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Article *in* Reviews in Aquaculture · February 2025

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Revisiting the History of Ornamental Aquaculture in Europe to Understand the Benefits and Drawbacks of Freshwater Fish Imports

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Received: 12 June 2024 | **Revised:** 23 December 2024 | **Accepted:** 10 January 2025

Funding: J.P. and L.K. were supported by the Technology Agency of the Czech Republic within the project, "DivLand" (SS02030018). A.M.V. was supported by Fundació Barcelona Zoo. This paper belongs to the portfolio of activities of the Indonesian Centre for Research on Bioinvasions. Support for this study was provided to J.M.F. by the Coastal and Marine Research Centre and Cities Research Institute, Griffith University.

Keywords: air transport | aquarium | fishkeeping | history | international trade | ornamental fish | pet trade

ABSTRACT

Ornamental aquaculture and fishkeeping are very popular with millions of enthusiasts worldwide. The number of newly imported fish species for ornamental purposes grew slowly from World War I until the 1980s. It then exponentially increased until now with more than 7900 species and a large number of scientifically undescribed morphotypes. Here we present the first comprehensive review of freshwater and brackish fish importations during the boom of ornamental fish keeping at the turn of the Millennium and discuss this with a cultural and socio-economic lens in the European context. The increase in imports accelerated following the availability of air transport and the end of the Cold War. From the list of traded species, the largest number of species imported for ornamental purposes was found in the following groups: armored loricariid catfish (family Loricariidae), cory catfish (family Callichthyidae, subfamily Callichthyinae), cichlids of African Great Lakes (order Cichliformes), killifish (egg-laying species of the order Cyprinodontiformes), and characids (order Characiformes). These taxa represent ca. 74% of all fresh and brackish water ornamental fish species. The species of fish with the ability to absorb atmospheric oxygen (e.g., Belontidae, including gouramis and bettas) have dominated the market, but their ratio to the other species has declined during the modern era of ornamental aquaculture (after the end of WWI). By identifying the most popular aquarium species traded through the

history of the aquarium trade, our findings aim to guide present-day management of ornamental aquaculture and better inform invasion risk assessments.

1 | Introduction

The aquarium hobby and the related pet industry (hereafter ornamental aquaculture) are a socio-economically important and growing sector with millions of enthusiasts worldwide [1–4]. Ornamental aquaculture has also contributed to scientific research and conservation interventions both positively, for example, a study of life requirements, reproduction, growth, ethology, ecology, and taxonomy [5–11] and negatively, for example, biological invasions, spread of associated symbionts, including pathogens, poaching, and overharvesting [12–18]. Keeping ornamental fish and other freshwater biota has a long history dating back to ancient times [19, 20], however, the modern era of ornamental aquaculture only started in the second half of the 19th century when the first tropical fish species were imported into Europe and the USA specifically for ornamental purposes [3, 21–23]. Contrary to the vast quantity of peer-reviewed literature published for the commercial aquaculture industry, which produces aquatic organisms for human consumption, the history of modern freshwater ornamental aquaculture was largely ignored prior to recent comprehensive review of its development [3]. Since the period of development discussed in Novák, Kalous, and Patoka [3] ended at the end of World War I in 1918, here we survey the ongoing era from 1919 until the present time.

Information about the first imports of freshwater and brackish (hereafter: "freshwater") ornamental fish and the numbers of species traded was collected primarily from published articles, monographs, websites, and databases; including the Food and Agriculture Organization of the United Nations (FAO, www.fao.org). Not only scientific sources were surveyed but also focused hobby and commercial magazines and books were included. Many of them are written in local languages (e.g., German and Czech), and these publications are commonly overlooked by researchers. Thus, we harvested the data as comprehensively as possible. All recorded valid species, subspecies, geographical forms, and differentiable wild forms and phenotypes indicated just by codes [24], locality, or by stating "sp." or "cf." were evaluated to estimate the total number of imported taxa. For this purpose, all breeding forms were omitted and excluded from the analysis. All scientific names were verified using an electronic version of Eschmeyer's Catalog of Fishes (www.calacademy.org/scientists/projects/eschmeyers-catalog-of-fishes; [25]). Common fish names from FishBase (www.fishbase.se) [26] were used. Most data are from Europe which was a key region in the development of ornamental aquaculture [27]. Although the numbers of species imported may differ for other regions (e.g., the USA, Africa, Asia, or Australia), the differences are minor and can be given specifically in the total volume of traded fish individuals [2].

Based on their popularity as ornamentals and socio-economic importance, the following nine groups of freshwater fish taxa are discussed in greater detail: (i) armored catfish (order Siluriformes, families Loricariidae and Callichthyidae), (ii) endemic cichlids (family Cichlidae) of the Rift Valley (i.e., African Great Lakes: Malawi and Tanganyika), (iii) killifish (egg-laying taxa from orders Cyprinodontiformes: families Aplocheilidae, Cyprinodontidae, Fundulidae, Nothobranchiidae, Profundulidae, Rivulidae, Valenciidae; and Beloniformes: family Adrianichthyidae), (iv) characids (order Characiformes), (v) dwarf South American cichlids of the genus *Apistogramma* s.l., (vi) livebearers (both viviparous and ovoviviparous taxa from orders Cyprinodontiformes: families Anablepidae, Goodeidae, Poeciliidae; and Beloniformes: family Hemiramphidae), (vii) rainbowfish (order Atheriniformes: families Bedotiidae, Melanotaeniidae, Pseudomugilidae, and Telmatherinidae), (viii) cyprinids (order Cypriniformes), and (ix) labyrinth fish (order Anabantiformes, suborder Anabantoidei).

2 | A Brief Note on the Early Developmental Period Before 1918

Novák, Kalous, and Patoka [3] reported that ca. 470 freshwater fish taxa had been imported as ornamentals before the end of WWI. However, certain species were later renamed, revised as several different species, or synonymized. Moreover, some of the details, such as the year of the first ornamental cichlid import, needed to be updated. The chameleon cichlids *Australoheros autochthon* (=*A. oblongus*), not *A. facetus*, was introduced to Paris, France by Jeunet in 1889 [28], and *Australoheros facetus* was imported into Berlin, Germany by Nitsche in 1894. Despite its taxonomic uncertainty of *A. autochthon* [29], France has a priority in this regard. Subsequently, further import of species from this genus was likely undocumented or misidentified as *A. angiru*, which was described later [30]. Hohl [31–33] draws attention to the difficulties with the correct identification of imported taxa presented in historical hobby literature on painted illustrations and emphasizes the need for the objectification of determination. Among others, the most iconic ornamental fish species, the small, live-bearing, freshwater teleost, the guppy *Poecilia reticulata*, was also introduced into Europe during this period [3].

3 | Snowball Effect Period (1918–1970s)

Based on Arnold [34], Arnold and Ahl [35], Holly et al. [36], and Rachow [37], the number of new and exotic ornamental freshwater fish imported to Europe between WWI and World War II (WWII) was estimated to be (number of newly imported taxa; cumulative number of ornamental taxa): 1921–1930 (95; 592), 1931–1938 (242; 834), 1939–1945 (10; 844) Figure 1. Changes in social and economic conditions resulting from the armament of Germany in the 1930s led to a brief economic upturn, which was reflected in the number of new ornamental fish imported between 1933 and 1936. Introductions were greatest for any single year in 1935 when 56 new ornamental fish taxa were imported into Europe [35]. Characids increased in popularity and dominance of the aquarium trade and hobby in the 1930s, which Hohl [38] described as the "Decade of Characids." This was in conjunction with their successful propagation given a

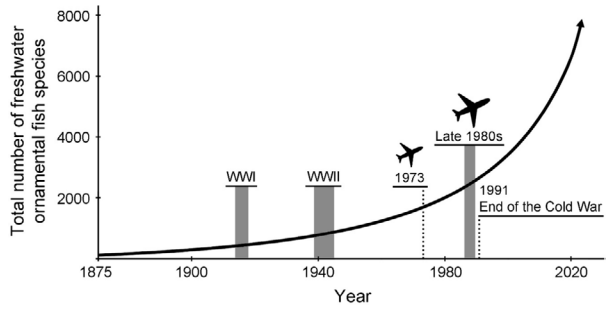

FIGURE 1 | The total number of freshwater fish species imported for ornamental purposes through time with key events indicated: WWI (1914–1918); WWII (1939–1945); Federal Express (i.e., FedEx) foundation in 1973; large cargo aircraft into service in the late 1980s; the end of the Cold War in 1991.

greater understanding of their life history and water chemistry requirements. Following this period there was a decline in the importation of new species into Europe caused by the outbreak of WWII.

During and immediately following WWII, the number of newly imported ornamental fish in Europe and the USA increased slightly, see Innes' book "Exotic Aquarium Fishes" published repeatedly in this period [39]. The final edition of this book contains a supplement that records only four new ornamental fish species imported [39]. The following year, Arnold [34] listed 870 species in culture, which agrees with the monographs of Holly et al. [36], see Zarske and Berkenkamp [40].

In the 1950s, an average of 15 new ornamental species were imported to Europe per year, all of which were imported to Germany [38]. By 1959, a total of 1003 ornamental fish taxa had been imported [41] and the necessary equipment for fish culture and propagation was available, for example, aquarium illumination, electric pumps, compressed air sources, water quality tests, thermometers, aquarium heaters, feeds, medicines, and anesthetics for fish [38]. Moreover, the commercial production of artificial fish food had commenced since 1951 in Melle, Germany, where Dr. Ulrich Baensch founded the company (Tetra Werke; https://www.tetra-fish.com/about-us.aspx) and pioneered the development of flake fish food—an innovation that revolutionized the industry [23], but the number of new ornamental fish species only increased slightly during this period. Sterba [42] reported that, by 1977, 1165 ornamental fish species had been imported.

From the 1950s onwards, the human dimension and professional qualifications of hobbyists increased with greater specialization and focus on specific fish taxa. Focused associations, organized meetings, symposia, and exhibitions developed in various countries, for example, Germany and Czechoslovakia [38, 43]. For instance, the first imports of endemic cichlids from the African Great Lakes, such as Malawi and Tanganyika, to Europe began in 1958 [38] and became more frequent beginning in the 1970s [44]. Many of the original 28 ornamental species imported remain iconic. However, uncertainty in identifying or misidentifying certain imported individuals/taxa also increased. Formally unknown species were imported [38] but were accidentally or mistakenly packaged in defined fish consignments as "bycatch" ("Beifang" in German; [45, 46]). Consequently, Brühlmeyer and Frotzler started to identify unspecified forms/taxa from Lake Malawi with the letter M and a unique number in the early 1970s ([47]). Moreover, cichlids from the genus *Haplochromis* were coded as CH and number (C = cichlid, H = *Haplochromis*) but this system was discontinued in 1994 [48]. In particular, the great interest in Malawian cichlids as ornamental animals led to further imports, assembling information, and publishing of focused monographs, resulting in the 1970s and 1980s being referred to as the "Malawian Wave" [38].

Early publications that foreshadowed the emergence of scientific, breeding and commercial interest in cichlids include the typology of tropical waters related to ornamental fish reproduction [49, 50], the importance of egg spots in the fertilization process of ovophilic mouthbrooders [51], and the classification of the stages of early fish ontogeny [52]. Monographs followed including those on cichlids in general by Goldstein [53, 54] and Staeck [55], and more specifically from lakes Malawi and Tanganyika by Fryer and Illes [56], Axelrod and Burgess [57], and Neergard [58]. Scientific findings were shared through aquarium hobby journals, contributing to the successful breeding of characids and mouthbrooder cichlids [59].

Monographs were also produced for entire fish groups or families, including killifish [60], characids [61], and livebearers [62]. These works were in high demand. The growing number of monographs reflected the increasing number of fish species being kept as ornamentals, and certain keepers began focusing on specific taxa. This resulted in the establishment of specific, supraregional, or international working groups, clubs, and associations. From an international perspective, an extensive encyclopedia focused on ornamental aquaculture and ichthyology is a keystone output of this period [63].

Because of increasing economic prosperity in Western Europe in the 1970s, hobbyists travelled repeatedly to the tropics, which led to numerous private fish imports of various species for ornamental purposes. However, these fish were often reserved for a small group of particularly interested specialists, for example, enthusiasts imported 107 new species of killifish into Germany between 1971 and 1980 [38].

4 | Flourishing Period (1980–1990s)

In the late 1970s, the use of silicone rubbers for building aquariums commenced, and the large-scale production and greater durability of aquariums resulted in the keeping of ornamental fish being more accessible to novice enthusiasts (www.juwel-aquarium.de/en/company/history). During the 1980s, there was a significant increase in the number of new freshwater ornamental fish imported into Europe. An estimated 1165 ornamental fish species had been imported by 1977, which was increased to circa 2000 species in the 1980s [42, 64].

After 1987, it became difficult to account for all new species imports, and the exact number of newly imported species can only be estimated due to the continuously increasing number of imports and the lack of precision of the various information sources [3, 5]. The increasing commercialization of aquarium magazines

resulted in many new species imported being reported, and it became difficult to follow the increasing abundance of ornamental taxa in encyclopedias, for example, Baensch and Riehl [65–67], Riehl and Baensch [68, 69], and Sterba [64]; the exception being the "Aquarium Atlas" by Riehl and Baensch [70].

An increasing number of focused articles and books were published during the flourishing period. For instance, Fryer and Illes [56], was followed by publications detailing the evolution, life history, and keeping and breeding of cichlids in the African lakes Malawi and Tanganyika [71–78]. The growing interest in the ornamental fishkeeping community in Neotropical cichlids resulted in books by Koslowski [79], Schaefer [80], Schmettkamp [81], and Zenner and Hohl [82] dealing with the genus *Apistogramma*, and by Stawikowski and Werner [83] on Mesoamerican cichlids. Detailed information on ornamental catfish care [84], and comprehensive descriptions of livebearers [85] were also published. No comprehensive work on characids has been published since Géry [61].

During the 1980s, an increasing number of armored suckermouth catfishes (family Loricariidae) and cory catfishes (family Callichthyidae, subfamily Callichthyinae) were imported into Europe by commercial tropical fish wholesalers, and the popularity of these taxa increased rapidly [23].

At the end of the 1980s, political attempts were made in Germany to generate a "Positive list" containing a limited number of low-risk ornamental species for which keeping and breeding would be legal [86, 87]. The import and breeding of other species would be prohibited and restricted to reduce the risk of biological invasions and to avoid the suffering of wild fish in captivity. This initiative was abandoned following a protest with 25,000 signatures from ornamental fish keepers [38]. Considering the historical importance of the "German aquarium phenomenon" and industry [3], such restrictions would have negatively impacted various economies, resulting in potentially considerable loss of jobs in developing and donor countries and would also have negative social and cultural effects and hinder scientific-related education of the general public. Moreover, the benefits of ornamental aquaculture for species conservation will be reduced. It is still uncertain whether similarly focused and politically motivated restrictions could be expected in the future, for example, for the EU.

In the 1990s, major books were published, summarizing the developments of previous years, linking the knowledge of practical fishkeeping and relating commercial and basic research in the field of ecology [88–90]. Concurrently, symposia presenting scientific information on the study of animals in controlled aquatic systems directly applicable to keeping and breeding practices were organized [91, 92]. From these, the multidisciplinary field of aquariology, the study of the fauna and flora in aquariums, originated [93].

5 | Global Boom Period (1995–2005)

This period is characterized by a positive relationship between research, fish production, trade, and breeding practices [94, 95], and a boom in the publication of extensive books, both atlases and specialized monographs. Among the encyclopedias, the most comprehensive were "Aquarien-Atlas" [65–69], Axelrod [96] and Axelrod and Burgess [97]. Specialized books include publications on cichlids [98, 99], Neotropical cichlids [100–103], West African cichlids [104], *Apistogramma* dwarf cichlids [105–108], Central American cichlids [75], African cichlids [109, 110], cichlids of Lake Tanganyika [111], Malawian peacock cichlids of the genera *Aulonocara*, *Lethrinops*, *Taeniolethrinops*, *Tramitichromis*, and *Trematocranus* [112], blunthead cichlids of the genus *Tropheus* [113], catfish [114–116], African catfish [117], suckermouth armored catfish [118], cory catfish [119, 120], livebearers [121], killifish [122–124], rainbowfish [125, 126], and characids [127–129]. The growing interest in aquarium fishkeeping also led to the publication of highly specialized books on bichirs, that is, genus *Polypterus* [130], freshwater stingrays of the genera *Potamotrygon* and *Paratrygon* [131], freshwater and brackish puffers of the genera *Colomesus*, *Carinotetraodon*, and *Dichotomyctere* [132], and brackish water fish in general [133].

In the new Millennium, new and interesting fish species started being imported as ornamentals, and additional countries reportedly began supplying wild-caught and cultured fish species. In addition, new groups of freshwater taxa, for example, decapod crustaceans including crayfish, shrimps, and crabs, were introduced for ornamental aquaculture [134–138]. Imports from "traditional" countries (countries with a long history of ornamental aquaculture) became more difficult due to the political conditions and regulations in these countries, for example, Venezuela, while political normalization in other countries, for example, Southeast and South Asia, enabled access to many new species of fish and other freshwater and brackish taxa (e.g., [38, 139, 140]).

However, the increasing popularity of ornamental fishkeeping was no longer correlated with the development of focused clubs and associations. For instance, in Germany, membership in one of the leaders in ornamental aquaculture in Europe, the German Society of Aquaristic and Terraristic Associations (Verband Deutscher Vereine für Aquarien- und Terrarienkunde, VDA) was significantly reduced after the year 2000 [3]. By 2010, the number of clubs in this association had decreased to the levels of the 1960s, and the membership base declined [38]. The rise of the Internet and the subsequent increase in the availability of information and the opportunity to socialize on social media (e.g., Orkut/Facebook in 2004, YouTube in 2005, Twitter—currently X—in 2006, Instagram in 2010) are likely to be the primary contributing factors to this phenomenon [141, 142]. Compared to previous periods, mainstream media did not support ornamental fishkeeping. As a result, the social, cultural, and educational functions of this sector of aquaculture were neglected.

6 | Cornucopia Period (After 2005)

The increasing numbers of taxa traded and improved knowledge is an obvious and positive aspect of ornamental aquaculture highlighted in this era including: the biology, phylogeny, distribution, life history requirements, reproduction, sociality, behavior, diet, ecotoxicology, and symbionts, translated to the practice of keepers, traders, and producers, in synergy with science [143–146].

Ornamental aquaculture was established as a hobby with many enthusiasts in temperate, tropical, and subtropical countries that had previously only been perceived as suppliers/producers [138]. However, the boom in ornamental aquaculture resulted in an increase in the illegal release of large and unwanted fish into natural waterbodies, some of which became invasive or problematic, impacting the native biota of these habitats and posing a serious threat to native (and mostly endemic) biota and whole ecosystems in these regions [147, 148]. Examples of high-impact species are fish *Arapaima gigas*, *Polypterus senegalus*, *Potamotrygon* spp., *Pterygoplichthys* spp., "flowerhorn" cichlid (hybrid), and crayfish *Procambarus clarkii* and *Cherax quadricarinatus* in Indonesia [13, 149–155]. The mostly illegal release of unwanted ornamental species has been publicized with the help of social media, such as YouTube in Brazil [152, 156]. Regarding ornamental aquaculture, policymakers tend to protect endangered species and regulate the invasive ones, but the efficiency of this effort is at least disputable or ineffective in many cases [157–159].

Illustrated by the story of armored and cory catfish, Novák et al. [24] pointed out that without the aquarium hobby and commercial trade, science alone would probably not have uncovered the diversity of fish species. On the other hand, the actual trend of the focused printed or online aquarium hobby and trade journals, which are increasingly suffering from commercialization and becoming a magazine-like character, is in contradiction to this, and it is more and more difficult to reliably analyze the overall spectrum of ornamental aquaculture. Regarding ornamental fish, it is worth mentioning that the extent is probably underestimated because of misidentifications and false synonyms used by traders, moreover, not all new imports were published and remain neglected [160].

7 | Specific Examples

Each important group of freshwater ornamental fish species has specific characteristics influencing its popularity and marketability through various aspects, including biology, ecology, ethology, coloration, diet, life requirements, environmental tolerance, air-breathing ability, body size, reproduction, and so forth. Specific aspects and important notes according to each group are given below, while small to moderate-sized adult fish, attractive coloration, nonspecific diet requirements, and wide tolerance to water parameters are typical, at least for some of the species of each group listed. The number of ornamental species in each group chronologically during the evaluated period is given in detail in Table S1.

7.1 | South American Armored Catfish

Both valid and potential novel species belonging to South American suckermouth armored catfish (family Loricariidae) and cory catfish (family Callichthyidae) together represent 19.0% of all ornamental freshwater fish species imported. Various species are marketed under trade names or codes (C or CW plus number for the family Callichthyidae and L or LDA plus number for the family Loricariidae). Many of these codes are paired with the scientific names of the species, however, several codes were found to be used for different populations of a single species [24]. Despite numerous synonyms [161], with over 1500 traded species, these catfishes represent the largest group of imported entities (species/forms) of ornamental freshwater fish. Keeping and breeding armored catfish in captivity is challenging for many of the taxa, with certain exceptions, for example, *Ancistrus* spp. Therefore, captive-bred fish do not form a significant portion of fish in the market, but wild-captured fish do not adequately represent their full diversity [24]. Even if not introduced only via ornamental aquaculture, certain species of armored catfish, specifically *Pterygoplichthys disjunctivus*, *P. pardalis*, *P. ambrosettii*, and their hybrids, have been successfully established in many tropical and subtropical countries [162–166] and were found also in temperate/Mediterranean areas [167, 168]. They are now considered among the most damaging introduced fish, posing a "very-high risk" of becoming invasive once introduced [169].

7.2 | Endemic Lacustrine East African Cichlids

The first cichlids imported from East Africa as ornamental species were the widespread and primarily riverine Nile tilapia (*Oreochromis niloticus*) and the Egyptian mouthbrooder (*Pseudocrenilabrus multicolor*) both in 1902. By 1914, the first predominantly lacustrine species was imported to Europe. This was the mouthbrooder *Haplochromis obliquidens* (due to uncertainty in the identification of the phenotypically similar forms of this taxon, for example, *H. latifasciatus*, we refer to these unspecified species as the "Zebra obliquidens complex"; [3]). The first cichlids endemic to Lakes Malawi and Tanganyika were imported to Germany in 1958 [38].

The total number of imported East African cichlid taxa is difficult to quantify due to their high degree of speciation and microhabitat preferences resulting in many reproductively isolated local forms. For example, at least 45 reproductively isolated forms of the Blunthead cichlids (genus *Tropheus*) from Lake Tanganyika were kept and bred around 2005 in the Czech Republic. These fish can justifiably be considered as potential novel species [170]. Similarly, in Lake Malawi, a large number of forms or species are found, especially within the Peacocks [112] and the ecologically isolated Mbuna [171] groups.

We estimate the total number of species traded as ornamentals, including well-known geographical forms of endemic cichlids in Lake Malawi, to be ca. 1000 species, based on Snoeks [172] and Weyl et al. [173]. All known forms of Lake Malawi cichlids may have already been imported into aquaria at least once. We believe that the same is true for Lake Tanganyika, where the total number of cichlid species (including the above-mentioned ca. 100 forms of the genus *Tropheus*) is estimated to be ca. 350. We estimate that cichlids endemic to Lakes Malawi and Tanganyika constitute 16.5% of all freshwater fish kept as ornamentals. This increase was facilitated by the development and expansion of air transport (see below) and the increased understanding of the biodiversity of Lakes Malawi and Tanganyika [172].

In contrast, the endemic cichlids from Lake Victoria are less popular. The total number of known species was estimated to be ca. 750; based on Seehausen [174] and Verheyen et al. [175]. However, only a small proportion of these are kept as

ornamentals, such as *Haplochromis nyererei*. For instance, Böhner [176] names 80 species or geographical forms kept in Germany. Since these species are very attractive in color and often show unique feeding behavior, their limited representation in aquaria is probably mainly due to specific geopolitical constraints. Moreover, the Lake Victoria ecosystem collapsed after the introduction of nonnative species, for example, Nile perch (*Lates niloticus*), Nile tilapia (*Oreochromis niloticus*), Blue spotted tilapia (*Oreochromis leucostictus*), Redbelly tilapia (*Coptodon zillii*), Lake Tanganyika sardine (*Stolothrissa tanganicae*), and water hyacinth (*Pontederia crassipes*) during the late 1950s and the early 1960s [177, 178]. The lack of ornamental species from Lake Victoria is probably also because the populations of the cichlids had decreased to be so low that they were below detection and are not suitable for exploitation at the current population levels.

7.3 | Killifish

Killifish were very popular fish during the early period of modern ornamental aquaculture due to their tolerance of low dissolved oxygen concentrations in water because of the ability of some species to absorb atmospheric oxygen through their skin and mucous membranes [179]. For example, Valencia toothcarp (*Valencia hispanica*) was introduced to Germany as early as 1881, followed by the Striped killifish or Striped mummichog (*Fundulus majalis*) in 1893.

It has been generally unprofitable for large-scale producers to breed and rear killifish. Therefore, these fish are supplied to the market mainly from wild-caught stocks or by hobbyists. Hohl [38] noted that during the 1970s, various formally undescribed populations of killifish were imported as ornamentals. Since the 1980s, a significant increase in the number of imported species/forms of killifish has been recorded. We estimate that killifish constitute ca. 20.3% of ornamental freshwater fish species. Many forms of killifish are imported at small scales by private individuals for culture (breeding and rearing) experts and focused enthusiasts.

7.4 | Characids

Characids formed ca. 20% of ornamental fish imports in 1918 [3]. The increase in the number of ornamental species was roughly linear; with significant import peaks between the years 1933 and 1935, and later in the 1990s deviated from this trend (Table S1). Currently, we estimate the share of characids to be 5.7% of the total number of freshwater ornamental fish. Although characids are not currently a particularly large component of the total number of species kept in captivity, the quantities traded are considerable for certain species. For example, the Cardinal tetra (*Paracheirodon axelrodi*) represents approximately 65% of all ornamental fish exports from Amazonas in Brazil (wild-caught; [180]) and approximately 10% from the Czech Republic (domestic production; [24]).

The Cardinal and Neon (*P. innesi*) tetras were instrumental in providing color to early hobbyist tanks [181]. Efforts to breed the Neon tetra in captivity have been significant, to the point they are now considered a domesticated species [182]. There are few wild animals to be found in the trade indicating the significant loss of economic revenue for local communities in Peru. The Cardinal tetra has been more difficult to breed in captivity, and there is still a robust wild fishery that supports remote communities in the Amazon basin [183]. However, there are aquaculture efforts for the Cardinal tetra, especially in the Czech Republic [24], that may have repercussions for the Brazilian communities that derive economic benefits from this wild fishery [9].

7.5 | Dwarf Cichlids of the Genus *Apistogramma*

Dwarf cichlids of the genus *Apistogramma* are popular due to attractive coloration, parental care, and tiny size ([184]). The specific code system used for traded ornamental tropical and subtropical South American dwarf cichlids of the genus *Apistogramma* was introduced by Koslowski [185] and formed an ascending numerical series beginning with a capital letter "A." The main purpose of this code was to present a complete and as definitive as possible guide to the enormous number of species of the genus *Apistogramma*. The codes were also paired with existing taxa, including forms that corresponded to the phenotype of described species (e.g., A1 = *Apistogramma taeniata* "Cupari," A2 = *A.* cf. *taeniata* "Tapajós," A3 = *A.* cf. *taeniata* "Arapiums"). The names of the locality/native range (area, river basin) or the designation of a typical coloration pattern were used as additional criteria (e.g., A11 = *A.* sp. "Wangenflecken/Cheek-spots"). Efforts were made to make the system as consistent as possible and to synonymize scientific, common, and trade names (e.g., A18 = *A. rubrolineata* = *A.* sp. "Beni" = *A.* sp. "Manu"). When released, the system contained a total of 243 codes plus one or more color photographs.

In comparison with the aforementioned codes for South American armored catfish, there is a difference from the philosophy of the "A concept": The A codes are based on published research outputs confirming the monophyly of the genus and defined phylogeny [186], and morphological and behavioral characteristics [108]. This concept is in line with recent species diagnoses, which often contain a reference to the relationship of the species to populations already kept as ornamentals [187]. The total number of species/potential species was estimated to be at least 250 and 3.2% of all freshwater ornamental fish.

7.6 | Livebearers and the Story of Guppies

At the end of the World War I, livebearers formed ca. 10% of the total number of ornamental fish species newly imported in Europe [3], while their current share was estimated as only 3.8% of all freshwater ornamental fish. However, this number says nothing about the unbroken popularity of this group of ornamental fish, which are bred in many varieties of coloration and shape in ornamental aquaculture [188, 189]. This is explained by the relatively limited native ranges and the narrow total number of species in this group. Some species, especially from the genera *Poecilia* and *Xiphophorus*, are suitable for further selecting body and fin coloration and shape forms.

These are mostly based on established standards and are assessed at national and international competitions (see e.g., justguppies.uk/ikgh/principles). Probably the most popular livebearer is guppy (*Poecilia reticulata*). The first known import of live guppies for ornamental fishkeeping to Europe was by a German company owned by Carl Siggelkow to Hamburg in 1908 [3]. This fish has a native range in Venezuela, Guyana, Surinam, northern Brazil, and several Lesser Antilles, including Trinidad and Tobago [190, 191]. At that time, all goods arriving from the tropics were disinfected by spraying their containers with prussic acid at ports of arrival, to prevent pathogen introduction. This practice killed many animals [192]. Nevertheless, guppies survived, and German hobbyists nicknamed this species the "Milionenfish" (million fish). Another popular name for the guppy was the missionary fish as it converted many people to ornamental fishkeeping [192, 193].

Easy reproduction, broad environmental tolerances, short generation period, fast maturation, and great variability in coloration, fin length, and shape gave rise to focused beauty contests [194]. Around 1920, an ornamental fishkeeping club in Leipzig, Germany, established the first system for judging guppies by score and held the first known guppy exhibition in November 1922. Around 1928, the first breeding form of guppy, the so-called double swordtail, was successfully isolated [192]. Whitern [195] also reported the culture of guppy in the United States in the early 1930s. The first albino guppies arose from an inbred line in 1941 [196].

In the 1950s, growing interests in selected fish breeding, especially guppies were recorded. The first international guppy exhibition was in Germany in 1954, showing the so-called veil tail guppy. Jordan [192] listed important personalities who bred various forms of guppies: P. Hahnel (veil tail guppy), W.G. Phillips (spade tail guppy and leopard guppy), and E. Schmidt Focke (half black guppy). The variety of forms that became an object in research on heredity was bred in subsequent years [190].

The most important association focused on the breeding of guppies is the International Board of Guppy Highbreeding (IKGH, Internationales Kuratorium Guppy Hochzucht, ikgh.org). There are 52 guppy clubs in 22 countries worldwide. Competition rules are specified by the International High-Breeding Standard (HIS) issued by the International Congress for Guppy High-Breeding. Together with Neon tetra (*Paracheirodon innesi*), guppy is the most popular ornamental fish kept in the United States, Czech Republic, Romania, and Turkey [23, 189, 197, 198], and the third most popular species in Brazil [199].

Guppies are also used as model organisms, especially in studies of behavior, life strategies, and evolution [200, 201]. Their popularity as ornamentals and the fact that nonbreeding forms are hardy creatures commonly used as biological control agents resulted in the establishment of nonnative and self-sustaining populations out of the native range of the species ([202, 203]). According to Froese and Pauly [26], guppies occur in at least 69 countries in which six they are native [15]. Moreover, other members of this fish group are known as invaders with negative effects on native fish, invertebrates, and amphibians, for example, species from genera *Gambusia*, *Poecilia*, *Xiphophorus*, and should be monitored and regulated in this regard [204–206].

7.7 | Rainbowfish

The first rainbowfish, the Murray River rainbowfish (*Melanotaenia fluviatilis*) was imported to Europe under the false name *Melanotaenia nigrans* in 1927. Rainbowfish have never spread widely among aquarium hobbyists despite the considerable abundance of species and wild local forms known today. It is caused by slow growth and late color maturity, which negatively affects their attractiveness for traders and keepers. Moreover, aquaculture production faces low growth rates and high mortality in the larval development of rainbowfish [207]. According to Hohl [38], imports of color-attractive Red rainbowfish (*Glossolepis incisus*), Banded rainbowfish (*Melanotaenia trifasciata*), and Boeseman's rainbowfish (*Melanotaenia boesemani*) started a focus of a small group of specialized enthusiasts who tried to maintain rainbowfish in ornamental aquaculture in the 1970s and 1980s. Their current proportion was estimated as only 1.9% of all freshwater ornamental fish.

7.8 | Cyprinids

Due to a recent revision of the family, this group contains "cyprinids" in a broad sense. In total, 46 species of cyprinids were introduced to ornamental fishkeeping before 1918 [3]. This increased to about 87 species by 1977 [42], 214 by 1987 [64], and 276 by 2002, were in trade [208]. A dramatic increase of species in trade was not recorded in this group of freshwater fish. This was probably due to the low popularity of cyprinids relative to other taxa, especially characids, which are usually smaller and more attractively colored. Their current proportion was estimated as 3.8% of all freshwater ornamental fish species. However, there are certain very popular ornamental cyprinids (e.g., *Danio rerio*, *Trigonostigma heteromorpha*, loaches and barbs). Goldfish (*Carassius auratus*) and Nishikigoi (*Cyprinus carpio*, *C. rubrofuscus* and their hybrids; so-called Koi) were probably the first freshwater fish taxa kept for ornamental purposes. These taxa stand out as being among the most popular ornamental fish worldwide. Renowned for their vibrant colors, elegant movements, and manageable care needs, goldfish especially appeal to both novice and seasoned aquarists. They are frequently housed in home aquariums, outdoor ponds, and even integrated into garden fountains or water features. The history of goldfish and Nishikigoi, and numerous selectively bred attractive forms, can be traced back to ancient times, with China and subsequently Japan being the major producers [20, 209, 210].

7.9 | Labyrinth Fish

The labyrinth fishes were a key group at the beginning of ornamental aquaculture and fishkeeping because they were able to survive long Oceanic transport due to their ability to breathe atmospheric oxygen [3]. But the total number of imported and kept species is relatively low: 41 species in 1977 [42], 83 in 1982 [211], and 180 in 2013 [212]. Nevertheless, among these taxa, very popular and commonly available

species can be found: Siamese fighting fish (*Betta splendens*), Paradisefish (*Macropodus opercularis*), Pearl gourami (*Trichopodus leerii*), Three spot gourami (*T. trichopterus*), Dwarf gourami (*Trichogaster lalius*), and Kissing gourami (*Helostoma temminckii*).

7.10 | Other Fish

Many other fish taxa have been imported as ornamentals, which, when combined with labyrinth fishes represent 25.9% of all freshwater ornamental fish. As an example, we will discuss catfishes. In comparison to the aforementioned armored catfish, other freshwater catfish are not abundant in ornamental aquaculture and trade. These catfish taxa were imported as ornamentals during the early history of ornamental aquaculture, but the total number of species was low (just 12 species imported by 1900, 29 by 1918, 84 by 1977, 92 by 1987, and 198 by 2002; [3, 63, 64, 208]). These fishes were not as popular in ornamental aquaculture due to their mostly nocturnal activity, large sizes, voracious appetites, predatory behavior, unremarkable and unattractive coloration, and are difficult to propagate in captivity [213]. Of about 500 African catfishes [117], only a dozen are commonly available on the market, none of which number among the most common species [23]. In general, the vast majority of freshwater catfish species are considered inappropriate for ornamental fishkeeping.

8 | Global Trends

Based on the survey of the literature and list of traded species, we compiled a timeline of the cumulative number of ornamental fish species imported. We present this timeline in Figure 1 and have included it with the timing of significant political and socio-economic events that have influenced the import of ornamental fish. We have also identified the most important fish groups that have contributed significantly to the current total number of ornamental fish species: 20.3% for killifish, 19.0% for armored catfish, and 16.5% for East African lacustrine cichlids.

The wide phenotypic plasticity in natural fish behavior associated with aerial respiration, including a combination of various strategies related to the different oxygen levels in the water, is a desirable trait in ornamental fish taxa [3]. Therefore, the fish species able to absorb atmospheric oxygen have dominated the market but their ratio to the others has gradually declined during the modern era of ornamental aquaculture from 98:2 in 1918 to 71:29 in 2024 (Figure 2). Technological progress and fast international transport have also allowed traders and keepers to import more species successfully, particularly those that cannot breathe or absorb atmospheric oxygen.

International trade was promoted by reducing or eliminating trade barriers such as tariffs or quotas in the General Agreement on Tariffs and Trade signed in 1947. However, even if crucial, the direct impact of this legal agreement on ornamental fish imports was not obvious. The foundation of the express air courier industry and subsequent separation of cargo and passenger transport in the first half of the 1970s [214], and the introduction of large cargo aircraft in the late 1980s [215], together with a deeper interest in ornamental aquaculture (Figure 1), have been the main relevant drivers of the rapid increase in commercial ornamental fish imports in the 1990s and the new Millennium. Simultaneously, the end of the Cold War in 1991 improved communication among countries, made more areas accessible and increased travelling safety [216]. The availability of a large variety of ornamental fish species has inspired a wide range of enthusiasts to start fishkeeping. This was also closely associated with increasing and deep interest in ornamental aquaculture in source countries as an economically valuable and profitable sector. Many previously overlooked species became popular, and their aquaculture or wild harvesting has increased rapidly (e.g., in *Dawkinsia denisonii*, which was introduced on the market not earlier than 1996; [217]). In addition, various

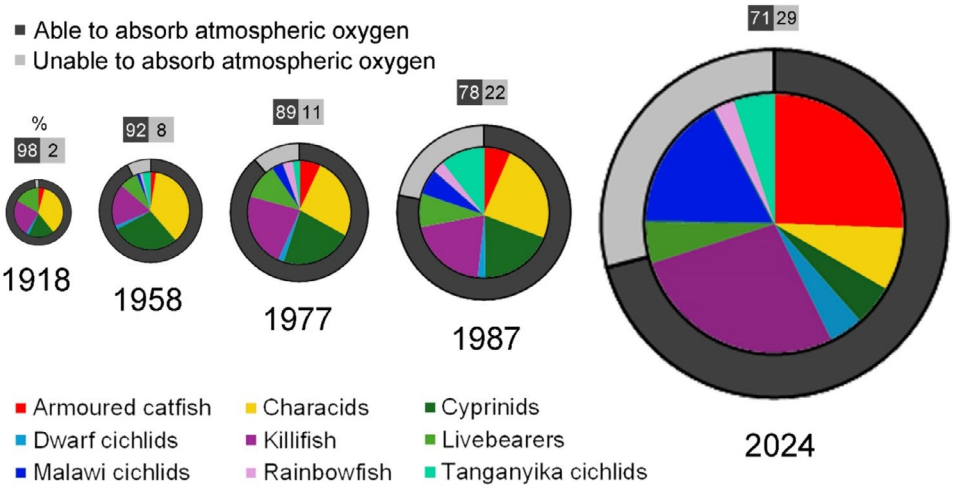

FIGURE 2 | The total number of freshwater ornamental fish species imported through time by the following groups: Armored catfish, Characids, Cyprinids, Dwarf cichlids, Killifish, Livebearers, Malawi cichlids, Rainbowfish, and Tanganyika cichlids. Each group is indicated by a specific color. The size of the circle indicates the total number of imported species until that year. The outer circle represents the ratio of species that are able to absorb atmospheric oxygen (dark grey) versus species that are not (pale grey). This ratio is also given above in %.

previously undescribed fish and invertebrate species were formally described due to their import and sale as ornamentals, for example, cyprinid fish advertised as "galaxy Rasbora" or "galaxy Microrasbora" which was later formally described as *Celestichthys margaritatus* and currently accepted as *Danio margaritatus* [218] or parastacid crayfish advertised as "Blue moon" and later formally described as *Cherax woworae* and *C. pulverulentus* [219, 220]. Based on the species and price lists from certain well-established wholesalers and local producers from the Czech Republic and Indonesia, two important traders and producers of ornamental fish, we updated the estimates of the total number of freshwater (and brackish) fish species kept more or less frequently as ornamentals to be presently ca. 7900, and increasing exponentially year-on-year ($y = -5402.01/[1 + (-8.6193 \times 10^{14}) \times e^{-0.0167324 \times x}]$, $R^2 = 0.9382$, x = year; Figure 1). We personally expect that the point where the market is fully saturated will be reached when the total number of ornamental freshwater fish reaches ca. 10,000 species. Since this value is just a rough estimation and our prediction and expectation, continuous and precise monitoring of the market is strongly recommended and required because, however, there will always be a bycatch, and the interest of specialists in new species and forms will remain undiminished.

There is no doubt that ornamental aquaculture offers many positive aspects. Indoor aquaria and outdoor ponds can serve as good models for education and nature conservation training, which can be well enhanced by practical experiments, personal experiences, and an intimate relationship with the animals, and whole ecosystems [5]. Also, conservationists and wildlife managers can use the higher popularity of species or groups of species for communication with the public and further education of stakeholders about both the benefits and risks related to ornamental aquaculture and biodiversity conservation [9].

However, ongoing commercialization in ornamental aquaculture is associated with the weakening of enthusiasts' associations and club activities. This trend was followed at the beginning of the new Millennium by a rapid decline in the membership base and a reduction nearly to the numbers of the mid-1930s [38]. Simultaneously, the many small local pet shops have disappeared replaced by large retail chains, DIY stores, and garden centers.

Within the last two decades, the Internet became the main information source, offering a further increase in commercialization, individualization, and a narrowing of the professional base of ornamental aquaculture with a growing ratio of online trade [221]. However, this has resulted in neglect of the wealth of knowledge and observations about ornamental fishkeeping published in over 100 years of magazines, books and journals, leading to oversimplification of the practice of fish culture by site authors and bloggers that do not have the experience of practically applying these techniques. The overload of information of varying quality on the internet erodes existing knowledge and expertise among hobbyists and aquarium owners. The lack of a supervisory body to vet the information posted on the Internet could seriously damage the field, the health, trade, and welfare of the organisms kept. As a result, some aquarium owners behave irresponsibly which includes purchasing species that grow too large for captivity, purchasing animals without sufficient knowledge about their life requirements, overstocking the tank, and so forth [6].

Ornamental aquaculture and the related pet trade are currently the primary sources of nonnative organisms released into natural water bodies, resulting in increased risks of biological invasion [14, 152, 222–225]. However, strict bans on high-risk and other species adopted for "positive lists" could paradoxically harm biodiversity due to the termination of domestic production and increased illegal wild capture. In addition, even if overharvesting and other risks associated with ornamental aquaculture are serious threats to endemic taxa, habitat destruction would continue as the major threat for many highly endangered species [5, 17].

Currently, scientists are working together with committed hobbyists and other stakeholders on international conservation breeding projects. These include, but are not limited to

- The Paro project for the conservation of gouramies of the genus *Parosphromenus* (https://parosphromenus-project.org),
- The Goodeiden project for the reintroduction of the Mexican highland splitfins (http://www.goodeidworkinggroup.com),
- The "Mata Atlântica" project for the conservation of the Brazilian cory catfish of the genus *Scleromystax* (http://www.oevvoe.org/scleromystax-mata-atl%C3%A1ntica),
- "Project Piaba" for the conservation of populations of the Cardinal tetra (*Paracheirodon axelrodi*) in Rio Negro Basin, Brazil (https://projectpiaba.org/),
- The "Peixes das Nuvens" project for the conservation of the 130 Brazilian killifish species (https://www.gov.br/icmbio/pt-br/assuntos/biodiversidade/pan/pan-rivulideos),
- The conservation project for killifish (tooth-carps) of the genus *Aphanius* (https://biodiversity.europa.eu/case-study-hub/mediterranean-killifish-aphanius-fasciatus),
- The Sulawesi Keepers focused conservation and breeding of various endangered freshwater fish, shrimps, crabs, and aquatic gastropods native to Sulawesi, Indonesia (https://sulawesikeepers.org).

The importance of practical ornamental fishkeeping for popular education and should also be emphasized [199, 226, 227]. In this sense, there have already been very good approaches in the past [228, 229], which have unfortunately been forgotten today. We consider better scientific education for all population levels indispensable (not only in destination countries but also in source countries/regions such as Sulawesi, Indonesia; [230]).

9 | Legislative Framework in Selected Important Countries

The aforementioned issues raise the fundamental question of the extent to which the state should intervene in importing and

trading ornamental fish, invertebrates, and plants through legislation. The approach to ornamental aquaculture, trade and welfare of ornamental animals in the countries concerned varies in some respects. For instance, in Germany, two political parties are currently calling for comprehensive regulations and restrictions on pet ownership. We believe that certain legal regulations and restrictions are fundamentally necessary, even if the species affected by hobby activities are more likely to be reptiles, birds, or mammals, and, to a lesser extent, fish. Since ornamental aquaculture is responsible for the introduction of numerous nonnative organisms outside of their native range, the identified species with high invasion potential *sensu* Vilizzi et al. [169] should be replaced by low-risk ones. Specific attention should be focused on vectors of nonnative diseases and pathogens [231]. This approach is potentially more effective than a total ban of whole pet-traded animal groups but must be accurately explained to the public and stakeholders to fully understand and accept the idea [140]. High-risk species are usually banned by national or international so-called blacklists such as in the European Union Regulation 1143/2014: list of Invasive alien species of Union concern. Even if the number of fish species listed in the current version is low (10 species), a future increase can be expected.

We believe that the legislative restriction on international trade in aquarium organisms should take place on the principle of "negative lists," that is, inventories of animals and plants that may, if required, not be traded (as an example see the CITES legislative system, https://cites.org), supplemented by national legislative acts built on the same principle. To ensure the welfare of farmed animals, individual countries can and do take legislative measures. Based on research, regionally focused blacklists of unwanted high-risk species are created and released, and these can be adopted also for the regulation of ornamental aquaculture.

Two forms of ornamental aquaculture are active in Europe:

i. Import from other countries, for example, Singapore, Indonesia, Thailand, Brazil, Colombia, Peru, and Nigeria;

ii. Domestic production with the Czech Republic and Germany being leaders.

Ornamental fish (but not invertebrates bar adult cephalopods) are protected against animal cruelty and suffering by Council Directive No. 98/58/EC concerning the protection of animals kept for production. Certain freshwater ornamental fish taxa are protected by Commission Regulation (EU) 2023/966 amending Council Regulation (EC) No. 338/97 on the protection of species of wild fauna and flora by regulating trade therein. Keeping ornamental aquatic animals and plants in pet shops and garden centers is regulated by Article No. 6 of Commission Decision 2006/656/EC laying down the animal health conditions and certification requirements for imports of fish for ornamental purposes or in facilities that are equipped with effluent treatment systems, which fulfil the set aims. Even if several pieces of legislation place regulations on ornamental aquaculture operations, including restrictions on specific taxa in the European Union, private breeders remain largely unregulated.

9.1 | Czech Republic

The regulations of ornamental aquaculture in the Czech Republic, a country with a long history of imports and domestic production of ornamental fish and serving as a hub for pet-traded animals in the European Union [23, 232, 233], are defined in particular in Act No. 114/1992 and Council Regulation (EC) No. 708/2007, which sets among others the rules for the use (transfer, release, stocking) of nonnative species in aquaculture. Ornamental fish are protected against animal cruelty and suffering by Act No. 246/1992. In particular, transport, euthanasia, and professional competence for trading and conducting experiments are subject to regulations. To regulate trade and to reflect the amendments adopted at the 19th meeting of the Conference of the Parties to the Convention on International Trade in Endangered Species of Wild Fauna and Flora, it was implemented into the Czech legislative measurements by Act No. 100/2004; listed were some South American freshwater stingrays, all members of the order Acipenseriformes, Asian bonytongues (*Scleropages formosus* and *S. inscriptus*), arapaima (*Arapaima gigas*), Mekong giant catfish (*Panasianodon gigas*), Zebra pleco armored catfish (*Hypancistrus zebra*), European eel (*Anguilla anguilla*), and Australian lungfish (*Neoceratodus forsteri*). Some native fish are among the species specially protected in the Czech Republic by Act No. 114/1992 (e.g., lampreys, Kessler's gudgeon [*Romanogobio kessleri*], native spined loaches [*Cobitis* spp. and *Sabanejewia* spp.], Bullheads of the genus *Cottus*, Eurasian minnow [*Phoxinus phoxinus*], and Ide [*Leuciscus idus*]) and permits are required for angling and any breeding. Keeping and breeding of genetically modified organisms, that is, fish such as Zebra danio (*Danio rerio*) and other species are restricted by Act No. 78/2004, which implements Directive 2001/18/EC of the European Parliament and of the Council on the deliberate release of genetically modified organisms and repeals Council Directive 90/220/EEC—Commission Declaration.

9.2 | Germany

In Germany, legal provisions prohibiting animal cruelty have existed since the beginning of the 19th century. This later gave rise to the Animal Protection Act (TierSchg.) of the Federal Republic of Germany, which entered into force as a federal law on October 1, 1972 and has since been amended several times. In May 2002, animal protection was included as a national objective in the Basic Law (Article 20a). This animal protection law is also of considerable importance for trade as well as for the breeding and rearing of aquarium fish. Section 2 requires that every animal owner has the necessary general knowledge and skills for appropriate nutrition, care and species-appropriate housing. In Section 11 ("breeding, keeping animals, trade in animals") the requirements are summarized much more specifically, as proof of competence under Section 11 of the Animal Welfare Act is required. This applies in particular to animal dealers and people involved in the sale of animals. This proof of competence is also required by organizers of animal fairs and exhibitions if these last longer than 3 days. As it is difficult for people to provide "proof of competence", two associations in Germany offer regular

and approved specialized training courses with exams and certificates. These associations are the "Federal Association for Appropriate Conservation of Nature and Species (BNA)" and the "Association of German Aquarium and Terrarium Associations (VDA)." The latter even offers these training courses at four locations in Germany. Moreover, the Federal Ministry for Food, Agriculture and Forestry, in cooperation with experts, released a "Guidance on minimum requirements for the keeping of reptiles" (1997) and another "Guidance on minimum requirements for the keeping of ornamental freshwater fish" (1998).

9.3 | Spain

In comparison, ornamental aquaculture in Spain is driven by imports of ornamental animals [234]. The aquarium trade in Spain is regulated by the general regulation of the pet trade in Europe (e.g., Common Entry Veterinary Document, Regulation 338/1997). Moreover, the trade, holding, and transport of certain exotic species is forbidden since the enforcement of the first "blacklist" of invasive species in Spain in 2011 (RD1628/2011) and subsequent updates (RD630/2013; RD 1143/2014). A major issue with this legislation is that a species is forbidden when there is a documented invasion elsewhere [235]. These researchers argue for a more proactive approach that tackles the root cause of pet-related invasions: pet abandonment. They propose, among other proactive measures, restricting the sale of low-cost, small-sized species at the point of purchase to discourage impulsive buying [235]. This is particularly relevant considering that many readily available species, like the Bala shark (*Balantiocheilos melanopterus*) or the Pleco (*Pterygoplichthys gibbiceps*), grow to sizes that most home aquariums cannot accommodate [234]. While the risk of invasion for these tropical species is low in mainland Spain, there are ethical concerns surrounding the sale of certain species with a high likelihood of improper care. It is also important to reduce pet abandonment or escapees from ornamental fish wholesalers because climate change with mild winter temperatures may increase the establishment of subtropical ornamental fish species or their parasites in Spanish freshwaters [235], as occurred in German freshwaters [236]. The new legislation on animal welfare, including regulations for pets (RD7/2023), seems to address these issues by developing a list of permitted species, often referred to as "whitelists" or "green lists." However, the specific details of this legislation and its potential impact on the trade of species that have been freely available for decades remain unclear (see [235]).

9.4 | USA and Canada

Regulations in North America for freshwater aquarium fish embody the aforementioned axiom that policymakers "tend to protect endangered species and regulate the invasive ones." Dictates impinging upon freshwater species imports to the United States include regulations by the US Fish and Wildlife Service (USFWS) and the US Department of Agriculture (USDA), which regulate the importation, interstate transport, and ownership of invasive species. Individual states also have regulations on bans of species, permitting requirements, and restrictions on collecting from the wild. A review of the risks of aquatic invasive species in commerce is supported by the US Department of the Interior, available at www.aisincommerce.org. Selected species are assessed by predicting models, for example, *Arapaima gigas* [237]. In addition, to minimize release of unwanted aquatic animals, the Pet Advocacy Network USFWS and the National Oceanic and Atmospheric Administration developed a consumer facing program called Habitattitude (https://www.habitattitude.net/). The message to avoid abandoning pets is being promoted in retail markets, industry trade shows, and in relevant magazines [238]. For endangered species, mandates are set in place by CITES, as well as the US Endangered Species Act (United States. Congress. "Endangered Species Act of 1973." 16 U.S.C. §§ 1531–1544.). Unique to the United States in terms of wildlife trade is the Lacey Act (United States. Congress. "Lacey Act." 16 U.S.C. §§ 3371–3378), which protects wildlife by making it illegal to import or export wildlife across state or national boundaries that is in violation of local laws. Data on inter-state commerce of ornamental fish are not well maintained, and thus total impact of this trade in terms of economic benefit and number of species is poorly understood. Environmental impacts of domestic aquaculture are regulated by the Environmental Protection Agency (EPA) through their National Pollutant Discharge Elimination System. A majority of ornamental aquaculture operations are not mandated to report this given that they are not considered a Concentrated Aquatic Animal Production Facility given that they discharge effluent less than 30 days per year. State-based aquaculture laws differ widely, and in Florida, the largest domestic ornamental fish producer, regulations that lead to production losses outweigh the financial cost of compliance [239]. The top regulatory burdens for growers included Interstate and international shipping (overseen by the United States Department of Agriculture), water access (overseen by the Florida Department of Environmental Protection), and drug and chemical approval (overseen by both the Food and Drug Administration and the EPA). In Canada, the Border Services Agency receives imports and then works with Fisheries and Oceans Canada (along with provinces and territories), the Canadian Food Inspection Agency, and Environment and Climate Change Canada for relevant species issues concerning aquatic invasive species, aquatic animal health, and CITES species, respectively. Provinces all have their individual mandates, many set in the form of avoid lists, and Canadian regulations regarding invasive species are summarized by Reid et al. [240].

9.5 | Brazil

The Brazilian aquarium trade is regulated by the Federal Law No. 9605 of 1998. This act emphasizes the trade regulation of nonnative aquatic species through vectors such as fish importation and the aquarium industry [158]. To reduce the likelihood of invasions in Brazil via aquarium trade, certain specific species were placed on the Federal Normative Instructions 202 and 203 of 2008 for saltwater and freshwater fish species, respectively. These laws were passed by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA), a Federal agency under the Ministry of Environment which determined the import, trade, culture, and transport of live specimens of these nonnative fish into the Brazilian aquarium

trade as illegal due to (i) irrelevance to the hobby (*Lutjanus sebae*, *Pangasianodon hypophthalmus*, *Channa argus*, *Channa striata*, *Clarias batrachus*, *Osphronemus gourami*, *Trichopodus pectoralis*); (ii) aggressive behavior (*C. argus*, *Channa lucius*, *Channa micropeltes*, *C. striata*, *C. batrachus*); and (iii) history of invasions in other countries (*Centropyge flavissima*, *T. pectoralis*, *O. gourami*, *C. micropeltes*, *C. striata*, *C. batrachus*) ([241]). Recently (i.e., January 16, 2017), IBAMA also banned import, trade, culture, and transport of the transgenic *Danio rerio* throughout Brazilian territory [242]. Despite being good laws, they are considered "dead-letters" (i.e., refers to existing—but unenforced—laws). The recent availability and ease in purchase of illegal species on the Brazilian market, such as *C. flavissima*, *P. hypophthalmus*, *T. pectoralis*, *O. gourami*, *C. argus*, *C. lucius*, *C. micropeltes*, *C. striata*, and *C. batrachus* indicate that the compliance of Normative Instructions No. 202 and 203 of 2008 is not effective [158]. Likewise, despite being banned, transgenic *D. rerio* and the Skirt tetra (*Gymnocorymbus ternetzi*) is very popular in pet stores in the five geopolitical regions of Brazil [242, 243] and is already introduced to Atlantic Forest creeks located in the southeast region ([244]; Magalhães ALB, personal observation for *G. ternetzi*). This scenario of lack of compliance with the Brazilian bans is due to IBAMA having a chronic shortage of officials on its staff since its creation in 1989, thus leading to an ineffective inspection, and lack of awareness of these laws by stakeholders (i.e., importers, wholesalers, retailers, pet store owners) involved in the Brazilian aquarium trade [158, 242, 245].

9.6 | Singapore

The ornamental fish industry in Singapore has a rich history dating back to the 1920s when Chinese immigrants began breeding fish for export. By the 1970s, Singapore emerged as a global hub for ornamental fish trading [246]. Today, it remains a significant player in the industry [2], with advanced breeding techniques and stringent quality control measures. Singapore's strategic location, favorable climate, and expertise have helped it maintain its status as a leading exporter of ornamental fish worldwide [247]. The legislative framework governing the ornamental fish industry in Singapore is comprehensive, comprising various regulations to ensure sustainable practices and aquatic life welfare. Regulated under the Animals and Birds Act (https://sso.agc.gov.sg/Act/ABA1965), the Wildlife Act (https://sso.agc.gov.sg/Act/WA1965), and the Endangered Species (Import and Export) Act (https://sso.agc.gov.sg/Act/ESIEA2006), these laws align with the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), administered by the National Parks Board (NParks: https://www.nparks.gov.sg/). NParks enforces additional regulations tailored to the ornamental fish industry, including licensing requirements for importers and exporters and guidelines for handling, housing, and transportation of ornamental fish. The Ornamental Fish (Licensing of Importers, Exporters, and Transhippers) Rules mandate obtaining a license from NParks, subject to conditions like animal welfare standards and biosecurity measures. This legislative framework ensures the industry operates sustainably, protecting fish welfare and the local ecosystem from environmental risks.

9.7 | Indonesia

Fisheries and aquaculture in Indonesia are regulated by Fisheries Law No. 31/2004, which emphasizes the crucial role of sustainable use of aquatic resources in the development of fisheries. The Directorate-General of Aquaculture Development, under the Ministry of Marine Affairs and Fisheries, manages all national-level aquaculture-related matters with authority and expertise [248]. Aquaculture contributes significantly to national food security, income and employment, and foreign exchange earnings, and plays an important role in Indonesian fisheries [249]. Indonesia (and Asia in general) have made significant strides in legislative regulations and acts related to aquaculture. The Southeast Asian Fisheries Development Center (SEAFDEC) has prepared the Regional Guidelines for Responsible Fisheries in Southeast Asia, which apply to aquaculture in marine, brackish, and freshwater environments, to facilitate the implementation of the FAO Code of Conduct for Responsible Fisheries [250]. The Regulation of the Minister of Maritime Affairs and Fisheries Number 47/PERMEN-KP/2020 clearly outlines the regulations governing the movement of fish in and out of Indonesia. This regulation asserts the supervision and control of food safety and quality, feed safety and quality, genetically modified products, genetic resources, biological agents, invasive species, and protected fish species that are introduced into, spread from one area to another, or removed from the territory of the Republic of Indonesia. The Minister of Marine Affairs and Fisheries has prohibited the entry, cultivation, and release of certain harmful fish species in Indonesia through Regulation 41/PERMEN-KP/2014. The regulation's effectiveness has been limited. Under this regulation, 152 species of fish have been declared illegal due to their harmfulness. However, it is important to note that there are still numerous high-risk ornamental fish species present in Indonesian waters, including: *Arapaima gigas*, *A. leptosome*, *Amatitlania nigrofasciata*, *Polypterus senegalus*, *Potamotrygon* spp. (e.g., [13, 149, 251]). It is worth mentioning that "ikan hias" is the Indonesian term for ornamental fish but also other aquatic ornamental animals are included (such as crayfish). The Minister of Maritime Affairs and Fisheries of the Republic of Indonesia has issued regulations on fish quarantine in Indonesia through Ministerial Regulation No. 8 of 2022. This regulation clearly outlines the commodities that require fish quarantine checks, as well as quality control and safety measures for fishery products. The Omnibus Law policy aims to unify several laws ("undang-undang") at once, including the simplification of regulations [252, 253]. Furthermore, all fish shipped to buyers must undergo a quarantine process. It is crucial to ensure that the Fish Quarantine Agency inspects every aspect during the inspection process to avoid any potential harm to economic actors and buyers.

9.8 | India

In the Indian ornamental fish trade, hundreds of alien species are prevalent, reflecting the increasing significance of this sector due to its social and economic impacts [254–256]. However, the unregulated influx of aquatic alien species across borders has drawn considerable attention from both scientists and policymakers, highlighting the need for stringent regulation and management [257–259]. Moreover, the presence of alien

aquarium species has been detected in natural water bodies across India, such as guppy, gourami, platy, and sucker catfish, indicating potential environmental implications [260, 261]. The Indian government has implemented a series of initiatives to promote the development of Ornamental Fisheries across the country. The National Fisheries Development Board has been instrumental in providing financial aid for various aspects of ornamental fisheries development, including the establishment of backyard rearing units, medium-scale rearing units, integrated breeding-cum-rearing units, aquarium fabrication units, and ornamental fish markets. Additionally, the Central Marine Fisheries Research Institute has spearheaded efforts such as the development of green certification for marine ornamental fish, standardization of breeding and seed production techniques, and the production of ornamental fish feeds using commercial extruders. The importation of ornamental fish into India is a subject of significant regulatory oversight and concern within the scientific community. The Department of Animal Husbandry, Dairying, and Fisheries (DAHDF) under the Government of India, has formulated comprehensive guidelines to regulate this practice. These guidelines, aimed at safeguarding human health, animal welfare, and environmental conservation, enforce stringent regulations prohibiting the import of species falling into specific categories. Such categories include those considered dangerous to humans or animals, listed under international conservation agreements, subject to national or international bans, or recognized as invasive with documented detrimental impacts. Exceptions may be made for cultured endangered species with proper certification, following risk analysis to assess potential invasiveness. Importation without a valid permit from the DAHDF is strictly prohibited to ensure adherence to regulatory standards and environmental preservation. Furthermore, the DAHDF has developed a detailed Sanitary Protocol for Import of Ornamental Fishes into India. This protocol regulates the import process to mitigate potential hazards and environmental risks associated with ornamental fish importation. Prohibited categories encompass species posing threats to humans or animals, those listed under international conservation agreements, species subject to import bans, invasive species with documented impacts, and genetically modified varieties. However, exceptions may be granted for cultured endangered species with proper certification. These measures aim to safeguard ecosystems and minimize the proliferation of harmful species. Additionally, the department has furnished a list of 92 ornamental fish permissible for import into India, subject to compliance with sanitary protocols and procedural requirements, including obtaining a No Objection Certificate (NOC) from the DAHDF along with the Ministry of Agriculture and Farmers' Welfare [262].

9.9 | Israel

Importing live ornamental fish to Israel is regulated under the responsibility of the veterinary services of the Israeli Ministry of Agriculture and was last updated in November 2020. In short, two types of importing licenses are regulated, based on the imported goods. The first license stands for the importing of ornamental tropical fish, where it is restricted to a publicly available "white list" of species, it does not require quarantine practices for the imported organism and is valid for 36 months. The second is dedicated to the importing of the cold-water species and their hybrids *Cyprinus rubrofuscus* (nishikigoi), *Carassius auratus*, *Ctenopharyngodon idella*, and *Tinca tinca*. This type of import permit is valid for 18 months and requires a quarantine procedure. The quarantine includes a monitored veterinary inspection and lasts from 30 to 180 days, depending on the imported species.

9.10 | South Africa

South Africa imports ornamental fish from 23 countries with about 75% of imports from Asia, predominantly Sri Lanka (23%), Indonesia (15%), Singapore (14%), and Thailand (12%) (Department of Forestry, Fisheries, and the Environment 2022). Import of live fish is regulated by the Animal Diseases Act 35 of 1984, Marine Living Resources Act 18 of 1998 (MLRA), Animal Health Act 7 of 2002, and the National Environmental Management: Biodiversity Act, 10 of 2004 (NEMBA), with the species prohibited from import listed in the Alien and Invasive Species Regulations (AIS Regulations); List 7: Prohibited Freshwater Fish. A veterinary import permit from the Directorate of Animal Health is required for the import of all animals or animal products into, or in transit through South Africa following the Animal Diseases Act, 35 of 1984 (Department of Agriculture, Forestry, and Fisheries 2015). The Department of Agriculture developed a list of Permitted Species in the 1990s, which importers could readily bring into the country as these species were not deemed to be a serious risk to South Africa's inland aquatic ecosystems. Importers of ornamental fish are primarily wholesalers that import fish regularly (often weekly) and who supply pet retailers across South Africa, although, import for personal and/or commercial purposes is permissible with the appropriate permits (Impson N.D., formerly of CapeNature, pers. comm.). Inspection of imported ornamental fish by customs officials is mandatory, however, identification of species can be problematic because of the large numbers of species imported and the need for inspectors to have expertise in fish identification. Transport of live fish across a provincial boundary requires import and export permits from the conservation authorities in the respective provinces, as detailed in the Cape Nature and Environmental Conservation Ordinance, 19 of 1974, Ciskei Nature Conservation Act 10 of 1987, KwaZulu-Natal Nature Conservation Ordinance 15 of 1974, Free State Nature Conservation Ordinance, 8 of 1969, Limpopo Environmental Management Act, 7 of 2003, and the Transvaal Nature Conservation Ordinance, 12 of 1983. Although these measures are in place, there is little enforcement of this requirement and in general, there is undocumented movement of ornamental fish across South Africa.

9.11 | Australia

The legislative framework governing ornamental aquaculture trade in Australia may involve three levels of Government. Commonwealth (i.e., Federal) environmental legislation, the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act) regulates imports and exports of wildlife, including assessment and approval of potential species for import, and whitelisting. Governments of the eight mainland States and

Territories may also regulate activities in the industry via a range of State-specific fisheries and biosecurity legislation (including blacklists of species): Millington et al. [263] identified 12 such examples of State legislation in their review. Local Governments (e.g., City, Regional Councils or Towns) may have additional regulations potentially influencing trade or operations in ornamental aquaculture. Illegal import of wildlife to Australia is well documented and known examples include species of fish, the turtle *Trachemys scripta elegans* [264] and the freshwater crayfish *Procambarus clarkii* [265]. It is unclear if illegally imported aquatic species intercepted at the border were destined for the ornamental aquarium trade, but it is understood that *P. clarkii* were actively being traded in Western Australia prior to confiscation in 2021 [266]. Similarly, despite the strict and extensive Commonwealth regulations governing imports to Australia, incursions and establishment of aquatic diseases and populations of exotic species in the wild (including ornamental fish) have not been uncommon (e.g., 22 species of fish; [267]). Similarly, challenges exist under State legislation. It is known that reporting of the species of fish, actually in trade, is incomplete within the Australian ornamental fish industry [263]. In part this is driven by (and also exacerbated by) issues with nomenclature impeding accurate species identification, and thus effective monitoring and regulation of the industry under State legislation. Similarly, a substantial part of the Australian ornamental freshwater fish trade is reportedly based on so-called "greylisted" species; species that have not been assessed and whitelisted (under Commonwealth legislation), nor blacklisted under State legislation. Shortcomings in the Australian legislative framework are well documented (e.g., [263, 267]) and various recommendations have been made to address previously identified issues in the industry (e.g., [268]). Appreciable amendments to legislation and regulations, plus reform within the industry are required in Australia.

Considering well-known positive aspects of ornamental aquaculture from a wide perspective such as the popularization of aquatic organisms and ecosystems, conservation and breeding of endangered taxa, education of the public including children, economic benefits, and various scientific discoveries including descriptions of new species, we appeal to decision-makers to find other solutions how to improve the situation and mitigate related risks than a total ban which can paradoxically end negatively.

10 | Summary

We documented the timeline of the number of freshwater ornamental fish species newly imported through time after the end of WWI. The important influence of advancements in air cargo transport is clear. The increasing economic prosperity in the majority of European and tropical countries likely represents a secondary major factor. The most common fish groups contributing to the total number of ornamental fish in trade are killifish (Cyprinodontiformes), armored catfish (families Loricariidae and Callichthyidae), and endemic lacustrine East African cichlids (Cichlidae from Lakes Malawi and Tanganyika). These groups contribute ca. 68% to the stock of freshwater ornamental fish species, in total some 4400 species and potential novel species. The impact of the era of globalization affecting the volume and speed of international transport can be called revolutionized global trade and is relevant for ornamental aquaculture and its related industry. Our findings support this assumption by highlighting the timeline of imported freshwater and brackish fish taxa. Modern practices and technologies have reduced the risks of mortality of fish in transport, enabling additional species that once were perceived as "problematic" to be quickly transported from the collector/producer to the ultimate customer. This information may be important for decision-makers, traders, producers, conservationists, and other stakeholders. Further exploration of opportunities for fostering innovation and diversification within the industry, as well as continuous structured monitoring of the market and pet trade, are recommended. A special focus should be on domestic markets that are frequently overlooked or ignored in this regard and on developing strategies to advocate responsible ornamental fishkeeping practices.

Author Contributions

Jindřich Novák: conceptualization, investigation, methodology, writing – original draft, data curation, resources, funding acquisition, formal analysis, supervision. **Dieter Hohl:** writing – review and editing, resources. **Martin Stuchlík:** methodology, formal analysis, investigation, software. **Jaroslav Hofmann:** writing – review and editing, resources. **Michael F. Tlusty:** writing – review and editing, validation, resources. **André Lincoln Barroso Magalhães:** resources, writing – review and editing. **Alberto Maceda-Veiga:** writing – review and editing, resources. **Surya Gentha Akmal:** resources, writing – review and editing. **Gen Hua Yue:** resources, writing – review and editing. **Pradeep Kumkar:** writing – review and editing, resources. **Sean M. Marr:** writing – review and editing, resources. **Joseph R. Sara:** writing – review and editing, resources. **Nir Stern:** writing – review and editing, project administration. **Andrew L. Rhyne:** writing – review and editing, resources. **James M. Furse:** writing – review and editing, resources, methodology. **Lukáš Kalous:** writing – review and editing, validation. **Jiří Patoka:** conceptualization, investigation, writing – original draft, writing – review and editing, visualization, methodology, project administration, supervision, formal analysis, data curation, software, funding acquisition.

Acknowledgments

J.P. and L.K. were supported by the Technology Agency of the Czech Republic within the project, "DivLand" (SS02030018). A.M.-V. was supported by Fundació Barcelona Zoo. This paper belongs to the portfolio of activities of the Indonesian Centre for Research on Bioinvasions. Any opinion, finding and conclusion or recommendation expressed in this material is that of the author(s) and the DSI-NRF, University of Limpopo (UL) do not accept any liability in this regard. Support for this study was provided to J.M.F. by the Coastal and Marine Research Centre and Cities Research Institute, Griffith University. We thank two anonymous reviewers or their constructive criticism. Open access publishing facilitated by Ceska Zemedelska Univerzita v Praze, as part of the Wiley - CzechELib agreement.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.