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REVIEW

A global perspective of fragmentation on a declining taxon — the sturgeon (Acipenseriformes)

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ABSTRACT: Acipenseriformes (sturgeons and paddlefishes) are considered to be one of the most globally imperiled taxon, with 25 of the 27 species listed by the International Union for the Conservation of Nature (IUCN). Overharvest, habitat degradation, fragmentation and water quality issues have contributed to their decline worldwide. These stressors have been ameliorated in some areas, but in others they remain a limiting factor to sturgeon. Barriers impeding upstream migrations to natural spawning areas and manifesting alterations to natural flows continue to compromise sturgeon recruitment and limit natural recovery. Watersheds in the Northern Hemisphere have been categorized as being strongly affected, moderately affected or unaffected based on the degree of fragmentation and water flow regulation. An overlay (i.e. intersect) of the sturgeons' status with this watershed categorization revealed that a small area remains in which sturgeon are not considered at risk and where rivers are unaffected in northern Canada. These relatively unperturbed populations provide a much needed opportunity to learn about sturgeon biology, habitat needs and reproductive potential in a natural riverine environment, which may facilitate conservation and recovery efforts in affected watersheds.

KEY WORDS: Acipenseriformes · Fragmentation · Imperiled

INTRODUCTION

Acipenseriformes (an order of basal ray-finned fishes that includes the sturgeons and paddlefishes) are considered to be one of the most globally imperiled vertebrate groups (Birstein et al. 1997, Pikitch et al. 2005). Sturgeon are unique and have been described as 'living fossils', dating back to the Lower Jurassic some 200 million years ago (Bemis & Kynard 1997, Bemis et al. 1997b, Pikitch et al. 2005) and have undergone few morphological changes since that time (Choudhury & Dick 1998). Rivers dominated the landscape during the period when sturgeon purportedly evolved; fossil records excavated strictly from these historical drainages support an ancestral affinity for flowing waters (Choudhury & Dick 1998). As such, extant species are highly migratory (Auer 1996, Welsh & McLeod 2010), spawning only in freshwater — including the many marine, anadromous sturgeon species (Rochard et al. 1990, Bemis & Kynard 1997). There are currently 27 recognized species of Acipenseriformes (25 species of sturgeon and 2 species of paddlefish) and they are found only in the Northern Hemisphere (Fig. 1; Bemis & Kynard 1997, Bemis et al. 1997a, Birstein et al. 1997), which is consistent with all sturgeon fossil locations (Bemis et al. 1997a). Eurasia supports the greatest diversity with 17 species of sturgeon, while North America hosts the remaining 10 species (Birstein 1993, Birstein et al. 1997, Billard & Lecointre 2001).

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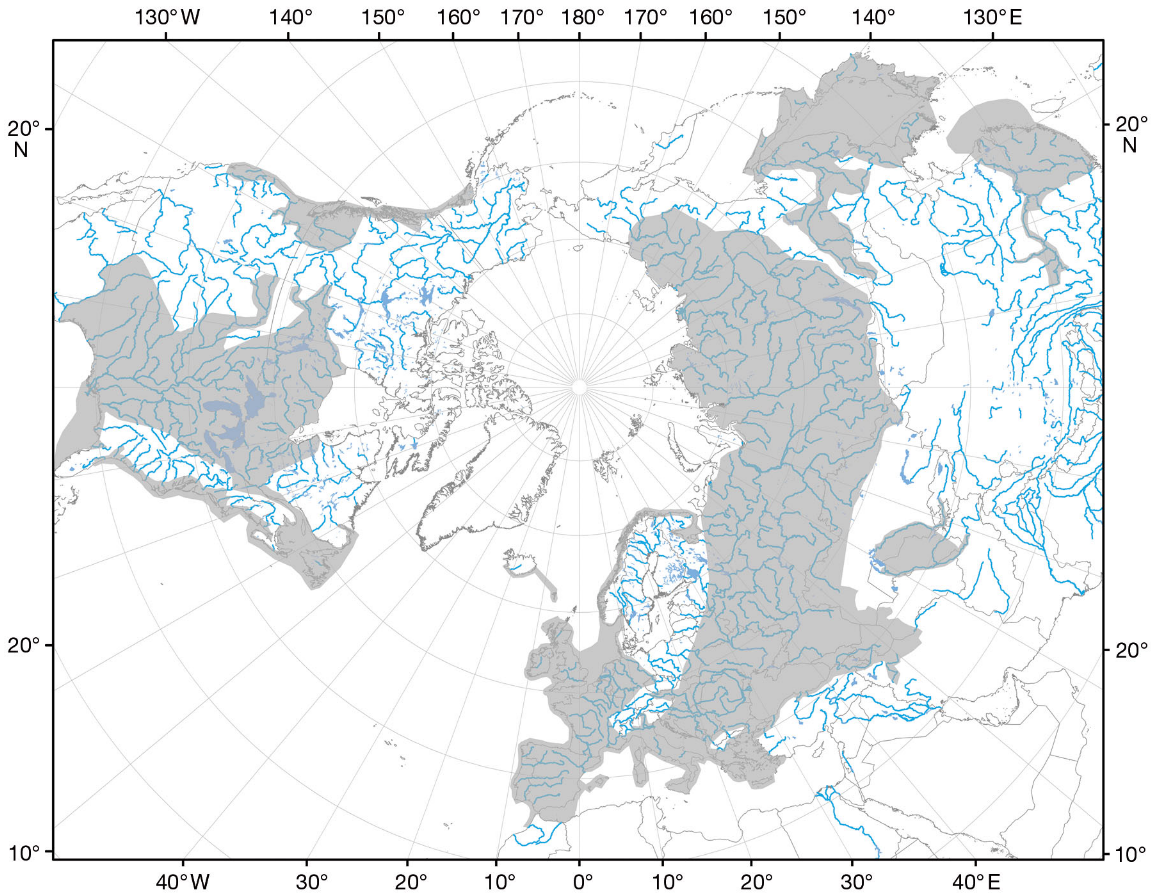

Fig. 1. Global distribution of the 27 Acipenseriformes species (depicted in gray)

GLOBAL DECLINE OF ACIPENSERIFORMES

Sturgeon are a resilient group, having adapted to large-scale global changes (Bemis & Kynard 1997) and survived mass global species extinctions (Jackson & Johnson 2000, Wang et al. 2014). However, many populations have become decimated despite their historical abundance and widespread distribution across the Northern Hemisphere (Birstein 1993, Bemis & Findeis 1994, DeVore et al. 1995). Non-regulated harvests for the highly sought caviar and meat of many sturgeon species initiated their decline in the mid-1800s in North America (Birstein 1993, Bemis & Findeis 1994, Pikitch et al. 2005), exacerbated stock declines from the Caspian Sea in the early 1960s (Khodorevskaya et al. 1997, Ivanov et al. 1999, Khodorevskaya & Krasikov 1999) and continue to depress or limit the recovery of some populations (Khodorevskaya et al. 1997, Williamson 2003, Peterson et al. 2007, Johnson & Iyengar 2015). Major alterations to many rivers were concurrent with, or subsequent, to overharvests. Dams were constructed on large rivers for mechanical or hydroelectric power, for navigation purposes or to facilitate transport of material downstream, directly blocking access to and/or altering sturgeon spawning habitat. Dramatic changes to water quality due to use of rivers for disposal of industrial or municipal effluent, deforestation and urbanization of watersheds were all prevalent practices in the period post over-harvesting concurrent with dam construction (Rochard et al. 1990, Birstein et al. 1997, Lenhardt et al. 2006). Consequently, riverine fish (i.e. fluvial-dependent species) including Acipenseriformes are among the most endangered species globally (Cooke et al. 2012).

RECENT IMPROVEMENTS AND CONTINUED THREATS

More recently, water quality conditions in many regions have improved (Hensel & Holcik 1997, Schram et al. 1999, Kampa et al. 2014) and stricter harvest controls have been implemented (Khodorevskaya et al. 1997, Baker & Borgeson 1999, Peterson et al. 2007) in addition to the enforcement of import

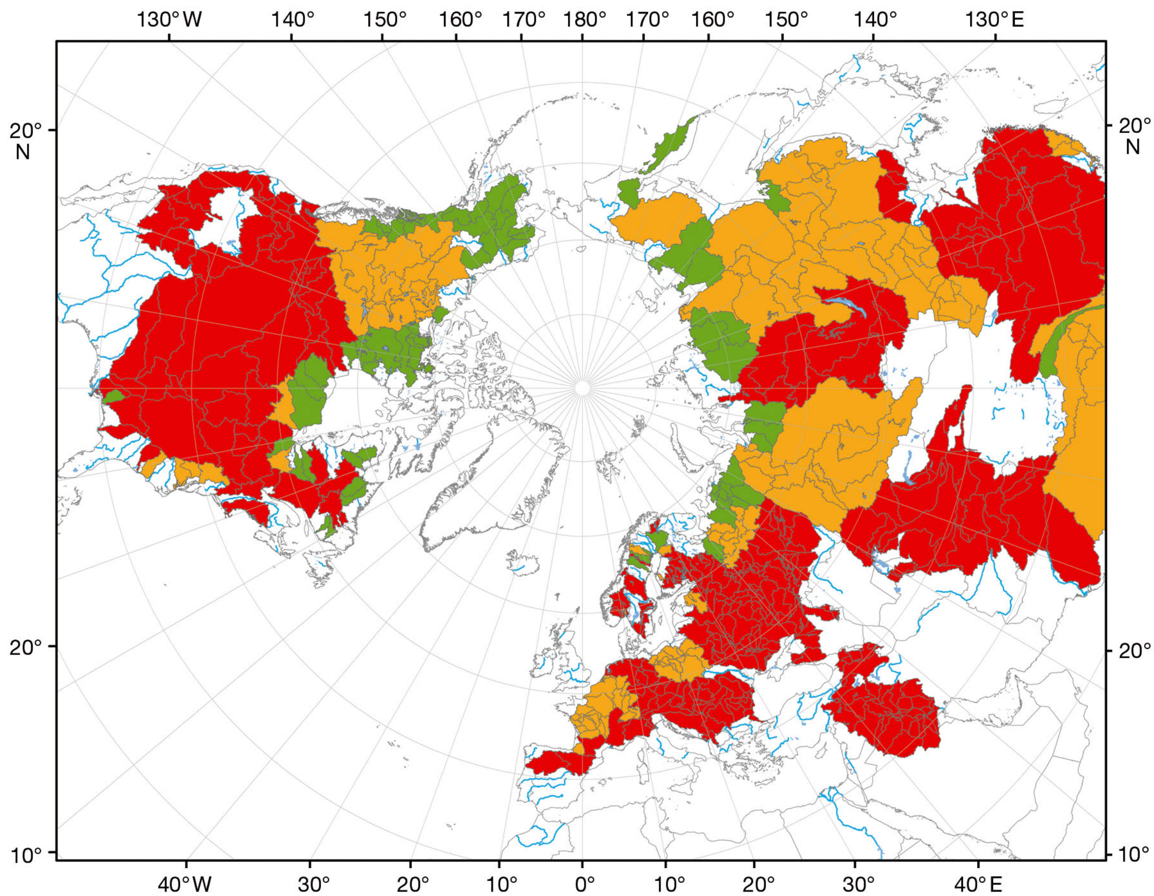

Fig. 2. Large river systems in the Northern Hemisphere as categorized by Dynesius & Nilsson (1994). Red: areas in which the large river systems are strongly affected by river regulation, amber: moderately affected areas, green: unaffected area

restrictions on many sturgeon species through the Convention on International Trade in Endangered Species (Williamson 2003, Lenhardt et al. 2006, Ludwig 2006). However, poaching purportedly remains a conservation concern for all sturgeon species, given the exorbitant prices of caviar (Cohen 1997, Pikitch et al. 2005); this seems to be especially relevant for European stocks (Khodorevskaya et al. 1997, Ivanov et al. 1999, Ludwig 2006). In addition, hydroelectric dams are a long-term fixture on the landscape. In fact, hydro development has recently undergone a renaissance as a source of renewable energy to meet growing demands (Nilsson et al. 2005, Grill et al. 2015, Zarfl et al. 2015), with over 3700 large dams either planned or currently under construction globally (Zarfl et al. 2015). River fragmentation has been extensive, with in excess of 45 000 large dams (i.e. >15 m height) in existence globally (Nilsson et al. 2005). Fragmentation has contributed to local extirpation of sturgeon in numerous rivers (Bemis & Findeis 1994, Ferguson & Duckworth 1997, Hensel & Holcik 1997). Dams act as barriers to upstream movement to historic spawning areas (Birstein 1993, DeVore et al. 1995, Wei et al. 1997), congregating migrating sturgeon and exposing them to harvest and the perils of poaching (Cohen 1997, Fernández-Pasquier 1999), and altering flows, affecting the success of natural sturgeon recruitment within rivers (Khoroshko 1972, Ivanov et al. 1999, Jager et al. 2002, Goto et al. 2015, Haxton et al. 2015). Moreover, variation in sturgeon abundance across the landscape has been attributed to the presence of hydroelectric generating stations (DeVore et al. 1995, Haxton & Findlay 2008, Haxton et al. 2014), demonstrating that dams can play a significant role in limiting the recovery processes for sturgeon.

The degree of fragmentation and water flow regulation has been categorized on a watershed basis for large river systems (those with mean annual discharge of at least 350 $m^3\ s^{-1}$ in a river channel within a catchment) on a global scale (Dynesius & Nilsson 1994, Nilsson et al. 2005). River watersheds have been classified, based on level of fragmentation and flow alteration, as strongly affected, moderately

Table 1. IUCN Red List status of sturgeon and paddlefish by continent in 2016. CR: Critically Endangered; EN: Endangered; VU: Vulnerable; NT: Near Threatened; LC: Least Concern

Species	Authority	Continent	Red List status	Year assessed
Acipenser baerii	Brandt, 1869	Eurasia	EN	2010
Acipenser brevirostrum	Lesueur, 1818	North America	VU	2004
Acipenser dabryanus	Duméril, 1869	Eurasia	CR	2010
Acipenser fulvescens	Rafinesque, 1817	North America	LC	2004
Acipenser gueldenstaedtii	Brandt & Ratzeburg, 1833	Eurasia	CR	2010
Acipenser medirostris	Ayres, 1854	North America	NT	2006
Acipenser mikadoi	Hilgendorf, 1892	Eurasia	CR	2010
Acipenser naccarii	Bonaparte, 1836	Eurasia	CR	2013
Acipenser nudiventris	Lovetsky, 1828	Eurasia	CR	2010
Acipenser oxyrinchus	Mitchill, 1815	North America	NT	2006
Acipenser persicus	Borodin, 1897	Eurasia	CR	2010
Acipenser ruthenus	Linnaeus, 1758	Eurasia	VU	2010
Acipenser schrenckii	Brandt, 1869	Eurasia	CR	2010
Acipenser sinensis	Gray, 1835	Eurasia	CR	2010
Acipenser stellatus	Pallas, 1771	Eurasia	CR	2010
Acipenser sturio	Linnaeus, 1758	North America	CR	2010
Acipenser transmontanus	Richardson, 1836	North America	LC	2004
Huso dauricus	Georgi, 1775	Eurasia	CR	2010
Huso huso	Linnaeus, 1758	Eurasia	CR	2010
Pseudoscaphirhynchus fedtschenkoi	Kessler, 1872	Eurasia	CR	2010
Pseudoscaphirhynchus hermanni	Kessler, 1877	Eurasia	CR	2010
Pseudoscaphirhynchus kaufmanni	Kessler, 1877	Eurasia	CR	2010
Scaphirhynchus albus	Forbes & Richardson, 1905	North America	EN	2004
Scaphirhynchus platorynchus	Rafinesque, 1820	North America	VU	2004
Scaphirhynchus suttkusi	Williams & Clemmer, 1991	North America	CR	2004
Polyodon spathula	Walbaum, 1792	North America	VU	2004
Psephurus gladius	Martens, 1862	Eurasia	CR	2010

affected or unaffected (Fig. 2; Dynesius & Nilsson 1994, Nilsson et al. 2005). Rivers in which less than one-quarter of the main channel was left without dams were considered strongly affected. Unaffected rivers contained no dams in their main channel, although dams in tributaries were permitted if the mean annual discharge was changed by less than 2%. Rivers that fell between these 2 categories were considered moderately affected (Dynesius & Nilsson 1994). In the Northern Hemisphere, within the sturgeon's historical range, approximately 75% of river discharge was considered to have been moderately to strongly affected by river regulation (Dynesius & Nilsson 1994).

Impacts of habitat fragmentation resulting from dam construction are widespread and well documented (Wozney et al. 2011, McDermid et al. 2011, Haxton et al. 2014). Barriers can present significant obstacles to the continued presence of sturgeon in historically occupied waters given that sturgeon often utilize entire river systems (Welsh & McLeod 2010, Gerig et al. 2011) to find the habitat necessary to fulfill the requirements of particular stages of the life cycle (Smith & King 2005). While safe, unimpeded movement up and downstream at barriers could possibly ameliorate the situation, passage efficiency in the limited instances where it is known to occur has been minimal (Cooke et al. 2002, Parsley et al. 2007, Thiem et al. 2011, 2016) and at a high energetic cost to the fish (Thiem et al. 2016). Recovery of sturgeon populations in highly fragmented rivers could therefore be limited or reliant on artificial propagation given the negative effects dams could have on recruitment (e.g. Khodorevskaya et al. 1997, Khodorevskaya & Krasikov 1999, Schram et al. 1999). Furthermore, the effects of fragmentation and adult mortality can be confounding. Fragmentation can affect recruitment, which impedes recovery, whereas poaching generally targets adults. Species or populations that are vulnerable to poachers may never naturally recover when they inhabit a fragmented river.

INTERSECT: RIVER FRAGMENTATION AND STURGEON STATUS

These multiple stressors have led the International Union on the Conservation of Nature (IUCN; www.iucnredlist.org) to list (i.e. categorize based on the risk of extinction) 25 of the 27 Acipenseriformes (Table 1,

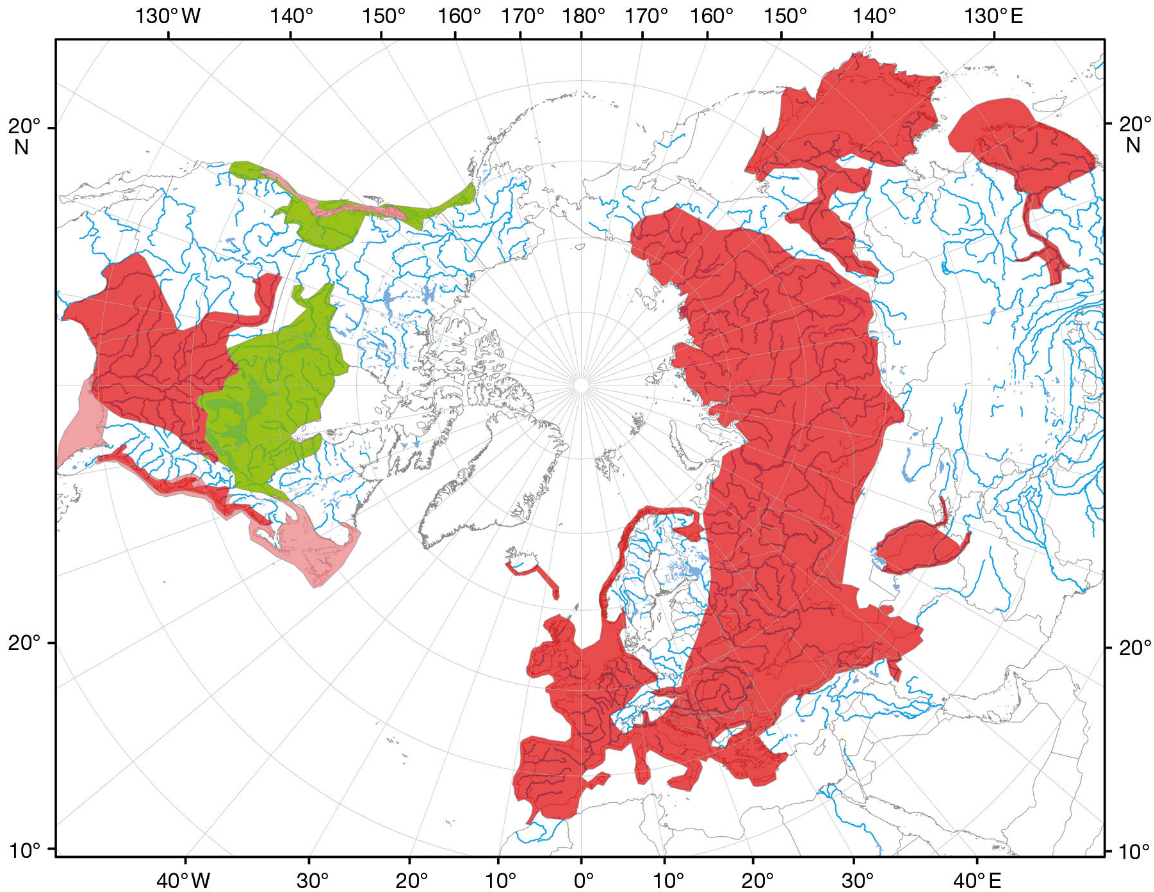

Fig. 3. IUCN's Red List status of the 27 sturgeon and paddlefish species globally. Status is indicated by colour — red: Critically Endangered or Endangered; peach: Near Threatened or Vulnerable; green: Least Concern

Fig. 3) worldwide. Only 2 sturgeon species, lake sturgeon *Acipenser fulvescens* Rafinesque, 1817 and white sturgeon *Acipenser transmontanus* Richardson, 1836, are considered by the IUCN to be not at risk (i.e. categorized as Least Concern) globally (Table 1); however, their status varies widely across their natural range at national or state/province scales.

On a global scale, few areas remain in which sturgeon populations are not considered to be at risk and where large rivers remain intact. An intersect (a geometric intersection; see the Appendix) of river fragmentation categorization (Fig. 2; Dynesius & Nilsson 1994, Nilsson et al. 2005) on sturgeon distribution and status (Fig. 3) identified those areas where sturgeon populations were not at risk and where rivers were not fragmented (Fig. 4). White sturgeon, indigenous to the west coast of North America, are anadromous, spawning in only 3 rivers: the Sacramento, Columbia and Fraser Rivers (Billard & Lecointre 2001). These rivers are all highly fragmented and as such, extensive management has been required to sustain or facilitate recovery of white sturgeon populations (e.g. Ireland et al. 2002, Parsley et al. 2002, 2007, Crossman & Hildebrand 2014). Lake sturgeon, a potamodromous species, is the only species of sturgeon not considered at risk by the IUCN that inhabits an area categorized as unaffected by fragmentation and barriers (Fig. 4). Northern Canada supports populations of lake sturgeon that purportedly avoided decimation in the late 1800s and early 1900s given the remoteness of the area (Bemis & Findeis 1994, Ferguson & Duckworth 1997). While robust lake sturgeon populations exist in areas categorized as strongly affected (e.g. Lake Winnebago, Wisconsin, Bruch 1999; the St. Lawrence River, Quebec, Mailhot et al. 2011; Lake of the Woods, Ontario, Rusak & Mosindy 1997), they are generally associated with large lakes accompanied with altered tributaries.

SUMMARY AND RECOMMENDATIONS

Sturgeon recovery efforts have historically been extensive and expensive (Bacalbasa-Dobrovici &

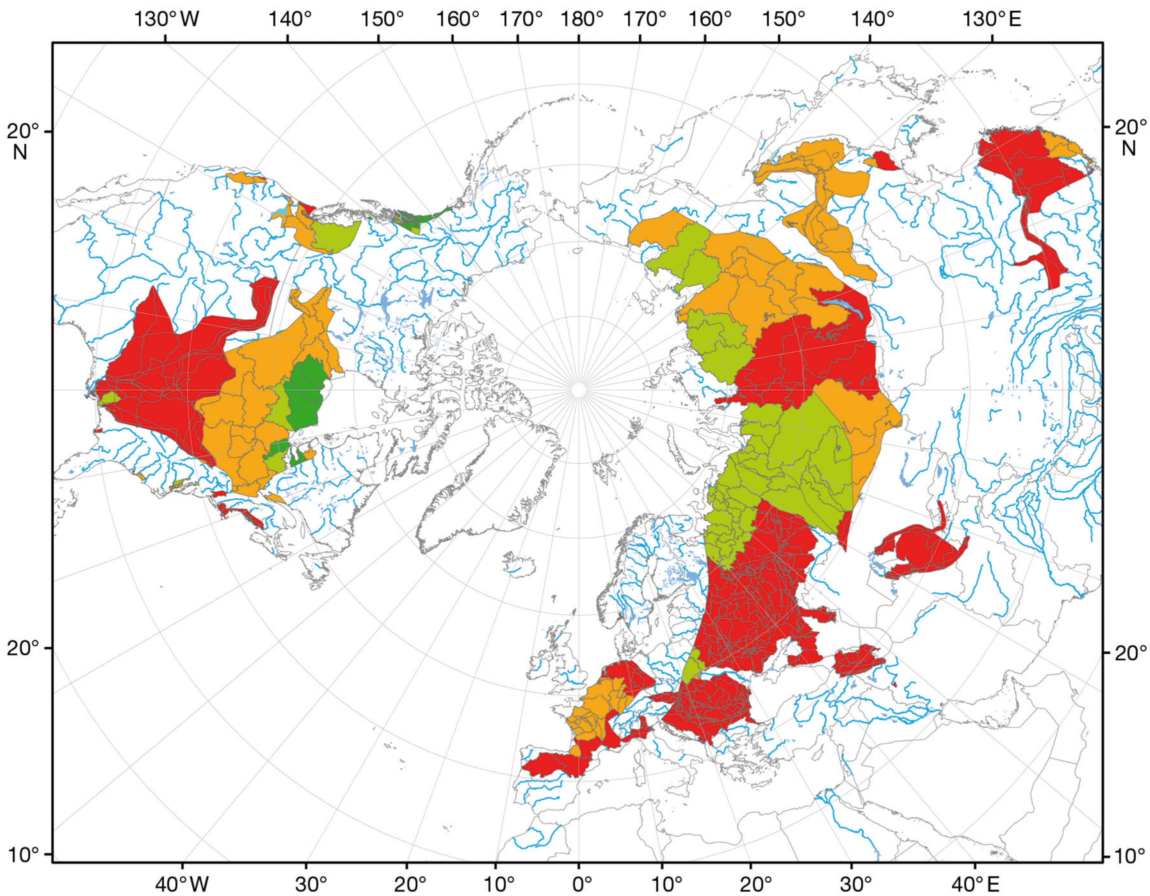

Fig. 4. Intersect of large river system categorization (Dynesius & Nilsson 1994) with sturgeon status and distribution (see Appendix). Dark green: areas where the species is not listed and where watersheds are unaffected. Light green: areas where species are listed but watersheds are unaffected. Amber: areas where species are not listed or listed as Near Threatened or Vulnerable with moderate fragmentation. Red: areas that are highly fragmented and species are listed

Patriche 1999, Lenhardt et al. 2006, 2008, Guti 2014) in areas where populations have drastically declined, such as the Danube River (Hensel & Holcik 1997) or Yangtze River (Wei et al. 1997, Dudgeon 2010). The relatively unperturbed populations in northern Canada provide an opportunity to learn about sturgeon biology, and to identify habitat needs and reproductive potential in a natural riverine environment. There is an identified need to learn more about endangered riverine fish, especially in unperturbed natural ecosystems (Cooke et al. 2012). Such research could help ascertain the life-history requirements of a fluvial-dependent species, which may facilitate conservation and recovery efforts in perturbed systems, and potentially unaltered systems in northern regions.

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Appendix.

To determine areas of low fragmentation and non-threatened sturgeon populations, an intersect was conducted in ArcMap v.10.1 (ESRI) of the categorization of fragmentation in large river systems (Fig. 2) (Dynesius & Nilsson 1994, Nilsson et al. 2005) and IUCN's Red List status (Fig. 3). A numerical value was assigned to the categorization for both fragmentation and status (fragmentation: unaffected = 1, moderately affected = 5, strongly affected = 10; status: Least Concern = 1; Near Threatened = 2, Vulnerable = 3, Endangered = 4, Critically Endangered = 5). The product of the 2 values provided an indication of Red List status and fragmentation (Fig. 4). A value of 1 represents areas where the species is not listed and watersheds are unaffected. Values between 2 and 9 represents areas where species are listed but watersheds are unaffected. Values between 10 and 19 represent areas where species are not listed or listed as Near Threatened or Vulnerable with moderate fragmentation. Values greater than 20 represent areas that are highly fragmented and species are listed.

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