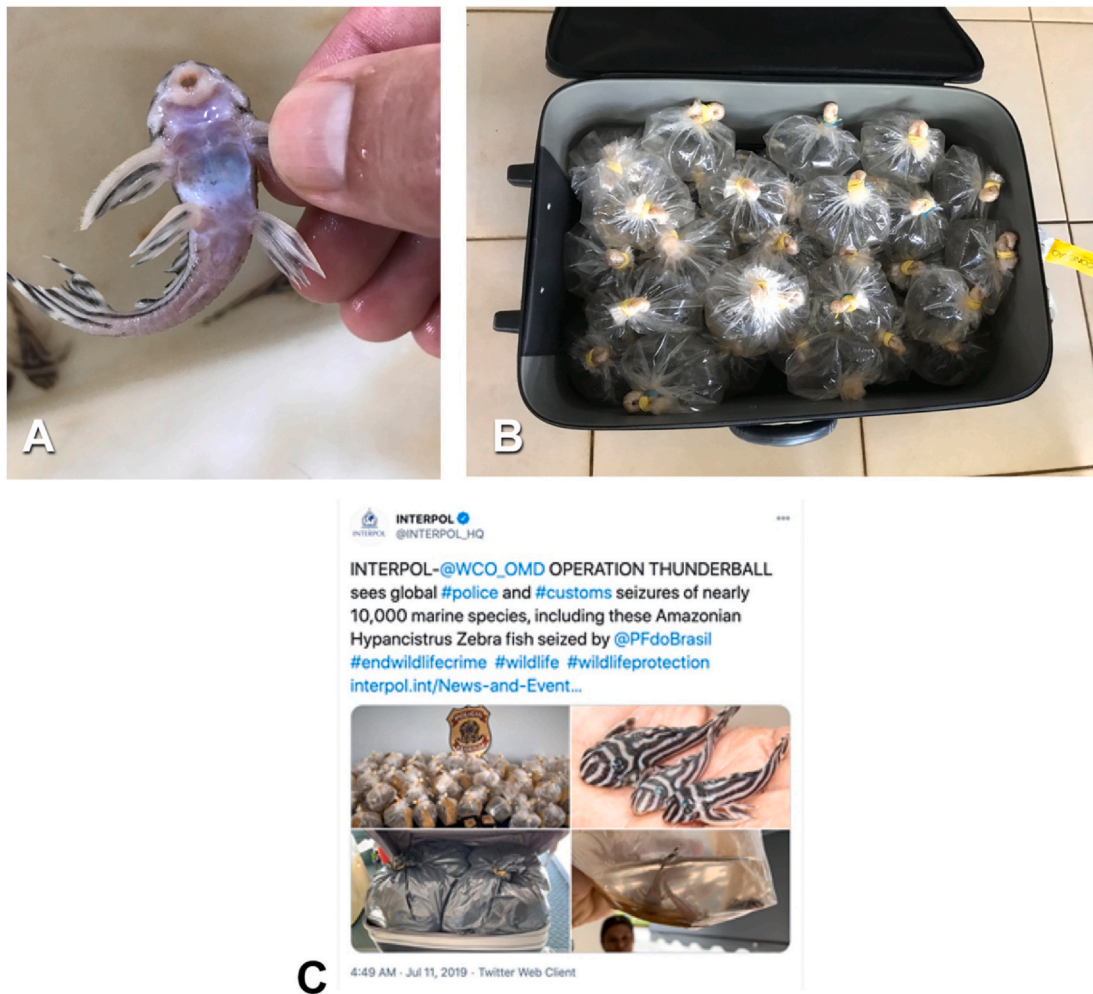


**Fig. 12.** Common trafficking routes for illegally caught and exported *H. zebra*. While fish are sent to international destinations directly from Bogotá, from Iquitos they are first sent to Lima, where they are loaded onto international flights. Internal shipments of zebra plecos to the national market are also shown but represent but a small fraction of the internationally trafficked specimens NA = North America.

hidden within a shipment declared to contain *Peckoltia vittata* and *Pseudohemiodon apithanos* destined for Osaka, Japan. The same year a larger shipment of over 1000 fish was found to contain 20 hidden zebra plecos from the same exporter destined for England. Several other similar examples have been reported from both Peru and Colombia.

In Brazil heavy fines are placed not only on illegally smuggled species, but also on small technical errors, such as mislabelled boxes, for the tightly controlled legal exporters (interview, E2). To many exporters, it is worthwhile to send legal fishes undeclared (and thus illegally) via Colombia and Peru instead of being liable to receive fines frequently levied on legal operations. This is seen in recent seizures of legal to export fishes (e.g., *Panaque armbrusteri*, *Hypancistrus* sp. L333, *Scobinancistrus pariolispos*, *Scobinancistrus* sp. L82, etc.), found in traffickers' shipments alongside *H. zebra*. Export quotas following the same model of Amazonian stingrays before their CITES listing (e.g., IBAMA and MMA, 2017) to allow for legal export of *H. zebra* and reduce the frequency of trafficking (interviews, E1–5).

Since 2004, zebra plecos are collected by the fishermen in the Volta Grande to fulfill orders from traffickers who transport the fishes to Manaus. Currently, the price at the river is around \$US 5–10 (Figs. 10b, 12) (interview, Fishermen; Bourscheit, 2019). Once at the border the fish are sold for \$US 15–30 (interview, E3, 4), depending on the quantity (Fig. 12). It is not uncommon for Peruvian and Colombian exporters to buy a few zebra plecos for up to US \$45 each, reselling them as loss-leaders to earn or retain customers purchasing local (legal) species (interview, E4, 5).



**Fig. 13.** A) Photograph of a malnourished *H. zebra* seized in Altamira in December 2020. The seizure comprised 160 trafficked fishes, including 128 zebra plecos. The fish were being smuggled by commercial air travel in checked luggage (B). Photographs by L. Sousa; C) Screen capture of Tweet showing zebra plecos seized during Operation Thunderball in 2019, © Interpol, used with permission (Interpol, 2019).

Since the addition of *H. zebra* to CITES Appendix III, the market for illegal fishes has changed. North American ports of entry, well protected by federal agencies in Canada and the US, have seen a substantial reduction in wild *H. zebra* imports, accounting for only an estimated 2% of the trafficked specimens (interview, E2). Europe, with more countries and ports of entry, customs officials trained to different levels of expertise to inspect and enforce tropical fish imports (interview, Customs Official) now accounts for an estimated 8% of trafficked zebra plecos (interview, E2). As stated by Exporter 2 (interview, October 2020), this leaves an estimated 90% of trafficked zebra plecos heading to Asia, primarily to China, Singapore and Thailand (Fig. 12). On occasion, large international efforts to curb wildlife trafficking also result in the seizure of zebra plecos, as was the case in 2019 through the Interpol and World Customs Organization led Operation Thunderball (Fig. 13c) (Interpol and World Customs Organization, 2019).

The large number of captive bred specimens available for sale, trade and auction from electronic retailers and informal networks should have reduced the demand for trafficked wild specimens but this does not seem to be the case, as seizures of fish (e.g., Fig. 13) still occur on a regular basis. Yet, as reported by Exporter 2, up to 10,000 specimens are trafficked from the Xingu River on a monthly basis, of which the majority (70%) are sent to China (~35,000 specimens per year accounting conservatively for the 50% mortality rate). The mortality rate of the trafficked fish is highest during the first legs of the journey from when they are caught to when they arrive in Bogotá or Iquitos due to the poor conditions in which they are trafficked (Fig. 13a). The trafficked specimens are often overcrowded, packed with many specimens per bag, without supplemental oxygen or insulation. At sustained temperatures above 32 °C the fish will usually die or get damaged beyond recovery. Exhaled ammonia built up in shipping bags containing dead specimens or insufficient oxygen are the other likely causes to lead to the unusually high mortality rate in specimens transported in luggage or buckets over long periods of time. In comparison, normal mortality rates for legally exported fishes from Brazil are low, below 2% for nearly all species (unpub. import records). The high value and/

or rheophile Loricariidae are generally single packed (one per bag) by trained staff after an extended quarantine period, with well purged stomachs and pure oxygen added to the bags. The fish are transported in insulating Styrofoam boxes with heat packs to regulate temperature in transit.

International shipments and seizures of zebra plecos upon import were difficult to quantify. The data provided by the FOIA requests of declared live fish imports to the United States as recorded in the Office of Law Enforcement's Law Enforcement Management Information System (LEMIS) database originated from USFW Form 3–177. These results were supplemented by previously obtained LEMIS data from (Eskew et al., 2020) dating back to 2000. The results indicated 126 records of *Hypancistrus* sp. shipments (declared quantities of 1–400 fish) with the majority from 2009 onwards originating primarily from Colombia, Brazil and Germany. Of these, only five (originating from Peru, Colombia and Germany) were refused by USFW. Despite exporters required to complete species names on form 3–177, this resolution was not retained in the report. Due to this lack of resolution, it is not possible to quantify how many zebra plecos were shipped to the United States with certainty prior to the CITES listing in 2017. Since 2017, 4558 declared specimens were shipped from Indonesia, 122 from Taiwan and 9 from Colombia (this last shipment was refused) (Fig. 12). The CFIA and ECCC FOIA requests returned no results. The response from the CFIA stated that *H. zebra* is not regulated by the CFIA, and as a result no documents exist concerning the requested information. Since 2017, 105 specimens were imported from Indonesia and 85 from the Netherlands (re-exported from Indonesia) (Fig. 12). The response from the EU-TWIX request stated in an email communication (October 2020) that it is restricted and available only to European enforcement agencies. Since 2017, 12,301 captive bred specimens were recorded shipped to Europe (including the UK) (Fig. 12). The TRAFFIC Wildlife Trade Portal contained two records of *H. zebra* seizures, one from 2017 of 672 fish (reported by Maisonnave, 2017) and one from 2019 consisting of 505 in transit from Altamira to Manaus (TRAFFIC International, 2021). No response was received from the UNODC World WISE database.

The zebra pleco is one of many species affected by wildlife trafficking (UNODC, 2020). Over 30 species of fish were identified by IBAMA/ICMBIO as being commonly trafficked from Brazil in large numbers over the 2012–2019 period (Charity and Ferreira, 2020). For example, some freshwater stingrays (e.g., *Potamotrygon albimaculata*) (IBAMA and MMA, 2017), *Corydoras* spp. (Charity and Ferreira, 2020), and some highly endemic species such as the catfish *Conorhynchus conirostris* from the São Francisco River also continue to be targeted by traffickers. A recent (November 2020) seizure of 28 specimens of *C. conirostris* in Altamira, 2000 km by road from their collection point, underlines the intricate network and ongoing problem with trafficked fishes in Brazil. The single piece of luggage with the 28 specimens would have a wholesale value of over \$US 10,000.

The long-awaited change in Brazilian export legislation, Instrução Normativa N° 10 from April 17, 2020 (Ministerio do Estado do Meio Ambiente MAPA, 2020) later updated by Portaria SAP/MAPA N° 17, from January 26, 2021 (Ministério da Agricultura, Pecuária e Abastecimento/Secretaria de Aquicultura e Pesca, 2021), which removed the 'positive' ornamental fish export list (last updated in 2012) does not affect *H. zebra*. While this change allows for the export of native ornamental species, it does not apply to those listed on CITES Appendices or those listed as endangered (e.g., (Instituto Chico Mendes de Conservação da Biodiversidade, 2018)). With China currently the largest market for tropical fish exports (e.g., ~60% of the legal wild caught Loricariids exported from Brazil) and trafficked fish (e.g., ~70% of trafficked *H. zebra*), legislative changes in China could have profound effects on supply chains. For example, as explained by Importer 4 (interview, September 2020), there are changes to China's live fish import legislation under consideration to ban all catfish and characin species, regardless of origin. If passed, such a change would likely have a negative impact on both legal and illicit supply chains as was seen in India when both the United States and Canada banned the import of all Channidae (i.e., snakehead fishes) (US Department of the Interior, 2002).

Other than the discussion in Charity and Ferreira (2020), the inclusion of freshwater ornamental fish in national and global trafficking reports is rare. In other cases, such as the FAO commissioned report from Monticini (2010), the importance of Brazil, and other South American countries in the ornamental freshwater fish trade is erroneously downplayed with a focus on large scale ornamental fish farming in South East Asia dominating the market; the large illicit trade from South America is omitted from discussion. In most cases, analysis of flagship species which dominate the illegal wildlife trade in volume and value (e.g., Pangolins, Tigers, Elephant Ivory, etc.) remain the primary focus of agencies worldwide (e.g., UNODC, 2016,) and illegal activities in fisheries are primarily assessed in terms of the food sector (e.g., (UNODC, 2020)). As a consequence, the illegal trade in ornamental freshwater fish operates nearly without impunity. Nevertheless, regardless of the level of enforcement, the illegal market for wildlife will continue as long as there is a demand from consumers (Nijman, 2010). Increased education and local stakeholder engagement (e.g., Ng and Tan, 1997; Rosen and Smith, 2010; Verissimo et al., 2012, broad availability of captive bred specimens at competitive prices and changes in perceptions from hobbyists are needed to conserve *Hypancistrus zebra* in the wild.

#### 4. Recommendations – the way forward

Based on our findings of the difference between the estimate of available captive bred specimens and number of trafficked fish, there is currently not a large enough supply of aquarium bred specimens to satisfy the worldwide demand for the zebra pleco. Were such breeding facilities to be permitted in Brazil, with proper captive breeding (e.g., Janssen and Chng, 2018) focusing on the hobbyist market, we believe it would decrease the pressure on the wild population. Based on the domestication levels of aquarium fish described in (Teletchea, 2016), the zebra pleco can be considered as a level 4 (entire life cycle closed in captivity) to level 5 (selective breeding programs are used focusing on specific goals) species. The commercial breeding facilities in Indonesia in particular are actively breeding rare color morphs. This advanced stage of domestication supports our argument that captive breeding is feasible.

*Hypancistrus zebra* is totally absent from Brazilian aquariums, except for a few university laboratories that occasionally receive seized fishes and a few unauthorized hobbyists. Issuing permits for commercial breeding of endangered species remains taboo among Brazilian agencies and, to date, no company has ever received authorization from IBAMA or another regulatory agency to commercially breed *H. zebra*. This conundrum highlights how complex the subject of Brazilian law can be on this issue. The reason for not allowing companies to breed and sell zebra plecos is to prevent these companies from selling wild caught juveniles, passed off as aquarium bred. But, by not allowing commercial breeding in Brazil specifically for commercialization (i.e., not for maintaining wild populations), the regulatory agencies are partially responsible for keeping the demand for trafficked animals high because there is no other source to supply the market in large enough volumes. A well-regulated network of commercial breeders in Brazil would greatly benefit the conservation of the species in nature (i.e., less pressure) as well as the captive breeding projects around the world, as new bloodlines from different stocks in Brazil could be sent to farms internationally that have not legally obtained new breeding stock for almost 20 years. Precedent for a similar system in Brazil can be seen with the CITES Appendix II listed Red-footed tortoise (*Chelonoidis carbonarius*) where thousands of captive bred specimens are exported yearly (Sinovas et al., 2017).

Contrary to statements by Pereira and Henriques (2019), indoor breeding facilities for the zebra pleco have shown to be profitable and sustainable long term. We disagree that the retail price of the zebra pleco must be increased for captive breeding to be profitable. Rather, further research is needed to optimize the scenario for Brazilian facilities. For instance, the historical prices worldwide indicate that the market would not sustain prices over \$US 250 per fish as recommended by those authors. Instead, given that the wholesale and retail prices were shown to have been decreasing since 2011, we argue that there is an even larger market of more conventional aquarists for zebra plecos outside of dedicated catfish enthusiasts, who would purchase large numbers if the price were to be more broadly accessible.

Furthermore, we argue that allowing a grassroots breeding project for exporting zebra plecos from Brazil would have a positive socioeconomic effect on the livelihoods of the local community (e.g., fisherman and their families) and allow them to better understand the value of the biodiversity in the river, aiming to greatly reduce the number of fishes captured illegally. In addition, an inclusive well-designed program of local and national education is needed to shed light on the battle for the conservation of the freshwater fish biodiversity unique to the Brazilian Shield, a hotspot for fishes. At the same time, Brazilian agencies must regulate commercial breeding of *H. zebra* to decrease the demand of wild specimens. Internationally, instructing aquarium hobbyists in the value of preserving the many Xingu species in situ, may be more effective in reducing the demand for trafficked zebra plecos than the current CITES legislation and export ban (e.g., Wong et al., 2020).

Law enforcement both in Brazil and internationally need more financial resources, better training to recognize the species in trafficked shipments and consistent access to existent and emergent tools to combat trafficking (e.g., World Bank, 2018). Digital media dedicated to helping identify the main species, if properly catalog and organized, would allow experts to readily assess a photograph of the fish to confirm the identity. As described in Charity and Ferreira (2020), misidentifications among law enforcement seizures abound and hamper proper quantification of the problem. More accurate and higher resolution taxonomic information required for imports and exports (e.g., Biondo and Burki, 2020; Eskew et al., 2020; King, 2018; Allen et al., 2017; Smith et al., 2008) would further facilitate enforcement of wildlife laws. If law enforcement would be more receptive to work with scientists and industry in Brazil, wildlife trafficking could be curtailed. Indigenous people and populations of developing countries often share impacted ecosystems with species targeted by traffickers. Greater cooperation with law enforcement is essential to also empower these communities to protect their natural heritage, and that of the entire planet.

It is important to consider the story of the zebra pleco in context with the thousands of other ornamental fishes. The issues Brazil is experiencing with conserving this species are not unique. Several other countries are grappling with similar challenges due to the aquarium trade (Tlustý, 2002). While the trade in ornamental fish is a largely sustainable industry (Evers et al., 2019), there are other exceptions besides *H. zebra* where the trade has negatively impacted the wild populations such as the red-line barb *Sahyadria denisonii* from India (Raghavan et al., 2018), and the bala shark *Balantiocheilos melanopterus* from the Malay Peninsula, Sumatra, and Borneo (Ng and Tan, 1997). For some species however, most notably *Sclerophagus formosus*, the Asian arowana, a CITES Appendix 1 listed species, captive breeding and strong legislation has all but eliminated the trade in wild caught specimens. Other species, such as *Chidongo saulosi*, a cichlid from Lake Malawi was heavily overfished by 2010 but has since been reintroduced in the natural range from captive breeding efforts (Artigas Azas, 2014). Most notably the Banggai cardinal fish (*Pterapogon kauderni*) has been overfished in its native range and an effort involving all stakeholders is working to conserve the species today. Here, a combination of protected areas, legislation, improved training for fishermen and shippers have led the way to help conserve this species (Moore and Ndohe, 2013).

## 5. Conclusions

With its easily recognizable pattern, large international following of dedicated aquarists and compelling story of habitat loss and pressure from trafficking, the zebra pleco would make a persuasive flagship species of not only Xingu River conservation. Ultimately, the fight for survival of the zebra pleco extends to the more than 500 valid species of fishes in that region, as well as the wealth of ethnic and cultural diversities of the indigenous people and others who depend on the river for their livelihoods. To effectively improve *Hypancistrus zebra* conservation, three main actions need to be taken: (1) strengthening of regulatory agencies to better target this flagship species with more effective government legislation in both import and export countries to enforce existing laws, (2) regulation of aquaculture with emphasis on domestic development to ensure sustainable alternative

livelihoods for fishermen and commercial companies in Brazil, and (3) convincing consumers around the world to support conservation efforts through purchase decisions prioritizing captive bred specimens.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.colsurfa.2021.126582](https://doi.org/10.1016/j.colsurfa.2021.126582).

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