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STURGEON PAPER

If you build it, will they come? Spawning habitat remediation for sturgeon

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Summary

Habitat loss is a widely recognized contributor to global declines in sturgeon populations yet habitat remediation has been limited for this highly endangered group of fish. In support of future sturgeon restoration efforts, this review examines habitat remediation needs and uncertainties. Consideration of the bio-spatial scale of remediation identified needs ranging from local to the whole river scale. Additionally, the context of remediation ranges from reintroducing sturgeon to habitats where they have been extirpated to conservation of currently functional habitat. While multiple remediation scales and contexts are discussed, the focus on spawning and early rearing habitat and associated biological and physical monitoring reflects the range of current projects and the importance of early rearing habitats. Four case studies are presented that examine four distinct remediation contexts (mitigation, rejuvenation, re-creation, repatriation) and three bio-spatial scales (whole river, spawning reach, spawning location) under which remediation has been attempted. Evaluation of existing remediation works indicates that many show limited long-term success, which is most often a response to substrate infilling in remediated habitats. Material presented in this review will help align sturgeon research and monitoring approaches in support of effective remediation. The limited number of remediation projects to-date attests to the importance of learning from existing projects and cross-species comparisons, to maximize the effectiveness of future restoration efforts.

1 | INTRODUCTION

Overfishing and habitat loss are the predominant causes of sturgeon declines worldwide (Rosenthal, Pourkazemi, & Bruch, 2006). Within the broad category of habitat loss, a wide array of anthropogenic habitat impacts have been identified, including river regulation for navigation, flood prevention, and power generation, as well as pollution from industrial activities (e.g., Gessner & Jarić, 2014; Luk'yanenko et al., 1999; Secor et al., 2002). River regulation has particularly strong effects on sturgeon in response to impacts including habitat fragmentation (Jager et al., 2001), blocked migration, and both direct (e.g., daily and seasonal flow modification) and indirect (e.g., temperature, nutrient levels, hydraulic conditions, substrate) effects of flow regulation (Petts, 1984; Petts et al., 1989; Ward and Stanford, 1989). Vulnerability of this ancient group of fishes to river regulation is further increased by their restriction to large rivers in the northern hemisphere, most of which are regulated or highly modified (Dynesius & Nilsson, 1994).

Human disruption of natural hydro-geomorphological processes that create and maintain riverine habitats as well as outright habitat destruction, has progressed to the point that remediation is essential to sustain habitat conditions for natural reproduction of many sturgeon. Despite widespread loss and alteration of sturgeon habitats worldwide, habitat restoration for this highly endangered group of fish has been limited. To date, three key factors may underlie the limited remediation and success. First, the ultimate causes of riverine habitat alterations that affect sturgeon (i.e., construction of shipping channels or large dams) are often considered irreversible impacts (Ligon et al., 1995; Petts et al., 1989). Second, biological uncertainty continues to limit the identification of effective remediation measures. Third, monitoring of past remediation works identifies the need for greater consideration of geomorphological effects, to ensure the continued effectiveness of the remediation (Kinzel, Nelson, Kennedy, & Bennion, 2016; Logan et al., 2011; McDonald et al., 2010). The dire conservation status of many sturgeon (Pikitch, Doukakis, Lauck, Chakrabarty, & Erickson, 2005) emphasizes the need for timely action. A few notable examples provide confidence that physical habitat remediation can be successful (e.g., Dumont et al., 2011), as does substantial experience with other fish species (e.g., salmonids; Wheaton et al., 2004).

Understanding current habitat limitations is an important requirement for effective habitat remediation (Rosenfeld & Hatfield, 2006) and, for most sturgeon, detailed knowledge of their habitat requirements limits remediation. General habitat use has been described for many species (Bemis & Kynard, 1997; Fox, Hightower, & Parauka, 2002; Hildebrand et al., 2016), however, few studies have specifically identified limiting habitats (e.g., McAdam, 2015). Restoration needs may vary depending on the causes of population declines. In some cases, remediation may be required throughout modified river corridors. In other cases site-specific remediation may be sufficient, for example, the remediation of spawning and early rearing habitats. While a broad spectrum of remediation needs is discussed (including fish passage and flow restoration), our focus on spawning and early rearing habitat reflects the focus of current remediation projects. Our focus also reflects the importance of early life history survival to recruitment and the identified links between recruitment failure and impacts to spawning and early rearing habitat (Gessner, Kamerichs, Kloas, & Wuertz, 2009; Hastings et al., 2013; McAdam, 2015; McAdam et al., 2005; Paragamian et al., 2009).

Conservation fish culture has also been employed to mitigate immediate extirpation risks for many populations, and if carried out with necessary precaution can provide interim compensation for low recruitment (Chebanov, Karnaukhov, Galich, & Chmir, 2002; Ireland et al., 2002; Secor et al., 2002). Genetic considerations associated with conservation fish culture include the importance of maintaining genetic diversity through practices such as factorial breeding and equalizing releases among families and years (Boscari, Pujolar, Dupanloup, Corradin, & Congiu, 2014; Ireland et al., 2002). Due to the high fecundity of sturgeon, failure to plan and monitor the genetic consequences of stocking creates the potential for negative effects on genetic diversity. Approaches such as the capture and rearing of wild progeny (e.g., feeding larvae) can have significant benefits for genetic diversity of released fish (Schreier and May, 2012). Additionally, the potential for phenotypic effects of captive rearing should be considered, which is reflected in recent research such as life-skills training in lake sturgeon (Sloychuk et al., 2016) and the carryover effects of early rearing habitats (Boucher, McAdam, & Shrimpton, 2014; Johnsson, Brockmark, & Näslund, 2014). Despite the importance of conservation fish culture within recovery programs, this is not specifically addressed in this review because of a) the focus of the review is on habitat remediation, and b) the principle of natural reproduction must be the ultimate goal of recovery efforts.

Our investigation of sturgeon restoration needs to identified the importance of contextual (Text Box 1) and bio-spatial factors that influence the scale of remediation (Text Box 2). For example, repatriation to formerly occupied rivers, potentially including the need for fish passage (e.g., European sturgeon (*Acipenser sturio)* and Baltic sturgeon *(Acipenser oxyrinchus*)) present substantially greater challenges due to their need for *de novo* habitat creation, plus the need to address multiple spatial scales and life stages. For most species, the presence of continued biological uncertainty means that a “build it and they will come” approach entails substantial risk. The large scale of potential recovery projects also means that economic risks may be substantial. Our consideration of multiple species emphasizes the potential for knowledge transfer among species (to-date often limited) to support more timely and effective recovery programs for sturgeon.

1.1 | Spawning habitat remediation

Our identification of four remediation contexts and three bio-spatial scales (Text Boxes 1 and 2) provides a structured way to examine remediation needs and their expected complexities (Table 1). The need to address remediation at the watershed scale is a function of the large river habitats occupied by sturgeon, and the long distance migrations of some species. The emphasis of current remediation on spawning and early rearing habitat likely reflects an insufficient consideration of sturgeon migratory needs when dams were constructed. In many cases, larger scale remediation may be required; our focus on current spawning and early rearing projects should not be interpreted as implying a lesser importance of larger scale restoration. Our discussion of the biological requirements are associated with the needs of sturgeon restoration progress from larger to small spatial scales.

Many sturgeon undergo large-scale migrations (e.g., 1,000 km for Chinese sturgeon, *Acipenser sinensis* (Wei et al., 1997), and the loss in connectivity is a widely recognized impact of river regulation. The high energetic cost of long-distance upstream migrations implies the presence of substantial biological benefits. Some species and populations are still able to undertake long distance migrations (Bruch, Haxton, Koenigs, Welsh, & Kerr, 2016; DFO, 2014; Duong et al., 2011; Phelps et al., 2016), and maintaining the current levels of riverine connectivity can be critical for those populations. While spawning downstream

TABLE 1 Categories of uncertainty associated with different contexts for sturgeon spawning habitat remediation (X = indicates uncertainty, XX = indicates high uncertainty)

Uncertainty	Repatriation	Re-creation	Remediation	Mitigation
Recolonization	XX			
Habitat use	XX	XX		
Habitat suitability	XX	XX	XX	X

Box 1

Mitigation: Functional populations are present and the goal is to increase or maintain the availability and quality of sturgeon habitat. Mitigation implies confidence in the efficacy of spawning habitat remediation, but may be challenging for species with persistent biological uncertainty.

Rejuvenation: Remediation is required to improve the quality of degraded habitats that continue to be used by spawning wild adults. For example, recent evidence (McAdam et al. 2005, Paragamian et al. 2009, McAdam 2015) supports the need for substrate remediation at spawning sites to address ongoing recruitment failures of white sturgeon. Even when contemporary spawning locations are known, ensuring the success of large scale remediation projects requires detailed information regarding spawning site selection and the biophysical properties that support recruitment.

Re-creation: Extensive habitat modification and destruction in some rivers leads to the need to create new spawning sites. Although adults are still present in such cases, complexity is elevated because suitable spawning locations and substrates may be unknown or assumed. Habitat re-creation requires knowledge about all life stages of sturgeon to ensure effective implementation and to diminish uncertainty regarding the recolonization and use of newly constructed habitat.

Repatriation: Returning sturgeon to rivers from which they have been extirpated (e.g., European sturgeon) represents the most complex form of remediation and faces substantial uncertainty. Evaluation of the habitat capacity of recipient rivers (Gessner and Bartel 2000, Arndt et al. 2006) is challenging in the absence of sturgeon, particularly when habitat modifications have been extensive. For species for which remediation work is just beginning, substantial gains may be achieved by cross species comparisons.

Box 2

Whole river scale: Long distance migrations are part of the life history of many sturgeons, and the negative effects of river impoundment on migration are widely recognized (Auer 1996a, Wei et al. 1997, Khodorevskaya et al. 2009). Large scale continuity of riverine habitat is also a suggested requirement for larval drift of pallid sturgeon (Braaten et al. 2012) and Chinese sturgeon (Zhuang et al. 2002). Rivers also integrate multiple watershed scale processes creating the potential need for upland habitat restoration to diminish their secondary downstream effects (e.g., runoff and sediment budget effects of deforestation).

Reach scale: Within a selected river reach, spawning habitat selection is predominantly influenced by hydraulic conditions, with spawning generally occurring in higher velocity areas (e.g. > 1 m/sec; Parsley and Beckman 1994, Ban, Du, Liu, & Ling, 2011, Bennion and Manny 2014). Detailed evaluation of hydraulic conditions (Zhang et al. 2009, Du et al. 2011, Muirhead 2014) also suggests the importance of elements such as turbulence, heterogeneous conditions and large roughness elements. Constant flow may also be important, as flow fluctuations (i.e., peaking) downstream of dams can negatively affect spawning (Auer 1996b). Repeated spatial patterns of spawning habitat use in lake sturgeon (Duong et al. 2011) also suggest the presence of additional (undefined) preferences at the sub-reach scale.

Spawning sites: Links between recruitment failure and altered substrate conditions at spawning sites demonstrate the critical importance of benthic substrates to the proper functioning of SER habitat (McAdam et al. 2005, Paragamian et al. 2009, Hastings et al. 2013). Negative effects of degraded substrates have been identified for eggs (Kock et al. 2006, Forsythe et al. 2013) and yolksac larvae (Gadomski and Parsley 2005b, Gessner et al. 2009, McAdam 2011, Boucher et al. 2014). Impacts upon feeding larvae (e.g. diminished food supply) are also possible (Howell and Mclellan 2011). While multiple attributes of spawning habitat have been described (e.g., depth, temperature) substrate is the attribute commonly addressed by remediation.

of migratory barriers is widely observed, such locations might not provide the biological benefits associated with upstream spawning locations (see below). For example, lost migratory access concentrates spawning in tailrace areas of hydroelectric facilities, which can contain either unsuitable habitats (Cooke & Leach, 2004; Terraquatic, 2011) or a much reduced area of potential spawning habitat (Chebanov & Savelyeva, 1999; Khodorevskaya et al., 2009; Zhang et al., 2013). Maintaining the existing connectivity is thus preferred (see Rupert River case study) in the absence of understanding how to fully mitigate the benefits accrued by migrating (see Brown et al., 2013).

Fish passage offers a potential means to restore connectivity; however, fish passage facilities are most often designed for other species (e.g., salmonids) and show a limited effectiveness for sturgeon. Use of fish passage facilities by sturgeon has been noted at fish ladders (Parsley et al., 2007; Bruch, 2008; Thiem et al., 2011, 2016), boat locks (Cooke, Leach, Isely, Van Winkle, & Anders, 2002) and fish lifts (Ducheney, Murray, Waldrip, & Tomichek, 2006; Warren and Beckman, 1993), although studies typically report low levels of passage. Recent laboratory studies have addressed specific requirements of sturgeon for fish passage (Cocherell et al., 2011; Kynard et al., 2011a; McDougall et al., 2014), and the larger size of sturgeon and their benthic orientation present important design requirements (Jager et al., 2016; McElroy et al., 2012; Thiem et al., 2011). Downstream passage also presents a critical challenge, since mortality associated with downstream passage may diminish the benefits of restoring upstream passage. Downstream passage survival rates vary, depending both on the passage route (e.g., turbines, spillway) and the size of the fish (Kynard & Horgan, 2001; McDougall et al., 2014). The large size of adult sturgeon can mean that the trashracks prevent downstream movement via turbines, and as a result the fish of intermediate size may be most vulnerable to mortality during turbine passage (Jager et al., 2016). While there are a few notable examples of successful upstream or downstream passage (e.g., Parsley et al., 2007; Thiem et al., 2011), current findings generally indicate the need for further research to identify methods for effective passage for sturgeon (see Cooke et al., 2002; Jager et al., 2016).

Identification of an extensive drift during the yolk-sac larval stage of some sturgeon (Braaten et al., 2012; Zhuang, Kynard, Zhang, Zhang, & Cao, 2002) suggests that contiguous sections of un-impounded riverine habitat are required to support population viability. The identification of both drift and hiding behaviour by yolk-sac larvae has critical implications for the spatial scale of habitat remediation for this life stage, and therefore represents a critical information requirement to plan remediation. While inferring natural behaviours from responses in altered environments and laboratory studies requires caution (Gessner et al., 2009; McAdam 2011), a recent study of pallid sturgeon (*Scaphyrhinchus albus*) provides clear evidence of early drift requirements for that species (DeLonay et al., 2015). For species that require long distance larval drift, mortality associated with movements into inhospitable reservoir environments may lead to recruitment failure (Guy et al., 2015). Restoration of contiguous riverine habitats represents a substantial and challenging undertaking that may require dam removal. Ongoing research for pallid sturgeon recovery provides the most extensive evaluation of the need for larval drift and potential remediation actions (Erwin & Jacobson, 2015; Jacobson et al., 2016), however, remediation actions to extend larval drift distances have not yet been implemented.

Flow restoration represents another remediation approach based on the association between sturgeon population declines and river flow regulation (Gessner & Bartel, 2000; Gessner, Spratte, & Kirschbaum, 2011; Luk'yanenko et al., 1999; Petts et al., 1989). The positive correlation between freshet flows and recruitment for some species (Dumont et al., 2011; Kohlhorst, Botsford, Brennan, & Cailliet, 1991; Nilo et al., 1997) suggest the importance of the magnitude of freshet flows. Unfortunately, the large-scale anthropogenic changes that affect river flow (dams, floodplain abstraction, inland navigation) make full restoration challenging and possibly unfeasible. In the absence of full-scale restoration of freshet flows, partial remediation requires a mechanistic understanding of how flow affects fish abundance. Without such knowledge it becomes uncertain whether partial solutions (e.g., the timing but not the full magnitude of historical freshet flows) will provide the desired outcomes (Wohl et al., 2015). Beneficial effects of a conservation base flow in the Rupert River (see case studies) provide a recent example of positive outcomes of flow mitigation for a new project. Potential benefits of flow restoration for white sturgeon (*Acipenser transmontanus*) recruitment have also been suggested (UCWSRI, 2013). However, experimental flow restoration in the Kootenai River provided no detectable recruitment response (Paragamian, 2012). Limited recruitment responses to naturally high flows in other cases (McAdam, 2015; McAdam et al., 2005) suggest that flow alone may be insufficient to restore recruitment. Understanding the relationship between river flow, sturgeon habitat and population responses is therefore paramount to the design and implementation of effective flow remediation.

Dam operations also affect reach scale habitat conditions, with the potential for both positive and negative effects. Short term flow fluctuations (e.g., in response to short term changes in electricity demand) have been associated with diminished use by spawning adults (Auer, 1996a), egg stranding (Gessner et al., 2011; DFO [Fisheries and Oceans Canada], 2014), and may stimulate larval drift (Crossman & Hildebrand, 2014). While the restoration of minimum flows is typically considered one of the first steps in a flow restoration program (Auer, 1996b), site-specific hydraulic models may be required to demonstrate beneficial effects (Hildebrand et al., 2014). For remediation works immediately downstream of dams, releases might also be adjusted to ensure the provision of suitable habitats conditions (i.e., maximize the area of spawning and early rearing habitat).

The need for reach scale restoration reflects the effects of hydraulic conditions on spawning habitat selection and reach scale fluvial geomorphology. Altered hydraulic conditions in spawning habitats (Muirhead, 2014; Paragamian et al., 2001; Zhang et al., 2009) should be addressed during planning stages of remediation works to ensure the utilization and maintenance of remediated areas (see case studies). The dynamic nature of river channels (Church, 1995) emphasizes that long-term persistence of remediation works will require detailed analysis of reach scale fluvial geomorphology in order to incorporate long-term channel changes at the project design stage. These considerations may be most important for remediation in non-tailrace locations where there may be a greater risk of underutilization if restored habitats are located in unsuitable areas (e.g., Vlasenko, 1974). It is also important to consider that manipulation of hydraulic conditions in spawning reaches may provide an opportunity to concentrate spawning in desired areas, or to avoid others; however, such applications will require an improved understanding of spawning habitat selection. The need for reach scale considerations is recognized in some recovery programs (KTOI [Kootenai Tribe of Idaho], 2009; DFO, 2014). While we found no current examples of completed works at this scale, reach scale restoration efforts for white sturgeon are underway on the Kootenai River (KTOI, 2016).

Selecting the location for site-specific remediation of spawning and early rearing habitat is a fundamental decision with potentially high uncertainty. In some cases, consistent spawning at a well-defined spawning site clearly identifies potential remediation sites, although spawning can persist in degraded spawning habitat (e.g., McAdam et al., 2005). However, spawning sites may not be known in all cases, which creates the potential that remediated habitats might not be fully utilized. For repatriation and recreation contexts, although historical sites might be known or inferred, current suitability may be limited by subsequent habitat alterations (Arndt, Gessner, & Bartel, 2006). Selecting remediation sites must also consider potential implications of spawning fidelity to specific reaches (Folz & Meyers, 1985; McAdam et al., 2005) or sites within a reach (e.g., Forsythe, Crossman, Bello, Baker, & Scribner, 2012). Failure to fully understand factors influencing the spawning habitat selection (e.g., hydraulic conditions) may lead to limited use of remediated habitats, particularly if the number of remediation sites is limited. In cases such as the Wolf River where rip-rap placement created multiple remediated sites, lake sturgeon selected the newly placed rip-rap when older sites had become covered with silt, debris or algae (Folz & Meyers, 1985). While the construction of multiple sites may allow habitat selection by spawning sturgeon and may support stronger recruitment responses, the potential impacts of dispersing spawners should be considered (e.g., if the numbers of spawning adults is low, as in some endangered populations).

Most successful examples of spawning and early rearing habitat remediation address the use of dam tailraces by lake sturgeon (Table 2). Such locations increase the potential for success because the sturgeon undertaking upstream spawning migrations are concentrated at the barrier created by the dam. Spawning locations are also fairly consistent due to the predictable hydraulic conditions in tailrace areas, and fine sediment inputs are limited due to the presence of upstream reservoirs. However, the area of available spawning habitat may be substantially reduced relative to the extent of inaccessible upstream habitat (Raspopov et al., 1994; Ruban and Khodorevskaya, 2011). Remediation at non-tailrace locations often shows limited long-term success due to factors such as inconsistent use by spawning adults (Khoroshko & Vlasenko, 1970), or the deposition of fine substrates leading to decreased egg or yolk-sac larvae survival (Table 2, case studies; Veshchev et al., 2011). Greater attention to reach scale hydraulic conditions and their effects on spawning location and substrate will hopefully lead to improved success for remediation in non-tailrace habitats.

Substrate augmentation is the most common method for remediating sturgeon spawning and early rearing habitat. Early remediation work was based on the replication of substrates found at natural spawning sites as well as being the fortuitous response to rip rap placed to improve bank stability (Folz & Meyers, 1985). More recently, support for substrate restoration has been based on links between recruitment failure and the deposition of fine substrates (McAdam 2015; McAdam et al., 2005; McDonald et al., 2010). Interstitial habitats provided by gravel/cobble substrates are important for the retention and survival of the egg and larval stages (Crossman & Hildebrand, 2014; Forsythe, Scribner, Crossman, Ragavendran, & Baker, 2013; Johnson et al., 2006b; McAdam 2011). The recent identification of strong egg adhesion to multiple substrates (Parsley and Kofoot, 2013) suggests that substrate type has a limited effect on egg retention. However, Johnson et al. (2006b) and Forsythe et al. (2013) found that the position of adhered eggs is important and that interstitial eggs showed decreased predation mortality relative to exposed eggs. Similar findings also apply to yolk-sac larvae (Gessner et al., 2009; Hastings et al., 2013, McAdam, 2011) for which substrates with suitable interstitial habitats increase larval retention (Crossman & Hildebrand, 2014) and decrease both predation and non-predation mortality (Boucher et al., 2014; Gadomski & Parsley, 2005a; McAdam, 2011). Recent identification of strong physiological benefits of enriched substrates (Baker, McAdam, Boucher, Huynh, & Brauner, 2014; Boucher et al., 2014; Gessner et al., 2009) provides further evidence for the importance of interstitial rearing of yolk-sac larvae.

The size and arrangement of placed sturgeon spawning substrates represents a critical design decision; placed substrates typically include large diameter materials to limit downstream displacement and smaller substrates that provide suitably-sized hiding habitat. Previous spawning habitat restoration projects have used 10-50 cm broken limestone or granite (Bruch & Binkowski, 2002; Roseman et al., 2011a, 2011b), 5-15 cm rounded igneous cobble (Manny et al., 2005) and 1-5 cm coal cinders (Nichols et al., 2003, Thomas & Haas, 2004). More recent projects have used a mixture of substrates sizes (see case studies). Use of substrates that are too large in diameter can limit the suitability for hiding by yolk-sac larvae, leading to downstream displacement of larvae (McAdam, 2011; Terraquatic (Terraquatic Resource Management), 2011). Zhang et al. (2009) suggested that a ‘pool and riffle’ structure was beneficial and enhances interstitial water flow, although under some circumstances bottom relief may contribute to sediment deposition and infilling of interstitial spaces. The total area of remediation sites also represents a critical design decision, due to the potential for egg overcrowding (Dumont et al., 2011; Khoroshko and Vlasenko, 1970). Additionally, in larger rivers, the location of sites below the photic zone may limit the negative effects of aquatic plants (Gendron, Lafrance, & LaHaye, 2002; Johnson et al., 2006b).

The long-term effectiveness of remediated habitats is also a critical consideration. Infilling of placed substrates is the most commonly observed limitation; however, growth of periphyton (Johnson et al., 2006b) can diminish long-term effectiveness. For example, half of the 18 examples presented in Table 2 are negatively affected by sediment infilling. Addressing this challenge will require greater input from the field of fluvial geomorphology. Sediment transport models that predict fine sediment movements at remediation sites can be used to guide the placement, composition and configuration of habitat remediation areas (Kinzel et al., 2016). Additionally, some recent projects (e.g., St. Louis River; see Aadland, 2010; Rupert River: see case studies) have given more attention to geomorphological effects. In some cases the current flow regimes may not be competent to provide the cleaning required maintain the quality of remediated habitat area (e.g., in the Nechako River; see Hildebrand et al., 2016), leading to the need for either (i) repeated physical cleaning or (ii) large-scale engineering to re-size the river channel for the regulated flow regime. The latter option entails substantial cost and biological uncertainty and would require extensive site-specific information.

Locating restored habitats in existing or constructed side channels may circumvent some of the challenges associated with mainstem locations, due to the potential for natural or artificially diminished bedload, but may increase limitations with regard to spawning site selection. In the extreme, use of off-channel habitats might entail physically moving spawners to enclosed off-channel raceways, which might function similar to salmonid spawning channels. While early experiences with this approach showed limited success (see Chebanov & Galich, 2011), positive results were achieved with shortnose sturgeon (*Acipenser brevirostrum*) (Kynard et al., 2011b). Factors such as fish size and the associated size of spawning channels as well as captivity stress (Genz et al., 2014) may be important limitations of this approach. Further

TABLE 2 Details of spawning habitat restoration projects undertaken for sturgeon (LS = lake sturgeon (*Acipenser fulvescens*), WS = white sturgeon, SVS = Sevryuga (*Acipenser stellatus*), RS = Russian sturgeon (*Acipenser gueldenstaedtii*))

River	Species	Area (m^2)	Velocity (m/sec)	Depth (m)	Material	Substrate depth (m)
Detroit and St. Clair (see Table 4)	LS	39, 000	0.5-0.7	5-10	Various (see Table 4; case study)	0.6
Eastmain	LS	Na	Na	Na	Na	Na
Kuban (upper)	SVS	1.9 ha	0.76-0.84	4-6	5-8 cm, coarse sand, quarry stone	0.30
Kuban (lower)	SVS	1.6 ha	0.88-0.94	4-5	Gravel, coarse sand, quarry stone	Na
Ottawa	LS	Na	Na	Na	15- 25 cm rock	Na
Des Prairies	LS	5, 000 and 8, 000	1.0	1.5-3.0	20-30 cm (area encircled with 30-50 cm rock with rows of 1 m rock)	0.3
Ouareau	LS	3050	0.8 -1.2 (m/sec)	0.5-1.5	Sedimentary blast rock and river rock (20-200 mm)	0.30 (min)
Upper Black River	LS	4 locations	Na	Na	Rip rap	Na
Saint- Maurice	LS	2100	Na	Na	Large boulder with 3-40 cm material downstream	Na
St. Lawrence (Odensberg)	LS	36 × 36	Na	4.3	4-7 cm	0.3
St. Lawrence (Iroquois)	LS	2 @ 929 m^2	0.6-0.7	10-12	5-10 cm, large boulders d/s	0.30
St. Lawrence (Beauharnois)	LS	3000	0.46- 0.98 (also intermittent low flow events)	2.0-4.5	17-65 mm and 65 mm-255 mm, with 1m x 5m blocks spaced at 8 m	0.30 (min.)
St. Louis	LS	Na	Na	Na	10-25 cm (24%) 30-90 cm (21%) 90-150 cm (54%)	Na
Volga	RS	~11,000	0.5-1.0	3-4	5-10 cm	
Wolf/Fox	LS	>50 sites	Up to 5 m/sec	Na	10-50 cm	Na
Columbia	WS	1, 000	Up to 3 m/sec	Variable	2.5-30 cm (see case study)	0.60
Nechako	WS	4,600	Up to 2 m/sec	1-3	25% 2-4 cm 35% 4-15 cm 40% 15-20 cm	0.30
Rupert	LS	2, 060	0.2-1.8	0.6-2.1	4-40 cm (see case study)	Na

research regarding spawning site selection would be highly beneficial for evaluating off-channel remediation options.

1.2 | Monitoring requirements

Monitoring the effectiveness of habitat remediation projects helps to ensure that desired biological and physical responses are achieved, and provides the basis for improved design of future projects. The duration of monitoring programs should reflect the time scale of expected biological (e.g., juvenile production, adult returns) and geomorphological (e.g., channel movement, substrate infilling) responses. Ideally, biological monitoring should demonstrate that habitat remediation is supporting all targeted life stages of sturgeon. We elaborate on these subjects in further detail below.

1.2.1 | Biological Response

Use by spawning adult sturgeon

Use of restored spawning habitat provides a straightforward metric of remediation effectiveness, with indicators of spawning ranging from the presence, density, and depositional pattern of eggs, to the number of spawners and their sex ratios. For example, recent genetic studies provide a means to estimate the number of spawning adults from collected wild progeny (Jay et al., 2014; Manny et al., 2015). Direct adult counts (see Rupert River case study) and DIDSON acoustic camera (Bray, Crossman, Martel, & Johnson, 2011) have also be used to detect spawning adults. Evaluation of changes in spawning habitat use over time should also be considered in combination with physical monitoring discussed below. For the re-creation and repatriation

Below dam (BD)/mid reach (MR)	Spawning (Y/N)	Year built	Comments	References
MR	N (Belle Isle), Y (other sites, some intermittent)	2004, 2008, 2012-16		(Manny et al., 2005), (Roseman et al., 2011b), (Thomas and Haas, 2004)
BD	Na	Na	Compensation for 890 m^2 habitat impact	(Environnement Illimité Inc., 2009)
BD (80 m)	Y	1966		(Khoroshko & Vlasenko, 1970)
BD (900 m)	Y - silted after 3 years	1966		(Vlasenko, 1974), (Chebanov, Galich, & Ananyev, 2008), (Kerr et al., 2010)
BD	TBD	2010/2012		Ron Threader (pers. comm.)
BD	Y (also increased egg to feeding larvae survival)	1985, 1996	13 m^2/female preferred, site sloped so effective at variable flows	(Dumont et al., 2011), (LaHaye et al., 1992)
MR (2.5 km down-stream)	N – at restored location, Y – at nearby natural site	2007, 2008	Landslide affected quality of natural spawning site	(LaHaye and Fortin, 1990), (MRNF-CARA, 2011)
BD (<2 km)	Na	1972	Sedimentation decreased effectiveness	(Smith and Baker, 2005)
BD	Y	1999	Multiple small sites	(Faucher, 1999), (Faucher & Abbott, 2001), (GDG Conseil Inc., 2001)
MR	Y (initially)	1993	Effectiveness decreased – siltation, periphyton, zebra mussels	(Johnson et al., 2006b)
Above and below	Y	2007		(McGrath, 2009)
BD	N	1998	Ineffective due to siltation, vegetation, unsuitable flow	(Gendron et al., 2002)
BD	Y spawning, assessment limited to date	2009	Stepped boulder clusters	(Aadland, 2010), Aadland, pers. comm.
MR	Rarely	1966	Site too far downstream of dam	(Khoroshko & Vlasenko, 1970)
MR	Y		Siltation at some sites	(Folz & Meyers, 1985), (Bruch & Binkowski, 2002)
BD	Unconfirmed	2011	Site degraded after 1 year	(Crossman & Hildebrand, 2014)
MR	Y	2011	Small recruitment response, sand deposition at 1 of 2 sites	Author's personal data, (nhc, 2013b)
MR	Y	2010		(Environnement Illimité Inc., 2013)

contexts, the presence of spawning sturgeon on newly created habitat is a special case of adult detection that may require sturgeon to stray from established spawning areas. The potential that low straying rates delay the re-establishment of spawning runs emphasizes the long-term nature of this metric. Cross-species comparisons and long-term research in controlled settings will also provide important reference studies of biological responses to construction of sturgeon spawning habitat (e.g., Forsythe et al., 2012; Pledger et al., 2013).

Early life stage survival and production of feeding larvae

Monitoring should ideally demonstrate survival through the egg, yolk-sac, and feeding larval stages, although this is rarely done. Quantifying stage-based survival may not be possible, however, systematic monitoring using standard techniques such as egg mats, benthic sampling and drift nets, can be used to estimate egg deposition (Caroffino, Sutton, Elliott, & Donofrio, 2010; Roseman et al., 2011a), egg loss (Johnson et al., 2006b), yolk-sac larvae survival (Johnson et al., 2006b; McAdam 2012) and larval dispersal (Crossman & Hildebrand, 2014; Dumont et al., 2011; Roseman et al., 2011a). Developmental staging of eggs or larvae allows the back-calculation of spawning time (Jay et al., 2014). Ontogenetic drift patterns (McAdam, 2011) and larval quality indicators (Baker et al., 2014) also offer potential biological indicators. For example, drift by newly-hatched larvae may be indicative of limited larval hiding in response to remediation (e.g., Crossman & Hildebrand, 2014; Khoroshko and Vlasenko, 1970; Raspopov et al., 1994). Ultimately, consistent monitoring of early life stages following remediation of spawning habitat (possibly using multiple methods) is one of the most important factors in determining remediation effectiveness.

Juvenile recruitment

Monitoring recruitment provides the ultimate measure of remediation success (see Dumont et al., 2011) and can be achieved through annual juvenile monitoring. Gill nets have typically been used for this application, although the delayed vulnerability to gill net capture leads to a muti-year lag in recruitment detection (Howell and Mclellan, 2011). Trawl nets have been also been used to detect early juveniles (Parsley and Beckman, 1994; Wanner et al., 2007), although the ability to use trawl nets may be limited in many applications (Steffensen, Wilhelm, Haas, & Adams, 2015).

Use by non-target species

While the main target of habitat remediation is sturgeon, the effects (positive or negative) on other species also warrant consideration. For example, substrate remediation may also benefit freshwater mussels (Haag and Williams, 2014), macro invertebrates (McManamay et al., 2013; Merz and Chan, 2005), salmonids (Jensen et al., 2009) and other lithophilic spawning fish (e.g., Jennings et al., 2010; Romanov et al., 2012). The potential for responses by non-target species to overwhelm responses from target species (Pine et al., 2009) must be seriously considered, and supports the need for broader monitoring programs. Sturgeon recovery, and particularly repatriation in highly altered habitats (e.g., European sturgeon; Arndt et al., 2006), is often included within a broader suite of ecosystem remediation objectives (e.g., KTOI, 2009; Hondorp et al., 2014). While linking sturgeon remediation to broader habitat remediation can yield important benefits, broadening recovery goals may also increase the probability of not achieving sturgeon restoration goals.

1.2.2 | Physical Response

Channel structure

River channel responses to flow regulation occur over decades or centuries (Church, 1995). Understanding long-term fluvial and geomorphological processes should be considered during project design. Consideration of the dynamic nature of river channels is important to ensure that remediation works are effective despite long-term changes in the river channel structure.

TABLE 3 Utilization by sturgeon of the man-made spawning ground at site KP 290, Rupert River, 2011 to 2014

	2011	2012	2014
Spawning period start	30 May	25 May	3 June
Spawning period end	6 June	8 June	9 June
Temperature (°C):	8.9 to 11.2	10.7 to 14.6	10.2 to 12.3
Sampling effort (number of egg traps):	37	42	38
Eggs captured:	6 346	2 366	2998
Spawners observed (maximum/day):	220	270	145

Hydraulic conditions

The importance of hydraulic conditions to spawning habitat selection (Du et al., 2011; Zhang et al., 2009) underscores the need for pre and post-project monitoring to ensure that hydraulic conditions are maintained or enhanced. Detailed modelling (Hildebrand et al., 2014; McDougall et al., 2013; nhc, 2008) and direct measurement (e.g., using ADCP; Elliott, Jacobson, & DeLonay, 2004; Johnson et al., 2006a, 2006b) have both been used to understand hydraulic responses. This aspect of physical monitoring is important to improve our understanding of spawning habitat selection at both the project design and monitoring stages.

Substrate condition

Infilling of restored spawning substrates with fine sediments is a key concern for both short and long-term effectiveness. Monitoring the effects of substrate (e.g., silt, sand or gravel) accumulation on remediated spawning habitat, and in other areas (e.g., downstream stretches, bank development, impacts on navigation), is a critical monitoring requirement. Monitoring techniques used to evaluate restored substrate quality have included video and diver observations of surficial characteristics (Dumont et al., 2011; Roseman et al., 2011b; Vaccaro et al., 2016) and freeze-core sampling of riverbed materials (nhc, 2013a). Ideally, assessments should develop a broad understanding of riverine sediment dynamics prior to remediation (e.g., sediment budget, spatial and temporal deposition patterns).

1.3 | Case studies

Sturgeon habitat remediation studies are not widely reported in the scientific literature; four case studies are therefore presented to provide examples across the range of remediation contexts and bio-spatial scales. These projects are at various stages of implementation, and identifying both successes and limitations should benefit future projects.

1.3.1 | Lake sturgeon-Rupert River (context = mitigation, bio-spatial scale = whole river and spawning site)

This case represents planned mitigation for lake sturgeon affected by newly-constructed diversion projects on the Rupert River (constructed in conjunction with two powerhouse projects, the Eastmain-1-A and Sarcelle powerhouses that are part of the La Grande Hydroelectric Complex). Changes to lake sturgeon habitat as a result of these projects include: reduced flow in the lower Rupert River downstream of the partial diversion; the creation of two diversion bays upstream of the diversion point (flooding of upland areas); and increased flow in the diversion zone up to the La Grande River watershed.

Impacts to lake sturgeon spawning habitat were addressed through pre-project evaluations of spawning habitat requirements and

TABLE 4 Characteristics of lake sturgeon (*Acipenser fulvescens*) spawning sites in the unobstructed St. Clair and Detroit rivers (sites listed from upstream to downstream)

Site	Area (ha)	Depth (m)	Substrate	Flow (m/s)	Egg density[a]	Duration of use (years)	Number of spawners
Port Huron	69.0	20-22	Cobble, gravel	2.0	Unknown	100	Thousands
Harts Light	1.54	10-12	Broken limestone	0.8	100s	2	
Pt. Au Chenes	0.61	10-12	Broken limestone	0.6	100s	2	
Middle Channel	0.3	7-10	Broken limestone	0.5	35	4	50
Mazlinkas	0.1	7-10	Coal cinders	0.6	50-1700	100	Hundreds
Belle Isle	0.11 expanded to 1.6	5-7	Limestone, cobble stone, coal cinders	0.7	0	0	2
Zug Island	0.1	9-10	Coal cinders	0.6	21	1	35
Fighting Island	0.3, expanded to 0.72	5-9	Broken limestone, cobble	0.7	0-330	6	35
Grassy Isle	1.62	8-10	Broken limestone	0.7	100s	1	

[a] eggs/m^2 on egg mats.

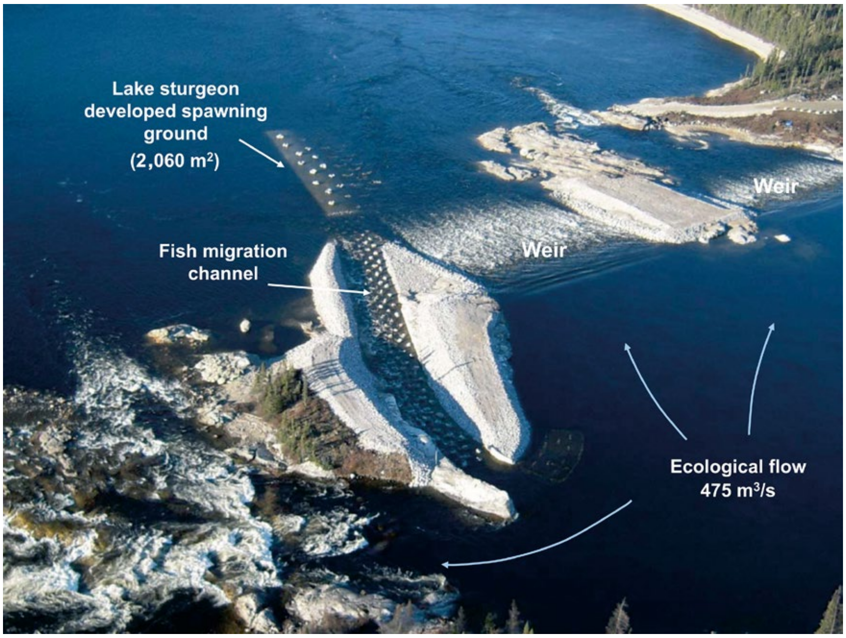

FIGURE 1 Aerial view of lake sturgeon, *Acipenser fulvescens*, developed spawning ground at site KP 290 of Rupert River

baseline habitat conditions, followed by the completion of mitigation and enhancement measures and associated effectiveness monitoring. In particular, the mitigation and enhancement measures included an in-stream flow regime, weirs and spur to maintain water levels, and the construction of fish passage channels and spawning grounds (complete project description in Hydro-Québec Production, 2004).

The in-stream flow regime for the Rupert River downstream of the diversion weir ensures that flows are sufficient to allow lake sturgeon to move between available habitats and provides appropriate hydraulic conditions at spawning sites. A 2,060 m^2 spawning ground was constructed in 2010, downstream of the diversion weir at site KP 290 (river km 290) of the Rupert River (Figure 1). Based on a review of 41 studies throughout the range of lake sturgeon (including six studies from the project area; Environnement Illimité Inc. et al., 2009, 2013a,b), the final design criteria for the site were:

- Location: adjacent to the thalweg, ideally at the foot of a major set of rapids
- Optimum velocity: 0.2 to 1.0 m/s (range 0.1 to 1.6 m/s)
- Optimum depth: 0.5 to 1.0 m (range 0.2 to 4.0 m)
- Spawning substrate: heterogeneous mix of 0%-10% large boulders (250-400 mm), 20%-70% boulders (150-250 mm), 25%-60% cobbles (80-150 mm), and 0%-20% pebbles (40-80 mm)

The constructed spawning ground was a shoal composed of two plateaus (6 m × 86 m – W x L), connected by a gentle 12 m long slope (8% gradient). About forty rock islets, each made up of three or four large boulders were placed in different spots over the spawning ground to provide shelter from the current. Modelled hydraulic conditions at the spawning ground showed that under expected spring flow conditions (i.e., the prescribed in-stream flow) the water should be 0.6 to 2.1 m deep and with velocities between 0.2 and 1.8 m/s.

Monitoring from 2011 to 2014 confirmed that the spring flow provides excellent hydraulic conditions in the spawning ground. Hydraulic conditions were measured in 2011 and 2012, when mean flow varied between 479 and 500 m^3/s, mean depth was constant at 1.3 m, and mean velocity remained between 0.66 and 0.76 m/sec. These conditions all met the design criteria, and their consistency reflects the proximity of monitoring locations to the upstream flow release structure.

Additionally, the spawning ground has maintained a consistently high level of physical integrity in terms of substrate cleanliness, developed area and stability since its construction in 2010 (Table 3). Utilization of the spawning ground was demonstrated by observation of adults (aerial counts) during the spawning period (daily counts ranged from 7 to 220 in 2011, 2 to 270 in 2012, and 35 to 145 in 2014). Egg mat sampling also confirmed the use of the site – especially the downstream portion (Table 2). The area used by spawning adults corresponded to roughly 65% (1,339 m^2) of the developed site area. Annual variation in the amount of spawning habitat used was anticipated, because the site was designed to provide suitable spawning habitat at a range of flow rates and water levels.

The effectiveness of the constructed spawning habitat for egg survival was evaluated through drift net capture of larvae (methods based on Verdon et al., 2013). Comparisons of larval captures at four sites (three downstream and one upstream control) were variable, however, the overall trend suggested that catches were either stable or increased, when comparing pre- and post-project larval captures (Figure 2). Post-project larval capture showed a statistically significant increase immediately below the constructed spawning site (river km 287 - Student *t*-test = 3.45, $p = .02$).

Future monitoring to demonstrate juvenile recruitment is planned, although currently the collective results based on adult, egg and larval monitoring all demonstrate that the in-stream flow regime and man-made spawning grounds at site KP 290 have effectively preserved available lake sturgeon spawning habitat. Stable flow for 45 days during the spring period may be particularly important due to an expected increase in egg survival relative to natural conditions, when egg mortality may occur as a result of decreased water levels.

1.3.2 | White Sturgeon-Columbia and Nechako rivers (context = rejuvenation, bio-spatial scale = spawning reach, spawning site)

White sturgeon populations in the upper Columbia and the Nechako rivers are legally listed as endangered, yet persistent recruitment failure was not recognized for more than 20 years in either case (DFO, 2014; Hildebrand et al., 2016). River regulation and industrial use have led to altered flow regimes and habitat degradation over several decades, thus targeted restoration is required to prevent extirpation. Spawning has been identified annually in both populations over the past decade, although at differing spatial scales. In the Upper Columbia River, spawning occurs at multiple locations (Howell and McLellan, 2007; Golder, 2008; Terraquatic (Terraquatic Resource Management), 2011; AMEC, 2014; BC Hydro, 2015). Most spawning sites occur within a 75 km stretch of river, with several immediately downstream of hydroelectric facilities. In the Nechako watershed, only one spawning site has been identified in a 4 km stretch of river (~140 km downstream of Kenney Dam), where decreased riverbed slope led to the historical presence of gravel bars (now largely with vegetation under the regulated flow regime). Spawning has been detected throughout the reach, with activity concentrated in four areas that show locally elevated water velocity (McAdam et al., 2005; Triton, 2009). Although the historical spawning locations are unknown, hydraulic modelling (nhc (Northwest Hydraulics Consultants), 2008) suggests that sturgeon spawned at a single site at the upstream end of the present spawning reach. For both the Columbia River and Nechako rivers the annual presence of wild spawners, coupled with the ability to implement experimental

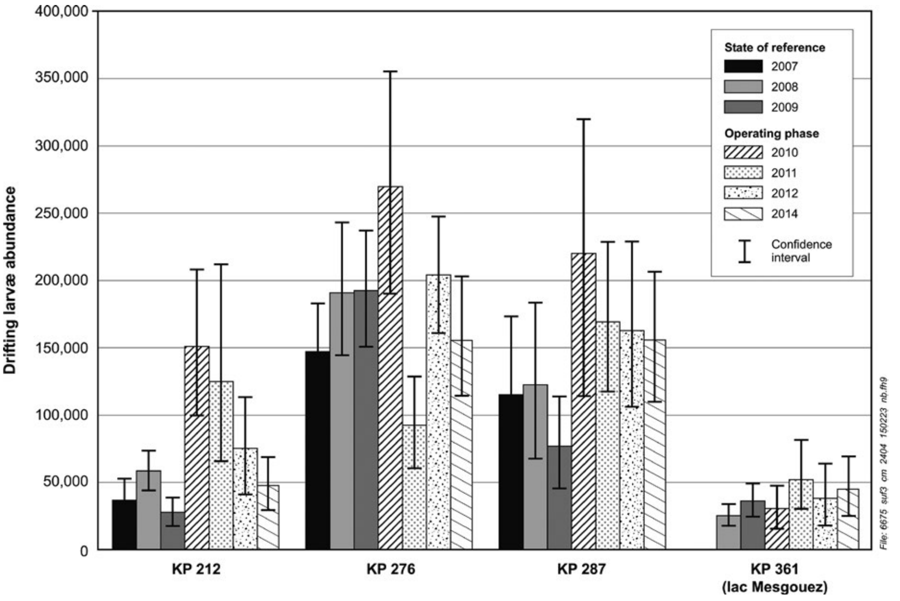

FIGURE 2 Estimated drifting larvae abundance at Rupert River sites KP 212, 276, 287 (downstream) and 361 (upstream) in spring 2007 to 2012 and 2014 (pre-project = 2007 to 2009, post-project = 2010 to 2014)

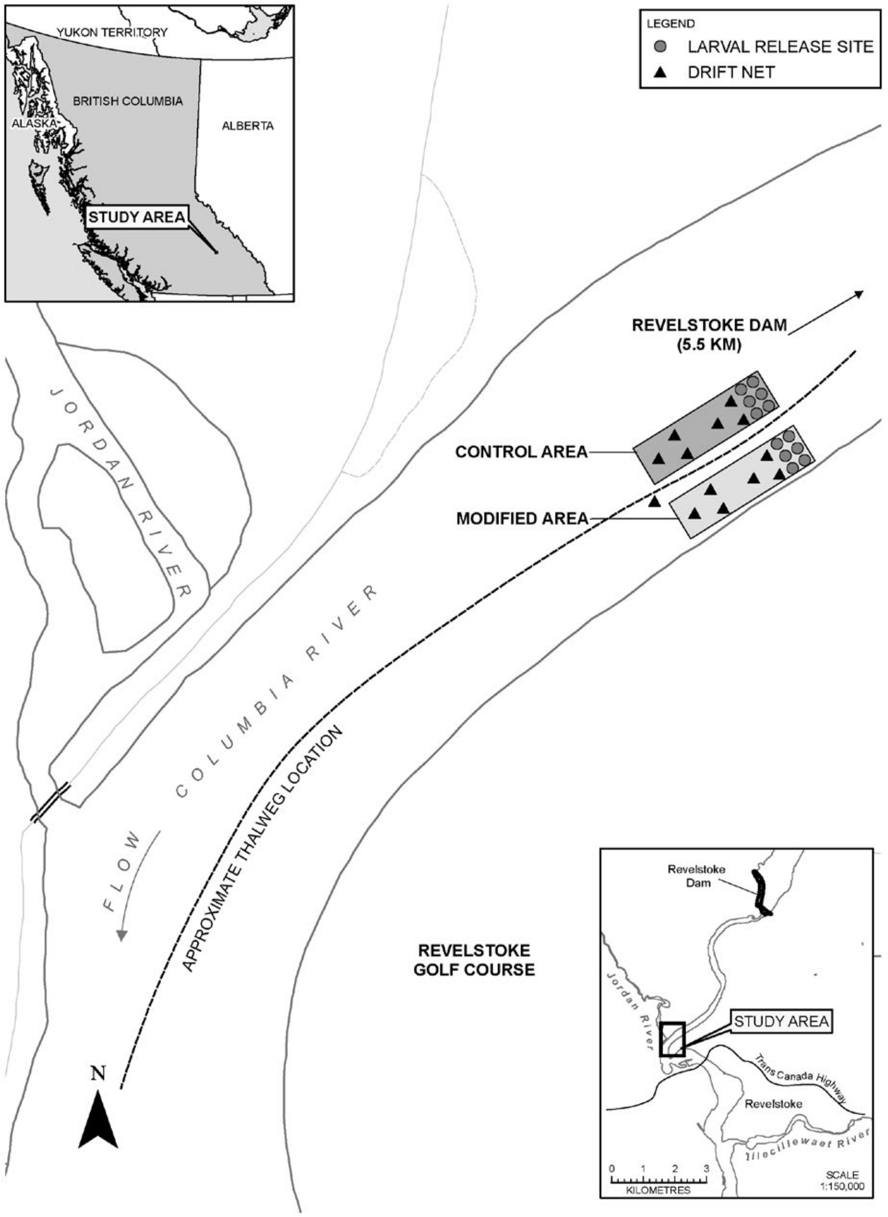

FIGURE 3 Map of Revelstoke Reach of Upper Columbia River showing location of white sturgeon, *Acipenser transmontanus*, spawning and early rearing habitat restoration in 2012. Site dimensions for control and modified sites are 10 m × 100 m. Figure reproduced from Crossman and Hildebrand (2014)

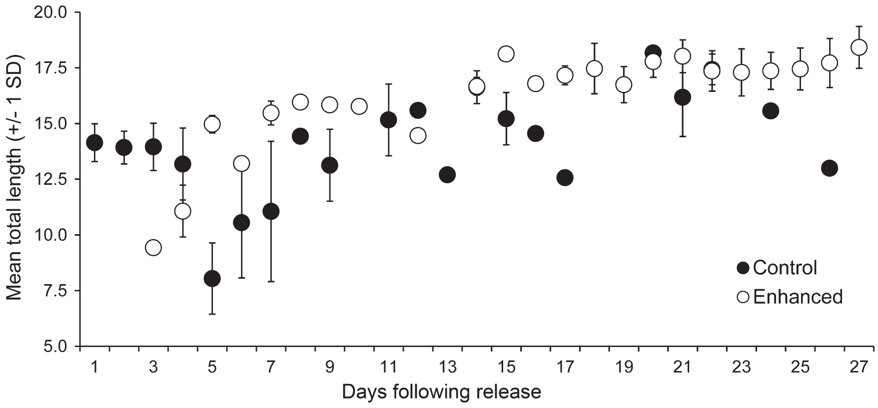

FIGURE 4 Number of larval white sturgeon *A. transmontanus* collected downstream of control and modified sites (histogram) and hourly mean discharge for each time interval (points, line). Figure reproduced from Crossman and Hildebrand (2014)

releases of early life stages (e.g., eggs and larvae), make these sites ideal settings to test the feasibility of spawning habitat remediation and determine the efficacy of different habitat remediation options.

Retrospective evaluations linking recruitment failure to substrate changes in white sturgeon spawning habitat (McAdam, 2015; McAdam et al., 2005) provide a strong foundation for pursuing substrate

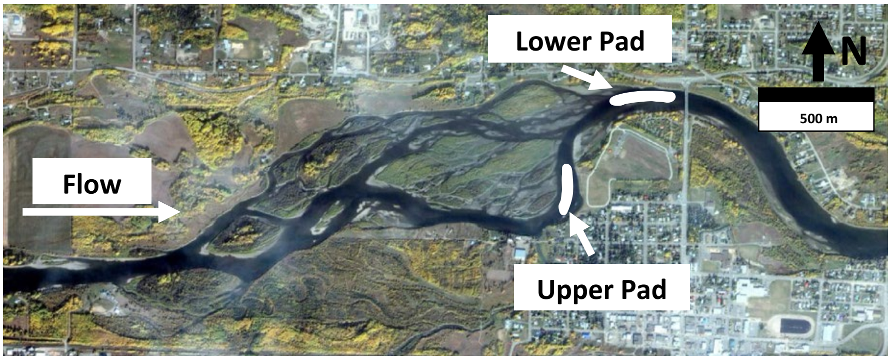

FIGURE 5 Aerial photo showing white sturgeon, *A. transmontanus*, spawning reach of Nechako River located near District of Vanderhoof. Substrate remediation was conducted at upper (upstream) and lower (downstream near bridge) pads in 2011

restoration as a means of population recovery in both rivers. Although bottom velocities at known spawning locations are within the suitable range (>1.0 m/s; Parsley et al., 1993), substrate surveys at several spawning areas show that high quality habitat is limited to a small proportion of surveyed sites (e.g., 3%-12% in the Upper Columbia River; nhc, 2012; Golder, 2013). Field studies in both rivers also demonstrate that larval catch is dominated by young yolk-sac larvae (Golder, 2009; Terraquatic (Terraquatic Resource Management), 2011) at most spawning sites, which is also indicative of a diminished quality of larval hiding habitat. Accordingly, habitat requirements of early life stages (particularly yolk-sac larvae) are used as the primary basis for designing spawning habitat remediation works that are a critical component of the federal recovery strategy for both populations (DFO, 2014).

Experimental spawning habitat remediation has been tested at one site in the Upper Columbia River (Figure 3). Remediation focused on a small area of known egg deposition (1 km^2) and the spawning substrate was modified with a combination of larger boulders and course gravel (90% > 200-300 mm diameter, 10% > 25-80 mm diameter), both of which were angular in shape to provide more interstitial space when settled. The spawning habitat was located below the minimum water level to avoid dewatering eggs or larvae (Golder, 2011). The effectiveness of the restored habitat was tested by stocking yolk-sac larvae (~1 day post hatch) over both modified and control sites (inclusion of a control site is notable, as suitable controls are often limited for such studies). Monitoring demonstrated that larvae released over substrates with increased interstitial space showed a greater tendency to hide, remained in the substrate regardless of the flow conditions, and dispersed downstream volitionally (Crossman & Hildebrand, 2014) (Figure 4). Although habitat conditions were improved, the modified spawning habitat deteriorated rapidly within two years (J. Crossman, BC Hydro, unpublished data). The highly variable flow regime in the study area resulted in the downstream displacement of restored substrate, demonstrating the importance of a thorough evaluation of site-specific hydraulics on substrate retention and maintenance prior to construction.

Experimental spawning habitat restoration in the Nechako River consisted of placing 2,100 m^3 of clean substrate on the riverbed at two sites (Figure 5) prior to the 2011 spawning season. The mixture of large and small materials (see Table 2) was designed to achieve both physical stability and a biological function (i.e., interstitial habitat suitable for yolk-sac larvae). While larval captures were limited in 2011, the detection of wild origin recruits from the 2011 year-class (*n* = 24; five times higher than other year-classes identified in the 2013-2016 juvenile sampling) provides evidence of a positive response to substrate remediation (S. McAdam, unpublished data). The limited recruitment response might be due to the rapid decrease in the habitat quality of enhanced substrates caused by an influx of sand over the majority of one gravel bed (lower pad - nhc (Northwest Hydraulics Consultants), 2012). Hydraulic conditions appear to be limiting or delaying further infilling and monitoring has confirmed the maintenance of biologically-functional substrate conditions at the upper pad in both 2012 and 2013 (Northwest Hydraulics Consultants, 2013b, nhc (Northwest Hydraulics Consultants, 2013a). Physical substrate cleaning was investigated in 2016 as a rapid, although temporary, remediation measure. While substrate cleaning was effective, it is too early to evaluate biological responses (nhc, 2016).

Experimental approaches in both rivers demonstrate the potential efficacy of substrate remediation. Further research regarding the geomorphology, substrate conditions, and hydraulic properties of all spawning sites is required to design remediation projects that maintain their effectiveness over the long term.

1.3.3 | Lake Sturgeon – Detroit and St. Clair rivers (context = re-creation, spatial scale = multiple spawning sites)

The Detroit and St. Clair rivers comprise an unobstructed, 160-km channel between two very large lakes (Figure 6) that has been highly altered and degraded by urban development (Edsall, Manny, & Raphael, 1988; Manny et al., 1988). Since 1900, the construction of more than 145 km of shipping channels led to the removal of more than 46 million cubic meters of rock-rubble from the Detroit River (Bennion & Manny, 2011) and similar amounts from the St. Clair River. The extent of the historical habitat destruction, including elimination of sturgeon spawning habitat, created unique challenges leading to the need to re-create historical habitats (Manny et al., 2005). Remediation of spawning habitat for native fishes, including lake sturgeon, is now an international goal in these rivers.

By 1925, habitat alteration and over-harvest reduced lake sturgeon in both rivers to less than 1% of their former abundance (Caswell, Peterson, Manny, & Kennedy, 2004; Manny and Mohr, 2011). Recent estimates indicate that 45,500 lake sturgeons occupy these two rivers, compared to an estimated historical population of 100,000 (Thomas

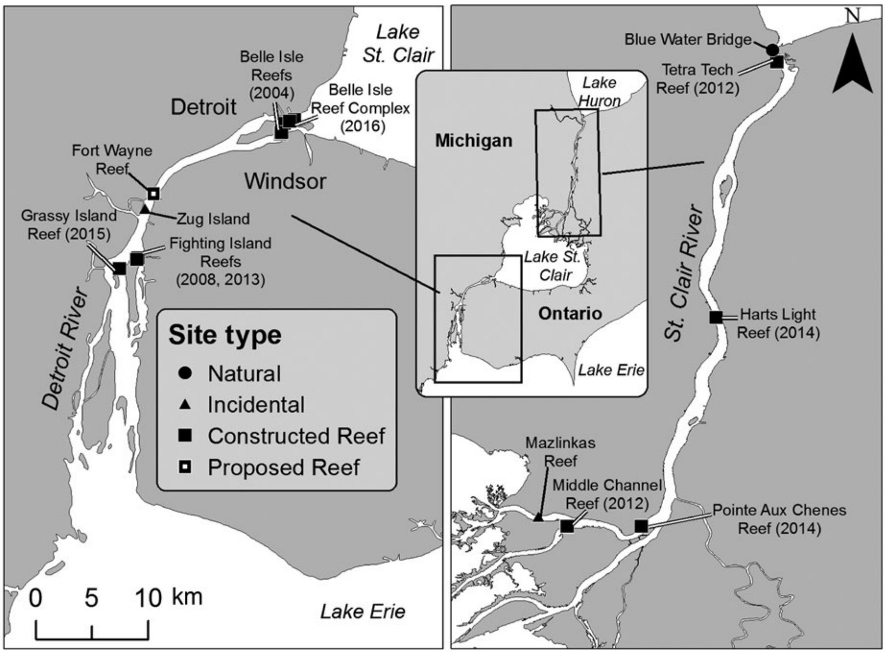

FIGURE 6 Map of unobstructed Huron-Erie corridor (St. Clair River/Lake St. Clair/Detroit River) showing locations of nine naturally-occurring, or restored, lake sturgeon, *A. fulvescens*, spawning sites

and Haas, 2002). Historical reports and interviews with retired commercial fishermen (Goodyear, Edsall, Dempsey, Moss, & Polanski, 1982) identified nine possible historical lake sturgeon spawning sites in the Detroit River.

The largest and highest quality lake sturgeon spawning site is located at the head of the St Clair River, near Port Huron, Michigan. This area is characterized by fast flow and rounded cobble and coarse gravel substrates, and was too deep to be affected by shipping channel construction (Boase & Hill, 2002). Spawning is also regularly detected at two additional areas where coal cinders were historically dumped; Mazlinkas reef in the St. Clair River (Nichols et al., 2003) and Zug Island in the Detroit River (Caswell et al., 2004). It is unclear whether these two sites were used by spawning lake sturgeon prior to the coal cinder dumping, or whether the addition of the coal cinders created new spawning sites.

Following an adaptive strategy, six spawning reefs have been constructed in the St. Clair – Detroit rivers since 2004 (Manny et al., 2015; Vaccaro et al., 2016). For all reef construction projects, the use of gravel less than 5 cm in diameter was avoided during reef construction, owing to its potential use by spawning sea lamprey (*Petromyzon marinus*) (Wigley, 1959) that are controlled throughout the Great Lakes. In the Detroit River at Belle Isle, an 0.11 ha reef was created in 2004 (Detroit River - total reef size 0.11 ha; Manny, 2006a). This previously unused site was chosen because of its location in the relatively unpolluted headwaters of the Detroit River and the presence of suitable water velocity [e.g., 0.37-0.80 m/s based on LaHaye et al., (1992)]. Site selection was based on a hydrodynamic geospatial model used to locate deep, fast-flowing areas (Bennion & Manny, 2014). The selection of substrates was based on the previous identification of large broken limestone (Bruch & Binkowski, 2002), rounded igneous rock (Manny et al., 2005), and coal cinders (Thomas and Haas, 1999, 2002) as suitable substrates (see Tables 2 and 4).

In 2008, a second spawning reef was constructed at Northeast Fighting Island (Detroit River), which was reputedly a historical spawning ground (Goodyear et al., 1982). Substrates used at this site were a mixture of 10-50 cm broken limestone, 5-10 cm broken limestone, and 10-20 cm rounded igneous rock. The initial 0.3 ha spawning reef was expanded in 2013 to a total of 0.72 ha. This location was selected based on the presence of high water velocity (> 0.5 m/s), year-round accessibility by adult sturgeon, a temperature of 11-16°C during the spawning period (Bruch & Binkowski, 2002), and a water depth of 9-12 m (Roseman et al., 2011b). In 2012, a third reef complex was constructed in the Middle Channel of the lower St. Clair River, using 10-20 cm broken limestone and 10-15 cm rounded, igneous stone. A Middle Channel reef was also constructed across the entire channel. Two reefs were placed in the St. Clair River during 2014 at Harts Light (1.54 ha) in the main channel, and at Pt. Au Chenes (0.61 ha) in the upper north channel of the river (Figure 6). These reefs were constructed of one large section of 10-20 cm fractured limestone oriented parallel to the current, along the edge of the river channel on the Michigan shore. In 2015, 1.62 ha of spawning reef was placed in the main channel of the Detroit River at Grassy Island, using similar stone and following the same orientation at Harts and Pt. Au Chenes in the St Clair River. Lastly, in the autumn of 2016, the 2004 Belle Isle reef was expanded to 0.5 ha of contiguous 10-20 cm limestone, and two additional reefs (0.4 and 0.7 ha) were placed upstream of Belle Isle in the Detroit River (Figure 6).

Assessments with various gear types indicate that all sturgeon age classes are present in the Detroit and St. Clair rivers (Boase et al., 2014), however, spawning habitat utilization is not uniform. Spawning by lake sturgeon has been confirmed at five of six constructed spawning sites (not the 2004 Belle Isle; Table 4). Additionally, eggs and larvae were not collected in all years that sampling was conducted (Roseman et al., 2011b; Thomas and Haas, 2004). For example, sturgeon eggs were collected only once (in 2001) at Zug Island (Caswell et al., 2004) until sampling was discontinued after 2008 (due to repeated gear loss). Sturgeon eggs and larvae were collected at Fighting Island in 2009, 2011, 2012, 2014, 2015, and 2016 but not in 2010 or 2013. No sturgeon eggs or larvae have been collected at the Belle Isle reef since it was constructed in 2004, despite repeated annual samplings from 2004 to 2014 (Hondorp et al., 2014, Manny 2006b). Eggs were collected on all other constructed reefs for at least two years following construction. These results suggest limited or intermittent use by spawning sturgeon of constructed spawning habitat. Captures of lake sturgeon yolk-sac stage larvae (Bouckaert, Auer, Roseman, & Boase, 2014) also suggest that substrates at some sites in the Detroit River may not be retaining early larval stages long enough for exogenous feeding to begin, possibly due to excessively large interstitial spaces (see Hastings et al., 2013; McAdam, 2011).

The physical conditions of constructed spawning reefs in the St. Clair and Detroit rivers (Table 4) have been assessed using divers and underwater cameras (Manny, 2006b; Roseman et al., 2011b). Within two years post construction, more than half of the area of the spawning reefs at Fighting Island and the entirety of the Middle Channel reef have filled in with sand and silt, resulting in embedded spawning substrates. Although some infilling was expected, factors affecting the magnitude and location of infilling are poorly understood. Beginning in 2014, an Acoustic Doppler Current Profiler, side-scan sonar, and sediment transport models have been employed to assess candidate reef sites prior to construction and avoid depositional areas (Fischer, Bennion, Roseman, & Manny, 2015; Kinzel et al., 2016; Vaccaro et al., 2016). These technologies are also used to monitor reef conditions and performance following construction. Continued monitoring and assessment is considered critical to understanding long-term changes to physical substrate conditions.

The need for a long term, comprehensive, monitoring program is one of the key lessons learned from various lake sturgeon spawning habitat remediation projects in the Detroit and St. Clair rivers (Manny et al., 2015; Vaccaro et al., 2016). This need is based on the potential for longer term, physical changes in the restored sturgeon spawning habitat, and the attendant biological effects. The optimum number, location, and size of restored sturgeon spawning sites are also important considerations, particularly when present and historical use provides limited guidance (Manny et al., 2015).

1.3.4 | Baltic Sturgeon – Odra River (context = repatriation; bio-spatial scale = whole river)

Remediation of the Baltic sturgeon in the Odra River represents the most complicated remediation context, since it requires the repatriation to habitats from which sturgeon have been extirpated. Extensive habitat changes in recipient watersheds also create numerous challenges for identifying, and restoring suitable habitats. For example, proposed spawning habitat remediation sites must be selected on the basis of expected, rather than confirmed, spawning habitats (Gessner, Arndt, Tiedemann, Bartel, & Kirschbaum, 2006).

Releases of *A. oxyrinchus* began in 2006, and 1 750 000 individuals of all age classes (feeding larvae to subadults of 1.5m length) have been released as of 2016. However, based on maturation rates of captive broodstock and survival rate estimates from early releases (Jaric and Gessner, 2013; McManamay, Orth, & Dolloff, 2013) returning spawners are not expected to be observed prior to 2020. Verification of spawning habitat use will therefore not be possible prior to this date. Despite this limitation, conceptual plans to improve the availability of adult spawning and staging habitat and the quality of early life phase habitats are being developed on the basis of a Project Group under the Helsinki Commission for the Baltic range states (Gessner et al., 2011).

In the absence of spawning adults, prospective spawning sites were identified by evaluating habitats in the vicinity of apparent historic spawning reaches identified from historical catches (Grabda, 1968; Przybyl, 1976). Habitat suitability in the vicinity of these areas was evaluated using well-established characteristics of spawning sites (e.g., depth, velocity, and substrate). Substrate quality was determined by mapping longitudinal sections of the river with transects at select locations to determine the dimensions of substrate aggregations, and by underwater video image analysis (Arndt, Gessner, & Raymakers, 2002).

Four potential spawning sites greater than 1000 m^2 were identified in the Odra catchment. All sites were in the vicinity of historic aggregation areas, mainly areas with erosion and deposition of substrate in areas of postglacial moraine deposits. Anthropogenic habitat alterations through damming, river channel modifications [e.g., channel straightening to increase water conveyance and surface water removal, in combination with groyne fields to stabilize the river bed, led to the loss of approximately 70% of the historical habitat (Grabda, 1968)]. Modelling of habitat availability, assuming 25,000 eggs/m^2 and that 10% of historical habitats remain suitable, suggests a present egg production capacity of 14 million eggs. However, the mobility of river substrates (mostly comprising fine and small gravel 0.1 – 6 mm grain size) means that potentially suitable substrates may show limited functionality for the early rearing of eggs and yolk-sac larvae due to filling with fine substrate (Arndt et al., 2006).

The main obstacles for effective remediation of habitat still persist (i.e., navigation and flood control) and limit the options for improvements to bank erosion, depth heterogeneity and sediment deposition. Currently the increased bank stability resulting from groynes and riprap leads to increased in-channel erosion and increased bedload transport. This has decreased riverbed elevation to the extent that it is below the alluvial deposition layers for gravel and rock, which limits the capacity for the natural regeneration of spawning sites. River channelization also prevents the establishment of a stable riverbed that provides sufficient habitat for bottom fauna, including juvenile sturgeon during downstream migrations. This leads to extremely high migration speeds in sections of the river with the highest bedload transport (Fredrich, Kapusta, Ebert, Duda, & Gessner, 2008).

Difficulties with remediation of mainstem sites suggest the need to consider alternatives, including remediation of spawning sites in major tributaries of the Odra River (e.g., Warta, Notec, Prosna, and Drawa rivers) and possibly the development of smaller scale mainstem remediation areas that allow limited reproduction at any single site. If smaller habitat patches are used they will need to be aligned with river currents and be sufficiently long (and stable) to allow drifting yolk-sac larvae to find shelter successfully. Approximations based upon behaviour experiments (Gessner et al., 2009) suggest the need for 30 m of continuous habitat, assuming a moderate drift duration of 15 sec at 0.8 m/sec. In case of longer drifts, multiple sites would clearly be beneficial, which is in line with the current targets that suggest lowland rivers should be comprised of roughly about 10% of coarse sediment (i.e., gravel and cobble) by area (Dahm et al., 2014). The habitat availability for feeding larvae is largely unknown; the presence of feeding larvae following release has not been successfully proven. However, the presence of multiple remediation sites may provide habitat that supports rearing by feeding larvae. It is hypothesized that groyne fields also provide productive habitat with suitable substrate for feeding larvae, although verification of utilization is currently lacking.

The need to restore all life stages of sturgeon in the Odra River (and other areas of their historical range in Europe) creates substantial challenges due to the need to restore all elements of suitable habitat for different life phases (i.e., reach selection, local scale hydraulic and substrate conditions). Monitoring of the initial repatriations into the Odra River provide critical guidance for subsequent efforts. As noted above, successful spawning of restocked fish will only be detectable after 2020. However, monitoring of particular life stages (e.g., larval out-planting experiments and lab-based research) may provide interim indications of habitat improvements. Conducting additional trials in different rivers or river sections would provide the opportunity to compare responses to different habitat remediation structures designed for various life stages while developing solutions that do not interfere with navigation targets.

2 | CONCLUSIONS

Our review of sturgeon habitat remediation identified that multiple contexts and bio-spatial scales must be considered for effective sturgeon habitat remediation. The dire global conservation status of sturgeon clearly indicates past failures to recognize and limit the impacts of anthropogenic changes to riverine habitats that affect sturgeon. While our review identified positive progress in the remediation of spawning and early rearing habitats, most sturgeon habitat remediation is still not able to address conservation concerns effectively. Current projects addressing lake sturgeon, *Acipenser fulvescens*, appear to show the most promise. Further applied research is needed to identify remediation measures that provide consistent long-term effectiveness. Until such measures are identified, we stress the need to maintain connectivity and the ability for long-distance migration, as well as the habitat mosaic required for successful recruitment. Most remediation projects to date have been conducted at the sub-reach scale and have focussed on substrate remediation to improve early life stage rearing in spawning habitats. The mixed success of past projects suggests that a 'build it and they will come' approach has not been sufficiently successful. We have identified three areas in particular where investigation will benefit future restoration efforts:

1) Mechanistic insight into factors affecting spawning site selection, including hydraulic conditions and fine-scale habitat specificity (see Duong et al., 2011).
2) Utilization of hydro-geomorphological process (e.g., reach scale) to identify a means to limit the incursion of fine substrates into restored spawning habitats and to clean substrates at spawning sites. Utilizing a river's own power is more desirable than repeated physical cleaning (Johnson et al., 2006b).
3) The role of habitat effects during early life history (e.g., survival, larval drift, first feeding) and early juvenile phases. A more nuanced understanding of habitat mediated effects would address such questions as: (i) do multiple factors affect larval drift decisions (e.g., ontogeny, food availability, the presence of predators, the characteristics of interstitial habitat); and (ii) what are the short and long term consequences of phenotypic responses to early life stage habitat conditions (Boucher et al., 2014; Du et al., 2014; Johnsson et al., 2014; Johnsson et al., 2014).

Both geomorphological and biological studies will necessarily require a combination of laboratory, modelled, and field studies. Both the urgent need for remediation and economic costs of large-scale remediation emphasize the value of information exchange among recovery programs for various sturgeon species.

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