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Perspective

**Decades of Global Sturgeon Conservation Efforts are Threatened by an Expanding Captive Culture Industry**

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**Abstract**

After centuries of overexploitation and habitat loss, many of the world's sturgeon (Acipenseridae) populations are at the brink of extinction. Although significant resources are invested into the conservation and restoration of imperiled sturgeons, the burgeoning commercial culture industry poses an imminent threat to the persistence of many populations. In the last decade the number and distribution of captive sturgeon facilities has grown exponentially and now encompasses diverse interest groups ranging from hobby aquarists to industrial-scale commercial facilities. Expansion of sturgeon captive culture has largely fallen outside the purview of existing regulatory frameworks, raising concerns that continued growth of this industry has real potential to jeopardize conservation of global sturgeon populations. Here, we highlight some of the most significant threats commercial culture poses to wild populations, with particular emphasis on how releases can accelerate wild population declines through mechanisms such as hybridization, introgression, competition, and disease transmission. We also note that in some circumstances commercial captive culture has continued to motivate harvest of wild populations, potentially accelerating species' declines. Given the prevalence and trajectory of sturgeon captive culture programs, we comment on modifications to regulatory frameworks that could improve the ability of captive culture to support wild sturgeon conservation.

## INTRODUCTION

Sturgeon (Acipenseridae) are one of the most ancient and unique clades of extant fishes. With little morphological change in their circa 200-million-year history, the 25 extant species of sturgeons are frequently referred to as living fossils for their primitive scutes and cartilaginous skeletons (Gardiner 1984). However, the natural history of these fishes has been anything but static. Subsistence fisheries by Indigenous peoples and early settlers had limited effect on populations and commercial interest for sturgeon products remained low throughout much of the 1800s. By the turn of the 20th century, increased efficiency in capture, storage, and transportation methods inspired the growth of a global fishing industry for sturgeon and demand for caviar and flesh intensified. This enterprise was short-lived, as serial depletion of regional and global stocks subsequently lead to collapse of many of the world's sturgeon populations in less than 100 years (Saffron 2002). Today, sturgeon are considered one of the world's most imperiled groups of fishes (IUCN 2022) and the majority of species are afforded regulatory protection within their native waterways (see Table 1). Despite these conservation measures, most populations have been slow to recover from legacy effects of overharvest and continue to be threatened by ongoing habitat loss and anthropogenic activity and most sturgeons have continued to decline despite conservation actions (IUCN 2022).

In the mid-1990s, amidst rising consumer demand for caviar and dwindling abundance of wild populations, the sturgeon culture industry saw a rise in the number and success of production facilities (Saffron 2002; Bronzi et al. 2019). Originally promoted as a means to alleviate harvest pressure on wild populations, commercial aquaculture for sturgeon is now a global enterprise that serves numerous consumer interests including caviar and meat production, pet trades, leather smithing, and isinglass manufacturing. Despite fluctuations in market value

and biomass production in the past decade, today there are over 2,300 commercial sturgeon facilities spread across at least 60 countries (Figure 1), with at least 13 of 25 known sturgeon species and numerous hybrids in captive production (Bronzi et al. 2019).

Sturgeon are also becoming more prevalent in conservation aquaculture programs. These programs, which use careful genetic and demographic planning to aid in species recovery, have been instrumental in the restoration of several sturgeon populations. However, conservation aquaculture is not the focus of this manuscript, as threats to wild populations are most likely to occur when individuals are released or escape from captive populations that have not been bred and reared for the explicit purposes of population restoration. As such, this manuscript focuses on the increasing prevalence in releases from captive populations that occur in commercial, private, and/or other research facilities.

We contend that growth of sturgeon captive culture has real potential to countermand decades of global conservation efforts and accelerate declines of many critically imperiled sturgeons. Moreover, given the projected expansion in the size, distribution, and scope of commercial aquaculture facilities, existing regulatory frameworks (Table 1) may be insufficient to protect future wild sturgeon populations. Here we highlight some of the most significant threats that the captive culture industry presents to native sturgeon populations. We then discuss modifications to existing regulatory frameworks that could help support the collective goals of conservation and sustainable consumerism of sturgeons.

## CAPTIVE STURGEONS IN THE WILD

As the number of sturgeon culture facilities has increased, so too has the number of reported incidents of sturgeon outside of their native waterways. The release of captive fishes, be it through intentional stocking or accidental release, has left one of the biggest footprints on global fisheries conservation (Lockwood et al. 2019). Yet, there are still few answers to the catastrophic declines in native fish communities that commonly follow the establishment of nonnative ichthyofauna. Physical, chemical, and genetic tools are available to control the spread of aquatic invasive species and populations, but these require significant resource investment and can result in further harm to native species. Even then, efforts largely focus on management of the nonnative population, as complete eradication is often impossible, particularly in large river systems and marine environments (Gozlan et al. 2010). Therefore, the best tool for limiting the spread of nonnative species is to minimize introduction pathways.

Below, we highlight the major introductory pathways for captive sturgeons into wild populations. Importantly, while unsanctioned release of captive sturgeon from research, commercial, and private facilities has been documented, limited monitoring and difficulty sampling sturgeon populations likely allows many incidences to go undetected. Moreover, many pathways that lead to captive sturgeon introductions may receive little attention as they involve release of relatively few individuals. However, the invasion histories of other species provide cautionary tales that colonization and spread of nonnative species can occur from small founding populations (Rachels 2021). In addition, the shared habitat requirements among sturgeons and the low abundance of many native populations suggest invasion success of released captive sturgeon could be high.

## Commercial Culture

The potential for commercial culture operations to negatively affect wild sturgeon populations is already being realized, as we have witnessed repeated incidences of accidental release of captive sturgeons from commercial facilities (Ludwig et al. 2009). In one example, a catastrophic flood in 2016 resulted in the escape of over 9.8 million kg of captive fish, including five nonnative sturgeon species, several sturgeon hybrids, and a nonnative paddlefish, into the Yangtze River, China (Ju et al. 2020). Escapees vastly outnumbered native species, including the critically endangered Chinese Sturgeon *Acipenser sinensis*, making hybridization and competition significant concerns (Gao et al. 2017). A similar event was documented in the United States in 2017, when flooding in the state of Idaho resulted in the release of approximately 3,000 captive adult White Sturgeon *A. transmontanus* into a nearby river, of which most were not recaptured (Idaho Power Company 2018).

In the Rioni River and Black Sea in the country of Georgia, nonnative Siberian Sturgeon *A. baerii* have been recently documented multiple times. Although the origin of these individuals is unknown, it is believed they were released or escaped from commercial aquaculture facilities. How Siberian Sturgeon will influence the conservation of four native sturgeons (Russian Sturgeon *A. gueldenstaedtii*, Stellate Sturgeon *A. stellatus*, Beluga Sturgeon *Huso huso*, and Ship Sturgeon *A. nudiventris*) is still under investigation. However, because native Rioni River sturgeons already exist in critically low abundance, presence of relatively few Siberian Sturgeon could result in significant declines and/or extirpation of native sturgeon (Fleur Scheele, Fauna and Flora International, written communication; see below for potential mechanisms of interaction between Rioni River sturgeons).

Effects of commercial culture are not always restricted to release of captive fishes. For example, investigations by Fauna and Flora International show that Georgian Black Sea fishers sometimes sell live Beluga Sturgeon and Stellate Sturgeon to local ponds, where owners mix wild and captive individuals with the goal of releasing offspring into the wild (Fleur Scheele, Fauna and Flora International, written communication). Effects of these releases are unlikely to be realized for several decades; however, even moderate amounts of interbreeding and competition may jeopardize the survival of several endemic, critically endangered sturgeons in the region.

**Research and Government Laboratories**

Damage to captive infrastructure typifies the catastrophic threats that high biomass commercial facilities pose to native fish communities. However, these events are generally isolated, well-documented, and often followed by increased management and surveillance. Conversely, poor biosecurity and uncontrolled trade likely present a more chronic and cryptic threat to wild populations. By nature, public documentation of unpermitted introductions is sparse. However, credible anecdotes implicate individuals, including career biologists, with the unsanctioned release of captive sturgeon, including the introduction of species outside of their native range. In the United States, a federally threatened Green Sturgeon *A. medirostris* native to the Pacific Coast of North America, was collected on April 23, 2010 in the Long Island Sound, an estuary of the Atlantic Ocean (Figure 1). Due to the conservation status of Green Sturgeon, the species is not permitted in private or commercial aquaculture. As such, it has been hypothesized that the nonnative Green Sturgeon was introduced from a nearby research facility; however, it is unclear when and how many individuals were released and how many may still be alive.

Although introductions are most frequently associated with nonnative species, the life history of sturgeon raises unique concerns about the invasion potential of captive individuals that are released within their native range but are genetically dissimilar to the local population. The philopatric tendency of sturgeon can create strong spatial genetic structuring among nearby populations, potentially leading to local adaptation to the unique physiochemical environments found in each river system (Schreier et al. 2012). As a result, the conservation value of a nonnative population of an otherwise native species is unknown. This question is currently being debated after a nascent population of Atlantic Sturgeon *A. oxyrinchus oxyrinchus* (a taxon listed under the United States Endangered Species Act) was discovered in the Connecticut River— a waterway where native Atlantic Sturgeon were thought to have been extirpated several decades ago (ASSRT 2007). Genetic analyses suggested the contemporary Connecticut River population was likely founded by individuals that originated from a population in the southeastern United States (Savoy et al. 2017). Atlantic Sturgeon are largely philopatric and show strong patterns of genetic isolation by distance, leading to genetically unique populations among most rivers (White et al. 2021). Therefore, while we cannot rule out the possibility that the Atlantic Sturgeon captured in the Connecticut River strayed from the southern Atlantic, it is more plausible that fish were released from a nearby research facility. At present, it is unclear if the population will adapt to the physiological requirements of a more northern climate. However, if the disjunct population persists, it may complicate future conservation efforts by conflating results of individual assignment and mixed-stock analyses, both of which are extensively used to understand regional and range-wide threats to Atlantic Sturgeon recovery (e.g., Kazyak et al. 2021).

**Private Pet Trade**

A rapidly emerging, and generally unregulated, threat to sturgeon conservation is the increased circulation of numerous sturgeons, including species of conservation concern, in hobby pet trades. The scale and scope of the pet trade for sturgeons is largely undocumented, and so their effect on native populations is unknown. However, ad hoc monitoring of popular consumer-to-consumer websites and online pet stores by the authors found numerous instances of both native and nonnative sturgeons being openly traded in the United States and abroad. Exotic pet trade has been unequivocally implicated with widespread biodiversity loss (Lockwood et al. 2019; Morton et al. 2021), and surveys of private aquarists have shown that up to 10% of fish owners admit to deliberately releasing aquarium fish into the wild (Chang et al. 2009; Strecker et al. 2011). Release of hobby sturgeon is a likely outcome, as sturgeon rapidly attain sizes that are too large for aquaria and small ponds and pet owners are often averse to euthanizing otherwise healthy animals (Holmberg et al. 2015). As such, the buying, selling, and transportation of hobby sturgeon is an expected pathway for nonnative invasions, as has already been documented by a Dutch public database (https://steuren.ark.eu/). This website monitors observations of native European Sturgeon *A. sturio* in the Netherlands, but has also documented nearly 50 occurrences of nonnative Siberian Sturgeon, Russian Sturgeon, and Sterlet *A. ruthenus* since 2010, with most occurring since 2020. The three nonnative species are likely derived from breeding facilities in eastern Europe and Asia, were sold in Europe as pond fish, and subsequently released into the wild. This finding is further corroborated by Brevé et al. (2022), who noted the occurrence of 11 nonnative sturgeon species in the Rhine–Meuse River delta, most of which could be attributed to unintentional and aided escape from garden and angling ponds.

## THREATS OF STURGEON CAPTIVE CULTURE TO WILD POPULATIONS

The full extent how captive sturgeon may impact wild populations is still unknown, as we have only recently started to document the invasion of captive sturgeons into wild populations (e.g., Ludwig et al. 2009). The outcome of an introduction likely depends on the number of individuals released, density of competitors, and habitat suitability. Therefore, we likely have not yet observed the full suite of potential negative interactions that may occur between captive and wild populations. Moreover, given the late maturation and long lifespan of sturgeon, it may take several decades before the consequences of present-day captive releases are fully realized. This underscores the importance of proactive regulation of captive sturgeon populations, as it may be too late to mitigate negative effects once declines in wild populations are detected.

**Hybridization**

A significant concern with release of captive individuals is the potential for interbreeding between domestic and wild lineages. The most significant threat is likely that of hybridization—the mating of individuals from different species or, rarely, different genera or families—which can cause rapid loss of native population fitness. Hybrid offspring are often sterile, and so the effect of hybridization may be restricted to loss of reproductive effort. For large populations, temporary reduction in fitness is unlikely to have significant, long-term genetic or demographic effects. However, in populations where few spawning individuals remain, as is the case in many imperiled sturgeon populations, hybridization has real potential to result in demographic swamping leading to collapse of local populations and even whole species extinction (Wolf et al. 2001).

When hybrid offspring are fertile, concerns arise over the potential for increased fitness of hybridized individuals relative to either parental species (i.e., hybrid vigor; Shivaramu et al. 2020). Hybrid vigor can lead to rapid displacement and loss of genomic signatures of the native species, ultimately resulting in declines in native populations through genetic swamping. One of the best documented cautionary tales of hybrid vigor comes from the prolific cutbow trout—a fertile hybrid from the mating of Cutthroat Trout *Oncorhynchus clarkii* and Rainbow Trout *O. mykiss*. Cutbow trout have physically displaced many populations of native Cutthroat Trout, including the Westslope Cutthroat Trout *O. clarkii lewisi*, which has experienced rapid declines in abundance and distribution due to habitat loss and erosion of genetic integrity from hybridization (Muhlfeld et al. 2009). Substantial resources are invested into ongoing efforts to identify and eradicate hybrids in an attempt to restore pure populations of Yellowstone Cutthroat Trout *O. clarkii bouvieri*. This case study underscores the potential long-term biologic and economic costs that can occur following release of nonnative species and the potential for hybridization to result in permanent genetic effects to native populations.

Hybridization has been well documented in wild and captive sturgeon populations, with over 20 different hybrid crosses reported in the literature (Table S1), including interfamilial hybridization between Russian Sturgeon and American Paddlefish *Polyodon spathula* (Káldy et al. 2020). Moreover, hybrids can be produced between species with differing ploidy levels, as exemplified by nonnative Siberian Sturgeon (~240 chromosomes) and native Sterlet (~120 chromosomes) hybrids in the Danube River (Ludwig et al. 2008). Although offspring of this cross were found to be sterile, hybrids from native Russian Sturgeon (~ 240 chromosomes) and Stellate (~120 chromosomes) in the Rioni River (Ludwig et al. 2009; Beridze et al. 2022; Figure 1) are viable. This success of hybrid sturgeons in wild environments is not well understood; however, hybridization between native Russian Sturgeon and nonnative Siberian Sturgeon in the Caspian Sea (Jenneckens et al. 2000), and subsequent laboratory studies documenting hybrid vigor (Shivarmu et al. 2019) suggests genetic swamping is a possible outcome of hybridization in sturgeons.

Sturgeon hybridization may occur readily in natural environments because many species have similar life history characteristics and spawning habitat requirements. In addition, sturgeon are broadcast spawners, which is a mode of reproduction that is associated with high hybridization rates in other taxa. Together, the documented ease and high probability of hybridization in sturgeon in captive and wild environments suggests that continued unregulated release of nonnative sturgeons has real potential to lead to population declines through demographic and/or genetic swamping. In addition, it is often difficult to discern hybrid individuals from purebred species using morphologic traits or genetic techniques, particularly after multiple generations of admixture and backcrossing. As the number of hybrid sturgeon in captive and wild populations increases, it may become increasingly challenging to identify purebred individuals in the field and trace the origin of commercial sturgeon products, both of which will complicate conservation efforts for native populations.

**Anthropogenically Mediated Gene Flow**

In addition to hybridization, sturgeon may also be prone to introgression, which we define as breeding between individuals of the same species but belonging to different populations. Introgression can improve population viability by increasing genetic diversity and long-term evolutionary potential. When executed successfully, as in many conservation aquaculture programs, introgression between wild and captive populations can be an effective conservation strategy for genetic rescue.

However, unintended introgression between wild and captive populations is likely to reduce fitness and survival of native populations. Wild-caught broodstock and juveniles are infrequently used in commercial production, and so generations of artificial selection can render captive individuals maladapted for wild environments. Under this scenario, introgression can lead to outbreeding depression and subsequent reduction in the fitness and survival of future generations—a phenomenon that has been well documented in salmonids (Araki et al. 2007). Moreover, introgression across large spatial scales can result in genetic homogenization and diminished long-term adaptive capacity. Together, loss of contemporary fitness and evolutionary potential may jeopardize the ability of native populations to persist and could severely undermine current efforts aimed at demographic recovery. Because many commercial facilities rear sturgeon outside of their native range, the threat of introgression is likely lower relative to hybridization. However, aforementioned examples of released captive Atlantic Sturgeon and White Sturgeon suggest the risk of introgression in contemporary populations is not negligible, and could increase with expansion in the size, scope, and location of commercial facilities.

**Competition And Depredation**

Negative effects of captive release can occur in the absence of reproduction, including the potential for resource competition and juvenile depredation. Given significant knowledge gaps about many aspects of sturgeon life history and ecology, the strength and outcome of competitive interactions may be difficult to predict. However, significant resource overlap among species and the global decline in sturgeon habitat suggests competition for already limited resources is likely to increase in future decades.

Although not causally linked to competition, malnourished Ship Sturgeon have been discovered during recent surveys in the Rioni River (Fleur Scheele, Fauna and Flora International, written communication); a potential indicator of negative interactions between native and introduced sturgeons (Figure 1). This is a discouraging finding, as Ship Sturgeon was believed to be extirpated from the Black Sea basin (Beridze et al. 2021) and now the long-term viability of the relict breeding population may be jeopardized by low fitness and survival.

Nonnative species, including sturgeon, but also other non-sturgeon species, can pose significant risk to recruitment through depredation. Although sturgeon develop bony scutes to deter predators, younger life stages have few natural defenses and are vulnerable to predation (Flowers et al. 2011). The risk of depredation may be particularly high when nonnative fishes are released near freshwater spawning and nursing habitats.

**Pathogens And Parasites**

Indirect effects of captive culture can be observed through the introduction of disease and parasites. High densities of fish in aquaculture facilities and mixing of multiple taxa in hobby aquaria increases the prevalence of viral, bacterial, and parasitic infections in captively reared individuals. Although many pathogens commonly found in captive facilities also occur in wild environments, human transport of captive fish across river basins introduces novel sources of disease to which native populations may have little natural immunity. Once released, captive individuals can then spread pathogens through entire ecosystems as they move through different habitats to complete their life cycle. Therefore, the pathogenic consequences of a single captive release may manifest across vast spatial scales, particularly for anadromous species like sturgeon.

Introduction of aquatic diseases during intentional stocking events has been implicated in population declines, loss of entire spawning year classes, and even complete extirpation of species in some areas (Zholdasova 1997). Presently, the largest disease risks in captive sturgeon populations appear to be bacterial (e.g., *Streptococcus iniae*, which also poses a disease risk to humans [Mugetti et al. 2022]) and viral infections including herpesviruses, White Sturgeon iridovirus, and potentially species of *Ranavirus* normally associated with amphibian declines (Waltzek et al. 2014). Although the threat of *Ranavirus* remains unclear, herpes viruses and White Sturgeon iridovirus are highly transmittable and have been correlated to necrotic infection and large mortality events. Viral infections of wild and captive sturgeon populations have been detected in multiple species and countries (e.g., Kurobe et al. 2010; Hofsoe-Oppermann et al. 2020), suggesting more widespread outbreaks could be forthcoming as the captive industry continues to expand.

**Continued Harvest of Wild Populations**

With most sturgeon species under strict harvest moratoria, captive facilities are now the most viable, and often only legal, source for caviar and other sturgeon products. However, large body size and late age of maturation can make sturgeon difficult to raise in captivity. Commercial fish culturists looking to reduce the space and resource requirements needed to support a self-sustaining captive sturgeon population or needing to compensate for incidental loss may continue to harvest individuals from wild populations. In Eurasia, wild sturgeon, particularly gravid females, are sometimes translocated to commercial facilities and temporarily held before being used as broodstock and/or harvested. This practice, which is illegal in many regions, perpetuates the stress on wild populations, and specifically monetizes removal of individuals during critical life stages. However, limited oversight and lack of critical inspection of many food labels still provide abundant opportunity for individuals to directly harvest or translocate individuals from wild populations (Dolan and Luque 2019; Figure 1).

## SUPPORTING STURGEON CONSERVATION IN THE ERA OF CAPTIVE CULTURE

Demand for caviar and other sturgeon products remains high, and continued loss and restriction of wild fisheries are likely to compel further development of the captive culture industry. Expansion of research laboratories, commercial facilities, and private pet trades presents serious challenges for conservation, as the scope and location of many captive facilities will likely fall outside the purview of current regulatory frameworks (see Table 1 for a list of policies that pertain to global sturgeon conservation). Specifically, the majority of current regulations aim to protect critical habitats, minimize individual harm, and regulate commercial harvest and transport of sturgeon and sturgeon products. While these challenges will remain into the future, emerging threats are likely to develop as the taxa's user group continues to expand. How this new era of sturgeon captive culture will affect wild populations remains to be seen; however, more stringent, effective, and targeted regulation would likely provide more opportunities for captive culture to be apposite to global conservation. Below we outline three major sectors of sturgeon captive culture and discuss possible regulatory changes that could improve the outlook of sturgeon conservation:

(1) **Commercial culture**. Commercial facilities account for the majority of captive sturgeon populations (Bronzi et al. 2019) and are likely to be the source of most nonnative sturgeon introductions. While many regulations already pertain to captive culturists (Table 1), there are still opportunities for improved oversight of this sector. Increased governance on allowable infrastructure, including restricted use of flow-through systems and banning facilities in flood-prone areas, would likely reduce the probability of high biomass escapes. Additional oversight on the location of large facilities may be particularly important given that catastrophic flood events are likely to increase under

future climate change scenarios. Another potential mechanism for reducing introduction pathways could be to severely restrict or prohibit the commercial sale of live sturgeon. However, across all commercial markets, more stringent investigation and castigation for mislabeled products is likely to reduce illegal harvest and minimize impacts on wild populations.

(2) **Research and government laboratories**. There is an expectation that fisheries professionals will uphold the highest standards of conservation. However, multiple observations presented in this article are consistent with unsanctioned releases of captive sturgeon from scientific facilities. In addition, fisheries research facilities are often highly trafficked, outdoor environments, which increases the biosecurity risk associated with these captive populations. Despite recent expansion in the number of sturgeon research programs, there are surprisingly few regulations that pertain to the proper handling of captive fish in these environments. For example, while academic research facilities in the United States operate under the oversight of animal care and use committees and may seek accreditation from the Association for the Assessment and Accreditation of Laboratory Animal Care International, accreditation is not mandatory for all federal research facilities. As such, within the United States there are no universal protocols pertaining to proper transport, handling, and disposal of captive individuals in laboratory environments. Likewise, there is no mechanism to assure that captive sturgeons are eliminated following laboratory testing, which is a requirement under federal permitting in the United States. Overall, the absence of consistent regulatory frameworks for academic and federal research facilities highlights a significant biosecurity gap, and an opportunity to enhance protocols pertaining to proper infrastructure, facility inspection,

and personnel training. For example, in Canada, captive facilities must satisfy requirements pertaining to disease transfer, husbandry methods, culture equipment, and fish holding densities, with more stringent requirements for listed species. Similar protocols in other countries may be particularly critical given that many research facilities are located near large waterbodies, and vulnerable infrastructure (i.e., flow-through systems) and insufficient maintenance has significant potential to be a source of unintentional captive escape.

(3) **Pet trade**. Although this sector has not yet been documented to have an impact on wild populations, rising popularity of sturgeon in the hobby pet trade foreshadows future negative consequences of private captive culture. This sector is very challenging to directly regulate due to the diffuse and poorly documented nature of private culture. Due to the challenges with regulating individual owners, and the near-certain probability that sturgeon growth will surpass all indoor aquaria, the strongest regulatory mechanism may be to prohibit all sale. Even with restrictions on sales, it may still be beneficial to increase surveillance for illegal trade of sturgeons. Automated approaches for monitoring the internet for trade of invasive species (e.g., Great Lakes Detector of Invasive Aquatics in Trade; https://bit.ly/3DIJ5Mu) have been developed and might provide a useful model for tracking the trade of sturgeons.

The captive culture industry represents an emerging threat to the recovery and conservation of critically imperiled sturgeon populations. Negative effects of captive culture programs, including intentional and unintentional release and ongoing harvest of wild populations, have already manifested in some populations. Under the current trajectory of the captive culture industry, nonnative invasion, introgression, and hybridization have real potential to reverse decades of conservation and drive one of the most ancient and globally revered groups of fishes further towards extinction. Increased attention to these emerging issues may help improve the outlook for sturgeon conservation programs.

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Table 1. Description of policies and resolutions that protect worldwide sturgeon populations against habitat loss, overharvest, and illegal trade.

| Resolution | Description | Application to Sturgeon | Resources |
|---|---|---|---|
| Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES) | Multinational agreement through which countries work together to ensure that international trade is not detrimental to the survival of the species in the wild. Member nations to CITES regulate and monitor international trade (import and export) through permits and certifications to ensure sustainable use. The CITES Secretariat is not a law enforcement authority and does not conduct investigations; instead, each country is to investigate within-county allegations if potential criminal activity lies with the relevant national law enforcement authorities of that country. | International trade led to a CITES listing of all species of Acipenseridae; since 1998, all sturgeon trade is regulated and all parts or derivates (e.g., caviar, meat, skin, etc.) require a CITES permit or certificate. Only Shortnose Sturgeon is listed under CITES Appendix I (threatened by extinction with trade permitted only in exceptional circumstances). All other sturgeons are listed in Appendix II (trade could threaten species persistence if not controlled).[1] | The Convention on the International Trade in Endangered Species of Wild Fauna and Flora provides country-specific contacts for reporting violations and information regarding illegal trade[2]; in the U.S. the U.S. Fish and Wildlife Service (USFWS) is the official CITES authority and provides opportunity to report violations.[3] |

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|---|---|---|---|
| U.S. Endangered Species Act (ESA) | Under the ESA, the National Marine Fisheries Service (NMFS) and the USFWS are required to conserve the ecosystems upon which endangered and threatened species depend on, provide a program for listed species conservation, and take appropriate steps toward recovery. Section 9 of the ESA outlines prohibitions including illegal "take" of a listed species which includes harm, capture and harassment and Section 10 describes penalties for illegal take. Under Section 7, federal actions are required to undergo a consultation to assess and reduce potential interactions with listed species and their designated critical habitat helps to conserve listed species. Limited federal dollars are also available for research. The ESA primarily protects foreign species by restricting trade and may prohibit certain activities, including import, export, take, commercial activity, interstate commerce, and foreign commerce. By regulating these activities, the United States ensures that people under its jurisdiction do not contribute to the further decline of a listed species. | Eight of the nine sturgeon species in the USA are currently listed under the ESA as either threatened or endangered and a review on the status of the Lake Sturgeon is scheduled for 2024. There are also eight sturgeon species that are not native to the United States listed under the ESA[4]. As described, the introduction of a nonnative species could harm listed sturgeon. | The National Oceanic and Atmospheric Administration (NOAA) is responsible mainly for marine wildlife[5] and USFWS for terrestrial and freshwater organisms[6]. Violations of the ESA should be reported to either NOAA by calling 1-800-853-1964 or USFWS via their online reporting[7]; photos and videos are encouraged |
| United Nations' Convention on the Conservation of | An environmental treaty of the United Nations designed to conserve migratory species, with special emphasis on protection of habitats and migration routes. CMS agreements range from legally binding treaties to less formal agreements. | European Sturgeon is listed under Appendix I (threatened with extinction) and 18 species are listed under Appendix II (species that would benefit from international cooperation). | |

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|---|---|---|
| Migratory Species of Wild Animals (CMS) | | |
| Bern Convention on the Conservation of European Wildlife and Natural Habitats | A binding international legal agreement among 50 countries and the European Union designed to conserve wild flora and fauna and their natural habitats, with special attention given to endangered and vulnerable species. | Adriatic, European, and Mediterranean populations of Beluga Sturgeon are listed as strictly protected while Sterlet, Stellate Sturgeon, and remaining Beluga Sturgeon populations are listed as protected. |
| International Union for the Conservation of Nature (IUCN) | Global environmental network of government and civil society organizations that uses expert panels to inventory the status of biological species. Using a set of precise criteria, these experts evaluate the extinction risk of thousands of species and subspecies. Species at risk of extinction are placed on the IUCN Red List. | The Sturgeon Specialist Group has over 50 experts contributing to conservation of sturgeon and paddlefish. As of the 2022 status assessment, all 26 species are imperiled to some degree, with 17 sturgeons identified as critically endangered, a listing that represents organisms at extremely high risk of extinction in the wild. |
| Species at Risk Act of Canada | Canadian legislation that provides legal protection for wildlife species and provides measures to assist in the recovery of threatened and endangered species. | Classification is often population-specific, but at least some populations of Atlantic Sturgeon, White Sturgeon, Green Sturgeon, Lake Sturgeon, and Shortnose Sturgeon are listed under Schedule 1 indicating populations that |

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|---|---|---|---|
| | | are endangered, threatened, or of special concern. Endangered populations are afforded federal protections of critical habitats and prohibitions on individual harm. | |
| U.S. Lacey Act | Administered by NMFS and USFWS, the Lacey Act makes it unlawful to any person to import, export, transport, sell, receive, acquire, or purchase fish, wildlife, or plants that were taken, possessed, transported, or sold in violation of any law or regulation of any state. | Illegal trade of sturgeon is punishable by felony fines with no innocent owner exceptions. | Violations of the Lacey Act can be reported at fws_tips@fws.gov or at 1-844-397-8477 |

[1] https://bit.ly/3U6XibC

[2] https://bit.ly/3DIjq6O

[3] https://bit.ly/3fjcQKj

[4] https://bit.ly/3SLslIR

[5] https://bit.ly/3NdZV98

[6] https://bit.ly/3ff1qr3

[7] https://bit.ly/3gQlZe3

Figure 1. The expanding scale and scope of sturgeon captive culture (center map; data from Bronzi et al. 2019; FAO 2020) presents an emerging threat to wild sturgeon populations around the world. Changes to existing regulatory frameworks would increase opportunities for captive culture to support wild sturgeon conservation.

# Decades of Global Sturgeon Conservation Efforts are Threatened by an Expanding Captive Culture Industry

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**Abstract**

After centuries of overexploitation and habitat loss, many of the world's sturgeon populations are at the brink of extinction. Although significant resources are invested into the conservation and restoration of imperiled sturgeons, the burgeoning commercial culture industry poses an imminent threat to the persistence of many populations. In the last decade the number and distribution of captive sturgeon facilities has grown exponentially and now encompasses diverse interest groups ranging from hobby aquarists to industrial-scale commercial facilities. Expansion of sturgeon captive culture has largely fallen outside the purview of existing regulatory frameworks, raising concerns that continued growth of this industry has real potential to jeopardize conservation of global sturgeon populations. Here, we highlight some of the most significant threats commercial culture poses to wild populations, with particular emphasis on how releases can accelerate wild population declines through mechanisms such as hybridization, introgression, competition, and disease transmission. We also note that in some circumstances commercial captive culture has continued to motivate harvest of wild populations, potentially accelerating species' declines. Given the prevalence and trajectory of sturgeon captive culture programs, we comment on modifications to regulatory frameworks that could improve the ability of captive culture to support wild sturgeon conservation.

**Introduction**

Sturgeon (family Acipenseridae) are one of the most ancient and unique clades of extant fishes. With little morphological change in their ca. 200-million-year history, the 25 extant species of sturgeons are frequently referred to as living fossils for their primitive scutes and cartilaginous skeletons (Gardiner 1984). However, the natural history of these fishes has been anything but static. Subsistence fisheries by indigenous peoples and early settlers had limited effect on populations and commercial interest for sturgeon products remained low throughout much of the 1800s. By the turn of the 20$^{th}$ century, increased efficiency in capture, storage, and transportation methods inspired the growth of a global fishing industry for sturgeon and demand for caviar and flesh intensified. This enterprise was short-lived, as serial depletion of regional and global stocks subsequently lead to collapse of many of the world's sturgeon populations in less than 100 years (Saffron 2002). Today, sturgeon are considered one of the world's most imperiled groups of fishes (IUCN 2022) and the majority of species are afforded regulatory protection within their native waterways (see Table 1). Despite these conservation measures, most populations have been slow to recover from legacy effects of overharvest and continue to be threatened by ongoing habitat loss and anthropogenic activity and most sturgeons have continued to decline despite conservation actions (IUCN 2022).

In the mid-1990s, amidst rising consumer demand for caviar and dwindling abundance of wild populations, the sturgeon culture industry saw a rise in the number and success of production facilities (Saffron 2002; Bronzi et al. 2019). Originally promoted as a means to alleviate harvest pressure on wild populations, commercial aquaculture for sturgeon is now a global enterprise that serves numerous consumer interests including caviar and meat production, pet trades, leather smithing, and isinglass manufacturing. Despite fluctuations in market value

and biomass production in the last decade, today there are over 2,300 commercial sturgeon facilities spread across at least 60 countries (Figure 1), with at least 13 of 25 known sturgeon species and numerous hybrids in captive production (Bronzi et al. 2019).

Sturgeon are also becoming more prevalent in conservation aquaculture programs. These programs, which use careful genetic and demographic planning to aid in species recovery, have been instrumental in the restoration of several sturgeon populations. However, conservation aquaculture is not the focus of this manuscript, as threats to wild populations are most likely to occur when individuals are released or escape from captive populations that have not been bred and reared for the explicit purposes of population restoration. As such, this manuscript focuses on the increasing prevalence in releases from captive populations that occur in commercial, private, and/or other research facilities.

We contend that growth of sturgeon captive culture has real potential to countermand decades of global conservation efforts and accelerate declines of many critically imperiled sturgeons. Moreover, given the projected expansion in the size, distribution, and scope of commercial aquaculture facilities, existing regulatory frameworks (Table 1) may be insufficient to protect future wild sturgeon populations. Here we highlight some of the most significant threats that the captive culture industry presents to native sturgeon populations. We then discuss modifications to existing regulatory frameworks that could help support the collective goals of conservation and sustainable consumerism of sturgeons.

**Captive Sturgeons in the Wild**

As the number of sturgeon culture facilities has increased, so too has the number of reported incidents of sturgeon outside of their native waterways. The release of captive fishes, be it through intentional stocking or accidental release, has left one of the biggest footprints on global fisheries conservation (Lockwood et al. 2019). Yet, there are still few answers to the catastrophic declines in native fish communities that commonly follow the establishment of nonnative ichthyofauna. Physical, chemical, and genetic tools are available to control the spread of aquatic invasive species and populations, but these require significant resource investment and can result in further harm to native species. Even then, efforts largely focus on management of the nonnative population, as complete eradication is often impossible, particularly in large river systems and marine environments (Gozlan et al. 2010). Therefore, the best tool for limiting the spread of nonnative species is to minimize introduction pathways.

Below we highlight the major introductory pathways for captive sturgeons into wild populations. Importantly, while unsanctioned release of captive sturgeon from research, commercial, and private facilities has been documented, limited monitoring and difficulty sampling sturgeon populations likely allows many incidences to go undetected. Moreover, many pathways that lead to captive sturgeon introductions may receive little attention as they involve release of relatively few individuals. However, the invasion histories of other species provide cautionary tales that colonization and spread of nonnative species can occur from small founding populations (Rachels 2021). In addition, the shared habitat requirements among sturgeons and the low abundance of many native populations suggest invasion success of released captive sturgeon could be high.

*Commercial culture*

The potential for commercial culture operations to negatively affect wild sturgeon populations is already being realized, as we have witnessed repeated incidences of accidental release of captive sturgeons from commercial facilities (Ludwig et al. 2009). In one example, a catastrophic flood in 2016 resulted in the escape of over 9,800,000 kg of captive fish, including five nonnative sturgeon species, several sturgeon hybrids, and a nonnative paddlefish, into the Yangtze River, China (Ju et al. 2020). Escapees vastly outnumbered native species, including the critically endangered Chinese Sturgeon (*Acipenser sinensis*), making hybridization and competition significant concerns (Gao et al. 2017). A similar event was documented in the United States in 2017, when flooding in the state of Idaho resulted in the release of approximately 3,000 captive, adult White Sturgeon (*A. transmontanus*) into a nearby river, of which most were not recaptured (Idaho Power Company 2018).

In the Rioni River and Black Sea in Georgia, nonnative Siberian Sturgeon (*A. baerii*) have been recently documented multiple times. Although the origin of these individuals is unknown, it is believed they were released or escaped from commercial aquaculture facilities. How Siberian Sturgeon will influence the conservation of four native sturgeons (Russian [(*A. gueldenstaedtii*], Stellate [*A. stellatus*], Beluga [*Huso huso*], and Ship [*A. nudiventris*]) is still under investigation. However, because native Rioni River sturgeons already exist in critically low abundance, presence of relatively few Siberian Sturgeon could result in significant declines and/or extirpation of native sturgeon (Fleur Scheele, Fauna & Flora International, written communication, 16 Feb 2022; see below for potential mechanisms of interaction between Rioni River sturgeons).

Effects of commercial culture are not always restricted to release of captive fishes. For example, investigations by Fauna & Flora International show that Georgian Black Sea fishers sometimes sell live Beluga and Stellate sturgeon to local ponds, where owners mix wild and captive individuals with the goal of releasing offspring into the wild (Fleur Scheele, Fauna & Flora International, written communication, 16 Feb 2022). Effects of these releases are unlikely to be realized for several decades; however, even moderate amounts of interbreeding and competition may jeopardize the survival of several endemic, critically endangered sturgeons in the region.

*Research and government laboratories*

Damage to captive infrastructure typifies the catastrophic threats that high biomass commercial facilities pose to native fish communities. However, these events are generally isolated, well-documented, and often followed by increased management and surveillance. Conversely, poor biosecurity and uncontrolled trade likely present a more chronic and cryptic threat to wild populations. By nature, public documentation of unpermitted introductions is sparse. However, credible anecdotes implicate individuals, including career biologists, with the unsanctioned release of captive sturgeon, including the introduction of species outside of their native range. In the United States, a federally threatened Green Sturgeon (*A. medirostris*) native to the Pacific Coast of North America, was collected on 23 Apr 2010 in the Long Island Sound, an estuary of the Atlantic Ocean (Figure 1). Due to the conservation status of Green Sturgeon, the species is not permitted in private or commercial aquaculture. As such, it has been hypothesized that the nonnative Green Sturgeon was introduced from a nearby research facility; however, it is unclear when and how many individuals were released and how many may still be alive.

Although introductions are most frequently associated with nonnative species, the life history of sturgeon raises unique concerns about the invasion potential of captive individuals that are released within their native range but are genetically dissimilar to the local population. The philopatric tendency of sturgeon can create strong spatial genetic structuring among nearby populations, potentially leading to local adaptation to the unique physiochemical environments found in each river system (Schreier et al. 2012). As a result, the conservation value of a nonnative population of an otherwise native species is unknown. This question is currently being debated after a nascent population of Atlantic Sturgeon (*A. oxyrinchus oxyrinchus*; a taxon listed under the United States Endangered Species Act) was discovered in the Connecticut River— a waterway where native Atlantic Sturgeon were thought to have been extirpated several decades ago (ASSRT 2007). Genetic analyses suggested the contemporary Connecticut River population was likely founded by individuals that originated from a population in the southeast United States (Savoy et al. 2017). Atlantic sturgeon are largely philopatric and show strong patterns of genetic isolation-by-distance leading to genetically unique populations among most rivers (White et al. 2021). Therefore, while we cannot rule out the possibility that the Atlantic sturgeon captured in the Connecticut River strayed from the South Atlantic, it is more plausible that fish were released from a nearby research facility. At present, it is unclear if the population will adapt to the physiological requirements of a more northern climate. However, if the disjunct population persists, it may complicate future conservation efforts by conflating results of individual assignment and mixed-stock analyses, both of which are extensively used to understand regional and range-wide threats to Atlantic Sturgeon recovery (e.g., Kazyak et al. 2021).

*Private pet trade*

A rapidly emerging, and generally unregulated, threat to sturgeon conservation is the increased circulation of numerous sturgeons, including species of conservation concern, in hobby pet trades. The scale and scope of the pet trade for sturgeons is largely undocumented, and so their effect on native populations is unknown. However, *ad hoc* monitoring of popular consumer-to-consumer websites and online pet stores by the authors found numerous instances of both native and nonnative sturgeons being openly traded in the United States and abroad. Exotic pet trade has been unequivocally implicated with widespread biodiversity loss (Lockwood et al. 2019; Morton et al. 2021), and surveys of private aquarists have shown that up to 10% of fish owners admit to deliberately releasing aquarium fish into the wild (Chang et al. 2009; Strecker et al. 2011). Release of hobby sturgeon is a likely outcome, as sturgeon rapidly attain sizes that are too large for aquaria and small ponds and pet owners are often averse to euthanizing otherwise healthy animals (Holmberg et al. 2015). As such, the buying, selling, and transportation of hobby sturgeon is an expected pathway for nonnative invasions, as has already been documented by a Dutch public database (https://steuren.ark.eu/). This website monitors observations of native European Sturgeon (*A. sturio*) in the Netherlands but has also documented nearly 50 occurrences of nonnative Siberian, Russian, and Sterlet (*A. ruthenus*) sturgeon since 2010, with most occurring since 2020. The three nonnative species are likely derived from breeding facilities in eastern Europe and Asia, were sold in Europe as pond fish, and subsequently released into the wild. This finding is further corroborated by Brevé et al. (2022), who noted the occurrence of 11 nonnative sturgeon species in the Rhine-Meuse river delta, most of which could be attributed to unintentional and aided escape from garden and angling ponds.

**Threats of Sturgeon Captive Culture to Wild Populations**

The full extent how captive sturgeon may impact wild populations is still unknown, as we have only recently started to document the invasion of captive sturgeons into wild populations (e.g., Ludwig et al. 2009). The outcome of an introduction likely depends on the number of individuals released, density of competitors, and habitat suitability. Therefore, we likely have not yet observed the full suite of potential negative interactions that may occur between captive and wild populations. Moreover, given the late maturation and long lifespan of sturgeon, it may take several decades before the consequences of present-day captive releases are fully realized. This underscores the importance of proactive regulation of captive sturgeon populations, as it may be too late to mitigate negative effects once declines in wild populations are detected.

*Hybridization*

A significant concern with release of captive individuals is the potential for interbreeding between domestic and wild lineages. The most significant threat is likely that of hybridization—the mating of individuals from different species or, rarely, different genera or families—which can cause rapid loss of native population fitness. Hybrid offspring are often sterile, and so the effect of hybridization may be restricted to loss of reproductive effort. For large populations, temporary reduction in fitness is unlikely to have significant, long-term genetic or demographic effects. However, in populations where few spawning individuals remain, as is the case in many imperiled sturgeon populations, hybridization has real potential to result in demographic swamping leading to collapse of local populations and even whole species extinction (Wolf et al. 2001).

When hybrid offspring are fertile, concerns arise over the potential for increased fitness of hybridized individuals relative to either parental species (i.e., hybrid vigor; Shivaramu et al. 2020). Hybrid vigor can lead to rapid displacement and loss of genomic signatures of the native species, ultimately resulting in declines in native populations through genetic swamping. One of the best documented cautionary tales of hybrid vigor comes from the prolific Cutbow Trout — a fertile hybrid from the mating of Cutthroat Trout (*Oncorhynchus clarkii*) and Rainbow Trout (*O. mykiss*). Cutbow Trout have physically displaced many populations of native Cutthroat Trout, including the Westslope Cutthroat Trout (*O. c. lewisi*) which has experienced rapid declines in abundance and distribution due to habitat loss and erosion of genetic integrity from hybridization (Muhlfeld et al. 2009). Substantial resources are invested into ongoing efforts to identify and eradicate hybrids in an attempt to restore pure Yellowstone Cutthroat Trout populations. This case study underscores the potential long-term biologic and economic costs that can occur following release of nonnative species and the potential for hybridization to result in permanent genetic effects to native populations.

Hybridization has been well-documented in wild and captive sturgeon populations, with over 20 different hybrid crosses reported in the literature (Table S1), including interfamilial hybridization between Russian Sturgeon and American Paddlefish (*Polyodon spathula* [Káldy et al. 2020]). Moreover, hybrids can be produced between species with differing ploidy levels, as exemplified by nonnative Siberian Sturgeon (~240 chromosomes) and native Sterlet (~120 chromosomes) hybrids in the Danube River (Ludwig et al., 2008). Although offspring of this cross were found to be sterile, hybrids from native Russian (~ 240 chromosomes) and Stellate (~120 chromosomes) sturgeon in the Rioni River (Ludwig et al. 2009; Beridze et al. 2022; Figure 1) are viable. This success of hybrid sturgeons in wild environments is not well understood; however, hybridization between native Russian and nonnative Siberian Sturgeons in the Caspian Sea (Jenneckens et al. 2000), and subsequent laboratory studies documenting hybrid vigor (Shivarmu et al. 2019) suggests genetic swamping is a possible outcome of hybridization in sturgeons.

Sturgeon hybridization may occur readily in natural environments because many species have similar life history characteristics and spawning habitat requirements. In addition, sturgeon are broadcast spawners, which is a mode of reproduction that is associated with high hybridization rates in other taxa. Together, the documented ease and high probability of hybridization in sturgeon in captive and wild environments suggests that continued unregulated release of nonnative sturgeons has real potential to lead to population declines through demographic and/or genetic swamping. In addition, it is often difficult to discern hybrid individuals from pure-bred species using morphologic traits or genetic techniques, particularly after multiple generations of admixture and backcrossing. As the number of hybrid sturgeon in captive and wild populations increases, it may become increasingly challenging to identify purebred individuals in the field and trace the origin of commercial sturgeon products, both of which will complicate conservation efforts for native populations.

*Anthropogenically mediated gene flow*

In addition to hybridization sturgeon may also be prone to introgression, which we define as breeding between individuals of the same species but belonging to different populations. Introgression can improve population viability by increasing genetic diversity and long-term evolutionary potential. When executed successfully, as in many conservation aquaculture programs, introgression between wild and captive populations can be an effective conservation strategy for genetic rescue.

However, unintended introgression between wild and captive populations is likely to reduce fitness and survival of native populations. Wild-caught broodstock and juveniles are infrequently used in commercial production, and so generations of artificial selection can render captive individuals maladapted for wild environments. Under this scenario, introgression can lead to outbreeding depression and subsequent reduction in the fitness and survival of future generations — a phenomenon that has been well documented in salmonids (Araki et al. 2007). Moreover, introgression across large spatial scales can result in genetic homogenization and diminished long-term adaptive capacity. Together, loss of contemporary fitness and evolutionary potential may jeopardize the ability of native populations to persist and could severely undermine current efforts aimed at demographic recovery. Because many commercial facilities rear sturgeon outside of their native range, the threat of introgression is likely lower relative to hybridization. However, aforementioned examples of released captive Atlantic and White sturgeon suggest the risk of introgression in contemporary populations is not negligible, and could increase with expansion in the size, scope, and location of commercial facilities.

*Competition and depredation*

Negative effects of captive release can occur in the absence of reproduction, including the potential for resource competition and juvenile depredation. Given significant knowledge gaps about many aspects of sturgeon life history and ecology, the strength and outcome of competitive interactions may be difficult to predict. However, significant resource overlap among species and the global decline in sturgeon habitat suggests competition for already limited resources is likely to increase in future decades.

Although not causally linked to competition, malnourished Ship Sturgeon have been discovered during recent surveys in the Rioni River (Fleur Scheele, Fauna & Flora International, written communication, 16 Feb 2022); a potential indicator of negative interactions between native and introduced sturgeons (Figure 1). This is a discouraging finding, as Ship Sturgeon was believed to be extirpated from the Black Sea basin (Beridze et al. 2021) and now the long-term viability of the relict breeding population may be jeopardized by low fitness and survival.

Nonnative species, including sturgeon but also other non-sturgeon species, can pose significant risk to recruitment through depredation. Although sturgeon develop bony scutes to deter predators, younger life stages have few natural defenses and are vulnerable to predation (Flowers et al. 2011). The risk of depredation may be particularly high when nonnative fishes are released near freshwater spawning and nursing habitats.

*Pathogens and parasites*

Indirect effects of captive culture can be observed through the introduction of disease and parasites. High densities of fish in aquaculture facilities and mixing of multiple taxa in hobby aquaria increases the prevalence of viral, bacterial, and parasitic infections in captively reared individuals. Although many pathogens commonly found in captive facilities also occur in wild environments, human transport of captive fish across river basins introduces novel sources of disease to which native populations may have little natural immunity. Once released, captive individuals can then spread pathogens through entire ecosystems as they move through different habitats to complete their life cycle. Therefore, the pathogenic consequences of a single captive release may manifest across vast spatial scales, particularly for anadromous species like sturgeon.

Introduction of aquatic diseases during intentional stocking events has been implicated in population declines, loss of entire spawning year classes, and even complete extirpation of species in some areas (Zholdasova 1997). Presently, the largest disease risks in captive sturgeon populations appear to be bacterial (e.g., *Streptococcus iniae*, which also poses a disease risk to humans [Mugetti et al. 2022]) and viral infections including herpesviruses, White Sturgeon iridovirus, and potentially species of *Ranavirus* normally associated with amphibian declines (Waltzek et al. 2014). Although the threat of *Ranavirus* remains unclear, herpesviruses and White Sturgeon iridovirus are highly transmittable and have been correlated to necrotic infection and large mortality events. Viral infections of wild and captive sturgeon populations have been detected in multiple species and countries (e.g., Kurobe et al. 2010; Hofsoe-Oppermann et al. 2020), suggesting more widespread outbreaks could be forthcoming as the captive industry continues to expand.

*Continued harvest of wild populations*

With most sturgeon species under strict harvest moratoria, captive facilities are now the most viable, and often only legal, source for caviar and other sturgeon products. However, large body size and late age of maturation can make sturgeon difficult to raise in captivity. Commercial fish culturists looking to reduce the space and resource requirements needed to support a self-sustaining captive sturgeon population or needing to compensate for incidental loss may continue to harvest individuals from wild populations. In Eurasia, wild sturgeon, particularly gravid females, are sometimes translocated to commercial facilities and temporarily held before being used as broodstock and/or harvested. This practice, which is illegal in many regions, perpetuates the stress on wild populations, and specifically monetizes removal of individuals during critical life stages. However, limited oversight and lack of critical inspection of many food labels still provide abundant opportunity for individuals to directly harvest or translocate individuals from wild populations (Dolan and Luque 2019; Figure 1).

**Supporting Sturgeon Conservation in the Era of Captive Culture**

Demand for caviar and other sturgeon products remains high, and continued loss and restriction of wild fisheries are likely to compel further development of the captive culture industry. Expansion of research laboratories, commercial facilities, and private pet trades presents serious challenges for conservation, as the scope and location of many captive facilities will likely fall outside the purview of current regulatory frameworks (see Table 1 for a list of policies that pertain to global sturgeon conservation). Specifically, the majority of current regulations aim to protect critical habitats, minimize individual harm, and regulate commercial harvest and transport of sturgeon and sturgeon products. While these challenges will remain into the future, emerging threats are likely to develop as the taxa's user group continues to expand.

How this new era of sturgeon captive culture will affect wild populations remains to be seen; however, more stringent, effective, and targeted regulation would likely provide more opportunities for captive culture to be apposite to global conservation. Below we outline three major sectors of sturgeon captive culture and discuss possible regulatory changes that could improve the outlook of sturgeon conservation:

(1) *Commercial culture* — Commercial facilities account for the majority of captive sturgeon populations (Bronzi et al. 2019) and are likely to be the source of most nonnative sturgeon introductions. While many regulations already pertain to captive culturists (Table 1), there are still opportunities for improved oversight of this sector. Increased governance on allowable infrastructure, including restricted use of flow-through systems and banning facilities in flood-prone areas, would likely reduce the probability of high biomass escapes. Additional oversight on the location of large facilities may be particularly important given that catastrophic flood events are likely to increase under future climate change scenarios. Another potential mechanism for reducing introduction pathways could be to severely restrict or prohibit the commercial sale of live sturgeon. However, across all commercial markets, more stringent investigation and castigation for mislabeled products is likely to reduce illegal harvest and minimize impacts on wild populations.

(2) *Research and government laboratories* — There is an expectation that fisheries professionals will uphold the highest standards of conservation. However, multiple observations presented in this article are consistent with unsanctioned releases of captive sturgeon from scientific facilities. In addition, fisheries research facilities are often highly trafficked, outdoor environments, which increases the biosecurity risk associated with

these captive populations. Despite recent expansion in the number of sturgeon research programs, there are surprisingly few regulations that pertain to the proper handling of captive fish in these environments. For example, while academic research facilities in the United States operate under the oversight of animal care and use committees and may seek accreditation from the Association for the Assessment and Accreditation of Laboratory Animal Care International (AAALAC), accreditation is not mandatory for all federal research facilities. As such, within the United States there are no universal protocols pertaining to proper transport, handling, and disposal of captive individuals in laboratory environments. Likewise, there is no mechanism to assure that captive sturgeons are eliminated following laboratory testing, which is a requirement under federal permitting in the United States. Overall, the absence of consistent regulatory frameworks for academic and federal research facilities highlights a significant biosecurity gap, and an opportunity to enhance protocols pertaining to proper infrastructure, facility inspection, and personnel training. For example, in Canada, captive facilities must satisfy requirements pertaining to disease transfer, husbandry methods, culture equipment, and fish holding densities, with more stringent requirements for listed species. Similar protocols in other countries may be particularly critical given that many research facilities are located near large waterbodies, and vulnerable infrastructure (i.e., flow-through systems) and insufficient maintenance has significant potential to be a source of unintentional captive escape.

(3) *Pet trade* — Although this sector has not yet been documented to have an impact on wild populations, rising popularity of sturgeon in the hobby pet trade foreshadows future negative consequences of private captive culture. This sector is very challenging to

directly regulate due to the diffuse and poorly documented nature of private culture. Due to the challenges with regulating individual owners, and the near-certain probability that sturgeon growth will surpass all indoor aquaria, the strongest regulatory mechanism may be to prohibit all sale. Even with restrictions on sales, it may still be beneficial to increase surveillance for illegal trade of sturgeons. Automated approaches for monitoring the internet for trade of invasive species (e.g., GLDIATR; https://www.glc.org/work/gldiatr) have been developed and might provide a useful model for tracking the trade of sturgeons.

The captive culture industry represents an emerging threat to the recovery and conservation of critically imperiled sturgeon populations. Negative effects of captive culture programs, including intentional and unintentional release and ongoing harvest of wild populations, have already manifested in some populations. Under the current trajectory of the captive culture industry, nonnative invasion, introgression, and hybridization have real potential to reverse decades of conservation and drive one of the most ancient and globally revered groups of fishes further towards extinction. Increased attention to these emerging issues may help improve the outlook for sturgeon conservation programs.

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Table 1. Description of policies and resolutions that protect worldwide sturgeon populations against habitat loss, overharvest, and illegal trade.

| Resolution | Description | Application to Sturgeon | Resources |
|---|---|---|---|
| Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES) | Multinational agreement through which countries work together to ensure that international trade is not detrimental to the survival of the species in the wild. Member nations to CITES regulate and monitor international trade (import and export) through permits and certifications to ensure sustainable use. The CITES Secretariat is not a law enforcement authority and does not conduct investigations; instead, each country is to investigate within-county allegations if potential criminal activity lies with the relevant national law enforcement authorities of that country. | International trade led to a CITES listing of all species of Acipenseridae; since 1998 all sturgeon trade is regulated and all parts or derivates (e.g., caviar, meat, skin, etc.) require a CITES permit or certificate. Only Shortnose Sturgeon is listed under CITES Appendix I (threatened by extinction with trade permitted only in exceptional circumstances). All other sturgeons are listed in Appendix II (trade could threaten species persistence if not controlled).[1] | CITES provides country-specific contacts for reporting violations and information regarding illegal trade[2]; in the U.S. the U.S. Fish and Wildlife Service (USFWS) is the official CITES authority and provides opportunity to report violations.[3] |

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|---|---|---|---|
| U.S. Endangered Species Act (ESA) | Under the ESA, the National Marine Fisheries Service (NMFS) and the USFWS are required to conserve the ecosystems upon which endangered and threatened species depend on, provide a program for listed species conservation, and take appropriate steps toward recovery. Section 9 of the ESA outlines prohibitions including illegal "take" of a listed species which includes harm, capture and harassment and Section 10 describes penalties for illegal take. Under Section 7, federal actions are required to undergo a consultation to assess and reduce potential interactions with listed species and their designated critical habitat helps to conserve listed species. Limited federal dollars are also available for research. The ESA primarily protects foreign species by restricting trade and may prohibit certain activities, including import, export, take, commercial activity, interstate commerce, and foreign commerce. By regulating these activities, the U.S. ensures that people under its jurisdiction do not contribute to the further decline of a listed species. | Eight of the nine sturgeon species in the U.S. are currently listed under the ESA as either threatened or endangered and a review on the status of the Lake Sturgeon is scheduled for 2024. There are also eight sturgeon species that are not native to the United States listed under the ESA[4]. As described, the introduction of a nonnative species could harm listed sturgeon. | NOAA is responsible mainly for marine wildlife[5] and USFWS for terrestrial and freshwater organisms[6]. ESA violations should be reported to either NOAA by calling 1-800-853-1964 or USFWS via their online reporting[7]; photos and videos are encouraged |
| United Nations' Convention on the Conservation of | An environmental treaty of the United Nations designed to conserve migratory species, with special emphasis on protection of habitats and migration routes. CMS agreements range from legally binding treaties to less formal agreements. | European Sturgeon is listed under Appendix I (threatened with extinction) and 18 species are listed under Appendix II (species that would benefit from international cooperation). | |

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|---|---|---|
| Migratory Species of Wild Animals (CMS) | | |
| Bern Convention on the Conservation of European Wildlife and Natural Habitats | A binding international legal agreement among 50 countries and the European Union designed to conserve wild flora and fauna and their natural habitats, with special attention given to endangered and vulnerable species. | Adriatic, European, and Mediterranean populations of Beluga sturgeon are listed as strictly protected while Sterlet, Stellate, and remaining Beluga sturgeon populations are listed as protected. |
| International Union for the conservation of Nature | Global environmental network of government and civil society organizations that uses expert panels to inventory the status of biological species. Using a set of precise criteria, these experts evaluate the extinction risk of thousands of species and subspecies. Species at risk of extinction are placed on the IUCN Red List. | The Sturgeon Specialist Group has over 50 experts contributing to conservation of sturgeon and paddlefish. As of the 2022 status assessment, all 26 species are imperiled to some degree, with 17 sturgeons identified as critically endangered, a listing that represents organisms at extremely high risk of extinction in the wild. |
| Species at Risk Act (SARA) of Canada | Canadian legislation that provides legal protection for wildlife species and provides measures to assist in the recovery of threatened and endangered species. | Classification is often population-specific, but at least some populations of Atlantic, White, Green, Lake, and Shortnose sturgeon are listed under Schedule 1 indicating populations that are endangered, threatened, or of |

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|---|---|---|---|
| | | special concern. Endangered populations are afforded federal protections of critical habitats and prohibitions on individual harm. | |
| U.S. Lacey Act | Administered by NMFS and USFWS, the Lacey Act makes it unlawful to any person to import, export, transport, sell, receive, acquire, or purchase fish, wildlife, or plants that were taken, possessed, transported, or sold in violation of any law or regulation of any state. | Illegal trade of sturgeon is punishable by felony fines with no innocent owner exceptions. | Violations of the Lacey Act can be reported at fws_tips@fws.gov or at 1-844-397-8477 |

[1] https://cites.org/eng/prog/sturgeon.php

[2] https://cites.org/eng/parties/country-profiles/us/national-authorities

[3] https://www.fws.gov/program/international-affairs/contact-us

[4] https://www.ecfr.gov/current/title-50/chapter-I/subchapter-B/part-17/subpart-B/section-17.11

[5] https://www.fisheries.noaa.gov/species-directory/threatened-endangered

[6] https://www.fws.gov/program/endangered-species/species

[7] https://www.fws.gov/story/how-report-wildlife-crime

Figure 1. The expanding scale and scope of sturgeon captive culture (center map; data from Bronzi et al. 2019, FAO 2020) presents an emerging threat to wild sturgeon populations around the world. Changes to existing regulatory frameworks would increase opportunities for captive culture to support wild sturgeon conservation

# CAPTIVE STURGEON

*A RISING THREAT TO GLOBAL CONSERVATION*

Following centuries of overharvest and habitat loss, many sturgeon populations are at the brink of extinction. Reduced wild production and harvest moratoria for many sturgeon species has prompted the growth of a global industry for sturgeon captive culture. Sturgeon aquaculture was originally intended to reduce harvest pressure on wild stocks while meeting growing consumer demands for caviar and other sturgeon products. However, rapid, and often unregulated, growth of sturgeon captive culture operations now threatens global conservation programs.

Captive culture may have a broad array of negative effects on critically imperiled sturgeon populations. As this sector grows and diversifies into new markets, regulatory changes could help limit negative interactions between captive and wild populations.

## NONNATIVE RELEASE

Sturgeons are often intentionally or unintentionally released from captive facilities.

Captive individuals have potential to harm wild populations through a large suite of genetic and non-genetic mechanisms.

In the United States, Green Sturgeon native to the west coast have been detected in the Long Island Sound, which is within the native range of Atlantic and Shortnose sturgeon.

## COMPETITIVE INTERACTIONS

Captive sturgeon released into the wild are likely to compete with wild populations for resources.

Given that global sturgeon habitat is declining, the strength of competitive interactions is likely to increase with time.

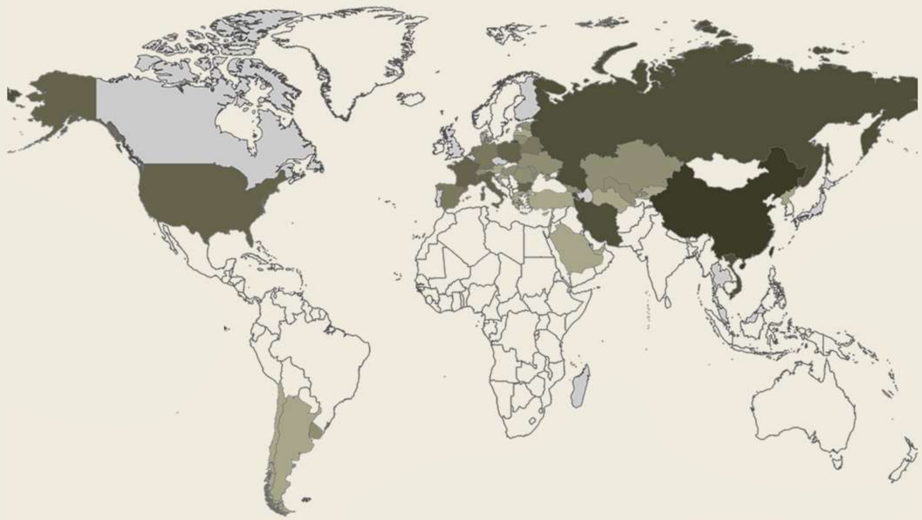
Malnourished Ship Sturgeon have been detected in the Rioni River, Georgia along with nonnative Siberian Sturgeon. Although the strength of potential competitive interaction is unknown, Ship Sturgeon are nearing extinction and any competition could compromise recovery efforts.

## INTERSPECIFIC HYBRIDIZATION

Nonnative sturgeons can breed with native individuals and create hybrid offspring.

Hybridization has the potential to negatively effect wild populations through genetic and demographic swamping.

Hybridization readily occurs between native and nonnative sturgeons in the Rioni River, Georgia, including native Stellate and Russian sturgeon (pictured). Although not all crosses produce fertile offspring, demographic and genetic swamping could challenge conservation of imperiled sturgeons in the region.



## CONTINUED WILD HARVEST

Wild-caught sturgeon products continue to be illegally harvested and sold under the guise of captive origin.

Translocation of living individuals to commercial captive facilities is also a common practice to increase yield or to augment existing broodstock.

An adult sturgeon for sale at a market in Tskaltsminda, Georgia. Evidence suggests that sturgeon from this market originate from both captive and wild sources.

## MEETING FUTURE DEMANDS

As captive culture continues to expand into new sectors, changes to current regulatory frameworks may help ensure the industry can support global sturgeon conservation needs. Regulatory changes may be particularly beneficial for improving infrastructure and reducing the number and modes of nonnative species introductions.

### RESEARCH

There are few regulations that broadly and consistently apply to captive sturgeon populations in government and academic research facilities. As the number of research programs expands, the lack of stringent oversight could represent a future biosecurity threat.

Protocols for proper facility design, inspection, and personnel training, with penalties for individual or facility non-compliance, could decrease the risk of escape from research facilities.

### COMMERCIAL

Most captive sturgeon are contained in large commercial aquaculture facilities and are often located near waterbodies with native sturgeon populations. Restrictions on facility infrastructure and location could reduce the probability and impact of large-scale escape events.

Commercial sale of wild-caught sturgeon products continues to threaten wild populations. Increased surveillance of illegal harvest may help protect wild populations.

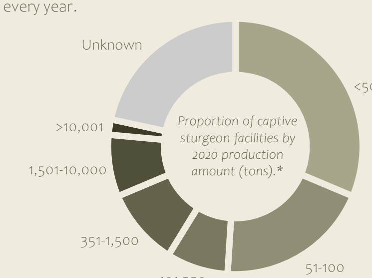
### PET TRADE

Sturgeon have only recently been identified as a target species in hobby pet trades. Given the large size and long lifespan of sturgeons, release of hobby sturgeon into the wild is an imminent threat that will be difficult to regulate given the diffuse nature of private ownership

A prohibition on the sale of life sturgeons and/or more stringent permitting may help minimize the risk of the consumer pet trade on wild populations.

## THE RISE OF CAPTIVE CULTURE

Sturgeon aquaculture experienced a sharp rise in the number and size of facilities in the 1990s. Captive culture programs can now be found in over 50 countries, with new operations being added every year.




* Data for map and chart from Bronzi et al. (2019); FAO (2022)

Perspective

# Decades of Global Sturgeon Conservation Efforts are Threatened by an Expanding Captive Culture Industry

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## Abstract

After centuries of overexploitation and habitat loss, many of the world's sturgeon (Acipenseridae) populations are at the brink of extinction. Although significant resources are invested into the conservation and restoration of imperiled sturgeons, the burgeoning commercial culture industry poses an imminent threat to the persistence of many populations. In the last decade the number and distribution of captive sturgeon facilities has grown exponentially and now encompasses diverse interest groups ranging from hobby aquarists to industrial-scale commercial facilities. Expansion of sturgeon captive culture has largely fallen outside the purview of existing regulatory frameworks, raising concerns that continued growth of this industry has real potential to jeopardize conservation of global sturgeon populations. Here, we highlight some of the most significant threats commercial culture poses to wild populations, with particular emphasis on how releases can accelerate wild population declines through mechanisms such as hybridization, introgression, competition, and disease transmission. We also note that in some circumstances commercial captive culture has continued to motivate harvest of wild populations, potentially accelerating species' declines. Given the prevalence and trajectory of sturgeon captive culture programs, we comment on modifications to regulatory frameworks that could improve the ability of captive culture to support wild sturgeon conservation.

## INTRODUCTION

Sturgeon (Acipenseridae) are one of the most ancient and unique clades of extant fishes. With little morphological change in their circa 200-million-year history, the 25 extant species of sturgeons are frequently referred to as living fossils for their primitive scutes and cartilaginous skeletons (Gardiner 1984). However, the natural history of these fishes has been anything but static. Subsistence fisheries by Indigenous peoples and early settlers had limited effect on populations and commercial interest for sturgeon products remained low throughout much of the 1800s. By the turn of the 20th century, increased efficiency in capture, storage, and transportation methods inspired the growth of a global fishing industry for sturgeon and demand for caviar and flesh intensified. This enterprise was short-lived, as serial depletion of regional and global stocks subsequently lead to collapse of many of the world's sturgeon populations in less than 100 years (Saffron 2002). Today, sturgeon are considered one of the world's most imperiled groups of fishes (IUCN 2022) and the majority of species are afforded regulatory protection within their native waterways (see Table 1). Despite these conservation measures, most populations have been slow to recover from legacy effects of overharvest and continue to be threatened by ongoing habitat loss and anthropogenic activity and most sturgeons have continued to decline despite conservation actions (IUCN 2022).

In the mid-1990s, amidst rising consumer demand for caviar and dwindling abundance of wild populations, the sturgeon culture industry saw a rise in the number and success of production facilities (Saffron 2002; Bronzi et al. 2019). Originally promoted as a means to alleviate harvest pressure on wild populations, commercial aquaculture for sturgeon is now a global enterprise that serves numerous consumer interests including caviar and meat production, pet trades, leather smithing, and isinglass manufacturing. Despite fluctuations in market value

and biomass production in the past decade, today there are over 2,300 commercial sturgeon facilities spread across at least 60 countries (Figure 1), with at least 13 of 25 known sturgeon species and numerous hybrids in captive production (Bronzi et al. 2019).

Sturgeon are also becoming more prevalent in conservation aquaculture programs. These programs, which use careful genetic and demographic planning to aid in species recovery, have been instrumental in the restoration of several sturgeon populations. However, conservation aquaculture is not the focus of this manuscript, as threats to wild populations are most likely to occur when individuals are released or escape from captive populations that have not been bred and reared for the explicit purposes of population restoration. As such, this manuscript focuses on the increasing prevalence in releases from captive populations that occur in commercial, private, and/or other research facilities.

We contend that growth of sturgeon captive culture has real potential to countermand decades of global conservation efforts and accelerate declines of many critically imperiled sturgeons. Moreover, given the projected expansion in the size, distribution, and scope of commercial aquaculture facilities, existing regulatory frameworks (Table 1) may be insufficient to protect future wild sturgeon populations. Here we highlight some of the most significant threats that the captive culture industry presents to native sturgeon populations. We then discuss modifications to existing regulatory frameworks that could help support the collective goals of conservation and sustainable consumerism of sturgeons.

## CAPTIVE STURGEONS IN THE WILD

As the number of sturgeon culture facilities has increased, so too has the number of reported incidents of sturgeon outside of their native waterways. The release of captive fishes, be it through intentional stocking or accidental release, has left one of the biggest footprints on global fisheries conservation (Lockwood et al. 2019). Yet, there are still few answers to the catastrophic declines in native fish communities that commonly follow the establishment of nonnative ichthyofauna. Physical, chemical, and genetic tools are available to control the spread of aquatic invasive species and populations, but these require significant resource investment and can result in further harm to native species. Even then, efforts largely focus on management of the nonnative population, as complete eradication is often impossible, particularly in large river systems and marine environments (Gozlan et al. 2010). Therefore, the best tool for limiting the spread of nonnative species is to minimize introduction pathways.

Below, we highlight the major introductory pathways for captive sturgeons into wild populations. Importantly, while unsanctioned release of captive sturgeon from research, commercial, and private facilities has been documented, limited monitoring and difficulty sampling sturgeon populations likely allows many incidences to go undetected. Moreover, many pathways that lead to captive sturgeon introductions may receive little attention as they involve release of relatively few individuals. However, the invasion histories of other species provide cautionary tales that colonization and spread of nonnative species can occur from small founding populations (Rachels 2021). In addition, the shared habitat requirements among sturgeons and the low abundance of many native populations suggest invasion success of released captive sturgeon could be high.

**Commercial Culture**

The potential for commercial culture operations to negatively affect wild sturgeon populations is already being realized, as we have witnessed repeated incidences of accidental release of captive sturgeons from commercial facilities (Ludwig et al. 2009). In one example, a catastrophic flood in 2016 resulted in the escape of over 9.8 million kg of captive fish, including five nonnative sturgeon species, several sturgeon hybrids, and a nonnative paddlefish, into the Yangtze River, China (Ju et al. 2020). Escapees vastly outnumbered native species, including the critically endangered Chinese Sturgeon *Acipenser sinensis*, making hybridization and competition significant concerns (Gao et al. 2017). A similar event was documented in the United States in 2017, when flooding in the state of Idaho resulted in the release of approximately 3,000 captive adult White Sturgeon *A. transmontanus* into a nearby river, of which most were not recaptured (Idaho Power Company 2018).

In the Rioni River and Black Sea in the country of Georgia, nonnative Siberian Sturgeon *A. baerii* have been recently documented multiple times. Although the origin of these individuals is unknown, it is believed they were released or escaped from commercial aquaculture facilities. How Siberian Sturgeon will influence the conservation of four native sturgeons (Russian Sturgeon *A. gueldenstaedtii*, Stellate Sturgeon *A. stellatus*, Beluga Sturgeon *Huso huso*, and Ship Sturgeon *A. nudiventris*) is still under investigation. However, because native Rioni River sturgeons already exist in critically low abundance, presence of relatively few Siberian Sturgeon could result in significant declines and/or extirpation of native sturgeon (Fleur Scheele, Fauna and Flora International, written communication; see below for potential mechanisms of interaction between Rioni River sturgeons).

Effects of commercial culture are not always restricted to release of captive fishes. For example, investigations by Fauna and Flora International show that Georgian Black Sea fishers sometimes sell live Beluga Sturgeon and Stellate Sturgeon to local ponds, where owners mix wild and captive individuals with the goal of releasing offspring into the wild (Fleur Scheele, Fauna and Flora International, written communication). Effects of these releases are unlikely to be realized for several decades; however, even moderate amounts of interbreeding and competition may jeopardize the survival of several endemic, critically endangered sturgeons in the region.

**Research and Government Laboratories**

Damage to captive infrastructure typifies the catastrophic threats that high biomass commercial facilities pose to native fish communities. However, these events are generally isolated, well-documented, and often followed by increased management and surveillance. Conversely, poor biosecurity and uncontrolled trade likely present a more chronic and cryptic threat to wild populations. By nature, public documentation of unpermitted introductions is sparse. However, credible anecdotes implicate individuals, including career biologists, with the unsanctioned release of captive sturgeon, including the introduction of species outside of their native range. In the United States, a federally threatened Green Sturgeon *A. medirostris* native to the Pacific Coast of North America, was collected on April 23, 2010 in the Long Island Sound, an estuary of the Atlantic Ocean (Figure 1). Due to the conservation status of Green Sturgeon, the species is not permitted in private or commercial aquaculture. As such, it has been hypothesized that the nonnative Green Sturgeon was introduced from a nearby research facility; however, it is unclear when and how many individuals were released and how many may still be alive.

Although introductions are most frequently associated with nonnative species, the life history of sturgeon raises unique concerns about the invasion potential of captive individuals that are released within their native range but are genetically dissimilar to the local population. The philopatric tendency of sturgeon can create strong spatial genetic structuring among nearby populations, potentially leading to local adaptation to the unique physiochemical environments found in each river system (Schreier et al. 2012). As a result, the conservation value of a nonnative population of an otherwise native species is unknown. This question is currently being debated after a nascent population of Atlantic Sturgeon *A. oxyrinchus oxyrinchus* (a taxon listed under the United States Endangered Species Act) was discovered in the Connecticut River— a waterway where native Atlantic Sturgeon were thought to have been extirpated several decades ago (ASSRT 2007). Genetic analyses suggested the contemporary Connecticut River population was likely founded by individuals that originated from a population in the southeastern United States (Savoy et al. 2017). Atlantic Sturgeon are largely philopatric and show strong patterns of genetic isolation by distance, leading to genetically unique populations among most rivers (White et al. 2021). Therefore, while we cannot rule out the possibility that the Atlantic Sturgeon captured in the Connecticut River strayed from the southern Atlantic, it is more plausible that fish were released from a nearby research facility. At present, it is unclear if the population will adapt to the physiological requirements of a more northern climate. However, if the disjunct population persists, it may complicate future conservation efforts by conflating results of individual assignment and mixed-stock analyses, both of which are extensively used to understand regional and range-wide threats to Atlantic Sturgeon recovery (e.g., Kazyak et al. 2021).

**Private Pet Trade**

A rapidly emerging, and generally unregulated, threat to sturgeon conservation is the increased circulation of numerous sturgeons, including species of conservation concern, in hobby pet trades. The scale and scope of the pet trade for sturgeons is largely undocumented, and so their effect on native populations is unknown. However, ad hoc monitoring of popular consumer-to-consumer websites and online pet stores by the authors found numerous instances of both native and nonnative sturgeons being openly traded in the United States and abroad. Exotic pet trade has been unequivocally implicated with widespread biodiversity loss (Lockwood et al. 2019; Morton et al. 2021), and surveys of private aquarists have shown that up to 10% of fish owners admit to deliberately releasing aquarium fish into the wild (Chang et al. 2009; Strecker et al. 2011). Release of hobby sturgeon is a likely outcome, as sturgeon rapidly attain sizes that are too large for aquaria and small ponds and pet owners are often averse to euthanizing otherwise healthy animals (Holmberg et al. 2015). As such, the buying, selling, and transportation of hobby sturgeon is an expected pathway for nonnative invasions, as has already been documented by a Dutch public database (https://steuren.ark.eu/). This website monitors observations of native European Sturgeon *A. sturio* in the Netherlands, but has also documented nearly 50 occurrences of nonnative Siberian Sturgeon, Russian Sturgeon, and Sterlet *A. ruthenus* since 2010, with most occurring since 2020. The three nonnative species are likely derived from breeding facilities in eastern Europe and Asia, were sold in Europe as pond fish, and subsequently released into the wild. This finding is further corroborated by Brevé et al. (2022), who noted the occurrence of 11 nonnative sturgeon species in the Rhine–Meuse River delta, most of which could be attributed to unintentional and aided escape from garden and angling ponds.

## THREATS OF STURGEON CAPTIVE CULTURE TO WILD POPULATIONS

The full extent how captive sturgeon may impact wild populations is still unknown, as we have only recently started to document the invasion of captive sturgeons into wild populations (e.g., Ludwig et al. 2009). The outcome of an introduction likely depends on the number of individuals released, density of competitors, and habitat suitability. Therefore, we likely have not yet observed the full suite of potential negative interactions that may occur between captive and wild populations. Moreover, given the late maturation and long lifespan of sturgeon, it may take several decades before the consequences of present-day captive releases are fully realized. This underscores the importance of proactive regulation of captive sturgeon populations, as it may be too late to mitigate negative effects once declines in wild populations are detected.

**Hybridization**

A significant concern with release of captive individuals is the potential for interbreeding between domestic and wild lineages. The most significant threat is likely that of hybridization—the mating of individuals from different species or, rarely, different genera or families—which can cause rapid loss of native population fitness. Hybrid offspring are often sterile, and so the effect of hybridization may be restricted to loss of reproductive effort. For large populations, temporary reduction in fitness is unlikely to have significant, long-term genetic or demographic effects. However, in populations where few spawning individuals remain, as is the case in many imperiled sturgeon populations, hybridization has real potential to result in demographic swamping leading to collapse of local populations and even whole species extinction (Wolf et al. 2001).

When hybrid offspring are fertile, concerns arise over the potential for increased fitness of hybridized individuals relative to either parental species (i.e., hybrid vigor; Shivaramu et al. 2020). Hybrid vigor can lead to rapid displacement and loss of genomic signatures of the native species, ultimately resulting in declines in native populations through genetic swamping. One of the best documented cautionary tales of hybrid vigor comes from the prolific cutbow trout—a fertile hybrid from the mating of Cutthroat Trout *Oncorhynchus clarkii* and Rainbow Trout *O. mykiss*. Cutbow trout have physically displaced many populations of native Cutthroat Trout, including the Westslope Cutthroat Trout *O. clarkii lewisi*, which has experienced rapid declines in abundance and distribution due to habitat loss and erosion of genetic integrity from hybridization (Muhlfeld et al. 2009). Substantial resources are invested into ongoing efforts to identify and eradicate hybrids in an attempt to restore pure populations of Yellowstone Cutthroat Trout *O. clarkii bouvieri*. This case study underscores the potential long-term biologic and economic costs that can occur following release of nonnative species and the potential for hybridization to result in permanent genetic effects to native populations.

Hybridization has been well documented in wild and captive sturgeon populations, with over 20 different hybrid crosses reported in the literature (Table S1), including interfamilial hybridization between Russian Sturgeon and American Paddlefish *Polyodon spathula* (Káldy et al. 2020). Moreover, hybrids can be produced between species with differing ploidy levels, as exemplified by nonnative Siberian Sturgeon (~240 chromosomes) and native Sterlet (~120 chromosomes) hybrids in the Danube River (Ludwig et al. 2008). Although offspring of this cross were found to be sterile, hybrids from native Russian Sturgeon (~ 240 chromosomes) and Stellate (~120 chromosomes) in the Rioni River (Ludwig et al. 2009; Beridze et al. 2022; Figure 1) are viable. This success of hybrid sturgeons in wild environments is not well understood; however, hybridization between native Russian Sturgeon and nonnative Siberian Sturgeon in the Caspian Sea (Jenneckens et al. 2000), and subsequent laboratory studies documenting hybrid vigor (Shivarmu et al. 2019) suggests genetic swamping is a possible outcome of hybridization in sturgeons.

Sturgeon hybridization may occur readily in natural environments because many species have similar life history characteristics and spawning habitat requirements. In addition, sturgeon are broadcast spawners, which is a mode of reproduction that is associated with high hybridization rates in other taxa. Together, the documented ease and high probability of hybridization in sturgeon in captive and wild environments suggests that continued unregulated release of nonnative sturgeons has real potential to lead to population declines through demographic and/or genetic swamping. In addition, it is often difficult to discern hybrid individuals from purebred species using morphologic traits or genetic techniques, particularly after multiple generations of admixture and backcrossing. As the number of hybrid sturgeon in captive and wild populations increases, it may become increasingly challenging to identify purebred individuals in the field and trace the origin of commercial sturgeon products, both of which will complicate conservation efforts for native populations.

**Anthropogenically Mediated Gene Flow**

In addition to hybridization, sturgeon may also be prone to introgression, which we define as breeding between individuals of the same species but belonging to different populations. Introgression can improve population viability by increasing genetic diversity and long-term evolutionary potential. When executed successfully, as in many conservation aquaculture programs, introgression between wild and captive populations can be an effective conservation strategy for genetic rescue.

However, unintended introgression between wild and captive populations is likely to reduce fitness and survival of native populations. Wild-caught broodstock and juveniles are infrequently used in commercial production, and so generations of artificial selection can render captive individuals maladapted for wild environments. Under this scenario, introgression can lead to outbreeding depression and subsequent reduction in the fitness and survival of future generations—a phenomenon that has been well documented in salmonids (Araki et al. 2007). Moreover, introgression across large spatial scales can result in genetic homogenization and diminished long-term adaptive capacity. Together, loss of contemporary fitness and evolutionary potential may jeopardize the ability of native populations to persist and could severely undermine current efforts aimed at demographic recovery. Because many commercial facilities rear sturgeon outside of their native range, the threat of introgression is likely lower relative to hybridization. However, aforementioned examples of released captive Atlantic Sturgeon and White Sturgeon suggest the risk of introgression in contemporary populations is not negligible, and could increase with expansion in the size, scope, and location of commercial facilities.

**Competition And Depredation**

Negative effects of captive release can occur in the absence of reproduction, including the potential for resource competition and juvenile depredation. Given significant knowledge gaps about many aspects of sturgeon life history and ecology, the strength and outcome of competitive interactions may be difficult to predict. However, significant resource overlap among species and the global decline in sturgeon habitat suggests competition for already limited resources is likely to increase in future decades.

Although not causally linked to competition, malnourished Ship Sturgeon have been discovered during recent surveys in the Rioni River (Fleur Scheele, Fauna and Flora International, written communication); a potential indicator of negative interactions between native and introduced sturgeons (Figure 1). This is a discouraging finding, as Ship Sturgeon was believed to be extirpated from the Black Sea basin (Beridze et al. 2021) and now the long-term viability of the relict breeding population may be jeopardized by low fitness and survival.

Nonnative species, including sturgeon, but also other non-sturgeon species, can pose significant risk to recruitment through depredation. Although sturgeon develop bony scutes to deter predators, younger life stages have few natural defenses and are vulnerable to predation (Flowers et al. 2011). The risk of depredation may be particularly high when nonnative fishes are released near freshwater spawning and nursing habitats.

**Pathogens And Parasites**

Indirect effects of captive culture can be observed through the introduction of disease and parasites. High densities of fish in aquaculture facilities and mixing of multiple taxa in hobby aquaria increases the prevalence of viral, bacterial, and parasitic infections in captively reared individuals. Although many pathogens commonly found in captive facilities also occur in wild environments, human transport of captive fish across river basins introduces novel sources of disease to which native populations may have little natural immunity. Once released, captive individuals can then spread pathogens through entire ecosystems as they move through different habitats to complete their life cycle. Therefore, the pathogenic consequences of a single captive release may manifest across vast spatial scales, particularly for anadromous species like sturgeon.

Introduction of aquatic diseases during intentional stocking events has been implicated in population declines, loss of entire spawning year classes, and even complete extirpation of species in some areas (Zholdasova 1997). Presently, the largest disease risks in captive sturgeon populations appear to be bacterial (e.g., *Streptococcus iniae*, which also poses a disease risk to humans [Mugetti et al. 2022]) and viral infections including herpesviruses, White Sturgeon iridovirus, and potentially species of *Ranavirus* normally associated with amphibian declines (Waltzek et al. 2014). Although the threat of *Ranavirus* remains unclear, herpes viruses and White Sturgeon iridovirus are highly transmittable and have been correlated to necrotic infection and large mortality events. Viral infections of wild and captive sturgeon populations have been detected in multiple species and countries (e.g., Kurobe et al. 2010; Hofsoe-Oppermann et al. 2020), suggesting more widespread outbreaks could be forthcoming as the captive industry continues to expand.

**Continued Harvest of Wild Populations**

With most sturgeon species under strict harvest moratoria, captive facilities are now the most viable, and often only legal, source for caviar and other sturgeon products. However, large body size and late age of maturation can make sturgeon difficult to raise in captivity. Commercial fish culturists looking to reduce the space and resource requirements needed to support a self-sustaining captive sturgeon population or needing to compensate for incidental loss may continue to harvest individuals from wild populations. In Eurasia, wild sturgeon, particularly gravid females, are sometimes translocated to commercial facilities and temporarily held before being used as broodstock and/or harvested. This practice, which is illegal in many regions, perpetuates the stress on wild populations, and specifically monetizes removal of individuals during critical life stages. However, limited oversight and lack of critical inspection of many food labels still provide abundant opportunity for individuals to directly harvest or translocate individuals from wild populations (Dolan and Luque 2019; Figure 1).

## SUPPORTING STURGEON CONSERVATION IN THE ERA OF CAPTIVE CULTURE

Demand for caviar and other sturgeon products remains high, and continued loss and restriction of wild fisheries are likely to compel further development of the captive culture industry. Expansion of research laboratories, commercial facilities, and private pet trades presents serious challenges for conservation, as the scope and location of many captive facilities will likely fall outside the purview of current regulatory frameworks (see Table 1 for a list of policies that pertain to global sturgeon conservation). Specifically, the majority of current regulations aim to protect critical habitats, minimize individual harm, and regulate commercial harvest and transport of sturgeon and sturgeon products. While these challenges will remain into the future, emerging threats are likely to develop as the taxa's user group continues to expand. How this new era of sturgeon captive culture will affect wild populations remains to be seen; however, more stringent, effective, and targeted regulation would likely provide more opportunities for captive culture to be apposite to global conservation. Below we outline three major sectors of sturgeon captive culture and discuss possible regulatory changes that could improve the outlook of sturgeon conservation:

(1) **Commercial culture**. Commercial facilities account for the majority of captive sturgeon populations (Bronzi et al. 2019) and are likely to be the source of most nonnative sturgeon introductions. While many regulations already pertain to captive culturists (Table 1), there are still opportunities for improved oversight of this sector. Increased governance on allowable infrastructure, including restricted use of flow-through systems and banning facilities in flood-prone areas, would likely reduce the probability of high biomass escapes. Additional oversight on the location of large facilities may be particularly important given that catastrophic flood events are likely to increase under

future climate change scenarios. Another potential mechanism for reducing introduction pathways could be to severely restrict or prohibit the commercial sale of live sturgeon. However, across all commercial markets, more stringent investigation and castigation for mislabeled products is likely to reduce illegal harvest and minimize impacts on wild populations.

(2) **Research and government laboratories**. There is an expectation that fisheries professionals will uphold the highest standards of conservation. However, multiple observations presented in this article are consistent with unsanctioned releases of captive sturgeon from scientific facilities. In addition, fisheries research facilities are often highly trafficked, outdoor environments, which increases the biosecurity risk associated with these captive populations. Despite recent expansion in the number of sturgeon research programs, there are surprisingly few regulations that pertain to the proper handling of captive fish in these environments. For example, while academic research facilities in the United States operate under the oversight of animal care and use committees and may seek accreditation from the Association for the Assessment and Accreditation of Laboratory Animal Care International, accreditation is not mandatory for all federal research facilities. As such, within the United States there are no universal protocols pertaining to proper transport, handling, and disposal of captive individuals in laboratory environments. Likewise, there is no mechanism to assure that captive sturgeons are eliminated following laboratory testing, which is a requirement under federal permitting in the United States. Overall, the absence of consistent regulatory frameworks for academic and federal research facilities highlights a significant biosecurity gap, and an opportunity to enhance protocols pertaining to proper infrastructure, facility inspection,

and personnel training. For example, in Canada, captive facilities must satisfy requirements pertaining to disease transfer, husbandry methods, culture equipment, and fish holding densities, with more stringent requirements for listed species. Similar protocols in other countries may be particularly critical given that many research facilities are located near large waterbodies, and vulnerable infrastructure (i.e., flow-through systems) and insufficient maintenance has significant potential to be a source of unintentional captive escape.

(3) **Pet trade**. Although this sector has not yet been documented to have an impact on wild populations, rising popularity of sturgeon in the hobby pet trade foreshadows future negative consequences of private captive culture. This sector is very challenging to directly regulate due to the diffuse and poorly documented nature of private culture. Due to the challenges with regulating individual owners, and the near-certain probability that sturgeon growth will surpass all indoor aquaria, the strongest regulatory mechanism may be to prohibit all sale. Even with restrictions on sales, it may still be beneficial to increase surveillance for illegal trade of sturgeons. Automated approaches for monitoring the internet for trade of invasive species (e.g., Great Lakes Detector of Invasive Aquatics in Trade; https://bit.ly/3DIJ5Mu) have been developed and might provide a useful model for tracking the trade of sturgeons.

The captive culture industry represents an emerging threat to the recovery and conservation of critically imperiled sturgeon populations. Negative effects of captive culture programs, including intentional and unintentional release and ongoing harvest of wild populations, have already manifested in some populations. Under the current trajectory of the captive culture industry, nonnative invasion, introgression, and hybridization have real potential to reverse decades of conservation and drive one of the most ancient and globally revered groups of fishes further towards extinction. Increased attention to these emerging issues may help improve the outlook for sturgeon conservation programs.

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Table 1. Description of policies and resolutions that protect worldwide sturgeon populations against habitat loss, overharvest, and illegal trade.

| Resolution | Description | Application to Sturgeon | Resources |
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| Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES) | Multinational agreement through which countries work together to ensure that international trade is not detrimental to the survival of the species in the wild. Member nations to CITES regulate and monitor international trade (import and export) through permits and certifications to ensure sustainable use. The CITES Secretariat is not a law enforcement authority and does not conduct investigations; instead, each country is to investigate within-county allegations if potential criminal activity lies with the relevant national law enforcement authorities of that country. | International trade led to a CITES listing of all species of Acipenseridae; since 1998, all sturgeon trade is regulated and all parts or derivates (e.g., caviar, meat, skin, etc.) require a CITES permit or certificate. Only Shortnose Sturgeon is listed under CITES Appendix I (threatened by extinction with trade permitted only in exceptional circumstances). All other sturgeons are listed in Appendix II (trade could threaten species persistence if not controlled).[1] | The Convention on the International Trade in Endangered Species of Wild Fauna and Flora provides country-specific contacts for reporting violations and information regarding illegal trade[2]; in the U.S. the U.S. Fish and Wildlife Service (USFWS) is the official CITES authority and provides opportunity to report violations.[3] |

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| U.S. Endangered Species Act (ESA) | Under the ESA, the National Marine Fisheries Service (NMFS) and the USFWS are required to conserve the ecosystems upon which endangered and threatened species depend on, provide a program for listed species conservation, and take appropriate steps toward recovery. Section 9 of the ESA outlines prohibitions including illegal "take" of a listed species which includes harm, capture and harassment and Section 10 describes penalties for illegal take. Under Section 7, federal actions are required to undergo a consultation to assess and reduce potential interactions with listed species and their designated critical habitat helps to conserve listed species. Limited federal dollars are also available for research. The ESA primarily protects foreign species by restricting trade and may prohibit certain activities, including import, export, take, commercial activity, interstate commerce, and foreign commerce. By regulating these activities, the United States ensures that people under its jurisdiction do not contribute to the further decline of a listed species. | Eight of the nine sturgeon species in the USA are currently listed under the ESA as either threatened or endangered and a review on the status of the Lake Sturgeon is scheduled for 2024. There are also eight sturgeon species that are not native to the United States listed under the ESA[4]. As described, the introduction of a nonnative species could harm listed sturgeon. | The National Oceanic and Atmospheric Administration (NOAA) is responsible mainly for marine wildlife[5] and USFWS for terrestrial and freshwater organisms[6]. Violations of the ESA should be reported to either NOAA by calling 1-800-853-1964 or USFWS via their online reporting[7]; photos and videos are encouraged |
| United Nations' Convention on the Conservation of | An environmental treaty of the United Nations designed to conserve migratory species, with special emphasis on protection of habitats and migration routes. CMS agreements range from legally binding treaties to less formal agreements. | European Sturgeon is listed under Appendix I (threatened with extinction) and 18 species are listed under Appendix II (species that would benefit from international cooperation). | |

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| Migratory Species of Wild Animals (CMS) | | |
| Bern Convention on the Conservation of European Wildlife and Natural Habitats | A binding international legal agreement among 50 countries and the European Union designed to conserve wild flora and fauna and their natural habitats, with special attention given to endangered and vulnerable species. | Adriatic, European, and Mediterranean populations of Beluga Sturgeon are listed as strictly protected while Sterlet, Stellate Sturgeon, and remaining Beluga Sturgeon populations are listed as protected. |
| International Union for the Conservation of Nature (IUCN) | Global environmental network of government and civil society organizations that uses expert panels to inventory the status of biological species. Using a set of precise criteria, these experts evaluate the extinction risk of thousands of species and subspecies. Species at risk of extinction are placed on the IUCN Red List. | The Sturgeon Specialist Group has over 50 experts contributing to conservation of sturgeon and paddlefish. As of the 2022 status assessment, all 26 species are imperiled to some degree, with 17 sturgeons identified as critically endangered, a listing that represents organisms at extremely high risk of extinction in the wild. |
| Species at Risk Act of Canada | Canadian legislation that provides legal protection for wildlife species and provides measures to assist in the recovery of threatened and endangered species. | Classification is often population-specific, but at least some populations of Atlantic Sturgeon, White Sturgeon, Green Sturgeon, Lake Sturgeon, and Shortnose Sturgeon are listed under Schedule 1 indicating populations that |

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| | | are endangered, threatened, or of special concern. Endangered populations are afforded federal protections of critical habitats and prohibitions on individual harm. | |
| U.S. Lacey Act | Administered by NMFS and USFWS, the Lacey Act makes it unlawful to any person to import, export, transport, sell, receive, acquire, or purchase fish, wildlife, or plants that were taken, possessed, transported, or sold in violation of any law or regulation of any state. | Illegal trade of sturgeon is punishable by felony fines with no innocent owner exceptions. | Violations of the Lacey Act can be reported at fws_tips@fws.gov or at 1-844-397-8477 |

[1] https://bit.ly/3U6XibC

[2] https://bit.ly/3DIjq6O

[3] https://bit.ly/3fjcQKj

[4] https://bit.ly/3SLslIR

[5] https://bit.ly/3NdZV98

[6] https://bit.ly/3ff1qr3

[7] https://bit.ly/3gQlZe3

Figure 1. The expanding scale and scope of sturgeon captive culture (center map; data from Bronzi et al. 2019; FAO 2020) presents an emerging threat to wild sturgeon populations around the world. Changes to existing regulatory frameworks would increase opportunities for captive culture to support wild sturgeon conservation.