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REVIEWS

Water resource development and sturgeon (Acipenseridae): state of the science and research gaps related to fish passage, entrainment, impingement and behavioural guidance

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Abstract Acipenserids (sturgeons) live in large rivers and lakes in North America and Eurasia, where many species and populations are considered imperiled. One of the most pervasive threats across the global range of sturgeon is water resource development (e.g., hydropower dams, water intakes for irrigation, industrial use, or human consumption). We report on the outcome of a literature review focused on interactions between sturgeon and water resource development. We focused on the persistent issue of dam passage (both upstream and downstream), impingement, and entrainment, which are all relevant issues for both existing and planned facilities. We discuss aspects of sturgeon sensory physiology, and how knowledge of sensory physiology can be used for behavioural guidance. We also consider how the swimming ability and style of sturgeon is relevant for passage. Most of the literature emanated from research on just a few species (especially lake sturgeon, white sturgeon, green sturgeon, and shortnose sturgeon). Although there are several examples of apparent "success stories" (e.g., successful upstream fish passage, efforts to reduce impingement and entrainment), there are also many failures, and such examples are likely under-reported. Without significant investments in solutions-oriented research related to sturgeon-water resource development interactions, we submit that fish passage, entrainment and impingement problems for acipenserids will remain. There is a need for research that spans life-stages, compares different species, and considers how passage, entrainment, and impingement influence demography.

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Further, there is a need for investment into evidence-based implementation of mitigation infrastructure and management strategies to ensure conservation needs of sturgeons are adequately considered.

Keywords Dam · Fishway · Safe passage · Downstream · Upstream · Hydropower · Barrier · Connectivity

Introduction

For centuries, humans have engaged in various forms of water resource development on rivers to generate power or extract water for use in irrigation, industrial processes, or for human consumption. All of these forms of water resource development have some level of environmental consequence, but alteration of rivers via the addition of dams, diversions, and other engineering structures to enable generation of hydropower represents one of the greatest threats to aquatic ecosystems (Nilsson et al. 2005; Winemiller et al. 2016). The consequences of such hydropower facilities and their operations are many and varied. For example, the actual footprint of hydroelectric facilities typically means a loss of the productive capacity of habitats. Moreover, if a reservoir is created for storage and head, riverine reaches become more lentic, which can change habitat quality such that the riverine fish communities transition to reflect the change in habitat (Baxter 1997). Depending on dam operations, it is typical to see dramatic alterations in flows relative to pre-dam conditions, which has major influences on the diversity and function of downstream ecosystems (see Poff et al. 2007) via changes to available habitat, erosion, stranding, and bioenergetic costs of feeding (see Baxter 1997; Ligon et al. 1995; Collier et al. 2000; Nagrodski et al. 2012). Given the inherent connections between rivers and the adjacent riparian zone (Hynes 1975), effects on aquatic ecosystems can transcend realms to also affect terrestrial systems (Naiman et al. 2010). Another major consequence of hydropower infrastructure is fragmentation (Nilsson et al. 2005), affecting ecological (Taylor et al. 1993) and hydrologic connectivity (Pringle 2003). If effective bi-directional passage facilities are not provided, extirpations of some migratory fish populations are almost a certainty. Fish attempting downstream movement may become impinged or entrained (e.g., may pass through turbines or out diversion pipes), which can be lethal (Coutant and Whitney 2000; Gutowsky et al. 2016). Impingement and entrainment can also occur in other water abstraction activities, such as for irrigation, industrial processes, or for drinking water. Nonetheless, hydropower generation has the potential to be a reasonable means of generating electricity if it can be done in a manner that minimizes negative consequences for aquatic biota (Truffer et al. 2001, 2003) and aquatic ecosystems (Lapointe et al. 2014; Lynch et al. 2016).

Fish are greatly affected by hydropower infrastructure and operations, and other forms of water resource development. Consequently, there has been much research focused on quantifying impacts to inform compensation (i.e., off-setting), and to identify opportunities to mitigate threats. One group of fish that are regarded as being particularly susceptible to impacts related to water resource development are acipenserids—the sturgeon (Secor et al. 2002; Williot et al. 2002). Sturgeon have a circumpolar distribution, with some 27 species in the temperate, sub-tropical, and sub-Arctic regions of North America and Eurasia (Birstein et al. 2006). Sturgeon are long-lived and have late age of maturation (Billard and Lecointre 2000). Such life-history characteristics contribute to their relative sensitivity to anthropogenic stressors (Reynolds et al. 2005). It is believed that four sturgeon species are recently extinct (within last 100 years), with most species or populations sufficiently imperiled that they occur on the IUCN Red List and various national and regional threat assessment lists. As a family, sturgeon face many threats including fisheries exploitation (direct and indirect as bycatch) and pollution (Billard and Lecointre 2000), but one of the most pervasive threats across their range is hydropower development and operations, and other forms of water resource development (Rochard et al. 1990). Water resource development has the potential to influence all life phases of sturgeon—from access of mature adults to spawning grounds to early life history and rearing of juveniles to overwintering of fish of all ages—and of the migrations associated with different life phases as they transition among habitats.

There is a growing body of literature that can help to guide utilities and regulators in minimizing the effects of water resource developments on fish (Katopodis and Williams 2012), including sturgeon.

However, this literature would benefit from a synthesis to guide further work and inform management (as has recently been done for green sturgeon more broadly related to conservation issues; see Rodgers et al. 2019). Here, we report on the outcome of a literature review (see "Appendix" for details on methods used in literature review) that examined interactions between sturgeon and water resource development. In particular, while we recognize that the impacts of water resource development are varied and broad, we focused here on the persistent issue of passage (both upstream and downstream) at dams, as well as impingement and entrainment (in various contexts, including dams and other water-taking activities) that are relevant to both existing and planned facilities. We concentrate efforts on identifying solutions to the issues of passage, impingement, and entrainment by examining literature related to fish passage design, and use of various behavioural guidance tools. Based on the available literature, the review is primarily focused on hydropower, but we recognize that there is potential to learn from studies on entrainment and impingement related to water taking (e.g., for irrigation) and other activities such as dredge operations and boat use (e.g., propellers). Moreover, there is also opportunity to learn from fundamental studies on sturgeon swimming performance and incorporate such information into risk assessments and design of safer infrastructure where relevant. We also consider the sensory physiology of sturgeon, and how knowledge about sensory physiology has been or could be used for the purpose of improving behavioural guidance. The depth and breadth of different sections of the paper reflects inherent bias in the literature in that some topics have been reasonably well studied while others have received comparatively little attention.

On river development and the range distribution of acipenserids

The acipenserids, or sturgeons, are a family of fishes that use a variety of habitats across a large geographic range. Sturgeons are found solely in the northern hemisphere, with a circum-polar distribution spanning the sub-Arctic, temperate, and sub-tropical latitudes of North America, Europe, and Asia. With the exception of the sturgeons of genus Scaphirhynchus and lake sturgeon (*Acipenser fulvescens*), which spend the majority of their time in freshwater (note—this varies among populations), most sturgeons are diadromous, spending the majority of their life in coastal marine waters, or the brackish water of inlands seas or estuaries (Bemis and Kynard 1997). Although specific habitat requirements for growth as juveniles and adults vary, all sturgeon spawn in freshwater, usually in large flowing rivers but can include smaller streams and lentic systems (Billard and Lecointre 2000). Migrations by sturgeon can extend thousands of kilometers upstream of their adult foraging grounds (Auer 1996). Sturgeons reproduce intermittently (i.e., some take reproductive holidays), returning to their non-breeding home range (for growth and overwintering) before spawning again. However, sturgeons have a limited ability to overcome obstacles, requiring extensive stretches of connected waterways, or assistance, to pass both upstream and downstream of anthropogenic barriers such as dams (Jager et al. 2016).

The large rivers often used by sturgeon to reach spawning grounds are frequently impacted by human development, notably hydroelectric dams, which restrict passage by sturgeon and impose other negative effects on their populations through flow regulation and changes to hydrological conditions. A recent analysis estimated that globally, only 37% of the world's 246 largest rivers remain free-flowing, and these free-flowing rivers are restricted to the northern parts of North America and Eurasia, the Amazon and Orinoco basins in South America, the Congo Basin in Africa, and a few areas in Southeast Asia (Grill et al. 2019). A previous 1994 analysis of the level of fragmentation and flow regulation of large river systems north of the Tropic of Cancer found that at the time, only 23% of these remained unfragmented and unregulated, with the majority of unimpacted river systems occurring in remote areas of the far north (Dynesius and Nilsson 1994). Notably, the rate of hydropower development has increased in the decades since the previous analysis (Lehner et al. 2011; Zarfl et al. 2014). Haxton and Cano (2016) compared the distribution of rivers categorized by Dynesius and Nilsson (1994) to the historical range of the 27 extant sturgeon species, and found that the lake sturgeon in northern Canada are globally the only relatively undisturbed populations of sturgeon that remain. Despite recognition of the harm that hydroelectric dams cause to fish diversity through habitat fragmentation (Liermann et al. 2012), and the ecological benefits of restoring connectivity to river systems through dam removal (Bednarek 2001), the rate of hydropower development is on the rise globally (Zarfl et al. 2014). Hydropower is seen as a cheap, reliable, and clean source of electricity, which makes it an attractive candidate for countries looking to meet growing demand for electricity while attempting to curb greenhouse gas emissions and adapt to climate change (Berga 2016). If these concerns are considered foremost, hydroelectric dams will continue to be built on rivers that are used by sturgeon, further impairing their ability to reproduce and contributing to the decline of their ancient lineage.

Water resources from rivers and reservoirs are routinely used for agricultural, industrial, and municipal development throughout the arable Northern Hemisphere [see reviews by Matsui (2009), O'Hara (2010), Kassen and Williams (2011) and Carle (2015)]. For example, an abundance of valuable crops is grown in semi-arid regions in California because of a complex system of dams, reservoirs, and canals that are used for irrigation (Reisner 1993). However, this complex system presents many barriers to migrating fishes, including sturgeons. As such, the impacts of river development can extend beyond hydropower generation to include water withdrawal and other infrastructure and activities that can create barriers or sources of impingement or entrainment.

On sturgeon swimming ability and sensory physiology

Achieving successful fish passage requires knowledge of the swimming ability of sturgeon as well as their sensory physiology. For upstream migrating fish, it is necessary to attract fish to a passage facility that has appropriate hydraulic conditions and cues to enable safe and timely passage. In the case of impingement and entrainment, knowledge of fish swimming ability can be used to identify areas where entrainment risk is high, and then to implement various sensory cues to guide fish away from unsafe areas towards areas of reduced entrainment or impingement risk. In some cases, this may mean trying to assist fish to locate and enter downstream bypass facilities. We discuss aspects of behavioural guidance informed by sensory physiology later in the paper. However, it is worth briefly summarizing what is known about the swimming performance of sturgeon and considering the types of sensory physiology apparatuses used by sturgeon, as these details are relevant to any discussions of fish passage.

Sturgeon swimming ability is affected by factors of their morphology and physiology that are distinct from teleost fish. Historically, most fish passage facilities have been constructed with teleost fish in mind, particularly salmonids (Clay 1994; Katopodis et al. 2019). However, the sturgeon's asymmetrical heterocercal tail is less efficient at providing power than the homocercal tail of teleost fish. Additionally, the drag a sturgeon experiences is greater than that acting on a similarly sized salmonid (i.e., a prototypical teleost) at the same speed, possibly due to the boney scutes that cover its body (Webb 1986). These disadvantages require sturgeon to expend more energy to resist or progress against a current, while their routine oxidative metabolism and anaerobic capacity are lower than those of salmonids (Singer et al. 1990). Thus, sturgeon, (i.e., of the equivalent size) do not possess the ability to surpass the strong currents or vertical barriers for which salmonids are known (Scruton et al. 1998) emphasizing the risks and challenges with extrapolating across families. However, top sustained and burst swimming speeds are proportional to body size, and migrating sturgeon are often larger and longer than salmonids when they reach reproductive age. For example, adult white sturgeon (mean FL: 136 cm, range 123–225 cm) swam at 257 cm s^{-1} against a 210 cm s^{-1} current to ascend a 24.4-m-long, laboratory swimming flume (Cocherell et al. 2011). Although the large body size of sturgeon may offset some of their disadvantages in swimming speed, it decreases their maneuverability (Peake et al. 1997; Scruton et al. 1998; Thiem et al. 2016). A full review of sturgeon swimming ability is beyond the scope of this paper; however, the topic has been comprehensively reviewed elsewhere (see Peake 2004; Verhille et al. 2014; Katopodis et al. 2019) including swimming ability for 13 species of juvenile sturgeon (Katopodis et al. 2019).

Sturgeon observe and navigate the world using a variety of sensory organs attuned to physical, chemical, and electromagnetic stimuli. The most poorly developed sense in sturgeons is sight. For example, in larval white sturgeon, only green-sensitive rods and cones are found, allowing only basic discrimination of lighting intensity in the green range of the visible spectrum; by 10 months post-hatch, white sturgeon produce blue, green, and red-sensitive cones, allowing colour differentiation, and rods sensitive to green light that help judge the intensity of light (Loew and Sillman 1993). Nonetheless, this creates opportunities for behavioural guidance with coloured lights (see below). Both visual cues and mechanosensory stimuli are used by sturgeon in rheotaxis, the behavioural tendency to orient themselves parallel to currents. Rheotaxis is an essential aspect of navigation and reduces the amount of energy expended when holding position or swimming upstream. Interestingly, an experiment on green sturgeon found that mechanosensory stimuli are more effective than visual stimuli at triggering rheotaxis (Johnston et al. 2017). The mechanosensory systems used in maintaining rheotaxis are tactile feedback as well as the lateral line system. The lateral line system is a series of mucous-filled pores on the side of sturgeons (see Fig. 1), which are highly sensitive to water movement and fluctuations of pressure in its surrounding. As well as being used in rheotaxis, the information provided by the lateral line may be used in feeding, predator avoidance, and object discrimination (Montgomery et al. 1997; Bleckmann and Zelick 2009).

Associated with the lateral line are the ampullae of Lorenzini, which can detect electric fields in the sturgeon's environment. Foraging sturgeon may sense electromotor impulses in the bodies of prey, triggering feeding (Zhang et al. 2012). The ampullae of Lorenzini may also be used to navigate using the earth's magnetic field (Jørgensen 1980), and are able to detect human-made electric fields. The ampullae of Lorenzini are mostly located on the rostrum, the flat elongated snout of the sturgeon (see Fig. 1). The rostrum also supports the olfactory system of the sturgeon, used in tracking food and potential mates. For example, pre-spawning female shovelnose sturgeon produce chemical cues, which prespawning males' olfactory system can detect and use to locate them (Kynard and Horgan 2002). The amino acids glycine and alanine are also olfactory attractants to many species of sturgeon, in concentrations as low as 1 μM (Kasumyan 1999). Another chemosensory system involved in feeding is the gustatory system. In cases where up to 85% of the olfactory system is damaged, the gustatory system can adapt to compensate for its loss (Kasumyan 2008). The gustatory system involves extraoral receptors located on the rostrum and barbels (see Fig. 1), as well as intraoral receptors. Contact of the barbels with prey triggers the feeding reflex to strike (Kasumyan 2008). The extra- and intraoral gustatory system acts as gatekeepers, informing the sturgeon about the quality of forage, and whether it should be consumed or discarded (Kasumyan and Kazhlayev 1993). A thorough review of sturgeon olfaction and gustation can be found in Kasumyan (2008).

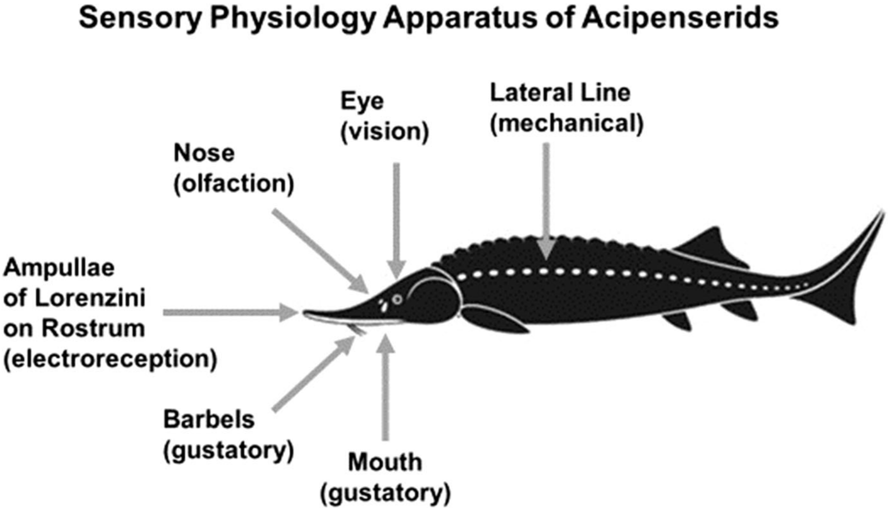


Fig. 1 Sensory physiology apparatus of sturgeon. As Chondrostei, sturgeon possess some unique sensory physiology apparatus. Sturgeon have the ability to sense and respond to diverse stimuli which is relevant to understanding fish–infrastructure interactions and for developing effective fish guidance strategies

In summary, sturgeon have a suite of sensory capabilities that help them navigate through their environment. Considering the suite of sensory systems used by sturgeon is important to understand how they perceive and navigate hydropower facilities and other water resource development infrastructure (Fig. 1). We acknowledge that it may be possible for transmission wires or other land-based infrastructure to influence sturgeon sensory physiology but there has been no research on that topic.

Safe passage

Upstream passage

Fish passage facilities are installed in an attempt to maintain (or re-establish) connectivity in fragmented systems. Engineers and biologists have struggled for decades to develop upstream fish passage facilities that work for the diversity of fish that have migratory tendencies. Fish passage facilities capable of passing salmonids are commonplace and tend to be highly effective. For that reason, many of the early attempts to develop fish passage for other fish (including acipenserids) simply involved adopting the designs that worked for salmonids with the assumption that they would work. After decades of failures, there have finally been dedicated studies focused on trying to identify the characteristics of effective sturgeon fishways. The literature base is still small, with most of the research limited to just a few sturgeon species (especially lake sturgeon and white sturgeon). The effects of dams on upstream passage of sturgeon in North America has been well documented (e.g., Auer 1996; Haxton and Cano 2016), but similar issues have also been identified in Russia (Pourkazemi 2006), Iran (Pourkazemi 2006), Azerbaijan (Pourkazemi 2006), Slovakia (Holcik et al. 2006), Romania (Kynard et al. 2002), Germany (Gessner et al. 2006), and China (Fan et al. 2006; Zhang et al. 2011; Liu et al. 2019).

Detailed field assessments of sturgeon passage facilities are generally lacking, aside from a few examples (lake sturgeon at a vertical slot fishway in Quebec; white sturgeon at two submerged orifice fishways in Washington; and shortnose sturgeon at two vertical lift fishways in Massachusetts). There are very few examples of attempts to install fish passage facilities at dams outside of North America, and where they have been used they have either not been properly assessed or deemed to be failures (but with little detail provided to inform future fish passage interventions; e.g., Chebanov et al. 2008). Even a synthesis of fish passage science for large migratory fish (with a focus on sturgeon) failed to provide any examples of where fish passage for sturgeon had been successful (Rosenthal et al. 2008). In some cases, failure to install fish passage facilities for sturgeon has been justified for reasons that are not entirely defensible. For example, Chang (2008) reported that on the Yangtze River at the Ghezouba Dam “to build fish passage particular for sturgeons was believed not at all to be useful because the fish were of considerable size and so would not use them”. Chebanov et al. (2008) provided some information on one of the few fish passages that have been studied in the context of sturgeon outside of North America. Two dams (the Fedorovskaya and the Krasnodarskaya Dams) on the Kuban River in Russia have blocked fish passage (including for historically strong populations of *A. stellataus* and *A. gueldenstaedtii*). Fishways of uncertain design were installed at the dams but it is unclear when; see Chebanov et al. 2008 for a somewhat confusing description) but they were deemed to be ineffective. One of the facilities in the system (the Krasnodar Dam; unclear its relation to the other two dams) had a fish lift that at times passed fish (including *A. ruthenus*), but the authors concluded that fish passage had yet to be resolved at the site with suggestions to focus more efforts on creating spawning habitat downstream. Kirschbaum et al. (2011) provided an overview of a series of fish passage facilities that were built at a weir at Geesthacht on the Elbe River in Germany. Previous fish passage facilities at the weir were presumably of insufficient size to pass adult sturgeon (*A. sturio* is the focal sturgeon species). First, attempts to enable sturgeon passage focused on building a side channel but apparently hydrological conditions did not allow large-scale migrations through the system (no other details provided). The new fish passage facility was scaled to enable sturgeon of 3.5 m to pass. The fishway is 500-m-long and 11-m-wide and is described by the authors as a double-slit pass (which we assume means a double vertical slot design). No details were provided regarding the effectiveness of the new fishway.

Fishway designs for upstream passage

Orifice fishways The first type of fishway to be extensively studied in the field for sturgeon passage was the overflow weir with orifice fishways on the Columbia River at the Dalles Dam (Fig. 2). The Dalles Dam has two such fishways [see Table 1 in Parsley et al. (2007) for full details on the design features of each fishway], although they differ in their configuration. The "east" fishway is larger than the "north" fish ladder. For example, the east fishway (9.1 m wide × 549 m long) is wider by 1.8 m and the submerged orifices are twice the size of the orifices in the north fishway (7.3 m wide × 536.8 m long). The lengths are quite similar. The north ladder has one entrance while the east ladder has three separate entrances. Entrance depths are typically 2.4 m or greater below tailwater elevation with a hydraulic head of 0.3–0.6 m at the entrances, and a water velocity of 0.5–1.2 m s^{-1} in the lower portions of the ladders. The slope in both fishways is 4.4%. The ladders are typically in operation throughout the year, except for several weeks during December, January, or February when they are dewatered for annual maintenance.

Fig. 2 The submerged east orifice fishway at the Dalles Dam on the Columbia River, USA. *Photo credit*: USGS

Extensive tracking studies (using both radio and acoustic telemetry) focused on white sturgeon (all > 95 cm TL) occurred between March 2004 and November 2005 to determine timing and routes of passage (Parsley et al. 2007). During the study, 17 of 90 tagged fish entered the two fishways one or more times: 11 entered only the east fishway; three entered only the north fishway; and three entered both fishways at some time during the study. Eight (out of a total of 90 tagged fish) complete ascents during the period were observed. Consequently, residence time within the fishways was variable, ranging from 1 min to nearly 6 months. There appeared to be differential performance between the two fishways. Only six fish successfully ascended the east fishway, one fish twice. The researchers suggest that differences in design between the north and east fishways may account for the greater apparent success of the east fishway (Parsley et al. 2007). Although both fishways at the Dalles Dam have overflow weirs with submerged orifices so fish can pass near the surface or along the bottom of the ladder, the one on the east side has a larger orifice and the fishway itself is 1.8 m wider (Parsley et al. 2007). The large body size of sturgeon requires thinking about the scale of fishways (especially at various constriction points) so that they can pass sturgeon.

Vertical slot fishways Vertical slot fishways can be scaled such that they are able to allow large bodied fish such as sturgeon to pass through the slots. Indeed, that is the premise behind the design of the Vianney–Legendre fishway located on the Richelieu River in Québec (Fig. 3). The river is 124 km long with an average annual discharge of 362 m^3 s^{-1} (measured at the dam site). The dam is 180° m wide and 3.4 m high, with a series of five submersible 30 m wide gates plus the Vianney–Legendre fishway. The fishway is 85 m long with 17 pools total (13 regular pools (3.5 × 3.0 m), two turning basins (2.75 m radius), and a large entrance and exit basin). There are 16 vertical slots (each 0.6 m width, 2.3–4.0 m height per slot, becoming higher toward downstream as a function of water depth and design constraints)

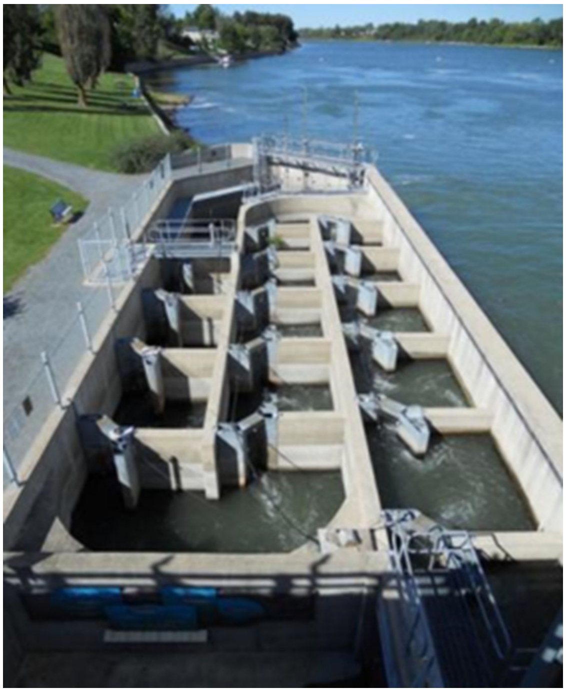


Fig. 3 The vertical slot fishway at the Vianney–Legendre fishway on the Richelieu River, Canada. *Photo credit*: Cooke Lab

throughout the fishway. The total rise is approximately 2.55 m with a total slope of 2.8%. Basins have a drop of 0.15 m, moving downstream. The top of the fishway contains a fish trap (2.2 × 2.0 × 2.15 m) in which fish that traveled up the fishway can be captured and enumerated. The fishway passes approximately 1 $m^3 s^{-1}$ of water with a capacity for an additional 6.5 $m^3 s^{-1}$ attraction flow (intended to attract fish to the entrance) near the entrance basin (Marriner et al. 2016).

The Vianney–Legendre fishway was intended to afford passage to a variety of key native fish species including lake sturgeon (*A. fulvescens*), copper redhorse (*Moxostoma hubbsi*), river redhorse (*M. carinatum*), American shad (*Alosa sapidissima*), American eel (*Anguilla rostrata*), and Atlantic salmon (*Salmo salar*). That is to say, this was designed as a multi-species fishway, but to be capable of passing lake sturgeon based on biological design criteria (especially body size of sturgeon). The Richelieu River contains a diverse fish assemblage with the Vianney–Legendre fishway being known to successfully pass at least 36 species (Desrochers 2009). Observations of adult lake sturgeon being captured routinely in the fishway exit trap prompted interest in conducting a more formal biological evaluation. To experimentally assess the effectiveness of the fishway, sturgeon were captured downstream, tagged (with PIT tags) and introduced just downstream of the entrance in an enclosure so the fish were unable to depart. As such, fish could either stay in the downstream enclosure or chose to enter the fishway (see Thiem et al. 2011). Over five trials, different groups of sturgeon were given 40–86 h to volitionally enter and pass the fishway. Although most sturgeon entered and attempted to pass the fishway (82.2%), passage efficiency was only 36.4%. Passage failure mainly occurred in the downstream portion of the fishway and the turning basins (i.e., where the fishway folds back on itself and thus there are 180° changes in flow necessitating a turning basin) presented a potential obstacle to sturgeon passage. Of the 56 individuals that failed passage, 20 failed in the two larger “turning” basins and fish spent disproportionately more time in the turning basins than in regular basins. The greatest failure rate occurred at the first turning basin. There was no effect of body size on passage efficiency which might suggest that the fishway was simply large enough for all size classes of sturgeon in the system. This experiment revealed two interesting findings: (1) that when essentially “introduced” into the fishway, success was still low; and (2) the turning basins were sources of significant delay.

One possible explanation for the low level of passage success was that the fish were simply not motivated to ascend the fishway. Because fish were captured downstream of the dam, it was possible that some of those fish were not in an endocrine state associated with migration. Indeed, subsequent blood sampling of fish downstream revealed that less than half of the fish were in a reproductive state, so may not have been motivated to ascend (Thiem et al. 2013). Moreover, egg mat surveys and a radio telemetry study downstream of the dam revealed that there was indeed suitable spawning habitat within 1 km of the dam tailrace (Thiem et al. 2013). As such, there was no necessity for fish to move upstream to spawn. The radio telemetry study revealed that very few fish approached the dam or fishway entrance suggesting that the majority of fish simply did not need nor want to move further upstream. Thus, vertical slot fishway seems to have the ability to pass adult lake sturgeon, assuming that fish are motivated to do so. This is promising for those considering fish passage on other systems, where there is not appropriate spawning habitat downstream of a dam.

As noted earlier, the turning basins were a significant source of delay during ascent. Often the term "resting basin" is used synonymously with turning basin so it is possible that fish were simply resting from physiological exertion and preparing for ascending the next reach. However, hydraulic engineers developed a computational fluid dynamics model of the turning basins, which revealed that the turning basins were characterized by highly complex vortices that presumably caused confusion for upstream migrating fish (Marriner et al. 2016). In silico modeling exercises suggested that the addition of a baffle could disrupt the vortex, and thus create a true resting environment while also making upstream flow cues more apparent (Marriner et al. 2016). That modification has yet to be implemented but is being considered by local resource managers.

The final aspect of research conducted on the Vainney-Legendre Fishway involved use of triaxial accelerometers to estimate the energetic expenditure (i.e., in terms of calories or joules) of swimming by lake sturgeon (Thiem et al. 2016). High-speed swimming was rarely observed during upstream passage through fishway basins, but when it did occur it was of short duration. As noted before in the PIT-tagging study, the turning basins delayed passage, elevating energetic expenditure. Interestingly, the rate at which energy was expended did not differ between successful and unsuccessful individuals (as estimated using calibrated accelerometer loggers). Energy expenditure metrics were not predictive of successful fishway passage, leading the authors to conclude that other endogenous or exogenous factors influence passage success. Of particular note was that energetic loss for lake sturgeon (3249–16,331 J kg^{-1}) associated with passage was equivalent to individuals travelling 5.8–28.2 km in a lentic system. In systems or years where fish condition is poor, fish passage may have significant negative consequences on fish unless they are able to pass rapidly.

Side baffle ladder In some cases, entirely new fishway designs have been developed in an effort to enable sturgeon passage. Kynard et al. (2012) developed and tested a prototype spiral side-baffle ladder for both upstream and downstream passage for wild adult male pre-spawning shortnose sturgeon. The ladder had two loops and spiraled upwards at 6% slope for 38.3 m around the outside wall of a 6.1 m diameter circle. The total rise was 1.92 m. The fishway was equipped with 28 triangular side baffles extending partway into the channel and alternative from the inside and outside wall. That configuration was chosen to create a sinusoidal flow down the ladder, as well as an eddy downstream of each side baffle. Passage success was positively associated with fish size and time provided to the fish to pass (i.e., more time in the ladder meant greater likelihood that they would eventually pass). For fish that spent 6 days in the ladder, 65% ascended to the top and 34.7% of all fish that did so also made round trips up and down the ladder, demonstrating bi-directional movement potential. The actual ascent times were usually short (< 1 h) once they committed to upstream movement, with most of such movements occurring at night. There was no evidence of injuries from baffles. The same prototype fishway was also studied using two sizes of cultured lake sturgeon (sub-adult; 105 cm TL, mean; adult; mean TL, 118 cm; see Kynard et al. 2011). Twenty-two fish were repeatedly tested in groups as juveniles in fall and spring periods. More of the juveniles entering the ladder ascended to the top in spring (72.7%) than in fall (40.9–45.5%). In addition, 90.9% of 11 adults, which ascended as juveniles (and then matured in subsequent year), ascended to the top. Some fish never swam to the top, potentially indicating differential motivation among individuals.

Fish lifts Fish lifts have been used in an attempt to enable passage of sturgeon and other large-bodied fish. The success of fish lifts depends on a number of factors, some germane to all devices. For example, fish need to find and enter the lift but may also face issues related to crowding and exclusion. There are also operational issues related to how often and when (e.g., at night) the lift should be operated, which may require on-site staff. Kynard (2008) describes an example where the science demonstrates that most sturgeon migrate upstream at night, yet the fish lift is only operated during the day. The best information available on fish lifts and sturgeon comes from a mini-review prepared by Kynard (2008). They highlight examples of sturgeon use of fish lifts with a particular focus on two lifts at the Holyoke Dam: one larger tailrace lift and a smaller spillway lift (Fig. 4). It

Fig. 4 The Robert E. Garrett fish lift (elevator) at the Holyoke Dam on the Connecticut River, USA. *Photo credit*: City of Holyoke

is important to note that neither lift was specifically designed for sturgeon. Nonetheless, it does pass sturgeon, although not particularly well. A few shortnose sturgeon (69–135 cm TL) were observed to enter the lift in spring, summer, and fall (0–16/day; mean for 22 years = 4.4/year; Kynard 1998, 2008).

Step plunge pool designs Bruch (2008) reported on passage of lake sturgeon at the Eureka Dam fishway on the Upper Fox River of Wisconsin. The fishway was built in 1988 (a three-step plunge pool design; see Fig. 5) and the dam itself was retrofitted in 1992–1993 to be a rock rapid design such that fish could potentially use both paths. Several years after construction, a rock wing deflector was added downstream to better direct flow in a manner to attract fish to the passage. The fishway along with the rock rapid weir design apparently enable unimpeded bi-directional movement of fish but details of the science to support that statement is lacking (reported as a personal communication).

Fig. 5 The three step plunge pool Eureka Dam fishway on the Upper Fox River, Wisconsin, USA. *Photo credit*: Wisconsin DNR

Factors affecting upstream passage performance

Several experimental studies have occurred in lab settings to better understand the interactions between fish and fishways. Cocherell et al. (2011) evaluated passage performance of adult wild-caught white sturgeon (123–225 cm TL) in a simulated mid-section of a 24.4-m-long experimental fishway incorporating vertical barriers, a 4% slope, and a series of five, paired vertical baffles (with 0.61-m slot widths). The study focused largely on comparing low and high tailwater conditions (i.e., water depth at the base of the fishway) and contrasting the performance of fish in various levels of physical condition. Approximately half of the "healthy" fish reached the upstream end of the flume in both the low (50% of the fish) and high (48%) tailwater treatments whereas only 5% of fish in poor condition did so. This study adds to the body of literature helping to explain differential success among individuals. Yet, even among the fish in good condition, only half of them ascended the fishway, again emphasizing the role of motivation and other, yet to be elucidated, factors.

Although there have been a number of swimming performance studies conducted in an effort to identify biological performance criteria for sturgeon [summarized briefly above, see Peake et al. (1997), Cheong et al. (2006)—as well as Katopodis et al. (2019) for a review of the research done on sub-adult sturgeon], few have done so in a manner that explicitly investigates how different fishway design elements (e.g., baffles) could influence performance, which would increase the relevance of the work to fish passage.

Webber et al. (2007) swam wild adult white sturgeon (TL 135–198 cm) in a variable-speed aluminum flume (24.4 m long 3 2.1 m wide 3 1.4 m deep) to evaluate swimming behavior around simulated fishway partial baffles. The researchers tested four baffle types, one horizontal ramp, and three different vertical slot designs, set in two configurations, at three velocity regimes (velocity range around baffles, 0.28–2.52 m/s). The authors reported that faster velocities (0.76–1.07 m/s) tended to cue fish to swim upstream sooner (i.e., within 100 s). The percentage exhibiting successful passage was variable among baffle types, but offset baffles (e.g., to more effectively slow the flow in the flume) did not work. The sturgeon tended to "burst" swim along straight paths, running into the offset baffles and halting their progress upstream. The authors concluded that fishways intended to be successful for white sturgeon should incorporate rapid-velocity (e.g., 0.84–2.52-m/s) sections, between somewhat slower (e.g., 0.51–0.68-m/s) sections for rest and recovery. This observation (and conclusion) is important in that it aligns with field observations (e.g., Thiem et al. 2011, 2016) and provides evidence that successful fishways require combinations of high flow areas and low flow areas [similar criteria incorporated into the prototype side-baffle fishway designed by Kynard et al. (2011, 2012)].

Entrance sills to fish lifts (and frankly all fishways) downstream of dams need to be as deep as possible, and ideally aligned with the bottom of the river to enable these benthic oriented fish access (Kynard 2008). In a study of shortnose sturgeon downstream of Holyoke Dam in the northeastern US, Kynard (cited by Kynard 2008, but unable to find original source) reported that even with appropriate attraction flow, sturgeon fail to find the entrance to the tailrace lift because it is positioned in shallow, turbulent water, away from areas used by the sturgeon.

More considerations for achieving upstream passage

After discussing potential fish passage solutions for sturgeon, it may seem counterintuitive to suggest that fish passage may not always be necessary or helpful. Although the idea of providing upstream passage for fish and thus re-establishing connectivity seems sensible, for a variety of reasons there may be certain instances where that is not the case. For example, there is evidence for some fish, including sturgeon, that upstream passage at dams may create ecological traps. An ecological trap is a scenario where anthropogenic change or rapidly changing environmental conditions lead organisms to settle in poor-quality environments with fish passage being but one example (Schlaepfer et al. 2002). In the context of fish passage, ecological traps occur when fish are moved from a lotic environment downstream of dam to a lentic environment upstream. Impounded reaches (i.e., reservoirs) are quite different from pre-impoundment conditions; they lack the original flow cues, have different thermal conditions, and different physical habitat. Reservoirs can also have different ecosystem structure, such as unfamiliar food sources, and there may be predators that do not exist in riverine reaches.

Beyond the concept of ecological traps, it is also possible that fish passage may not be needed if there is suitable spawning habitat downstream. Of course, this requires knowledge of spawning habitat use and distribution of sturgeon prior to dam construction, which may not always exist, and it requires that spawning habitat still exists downstream, given the alterations to the habitat caused by the dam. Thiem et al. (2013) affixed radio transmitters to lake sturgeon downstream of the Vienney–Legendre Fishway on the Richelieu River in Quebec and observed that very few fish approached the dam or fishway and instead spawned in habitats downstream of the dam. It is unclear whether the spawning habitats used were present before dam construction or if dam construction and subsequent operations helped to create habitat suitable for spawning. In that system, it was presumed that some fish spawned in upstream reaches, but the prevalence of upstream spawning was unknown. In that case, passage of fish upstream that intend to spawn downstream may in fact take them away from habitats that are fully suitable for spawning.

For the reason described in the previous paragraph, prior to considering the type of passage facility that is needed, the first question that needs to be asked is "is fish passage necessary or desirable" (Cooke and Hinch 2013). Ideally, information (from either scientific studies or traditional or stakeholder knowledge) will be able to identify the historic distribution of sturgeon in a given system. Moreover, it is important to understand the life history and population biology of a given species and population. For example, knowledge of age of maturation, frequency of reproduction, and population size is needed to truly understand if passage is needed and if so, what level of passage success is needed to achieve management targets. It may be the case that only a fraction of a given "downstream" population wants to or needs to pass in a given year. Again, the example from lake sturgeon in the Vianney–Legendre fishway is informative in that endocrinology studies revealed that only 30% of the fish downstream of the dam were in a hormonal state that would suggest they were going to reproduce that year. Designing a fishway that passes 100% of the sturgeon is simply not necessary; ideally, the fishway would pass 100% of the sturgeon that historically would have engaged in upstream migration to spawn. As noted above, the challenge is having sufficient baseline data to be able to project where fish need to go, and how many need to go there.

Downstream passage

Downstream passage has been poorly studied for sturgeon. Downstream passage is necessary for iteroparous species that undertake upstream spawning migrations, and then need to return to downstream waters to complete some aspects of their life cycle. Downstream passage is also necessary for offspring spawned by migrants, either during larval drift or after some level of upstream rearing. For larvae and juveniles, it is presumed to be a "go with the flow" model in which individuals are most likely to take the path where the majority of the water is going, which is often through a turbine (i.e., entrainment) if a dam exists. In instances where entrainment mortality is low for early life stages, turbine passage may suffice for downstream passage. However, it may be more desirable to create bypass channels or try to direct fish to the upstream entrance of fish passes primarily designed for upstream passage. At weirs, spillways, or sluiceways where water tops the dam infrastructure, it is presumed that some fish go over the top, particularly during high flows when they would be difficult to see or detect via traditional monitoring. The challenge with any downstream passage is trying to get fish to find the entrance, which is often rather small (especially for upstream fish passes). Often times the upstream "exit" of a fishway is placed in areas rather far from the intakes, to prevent immediate entrainment of fish that pass, but this presents added challenges in that the fish passage entrances are often spatially separated from the path where the bulk of the flow is going. Aside from anecdotes, there is very little known about downstream passage or how to make it effective. Locating the upstream exit (and thus entry point for fish moving downstream) can be quite a challenge for a fish attempting to navigate downstream. The behavioural guidance approaches discussed below will almost always be needed to attempt to concentrate fish (by repelling them from undesirable paths and attracting them to good ones), but we were unable to find examples of where this has been used successfully.

The need for adult fish to move downstream varies widely depending on the natural history and habitat mosaic for a given population. If spawning habitat is upstream of a dam, downstream movement, unless of great benefit for feeding or overwintering, may be costly. Efforts to understand the genetic and population-level consequences of downstream movements have been challenging, and there is still much to resolve. Although most of the work on downstream passage of sturgeon has been done in the context of impingement and entrainment of sub-adult fish, there are instances where adult fish have moved downstream through pathways that are comparatively safer than turbines. For example, at the Dalles Dam on the Columbia River, Parsley et al. (2007) released 58 adult white sturgeon in the forebay and tracked them with acoustic and radio telemetry. Eighteen of these tagged fish moved downstream, mostly through open spill gates. In this case, there were trash racks in place on the turbines to prevent entrainment of adult sturgeon, and it was unclear whether the movement of fish through open spill gates were volitional downstream movements or entrainment events. However, the fish appeared to survive downstream passage, so they have the potential to re-ascend the fishways. Sublethal consequences of such downstream passage events are poorly understood. Schulze (2017) experimentally passed adult lake sturgeon above a dam on the Menominee River in northwestern Michigan and northeastern Wisconsin, and tracked them to assess movement and habitat use. Interestingly, sturgeon exhibited a 17% probability of passing downstream of Park Mill Dam in the Lower Menominee River in spring (March, April, May) and an 8% probability in both summer (June, July, August) and fall (September, October, November) each month after upstream passage. Probabilities of downstream passage at Menominee Dam were 36, 42, and 33% for spring, summer, and fall, respectively. Given the configuration of the dams (a weir), the fish would have had to pass over the top of the facility or go through one of the turbines. A bypass has since been installed at the Menominee Dam. More work is needed to differentiate between volitional downstream movement, which is an important part of their life history that benefits the population, and entrainment that represents a loss to the population or upstream spawning population (Jager 2006).

Entrainment and impingement

Entrainment occurs when fish become involuntarily drawn into water control structures (e.g., turbines, water intakes in irrigation facilities). We found reports of Atlantic sturgeon entrainment at the Salem Nuclear Generating Station in New Jersey, USA at the intake trash rack in the Delaware River involving fish ranging from 443 to 713 mm (https://www.nrc.gov/docs/ML1310/ML13100A211.pdf; https://www.nrc.gov/docs/ML1333/ML13336A690.pdf). Entrainment may or may not result in injury or death (reviewed in Harrison et al. 2019; But see Algera et al. (2020) for a systematic review that concludes that immediate mortality is 235 times higher for temperate fish that are entrained either through or over hydropower infrastructure relative to controls), but in general, efforts are undertaken to reduce or prevent entrainment through use of water intake screens or racks. Unfortunately, this can lead to other issues such as impingement. Impingement occurs when free-swimming fish get “stuck” (due to negative pressure) to some form of water intake screen or rack (Barnthouse 2013). Poletto et al. (2014) placed individual juvenile green or white sturgeon in a laboratory swimming flume in the presence of standard fish screens (2 mm bar spacing) at two field-relevant water velocities (20.4 ± 0.1 and 37.3 ± 0.3 cm s^{-1}), at 18 °C for 15 min during the day or night. Green sturgeon contacted and impinged upon the screens twice as frequently as white sturgeon and differed in how their behaviors were altered by water velocities and time of day. In general, early life stages of fish may seem more susceptible to impingement on screens, but that is largely a function of bar/grid spacing in screens and racks (Danley et al. 2002; Grimaldo et al. 2009); adults can also be impinged, meaning that general rules governing impingement are difficult to establish (Barnthouse 2013). Given the usual sustained intake at hydropower facilities, once a fish is impinged, they tend not to be able to escape and eventually succumb to injuries related to water pressure that physically harm the body or impede respiration. For fish that do escape an impingement scenario, there is evidence that they may experience impairments in swimming performance and behaviour that could promote predation (OTA 1995).

Impingement of sturgeon has been observed at various facilities on the Hudson River, USA (http://cybrary.fomb.org/sturgeon/atlanticsturgeon2007statusreview.pdf). Between 1972 and 1998, 63 shortnose sturgeon ranging from 200 to 700 mm were observed impinged at six facilities (Applied Science Associates 1999). Interestingly, impingement was not uniform across the six facilities, with little insight into the driver of that variability. Impingement was sufficiently frequent on the Hudson that they were able to use impinged carcasses to study the diet of juvenile shortnose sturgeon (Carlson and Simpson 1987).

Understanding impingement and entrainment of sturgeon is a critical consideration for their conservation so that mitigation can be effectively implemented. To that end, there has been extensive research on trying to reduce sturgeon impingement and entrainment. For example, Prakash et al. (2014) used swimming capabilities to suggest that Atlantic and shortnose sturgeon can swim well enough to move away from the potential zone of influence of ship ballast intakes and avoid impingement. However, this does not consider whether the fish can detect the threat in time to swim away. Noise associated with some intakes (particularly at hydropower facilities) may be sufficient to limit impingement encounters, but there is little empirical evidence that this occurs (http://waves-vagues.dfo-mpo.gc.ca/Library/363356.pdf). Larger intake pipes enable closer bar spacing, or even use of screens, having the potential to yield low impingement rates while also dramatically reducing entrainment and subsequent mortality (http://waves-vagues.dfo-mpo.gc.ca/Library/363356.pdf). Impingement of eggs, larvae, and juveniles tends to be most common on screens with narrow mesh size, and tends to be highest when intakes are near spawning and rearing habitats. Mussen et al. (2014) examined avoidance behaviors and entrainment susceptibility of juvenile green sturgeon (35 ± 0.6 cm mean FL) to entrainment in a large (> 500-kl) outdoor flume with a 0.46-

m-diameter water-diversion pipe. Sturgeon entrainment was very high [range 26–61%, as compared with 0.8–8.5% for juvenile Chinook salmon in similar experiments (Mussen et al. 2013)], likely due to a lack of avoidance behavior prior to entering inescapable inflow conditions. These authors estimated that up to 52% of green sturgeon could be entrained after passing within 1.5 m of an active water-diversion pipe three times. Thus, juvenile green sturgeon are probably very vulnerable to unscreened water-diversion pipes, and additional research is needed to determine the potential impacts of entrainment mortality on declining sturgeon populations. Finally, data under various hydraulic conditions also suggest that entrainment-related mortality of these juveniles could be decreased by extracting water at slower diversion rates across longer periods of time, balancing agricultural needs for a desired volume of water with green sturgeon conservation (Mussen et al. 2014). In the last decade there have been a number of swimming performance studies published that focus on juveniles and provide data needed to help inform risk assessment and mitigation for impingement and entrainment [e.g., Deslauriers and Kieffer (2011, 2012); reviewed in Katopodis et al. (2019)].

In general, screens trade-off entrainment for impingement risk. Sturgeon mortality resulting from impingement seems to be greater than from entrainment given that escaping impingement is challenging but entrainment more frequently conveys fish to downstream reaches, although it can also be stressful, injurious, and certainly lethal in some circumstances. If entrainment simply represents loss from one system, but the fish survive passage and subsequently reside in a downstream reach, then that creates other opportunities for mitigation (e.g., safe passage back upstream) and is preferable to mortality of the individual. In such instances where entrainment is low or survival of entrainment rates is high (assuming that both of these rates represent reliable estimates), it may be undesirable to use intake screens given that it may introduce impingement mortality. For effective management, the trade-offs between entrainment and impingement need to be explored quantitatively and interfaced with reach-specific populations models specific to sturgeon species (Barnthouse 2013).

Behavioural guidance

Mitigating negative interactions between sturgeon and infrastructure benefits from guiding them away from danger and towards safety. However, effectively directing sturgeon towards safe pathways for undertaking upstream and downstream movements remains a challenge. Guidance techniques that lead fish away from hazardous areas such as hydropower turbines or unprotected water-intake pipes have also been explored (Schilt 2007). Although physical barriers (as discussed above largely in the form of screens) can be used to reduce likelihood of entrainment (e.g., Noatch and Suski 2012), fish may still become impinged upon them and both entrainment and impingement can be lethal. Behavioral guidance strategies aim to exploit the sensory modalities of target animals to achieve desirable outcomes (Coutant and Whitney 2000; Noatch and Suski 2012). Behavioural guidance can be used to either repel or attract sturgeon and can even be used in combination (e.g., repelling them away from an unsafe or undesirable area and attracting them to a desirable area). As described above, sturgeon have diverse and somewhat unique sensory physiological systems that provide varied opportunities for behavioural guidance. In general, relatively little is known about behavioural guidance of sturgeon. What is clear is that there is likely much interspecific variation as well as potential substantial variation among individuals of the same species, especially with respect to sex, maturation state, and ontogeny (e.g., Elvidge et al. 2019).

Behavioural guidance offers much potential for sturgeon given their diverse sensory physiology apparatus. Physical, visual, electro-physical and chemical guidance methods have revealed the complexity of guidance with respect to age, size, maturation, and species of sturgeon and it is still too early to generalize regarding what works best for a given species in a given situation (see below for example). Light, low-voltage electricity, and certain chemicals may show promise, but without field-scale trials, these tools remain unproven solutions to the pressing problems associated with entrainment and impingement of sturgeons at various water intakes and outlets in their spawning rivers. Louvers and bar racks have been well studied for other species (e.g., salmonids; see Coutant and Whitney 2000) but have received relatively little attention from sturgeon researchers.

Here we provide a brief overview of the literature related to these various behavioural guidance modalities specific to sturgeon.

Physical guidance Physical guidance devices can be used to guide fish and is most often used to direct fish away from areas of potential danger and towards areas of safety. Louvers represent the most common approach. The concept of a louver is that it serves both as a physical barrier (although they tend to have large enough spacing that fish can swim through them) and a means of creating flow characteristics that are detectable by fish and thus result in behavioural responses. We found relatively little research on use of louvers to guide sturgeon.

Kynard and Horgan (2001) conducted experiments in a shallow experimental flume (water depth of 37 cm) with yearling shortnose and pallid sturgeon. The researchers tested two guidance structures—vertical bar racks and louver arrays. The vertical bar rack configuration involved slats spaced 3.9 cm apart that were oriented directly into the approach flow at a 45° angle to the flow. The louver configuration involved slats spaced either 3.9 cm apart or 9.0 cm apart. For both spacings, the louver slats were oriented at a 90° angle to the flow. The row of slats was oriented at a 20° angle to the approach flow. The authors reported that both species were guided by the louver array (96–100% efficiency). Guidance efficiency was comparatively less for the bar rack (58–80%). There was also some evidence of diel variation in guidance efficiency with higher efficiency during the day. At night there was frequent contact between the sturgeon and the structures suggesting that they were presumably responding to visual cues as well as or instead of flow-related cues.

A flume study by Amaral et al. (2002) focused on juvenile lake sturgeon and shortnose sturgeon to determine guidance efficiency of angled bar racks and louvers. The researchers studied YOY lake sturgeon with the arrays angled at 45 and 15 degrees to the approach flow, and age-l lake and shortnose sturgeon were evaluated solely with the guidance structures set at a 15° angle. Experiments were replicated across three approach velocities (i.e., 0.3, 0.6, and 0.9 m/s). Overall, guidance efficiency of YOY lake sturgeon was low (< 37%) with the highest guidance efficiencies for YOY lake sturgeon observed at 0.3 m/s and the lowest at 0.9 m/s. The use of perpendicular bar racks failed to guide the YOY sturgeon. In contrast, guidance efficiencies for age-l lake and shortnose sturgeon were high (> 90% at all velocities) especially during tests of the bar racks and louvers with the solid bottom overlay installed. The authors concluded that the use of angled bar racks and louvers may not be appropriate for sturgeons less than about 20 cm in length but may be effective for large bodied individuals or species. This work clearly shows the important role of fish size in influencing swimming performance and thus how approach velocity may dictate the type of guidance method that should be used. Moreover, the researchers revealed that the presence of a bottom overlay influenced the overall performance of the louver and bar racks such that more work is needed to inform optimal overlay design.

Ford et al. (2017) studied the performance of a louver in a laboratory setting in combination with LED lights to guide juvenile white sturgeon (see "Visual guidance" section for detailed discussion) which also showed promise but emphasizes how guidance methods may work best when combined. Overall, there is some evidence that louvers and bar racks of various sorts can be effective but they seem to be context specific with respect to factors such as body size (presumably as a proxy for swimming performance), approach velocities, species, and diel period.

Visual guidance Based on visual physiology studies evaluating retinal sensitivity, it was determined that white sturgeon are sensitive to green light as larvae and then gain sensitivity to red as they mature and disperse deeper in the water column (Loew and Sillman 1993). Using that knowledge, Elvidge et al. (2019) conducted a study involving behavioural responses of live fish. They compared behavioural responses of age 1+ and 4+ lake sturgeon. Based on an initial y-maze dichotomous choice study in age 1+ fish during daytime, the researchers selected green, blue, orange, and full-spectrum white light, strobing at 1 Hz and then used those settings for further testing. At night, age 1+ sturgeon were most rapidly attracted by blue light; orange light was the least attractive initially, but fish spent the most time in the orange light. Conversely, at night, age 4+ sturgeon, demonstrated strong avoidance of blue light and white light. Age 4+ fish were negatively phototactic with orange light being the least repulsive. To guide 1+ lake sturgeon at night, blue light strobing at 1 Hz could therefore be used to attract fish in the 1+ age class and white light strobing at 1 Hz for their repulsion. For age 4+ fish, the authors recommended the use of blue light or white light strobing at 1 Hz for repulsion. This study further demonstrated the important role of ontogeny when considering the use of light for behavioural guidance. LEDs have emerged as a potential new tool for behavioural guidance, providing an adjustable light spectrum and strobing frequency. Ford et al. (2018) exposed age-0 white sturgeon to light strobing at 1 Hz, 20 Hz, or constant illumination with three colours (i.e., green, red, blue) matching the absorbance maxima of their retinal photopigments (based on literature studies of retinal activation). The researchers then assessed the behavioural responses of the sturgeon using y-maze dichotomous choice under light and dark conditions. Age-0 white sturgeon demonstrated positive phototaxis under all conditions and approached the LED array more often when light was continuous or strobing at 20 Hz compared to strobing at 1 Hz. Green light was the most "attractive" to the fish while red was mildly repulsive. This study suggests that varying both strobing frequency and colour has the potential to guide sturgeon. It is important to note that light may have unintended consequences on other non-acipenserid species which needs to be considered when using light for behavioural guidance although this is poorly understood.

In one of the few studies to combine different forms of behavioural guidance (in this case LED lights and a louver), Ford et al. (2017) revealed some reasonable success. Specifically, they tested an LED light array (with adjustable wavelength and strobing output) and a reverse-configured louver rack in a laboratory flume intended to simulate a bypass for age-0 white sturgeon. The researchers reported that in the absence of the LED array, louver slat spacing of 10 or 20 cm were reasonably effective at achieving downstream bypasses with greater success rates (ca. twofold greater) under night conditions than under day conditions. They then used the most attractive LED setting [green light (540 nm) strobing at 20 Hz] with the louver spacing of 10 or 20 cm to achieve bypass usage rates of 100% by day and 97% by night relative to a control treatment (no LED or louver) which had a 46% bypass rate. Tests with red light (605 nm) presented behind the louver failed to provide additional benefit over using green light to attract fish. The combination of light and louvers remains promising for behavioural guidance of sturgeon.

Electrophysical guidance Sturgeon have been shown to be sensitive to anthropogenic electrical signals and orient relative to them (Basov 2007). To our knowledge, only a single study has used electricity for behavioural guidance. Stoot et al. (2018) exposed two size classes of juvenile lake sturgeon to low-frequency (0.1–50 Hz) low-voltage (0.024–0.3 V) electric fields and assessed their behavioural response and the sublethal physiological consequences. Smaller, younger fish were more reactive to the electric stimulation of the fields than older, larger fish. Their results also revealed that individuals can acclimatize to electric fields in a relatively short time period and that the larger individuals tended to be less affected by low-frequency/low-voltage electric fields than smaller fish. This very preliminary study suggested that electricity for guiding sturgeon could be promising but more research is needed to determine the extent to which it could work in field settings.

Chemical guidance It appears that most of the research conducted thus far has focused on attempts to repel sturgeon but we also found several studies that attempted to attract sturgeon. Sturgeon behaviour is stimulated by pheromones (Kasumyan and Mamedov 2011) that could be applied to attract fish; for example, Kynard et al. (2012) used the odor of mature female shortnose sturgeon at the top of a prototype spiral fishway in an attempt to increase passage of male sturgeon. This attempt to use odor (presumably pheromones) failed to significantly enhance male sturgeon passage. Poletto et al. (2013) acclimated juvenile green sturgeon (ca. 4.5 mo. old, 38.0–52.5 cm TL) to either "fresh" water (salinity = 3.2 ppt) or "sea" water (34.1 ppt) for 8 weeks. Following acclimation, the two groups were further divided into experimental and control groups, where fish were individually introduced into a rectangular salinity-preference flume (maximum salinity gradient for experimental groups: 5–33 ppt). Controls were presented with only their acclimation water ("fresh" water or "sea" water) on both sides of the flume. Both "fresh" and "sea" water-acclimated experimental fish spent longer on the "sea water" side of the testing area, whereas both control groups spent an equal amount of time on each side of the flume (Poletto et al. 2013). These findings indicate that anadromous, juvenile green sturgeon were not only capable of detecting “sea” water within the first year of their lives, but might actively seek out more saline environments or currents as they move through a watershed. Besides providing a better understanding of this threatened species’ early life history, its salinity preferences suggest a possible guidance mechanism (salinity, as a chemical cue) to lead out-migrating fish to relatively safe routes past dams or other structures. Fish guidance via salinity gradients has been investigated in juvenile salmon (McInerney 1964); research on anadromous sturgeon could extend this knowledge using both laboratory and field studies. For example, laboratory studies could determine life-stage-specific threshold salinity responses, with complementary field studies examining the movements of ultrasonically tagged fish towards a simple pipe array diffusing saline solutions on the bottom of a reservoir (e.g., towards a safe exit downstream). Obviously, to minimize adverse effects on downstream biota (including possible crops), careful attention to the quantities of salt used in such guidance systems would be required.

Dam removal

While hydropower construction is globally on the rise, dam decommissioning or dam removal is increasingly attracting attention as a viable tool for river restoration, particularly in Europe and parts of the United States, where historical damming has been extensive (e.g., Bednarek 2001; Hart et al. 2002). Dam removals, even of small facilities, are typically large projects that involve complex social and institutional considerations (Magilligan et al. 2017), as well as ecological considerations (e.g., consequences of silt releases; McLaughlin et al. 2013). Examples of dam decommissioning and dam removal are still therefore relatively rare. However, the few examples that do exist suggest that such actions benefit sturgeon species. As one example, the Edwards Dam on the Kennebec River in Maine was previously a hydropower facility that was removed in 1999, when the Federal Energy Regulatory Commission (FERC) refused the renewal of the dam license due to excessive negative environmental impacts. Within a year after the dam removal, large numbers of Atlantic and shortnose sturgeon, among other species, were observed in upstream habitats that had been inaccessible to these species for 162 years since the dam construction (O’Donnell et al. 2001); in the years since, shortnose sturgeon have been observed spawning in this previously inaccessible upstream habitat (Wippelhauser et al. 2015). The extent to which sturgeon are opportunistic when presented with novel habitats is unclear but research from reef creational activities suggests that it is possible (Johnson et al. 2006).

As another example, California’s two native sturgeons, semi-anadromous white sturgeon (*A. transmontanus*) and anadromous green sturgeon (*A. medirostris*), must migrate up modified river systems such as the Sacramento and the Klamath to spawn (Schaffter 1997; Brown 2007). Heublein et al. (2009), using ultrasonic tracking of adult green sturgeon, found that their migrations up the Sacramento River were impeded by a springtime closure of gates at the Red Bluff Diversion Dam. The reservoir (Lake Red Bluff) behind this dam provided gravity-fed water for irrigation canals of the Central Valley Project, Operated by the U.S. Bureau of Reclamation. Due, in part, to the migratory obstruction of these US Endangered Species Act-listed sturgeon, the dam was decommissioned (i.e., gates remain open) in 2013. A pumping plant was constructed a short distance upstream to supply water to the irrigation canal system, and the Sacramento River now flows freely at this site. This is an example of a dam removal project that directly benefits sturgeon.

Synthesis

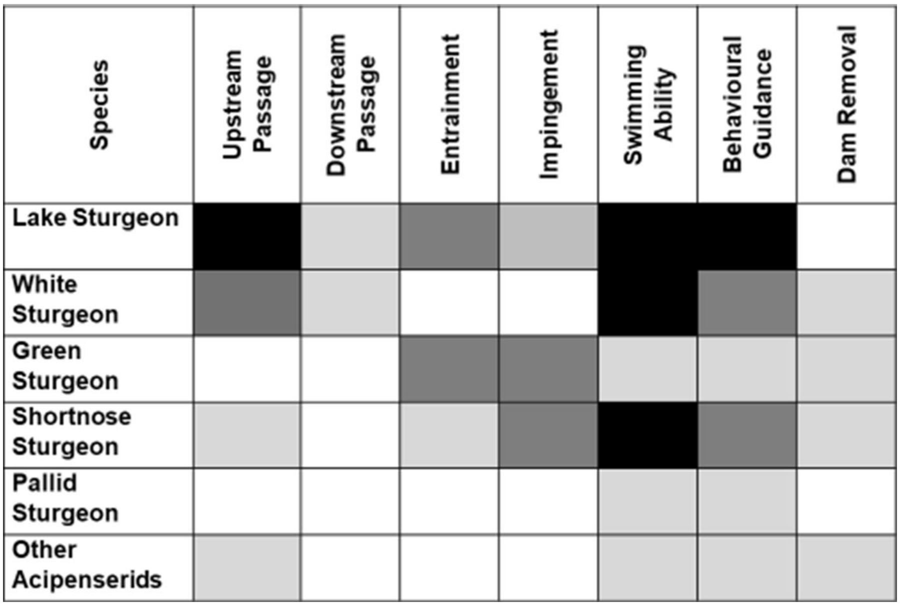
Our literature searchers identified theses, technical reports, and peer reviewed papers addressing topics specifically relevant to our aims. On the surface, this may seem like an impressive amount of information. However, in actuality, the distribution of research effort is taxonomically grouped; several species (i.e., lake sturgeon, white sturgeon, green sturgeon, Atlantic sturgeon, shortnose sturgeon) are reasonably well studied, while the remainder have been ignored entirely. There was also a clear trend with the majority of sturgeon literature pertaining to the topic of this review being conducted in North America, with almost negligible work in Eurasia [our literature search covered international English language journals, e.g., The Iranian Journal of Fisheries Sciences, Turkish Journal of Fisheries and Aquatic Sciences, Indian Journal of Fisheries, and Journal of Ichthyology (printed in both English and Russian)]. The geographic bias to North America is particularly worrisome, given that hydropower facilities are common in Eurasia (indeed, four of the 10 largest hydropower facilities in the world are in Russia and China), and suggests that hydropower development is being done without science to guide their mitigation decisions. Our literature review was limited to English and French, so it is possible that we missed studies conducted in regions where publication or dissemination in English is uncommon, but sturgeon conservation issues are abundant (e.g. Russia, China, Iran). However, we conducted cited reference searches using key historical papers that would most certainly be cited no matter the language, and we failed to identify a meaningful concentration of studies in other languages that were missed. We also found some papers that had been translated (from Russian). As such, we feel confident that we summarized the vast majority of the published literature on this topic.

The studies covered in our review spanned the lab, the computer (i.e., in silico modeling), and the field with relatively few studies spanning realms. This is problematic in that, with few exceptions (e.g., Mussen et al. 2014), lab studies are not being scaled up to determine if they work in the field, and field studies are not being dissected to determine (experimentally in a lab context) what we could do better, or to identify specific mechanisms. It is also problematic that there is little evidence of sustained research programs on the topics addressed in this review. The work has been done by many different groups, often at the level of one thesis, one paper, or one study within in a given research group. The issues covered in this review are complex, and would benefit from long-term focused effort in the form of a research program, rather than things being tackled as discrete one-off projects, which currently seems to be largely the norm.

Finally, we have reason to believe that there is some level of bias in the literature. Studies with “negative results” are much less likely to appear in the literature (i.e., the so-called “file drawer effect”). Therefore, we assume that many of the studies related to passage and entrainment that represent “failures” (e.g., no benefit of various interventions of installation of entire passage facilities that fail to pass sturgeon) are likely unpublished, and are far more common than represented through this review. We encourage researchers and practitioners to publish their work (even if only in case study format) so that lessons can be learned and shared across jurisdictions about both success and failure.

Research needs

The most obvious need is to conduct the kind of research summarized here on a greater diversity of acipenserids recognizing that it is impossible to do it all. The reality is that for most species (> 80%), there is simply no information to help inform issues described in this paper (Fig. 6). There is also much that could be learned from more focused effort on several species to try and understand all aspects of migration with the hopes that lessons learned could be exported. Even today the more well-studied species (lake sturgeon, white sturgeon, green sturgeon) are not studied so well that we know exactly how to mitigate hydropower or irrigation-related losses, and we know only a fraction of what one would want to know to properly inform evidence-based management. In an ideal world, we would conduct a meta-analysis where we quantitatively test the factors that influence, for example, passage success. Even if one were to group all acipenserids together, such quantitative analysis would be impractical. If one were to evaluate the quality of the research conducted to date and use rigid screening criteria (as is common in systematic reviews), it is entirely likely that many of the studies conducted here would be excluded. All of this is to say that the evidence base is shallow. We also fear that there is a major “file drawer effect” whereby there is a bias against publishing studies that show the failures of fish passage facilities, behavioural guidance strategies, or other mitigation efforts. Considering the great uncertainties and superficially poor passage rates for sturgeon observed in the literature (see discussion above re: motivation), it is worrisome to think that the studies that are published are the ones that might have the best levels of passage success. We need to encourage practitioners and local knowledge-keepers to share their observations about sturgeon passage, even if it is about a total failure, to inform our general understanding of fish passage. Doing so could help to reduce the likelihood of repeating past mistakes.



Species	Upstream Passage	Downstream Passage	Entrainment	Impingement	Swimming Ability	Behavioural Guidance	Dam Removal
Lake Sturgeon	■	░	▓	▒	■	■	□
White Sturgeon	▓	░	□	□	■	▓	░
Green Sturgeon	□	□	▓	▓	░	░	░
Shortnose Sturgeon	░	□	░	▓	■	▓	░
Pallid Sturgeon	□	□	□	□	░	░	□
Other Acipenserids	░	□	□	□	░	░	░

Fig. 6 Matrix of published research volume on different sturgeon water resource development topics. The shading ranges from black (most known—reasonable evidence base) to white (no research uncovered during our search). In many ways this is relative in that although lake and white sturgeon upstream passage is denoted as "black", we still know very little relative to salmonids or other diadromous species. For species for which there was published activity in more than two columns we report at the species level. However, what is remarkable is that for the vast majority of sturgeon species (last row), there is absolutely nothing known about this topic

As much as there is a need for studies on how sturgeon directly interact with hydropower or irrigation-related infrastructure (e.g., understanding fish–hydraulic interactions, as described above) and which mitigation strategies are effective (not just in the lab, but in the field), there are also major knowledge deficiencies regarding system-specific habitat and reproductive behaviour prior to dam construction. Routine monitoring that one would hope for when making decisions about potential interventions simply do not exist for most sturgeon populations. There is certainly need for research, but there is also a pressing need for long-term monitoring of fish populations and basic stock and habitat assessment work to enable modeling (e.g., Jager 2006). With respect to specific research needs, we urge further work on behavioural guidance, as fish require assistance in being guided to fishway entrances (for upstream passage) and bypasses (for downstream passage), while repelling them from areas where entrainment or impingement could occur. We also encourage more work that combines laboratory experiments (i.e., using flumes) with field-based studies, because the mechanistic understanding that can arise from doing so is informative. Experimental fishways or flumes that can be modified to do experiments on scales that would inform field application will be important for ensuring that investments in fish passage infrastructure are not wasteful. It also goes without saying that research on sturgeon fish passage should involve teams of experts with diverse backgrounds and perspectives including ecology, behaviour, biomechanics, and engineering (Silva et al. 2018). Investments in broad-scale (i.e., watershed-level) assessment of past and present sturgeon habitat, population trends, and population-specific life-history characteristics are needed to determine when passage is necessary. Given the threat status of the species and their vulnerability to the impacts of hydropower development, policy should integrate the value of actions that conserve sturgeon populations, e.g. changing operations or removing/retrofitting/denying construction of dams that affect these fish, against the value that can be generated from regulation for hydropower.

The issues described in this paper for sturgeon are also reasonably germane to non-salmonid fishes. A recent synthesis on the future of fish passage identified a number of research needs related to fish passage (Silva et al. 2018) and almost all of those research needs are applicable to acipenserids.

Moving forward

Here, we summarized the existing literature on strategies for addressing issues related to passage, entrainment and impingement of acipenserids. The evidence base is still sufficiently sparse that there is significant uncertainty regarding best management practices for even the most well-studied species, but there are some clues indicating that possible solutions exist, providing hope for acipenserids in the future. Despite uncertainty, action is needed. As noted by Secor et al. (2002), there is potential to "study sturgeon to extinction". Practitioners are faced with decisions on a daily basis regarding how to mitigate the issues described here given expanding hydropower development as well as relicensing which creates opportunities for conservation gains. Given that, we recommend the following (note—these are not prioritized but rather follow the same general structure of the paper):

- Although there is much to consider in terms of biology and engineering, Kynard (2008) suggests that most sturgeon fishways fail due to lack of institutional will (e.g., unwillingness to monitor and adapt operations or infrastructure; or lack of ongoing operational support, such as at night when sturgeon pass). In order to support sturgeon, there needs to be investment and commitment to supporting these fish.
- All too often, fish passage designs for sturgeon fail because of failure to consider their behaviour (Kynard 1993, 2008; although see Cocherell et al. 2011). Therefore, knowledge of species-specific behaviour as well as site- and population-specific natural history is essential for designing facilities that will work (e.g., including the successful reproduction of upstream migrants after passing barriers en route).
- If one is going to install upstream passage facilities, ensure that the passage facilities are sufficiently large that adult sturgeon can easily navigate through the infrastructure. Sturgeon are large and thus so must be the passage facilities (including width between vertical slots, orifices, and other elements of the infrastructure) but also design criteria that recognizes the swimming capabilities of large fish.
- Given the rheotactic nature of sturgeon, it is important to ensure that there is adequate attraction flow at the fishway entrance, and that the approach area is as close to the face of the dam as possible.
- Much of upstream passage activity seems to occur at night, so any fish passage solutions should be developed around that maxim.
- Sturgeon fishways seem to perform best (based on lab experiments, knowledge of sturgeon swimming performance, and field observations) when they combine high flow areas (that serve as cues for upstream movement) with opportunities for rest and recovery.
- Both vertical slot and overflow weir with orifice have been documented to pass sturgeon, but they need to be scaled appropriately (i.e., large orifices, wide spacing between vertical slots, generally wide fishways).
- Motivation is something that is hard to measure, but across studies, it is clear that fish that presumably have the capacity to move upstream may have no interest in doing so. This is relevant for assessing the performance of a fish passage facility and in setting realistic performance targets based on motivation (e.g., maturation status and reproductive preparedness).
- Entrance sills to fish passage facilities need to be aligned with the bottom of the river, ideally in deep water, to enable sturgeon to enter the fishway. Provision of attraction flows seems to be irrelevant if fish are forced to swim into very shallow water or encounter a "perched" entrance.
- Fish lifts are effective at passing large fish, but challenges exist with getting sturgeon to enter them (Kynard 2008). As such, investments in lifts should not occur without consideration for ensuring adequate attraction.
- There is virtually nothing known about downstream passage, aside from when the path involves entrainment. Given that the relative amount of water moving through turbines frequently exceeds (by many orders of magnitude) the volume of water moving through spillways, bypass structures, or fishways, there are inherent challenges with helping fish locate routes of safe passage. Use of

behavioural guidance strategies will almost certainly be needed to repel fish from “dangerous” paths and attract them to “safe” paths.

- Impingement of sturgeon of all life stages can occur and is almost always associated with attempts to prevent entrainment using screens and racks. It is therefore important to quantitatively explore the trade-offs between impingement and entrainment (especially if fish survive entrainment events) before installing screens and racks.
- Not surprisingly, impingement typically occurs when flows are high. Protection from entrainment often fails if spacing in bars/grids is too wide. One approach to address this issue is to use larger intakes so that bar or screen spacing can be smaller, while maintaining lower velocities across the entire surface of the intake. Another approach is to decrease water-diversion flows and associated diverted-water velocities such that sturgeon are better able to avoid impingement. This approach could balance water resource requirements (e.g., for irrigation) with conservation of resident or migrating fishes that are vulnerable to either screened or open diversion structures.
- Some behavioural guidance techniques show promise (e.g., for guiding fish towards desirable areas such as a fishway entrance or away from dangerous areas where entrainment could occur), but it is premature to identify a tool that is reliable recognizing that this may be species- and life-stage specific. Light and low-voltage electricity show promise but there is a lack of field-based trials, so it is unclear if these are effective. One laboratory study indicated that anadromous sturgeon may follow salinity cues. With further research, perhaps these fish could be led to “safe” passage areas or structures. With the low salt tolerance of stream insects, crop plants, etc., the appropriate concentrations and distributions of possible “salty currents” of water to lead anadromous sturgeon would have to be carefully examined.
- Dam removal could be of great benefit to sturgeon. When dam removal occurs on systems with sturgeon there is urgent need to explicitly study how sturgeon populations respond to the actual dam removal process and subsequent presumed improvements in ecological connectivity.

Conclusion

Without significant investments in research to identify solutions to fish passage, entrainment and impingement challenges, acipenserids will continue to be threatened with water resource development. Seventeen years later, we agree with the call by Secor et al. (2002) that it is (still) time for action, yet it is not clear what form action should take, with an evidence base to date only yielding partial clues as to what might work. Given inherent variation among species, life-stages, and populations, as well as the range of site configurations, operations, and environmental conditions, it is simply impossible to draw strong conclusions beyond what we present in this review. Although we have summarized the available literature, we must be clear that the evidence base is weak, and thus the conclusions based on it must reflect this uncertainty. It is our hope that this review will stimulate research necessary to generate the high-quality science needed to guide future decisions regarding efforts to mitigate effects of hydropower and water-diversions (e.g., for irrigation) on sturgeon. An expanded, high-quality evidence base would also enable systematic review with meta-analysis—something that was not possible here due to the sparsity of comparable studies. Next, we need the will and investment to act, when there are clear infrastructure options or management strategies that are likely to be beneficial. At this point, without the investment in research and action, we are failing sturgeon and the many people who depend on the ecosystem services generated by healthy and productive sturgeon populations.

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Appendix: methods for literature review

Given the sparsity of literature on sturgeon and water resource development, it was clear from the start of this project that it would not be possible to conduct a systematic review nor a meta-analysis. Nonetheless, where possible and practical we adopted best practices for evidence synthesis (see Haddaway et al. 2018). For example, we created a stakeholder advisory committee involving researchers and end users engaged in sturgeon management (Haddaway et al. 2017). We searched the Web of Science Core Collection and Google Scholar in November of 2018 using the following Boolean search string (“sturgeon*” or “acipenser* and “entrain*” or “dam” or “passage” or “fishway” or “fish way” or “impinge” or “guid” or “ladder” or “elevator” or “turbine” or “lift” or “swim*” or “screen*” or “rack*” or “intake” or “hydro*” or “irrigation” or “channel*” or “bypass”). We screened all papers located using these search strings based on title and abstract and retained those that dealt with the topic of this paper. We also searched several databases of screened papers for formal systematic reviews—one related to fish passage (https://osf.io/xvzbf/) and one related to entrainment (Rytwinski et al. 2017)—simply using the word “sturgeon*” and “acipenser*”. We did not restrict ourselves to peer reviewed documents and included many technical reports and theses. Our search was restricted to English but we located several non-English or translated documents (from Russia). Papers were not subject to critical appraisal as in most cases the research that was conducted focused on a single site and thus lacked replication or appropriate controls—something common in studies evaluating fish responses to water resource development.

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