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Reconnecting Fragmented Sturgeon Populations in North American Rivers

Henriette I. Jager

Environmental Sciences Division, Oak Ridge National Laboratory, Mail Stop 6036, P.O. Box 2008, Oak Ridge, TN 37831-6038. E-mail: jagerhi@ornl.gov

Michael J. Parsley

U.S. Geological Survey, Western Fisheries Research Center, Columbia River Research Laboratory, Cook, WA

Joseph J. Cech, Jr.

Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA

Robert L. McLaughlin

Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

Patrick S. Forsythe

Department of Natural and Applied Sciences, University of Wisconsin–Green Bay, Green Bay, WI

Robert F. Elliott

Green Bay Fish and Wildlife Conservation Office, U.S. Fish and Wildlife Service, New Franken, WI

Brenda M. Pracheil

Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN



The majority of large North American rivers are fragmented by dams that interrupt migrations of wide-ranging fishes like sturgeons. Reconnecting habitat is viewed as an important means of protecting sturgeon species in U.S. rivers because these species have lost between 5% and 60% of their historical ranges. Unfortunately, facilities designed to pass other fishes have rarely worked well for sturgeons. The most successful passage facilities were sized appropriately for sturgeons and accommodated bottom-oriented species. For upstream passage, facilities with large entrances, full-depth guidance systems, large lifts, or wide fishways without obstructions or tight turns worked well. However, facilitating upstream migration is only half the battle. Broader recovery for linked sturgeon populations requires safe “round-trip” passage involving multiple dams. The most successful downstream passage facilities included nature-like fishways, large canal bypasses, and bottom-draw sluice gates. We outline an adaptive approach to implementing passage that begins with temporary programs and structures and monitors success both at the scale of individual fish at individual dams and the scale of metapopulations in a river basin. The challenge will be to learn from past efforts and reconnect North American sturgeon populations in a way that promotes range expansion and facilitates population recovery.

Reconexión de poblaciones fragmentadas de esturión en los ríos de Norteamérica

La mayor parte de los grandes ríos en el norte de América están fragmentados por presas, lo que interrumpe la migración de peces de amplia distribución como los esturiones. La reconexión de hábitats es vista como un importante medio de protección de las especies de esturión en los ríos de Norteamérica, ya que estas especies han perdido entre 5 y 60% de sus rangos históricos de distribución. Infortunadamente, las instalaciones que sirven para que otros peces transiten entre hábitats, no han funcionado bien para los esturiones. Se aprovecharon aquellas instalaciones que operaron de forma exitosa para los esturiones y se acomodaron aquellas especies que son afines al fondo. En el caso de los pasajes río arriba, las instalaciones con entradas amplias, sistemas de guía de profundidad, elevadores grandes o bien aberturas grandes para peces y sin obstrucciones o vueltas cerradas, mostraron tener un mejor desempeño. Sin embargo, facilitar la migración río arriba es sólo la mitad del trabajo. Una recuperación generalizada que permita unir poblaciones fragmentadas de esturiones, requiere de pasajes que aseguren un “viaje redondo” que implica sortear varias presas. Las instalaciones río abajo más exitosas incluyen pasajes para que transiten los peces, que son similares a los encontrados en la naturaleza, tributarios amplios y compuertas en el fondo. En este estudio se muestra un enfoque adaptativo para implementar pasajes, que inicia con estructuras y programas temporales, y se hace un monitoreo del éxito a escala del traslado de cada pez por cada represa, así como también otras medidas más generales que indican la recuperación a nivel poblacional. El reto por delante será aprender de los errores del pasado y reconectar las poblaciones de esturiones en Norteamérica de tal forma que se promueva la expansión del rango de distribución y se facilite la recuperación de las poblaciones.

Relier les populations fragmentées d'esturgeons dans les fleuves d'Amérique du Nord

La majorité des grands fleuves d'Amérique du Nord sont fragmentés par des barrages qui interrompent les migrations d'un large éventail de poissons comme les esturgeons. Relier l'habitat est considéré comme un important moyen de protéger les espèces d'esturgeons dans les fleuves américains, car ces espèces ont perdu entre 5 et 60 % de leurs aires historiques. Malheureusement, des installations conçues pour laisser passer d'autres poissons ont rarement bien fonctionné pour ce poisson. Les installations de passage les plus réussies ont été dimensionnées de manière appropriée pour les esturgeons et les espèces de fond qui se sont adaptées. Pour le passage en amont, les installations avec de grandes entrées, les systèmes d'orientation pleine profondeur, les grands ascenseurs, ou les passes à poissons larges sans obstructions ou virages serrés ont bien fonctionné. Toutefois, faciliter la migration en amont ne représente que la moitié du chemin. Le rétablissement à plus grande échelle des populations d'esturgeons nécessite un passage « aller-retour » sûr impliquant de multiples barrages. Les installations de passage en aval les plus réussies incluent les passes à poissons pseudo-naturelles, les grandes rocadés de canal, et les portes d'écluses à poissons. Nous présentons une approche adaptative de la mise en œuvre d'un passage, qui commence par des programmes et des structures temporaires, et contrôle la bonne marche à l'échelle de chaque poisson passant par les barrages individuels et par des mesures plus larges de rétablissement de la population. Le défi sera d'apprendre des efforts du passé et de relier les populations nord-américaines d'esturgeons d'une manière qui favorise l'expansion de l'aire de répartition et facilite le rétablissement de la population.

INTRODUCTION

Impoundment of rivers by dams has blocked fish migrations in more than half of large river systems in the world (Nilsson et al. 2005). In the United States, fewer than 42 free-flowing sections of river over 200 km remained before the turn of the 21st century (Benke 1990). Because rivers are linear corridors, fragmentation by dams results in nearly complete blockage of animal movements (Jager et al. 2001; Fagan 2002). Not surprisingly then, range contractions and population declines have been attributed to dams for both resident (Nislow et al. 2011) and migratory fishes (Liermann et al. 2012). Sturgeons are no exception (Aadland et al. 2005; McLaughlin et al. 2006).

The International Union for Conservation of Nature considers all sturgeons at risk of extinction (Birstein 1993). Historically, sturgeons inhabited many large rivers, oceans, and inland seas of the Northern Hemisphere (Pikitch et al. 2005), and nearly every major river system in North America continues to support one or more sturgeon species (Figure 1). Based on NatureServe data (area of eight-digit hydrologic units

in historic vs. current species distribution data), all sturgeons in the conterminous United States have experienced range contraction (Figure 2). Overall, sturgeons have disappeared from 22% of their historical ranges. Compared with other fishes, a disproportionate fraction of sturgeon populations receive special conservation protection under the Endangered Species Act (United States) or Species at Risk Act (Canada).

Sturgeons typically fare poorly in highly fragmented rivers (Limburg and Waldman 2009), and restoring blocked migration patterns is considered an important path toward expanding species ranges and recovering sturgeon populations at risk. In the absence of barriers, sturgeons make riverine migrations. Adults may travel upstream to spawn and then return downstream. This cycle may be repeated multiple times during their lives. Early life stages (e.g., larvae) disperse downstream from spawning areas. Among anadromous and amphidromous populations, those lacking access to downstream estuaries grow more slowly than those with access (Beamesderfer et al. 1995). For populations above dams, downstream migration by adults

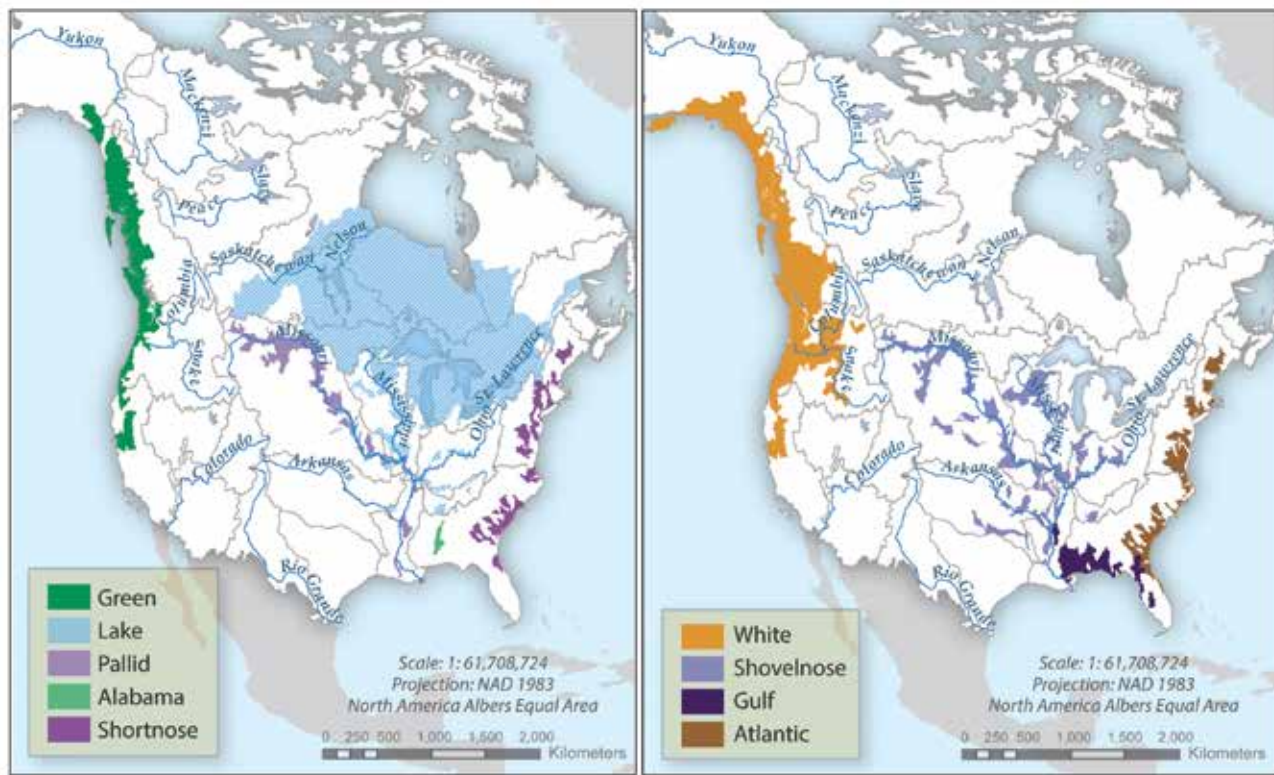


Figure 1. Distribution of sturgeons of special conservation concern in the United States and Canada. Sources: Scott and Crossman (1985). 2013 Data from NatureServe.

adds the risk of injury during passage through turbines (Amaral et al. 2002). Fragmentation causes spawning-ready adults to experience delays during upstream migration, sometimes resulting in reabsorption of eggs or spawning in unsuitable locations (Auer 1996). Export of smaller life stages downstream over or through dams depletes upstream populations over time.

Upstream passage, the “obvious” solution for recolonizing upstream reaches, has not always benefited sturgeon populations. Passage has resulted in moving sturgeons upstream into “ecological traps” (Brown et al. 2013). Reservoirs above dams often experience periods of high temperature and low dissolved oxygen. For example, anoxic conditions contributed to the mortality of 28 White Sturgeons *Acipenser transmontanus* in a low-flow year in a Snake River Reservoir in Idaho (K. Lepla, Idaho Power Company, personal communication to H.J.).

Finding viable solutions to the problem of sturgeon passage is urgent for declining populations lacking access to needed habitats. Our review synthesizes successes and failures of efforts to reconnect sturgeon populations in North American rivers. We provide guidance on designing passage technologies, learning from both rare successes and frequent failures. We also emphasize measuring broader-scale success across projects and river systems by improving access to needed habitats.

STURGEON HAVE SPECIAL NEEDS

In North America, most passage structures were designed for fish species such as clupeids and salmonids and have not worked well for sturgeons (Brown et al. 2013). Guidance systems for sturgeons must be focused on the river bottom and rely less on visual cues to attract fish. Impingement against screening devices is a more significant concern for sturgeons than for other species. Fishways and lifts designed for other

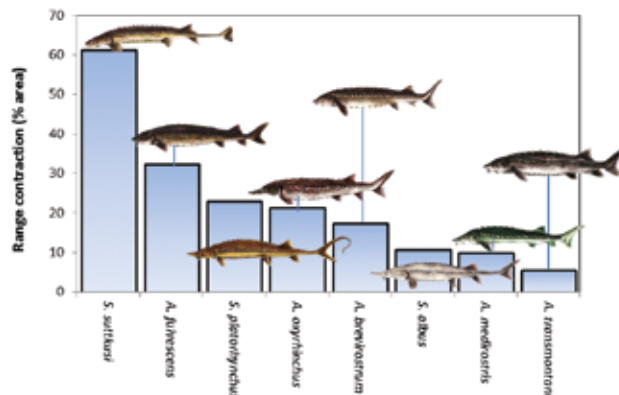
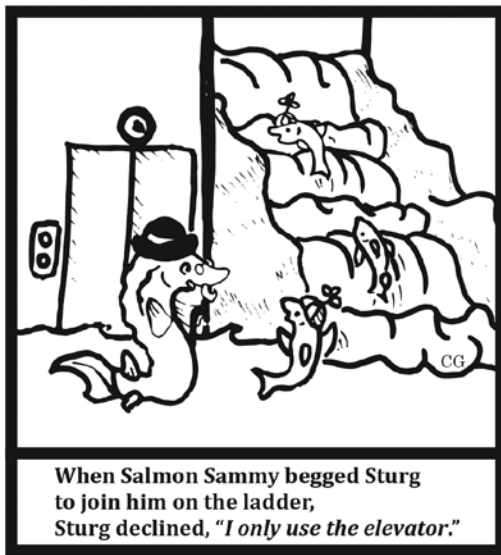


Figure 2. Range contraction in sturgeon species based on NatureServe data. Gulf and Atlantic sturgeon ranges are combined for this analysis.

species are typically too small for adult sturgeons. Sturgeon swimming performance follows different relationships with body size than it does with other fishes (Katopodis and Gervais 2012). Sturgeons prefer to swim straight upstream along the bottom against a steady flow (McElroy et al. 2012). In contrast, most fishways are designed to create hydraulic heterogeneity by using changes in slope, turning basins, and obstructions. Sturgeon-friendly solutions for downstream passage must also accommodate large, bottom-oriented species. We summarize successes and failures in Supplemental Online Table 1.

DESIGNING SUCCESSFUL RECONNECTION FOR STURGEON

Although efforts to reconnect North American sturgeon populations have met with limited success, many projects



Cartoon drawn by Catherine Graham.

included successful elements that hold promise for recovery and reconnection of sturgeon populations (see Supplemental Table 1). Below, we review guidance systems, locks and lifts, the design of fishways, nature-like fishways, downstream passage, and translocation.

Guidance Systems

Guidance systems are needed to attract sturgeons to both upstream and downstream passage facilities. Ideally, sturgeons traveling in the thalweg should be able to detect elevated flows leading to the structure (White and Mefford 2002). However, forebay flows should be low enough to prevent impingement (see Supplemental Table 1). Poor water quality in reservoirs may prevent sturgeons and other fishes from reaching passage structures. Sturgeons have been struck by turbines after aggregating in turbine bays below dams during dam maintenance, killing and injuring multiple individuals at once. This problem, which has been noted at dams across the United States, has been solved by installing racks in the turbine draft tubes to prevent adult sturgeons from entering turbine bays or by using fog horns to scare sturgeons away before resuming operation (see Supplemental Table 1).

Sturgeons large enough to be vulnerable to turbine blade strike can be excluded by appropriately spaced trash-bar racks or screens. However, sturgeons may be pinned against screens or trash bars when velocities exceed their critical swim speeds. In one study, sturgeons oriented downstream were more likely to be impinged on bar racks than on louvers (Kynard and Horgan 2001). Amaral et al. (2002) observed sturgeons becoming trapped between slats. Studies are needed to quantify impingement risk.

To be effective for bottom-oriented fishes like sturgeons, downstream guidance systems should ensure that the structures extend seamlessly to the river bottom (Kynard and Horgan 2001). For example, the bypass canal around Holyoke Dam was modified by blocking the space between the bottom of the canal and the frame of a louver array with timbers. This modified canal successfully guided sturgeon around Holyoke Dam (Ducheney et al. 2006). Louvers were more effective than bar racks at guiding Pallid Sturgeon *Scaphirhynchus albus* and Shortnose Sturgeon *A. brevirostrum* in flumes, particularly at nighttime (Kynard and Horgan 2001).

Screening is important in guiding sturgeon away from intakes to dam turbines and water diversions. Entraining juveniles into irrigation canals is a concern for Endangered Species Act-listed sturgeons (e.g., Mussen et al. 2014). Entrainment and impingement risks depend in part on species' critical swim speeds (Katopodis and Gervais 2012), which typically increase with body size and temperature. Fatigue curves relating fish swim speed in body lengths per second, U , as a function of swim time, t , follow the relationship $U/t = 4.328 t^{-0.185}$ for sturgeon species (Deslauriers and Kieffer 2012; Katopodis and Gervais 2012). This fatigue relationship is similar to that for eels and different from that for salmonids.

Locks and Lifts

Locks and lifts operate in a similar way, trapping water and fish below an unnavigable barrier on a river (e.g., waterfall or dam) and raising the volume of water, including fish, to the elevation of an upstream river. High-head dams often require lifts to pass sturgeons, whereas lower-head dams on low-gradient navigable rivers can use locks. On the Pacific Coast, approximately 1,500 White Sturgeons used fish lifts at Bonneville Dam, a high-head dam at the entrance to the Columbia River (Warren and Beckman 1993). However, operation of the lifts was discontinued in 1956 (Warren and Beckman 1993). On the Atlantic Coast, only the lift at Holyoke Dam on the Connecticut River is still used to pass sturgeon (Ducheney et al. 2006; Figure 3). Yet, during 22 years of operation, the Holyoke lift passed only 97 Shortnose Sturgeons, a small fraction of adults in the downstream population (Kynard 1998).

Large sturgeon-sized designs and well-timed operations produced the modest success reported at Holyoke Dam (Kynard 1998; Ducheney et al. 2006; Supplemental Table 2). Downstream passage was provided by a full-depth guidance system (i.e., without gaps near the substrate) leading to a large canal. Upstream passage was provided by large transport and crowding channels leading to an oversized hopper and spillway lift (Figure 3, left). Attraction flows and lift frequencies were increased during late May–October following high spring flow events that stimulated upstream migration by adults (Kynard 1998).

Several telemetry studies have demonstrated the ability of sturgeons to pass both downstream and upstream through spill gates, lifts, and navigation locks (Cooke et al. 2002). In the spring of 2015, a new facility on the Menominee River that features a fish lift and sorting facility began seasonal operation. During a couple of days of operation, 13 mature adult Lake Sturgeons *A. fulvescens* were passed above the dam and gained access to 34 km of upstream riverine habitat. Nevertheless, migration rates at other facilities have been low. For example, an ongoing telemetry study by South Carolina Department of Fish and Game detected only two Shortnose Sturgeons passing upstream of Pinopolis Dam in South Carolina, and no passage events were reported at this facility by Cooke and Leach (2004). The St. Steven fish lift in South Carolina passed only six Shortnose Sturgeons since it began operation in 1985 (W. Post, South Carolina Department of Fish and Game, personal communication). Monitoring at The Dalles Dam in Oregon (Parsley et al. 2007) failed to detect any White Sturgeon passage events at navigation locks.

Cooke et al. (2002) made three recommendations for improving the performance of navigation locks as passage structures: (1) fill locks slowly to minimize turbulence that



Figure 3. Fish passage facilities at Hadley Falls at the Holyoke Project on the Connecticut River. A fish lift is used to transport anadromous sturgeons upstream (left), and a large bypass canal permits return downstream (right). Photo credit: Duchenev et al. (2006).

might cause disorientation of sturgeons, (2) partially open a drain valve after upper gates are open to create a guiding flow, and (3) leave the upper gate open for an extended time and using an air horn or other methods to encourage fishes to exit. Structural changes may also be needed to help bottom-oriented fishes pass through locks. For example, sturgeons must swim over a 15-m sill to exit the Pinopolis lock, and smaller sturgeons may take up residence in drain ports that line the bottom of lock walls rather than exit (Cooke et al. 2002).

Fishway

Much has been learned in designing fishways for sturgeons (see Supplemental Table 1). Sturgeons generally swim straight upstream along the bottom, selecting for hydraulically heterogeneous, yet energy-inexpensive, routes (McElroy et al. 2012). Most fishways are designed to create hydraulic heterogeneity by using changes in slope, turning basins, and obstructions. These features impede sturgeons by creating crowded passages, preventing movement along the bottom (e.g., vertical baffles), and causing sturgeons to lose upstream focus, particularly at lower velocities (White and Mefford 2002; Webber et al. 2007). Obstructions such as baffles, used to create resting areas of low velocity, can impede sturgeon progress if they are closely spaced, tall, or sharp (Anderson et al. 2007). For example, turning basins impeded progress of Lake Sturgeons ascending a vertical-slot fishway at St. Ours Dam on the Richelieu River, Canada (Thiem et al. 2013). Only 36% of monitored fish passed, and most failures occurred as sturgeons attempted to navigate the first turning basin in the bottom half of the fishway (Thiem et al. 2013).

Moderately fast velocities encourage sturgeon to ascend fishways. Several studies have reported that upstream progress was more direct when velocities were higher (White and Mefford 2002; Webber et al. 2007), but efficiency may decrease with increasing depth and turbulence (Cheong et al. 2006; see Supplemental Table 1). White Sturgeons benefited from flow-straightening structures capable of dissipating flow without creating turbulence or eddies (Anderson et al. 2007). One successful design passed 54% to 63% of White Sturgeons in a 24-m experimental flume with three segments (Cocherell et al. 2011). Flow was constricted by wide, rounded baffles in the first segment; flow was straightened in the middle segment and expanded again in the third segment. White Sturgeons ascended the flume by swimming through water currents between 1.7 and 2.1 m/s (Webber et al. 2007; Cocherell et al. 2011).



Figure 4. The Dalles Dam on the Columbia River has both an east ladder (left) and north ladder (right). The wider east ladder passed more sturgeons. Photo credits: U.S. Geological Survey.

Fishways designed for salmon typically rely on fish jumping among a series of resting mini-pools. Pools can be useful to sturgeon, but only if they are sufficiently large to allow sturgeon to rest during ascent, and if they do not require jumping to proceed. Adult sturgeons are too large to jump, but adults can navigate elevated bed slopes (i.e., increasing elevation of substrate) against swift currents. Relatively steep fish ladders passed White Sturgeon at two Columbia River dams. Bonneville Dam passed 22 to 133 White Sturgeons annually between 1998 and 2012 (Parsley et al. 2007). Although this represents just a small fraction of the estimated million sturgeons in the estuary below the dam, this species might not choose to ascend in the absence of dams. Upstream at The Dalles Dam, more than 1,000 White Sturgeons have ascended two fishways (Figure 4) that rise 24 m over a length of approximately 540 m. The east ladder is 1.8 m wider than the north ladder, and its submerged orifices have twice the surface area as those in the north ladder and passed many more fish (943 vs. 104; Parsley et al. 2007). However, only a small proportion (6 of 90) of telemetered sturgeon passed upstream in a follow-up study, all via the east ladder (Parsley et al. 2007), and some individuals passed back downstream over spillways.

Nature-like Fishways

Low-gradient nature-like fishways provide a promising approach that can pass sturgeons in both directions at modest cost. In Minnesota, nature-like fishways have reconnected populations of Lake Sturgeon and other native fishes through a total of 36 barrier mitigations (Aadland 2010). These fishways have opened hundreds of miles of river habitat in the Red River Basin.

Nature-like fishways allow sturgeon to pass low-head dams. Sturgeon can ascend a relatively low slope and rest in plunge pools but do not have to jump to proceed. Rock-ramp fishways, designed as a semicircular weir, dissipate energy in the center of the channel to protect banks and create low-velocity eddies (Aadland 2010). Rock-arch rapids constructed with 3% to 5% slopes are expected to reconnect Lake Sturgeon populations at Christine and Hixon dams in the Red River Basin (Aadland 2010). Lake Sturgeon have ascended similar low-gradient structures on the Fox River, Wisconsin, where a 3-m rock-ramp fishway was constructed on Eureka Dam in 1989 (Bruch 2008). Other sturgeons can likely ascend low-gradient rock fishways as well. For example, White and Mefford (2002) determined that Shovelnose Sturgeons were twice as likely to ascend a rock fishway as either of two low-gradient slotted fishways. Nature-like fishways can also be constructed for somewhat higher dams. For example, nature-like bypass reaches were constructed around two approximately 2.2-m-high dams on the Otter Tail River, Minnesota (Aadland 2010).

Downstream Passage

Efforts to provide upstream passage must be accompanied by downstream passage to succeed. Downstream passage should be a priority because sturgeons passed upstream will otherwise experience a high risk of entrainment into turbines and blade strike (Brown et al. 2013). In one example, the use of a fish elevator at Conowingo Dam on the Susquehanna River was discontinued because mature adults that were passed upstream later experienced high turbine blade strike mortality during downstream migration after spawning (Normandeau Associates and Gomez and Sullivan Engineers 2011). Similarly, blade strike killed 50% of turbine-entrained sturgeon at Hadley Falls on the Connecticut River (cited in Kynard and Horgan 2001).

As the risk of turbine strike increases with length, the range of sturgeon sizes protected from strike depends on turbine design and trash-rack spacing. Very small juvenile sturgeons can pass through turbines safely (>90% survival; Kynard and Horgan 2001). Large sturgeons would experience a high risk of turbine strike, but trash-rack bars prevent them from entering turbine intakes. A passage model that included these size-related factors found that intermediate-length sturgeons were at greatest risk (Jager 2006) and that closer bar spacing could increase survival for intermediate-length sturgeons.

Safer alternative routes for larger fish include spillways and bypasses. Spillways located near the bottom are more likely to be used by sturgeons. Subadult and adult Lake Sturgeons in a Manitoba river experienced over 90% survival when moving downstream through bottom-draw sluice gates (McDougall et al. 2014). Sturgeons have passed via high spillways, and to our knowledge survival via this route has not been studied. For example, telemetered adult White Sturgeons in the Columbia River moved downstream over a high spillway (Parsley et al. 2007).

Bypass canals can pass sturgeons safely if the entrance is sufficiently large and the water depth at the entrance sufficiently deep to accommodate them (Kynard 1998). At the Holyoke Project on the Connecticut River, fish are guided to large canals (Figure 3, right) by louver arrays. On the Menominee River, angled guidance racks were constructed to direct both adult and juvenile Lake Sturgeon into a bypass channel around the turbine bays (Menominee/Park Mill Implementation Team 2009).

If adults do not require downstream habitat, retaining adults upstream using size-selective screens or trash-racks is one strategy for subsidizing downstream populations with juveniles produced by adults in an upstream reach with sufficient spawning habitat. This “screening” strategy, proposed by Jager (2006) for White Sturgeon, has not been experimentally tested.

Translocation

Translocating sturgeons can be an effective way to connect sturgeon populations in fragmented rivers. Translocation allows researchers and managers to monitor the outcomes that upstream passage has before investing in permanent structures. Translocation is flexible in two respects: (1) the ability to selectively target individuals of different life stages (and potentially exclude nontarget species, such as invasive species; McLaughlin et al. 2013) and (2) the ability to move sturgeons upstream or downstream past multiple dams (rather than just between adjacent segments). Choosing which life stage to relocate depends on the life history of the sturgeon species and which life stages are lacking habitat. In some cases, naturally spawned larval or juvenile fish can be captured from reaches lacking adequate rearing habitat and raised in hatcheries and

then planted out after a critical period that requires missing habitat. Translocation can be also be used to collect and move sturgeons to upstream reaches with suitable spawning habitat that lack adult spawners.

For sturgeon species that make well-defined seasonal spawning migrations, it is best to transport adults that are clearly moving upstream to spawn. For example, Lake Sturgeon spawners are transported around multiple dams on the upper Wolf and the Menominee rivers to historic spawning and juvenile rearing habitat (Coscarelli et al. 2011). On the Menominee River, a lift transfers sturgeons from the tailwaters of the first dam into a sorting facility, where adults ready to spawn are transported around two upstream dams (Coscarelli et al. 2011). However, for populations that do not make seasonal migrations, moving younger individuals may be a better option. For example, juvenile White Sturgeons collected by bottom trawls downstream of Bonneville Dam were transported to upstream impoundments where natural recruitment was low (Chapman 2012). Annual survival of transported fish averaged approximately 85% over 10 years (Chapman 2012).

FUTURE DIRECTIONS FOR SUCCESSFUL RECONNECTION

Monitoring at Two Scales

Monitoring studies should be designed at the scale of individual dams and the scale of river basins with the goal of achieving effective reconnection of fragmented populations. At the scale of the individual dam, monitoring the chain of events required to achieve overall success is more informative than overall passage success alone. Monitoring the following chain of events can help to isolate mechanisms responsible for fishway success or failure: (1) proportion of tagged upmigrating sturgeons attracted to structures or traps, (2) proportion that successfully pass upstream or are transported, (3) proportion that exhibit no impairment as a result of using passage structures or transport, (4) proportion that subsequently spawn upstream (e.g., use telemetry to distinguish successful spawners from those that “fall back” or fail to spawn), (5) young-of-year production (e.g., monitoring larval and juvenile life stages), and (6) proportions of all ages that safely return downstream (e.g., release studies at different points in the upstream reservoir).

Fortunately, methods for monitoring fish passage facilities exist (Roscoe and Hinch 2010). Video or hydroacoustic devices, such as dual-frequency identification sonars or passive integrative transponder (PIT) readers, can be installed in fishways to count numbers of sturgeon, along with real-time water quality recorders. These monitoring systems are already being used to monitor sturgeons and other species at the Vianney-Legendre Fishway, where tagged fish are used to quantify upstream passage success (Thiem et al. 2013). Similarly, PIT detectors installed in fishways (ladders) of the Columbia River dams track PIT-tagged White Sturgeon. Statistical analysis (e.g., mark-recapture) to relate fish passage success to relevant covariates, such as fish size, water quality, and hydraulic conditions in the fishway, can help to improve future designs.

The ultimate goal of successful reconnection is to restore sturgeons to their historical ranges and facilitate recovery (growth) of multiple conjoined populations. Success at this scale is assessed by monitoring population status and trends. At the scale of river basins, monitoring recovery of linked sturgeon populations may require more time than that required for other fishes. [The phrase “linked populations” refers here to sturgeon

inhabiting a series of river segments where the groups have an unspecified degree of migration between adjacent populations. Such populations are unlikely to conform to the definition of a classic metapopulation *sensu* Levins (1969).] Although a large female sturgeon may produce over one million eggs, sturgeons typically need many years to grow to large size and reach sexual maturity, and most females do not spawn annually. Therefore, it may be important to monitor advance signs of recovery, such as an increase in the proportion of sturgeon in younger age classes.

Passing individuals upstream or down is a necessary, but not sufficient, condition for recovery. Stable or growing population sizes and evidence of recruitment demonstrate that the conjoined population as a whole is recovering (Jager 2006) without any significant “sink” habitats or dangerous corridors linking them. Monitoring upstream populations can indicate whether sufficient upmigration is occurring to offset downstream migration of younger sturgeons. Proxies of success might include indicators of successful reproduction (recruitment indices, age structure) and evidence for population growth in above and below complexes of dams that have been reconnected.

Adaptive Reconnection

We define “adaptive reconnection” as a strategy leading toward success through a science-based process of experimentation and monitoring. Adaptive reconnection requires feedback on performance to measure success at both the scale of individuals passing single dams and the scale of linked populations navigating around “round-trip” permeable dams in a river system. We emphasize the broad goal of ensuring population-level success and recovery and not just the ability of an occasional individual to surmount a dam. At the scale of individual dams, temporary measures might include building structures that can be easily modified to improve performance. At the scale of multiple populations in a river basin, temporary measures include efforts to relocate individuals of different life stages to and from different river segments. Permanent structures would be built where monitoring suggests population-level benefits would be greatest.

CONCLUSIONS

Reconnection is most likely to succeed at dams where sturgeon passage is facilitated in both directions, and efforts considering only one or the other frequently fail. Surviving to reproduce and return downstream can be more challenging than simply passing upstream at a dam. The key to successful round-trip passage is to ensure that sturgeons migrating upstream past dams can survive travel through upstream reservoirs (avoiding ecological traps; Brown et al. 2013) and later pass safely downstream. The most successful examples of downstream passage include nature-like fishways, large canal bypasses (e.g., Holyoke Dam), and bottom-draw sluice gates (e.g., Slave Falls Dam). The most successful upstream passage facilities were sized appropriately for sturgeons and worked well for bottom-oriented species, with large entrances, full-depth guidance systems, large lifts, or wide fishways without obstructions or tight turns.

Achieving the goal of safe round-trip passage might involve staged, adaptive implementation that progresses from (1) experimental translocation programs, to (2) monitoring to ensure population-level success, and, ultimately, to (3) the design of structures that accommodate the special characteristics of sturgeons (size, bottom orientation, nonvisual) as well as those of other species. Despite its checkered history, we have gleaned

a promising catalog of sturgeon-tailored structural design features (see Supplemental Table 1) and alternative reconnection strategies, demonstrating that we can learn from past failures as well as from successes.

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SUPPLEMENTARY MATERIAL

Supplemental material for this article can be accessed on the publisher’s website at www.tandfonline.com/ufsh.

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