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Review

A review of lake sturgeon *Acipenser fulvescens* spawning sites in the Lower St. Lawrence and Ottawa river systems

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ABSTRACT

Knowledge concerning critical habitats such as spawning sites is crucial to the preservation of vulnerable fish species like sturgeons. For lake sturgeon *Acipenser fulvescens* populations in the Lower St. Lawrence and Ottawa river systems, knowledge about spawning sites has been documented primarily in the grey literature, unpublished reports, or notes, with very little published in peer-reviewed literature. Here, we reviewed over 100 reports, articles, and unpublished observations in the Lower St. Lawrence and Ottawa river systems to synthesize available information concerning the location of lake sturgeon spawning sites, the level of spawning activity, and the methodologies used for assessments. In this review, 38 lake sturgeon spawning sites were identified. Of these sites, 11 were enhanced or artificially created for lake sturgeon. In the Lower St. Lawrence River, 68% of known spawning sites were located downstream from a dam compared to 47% in the Ottawa River. The use of the two artificially created spawning sites in the Lower St. Lawrence River has not yet been confirmed, while one site established in the Ottawa River has had confirmed spawning activity, although the spawning run size is unknown. In contrast, spawning has been confirmed for the seven natural spawning sites that have been artificially expanded in these systems, and two of these sites have large spawning runs. Information revealed by this review suggests that lake sturgeon populations in these large river systems rely on multiple spawning sites and that expanding natural spawning grounds may be more effective than creating new ones.

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Introduction

Locating and mapping critical habitats such as spawning sites is essential to ensure adequate protection and management of long-lived fish species like sturgeons (Auer, 1996; Pollock et al., 2015; Baril et al., 2018). Sturgeons are lithophilous, obligate riverine spawners (Bruch and Binkowski, 2002) that can undergo extensive migrations (Auer, 1996) to their small-scale spawning sites. While perturbations or barriers to spawning sites can have marked effects on early life stages and negatively impact sturgeon recruitment and recovery effects (Gross et al., 2002; Vélez-Espino and Koops, 2009), knowledge concerning the location of spawning sites and the extent of spawning habitat utilization is often partial, incomplete, or scattered (i.e., personal observations, unpublished information, grey literature from government agencies; Baril et al., 2018). The lack of adequate synthesis and appropriate dissemination of information on critical sturgeon habitat sometimes prevents this crucial information from being considered by conservation biologists, fisheries managers, and stakeholders (Pollock et al., 2015).

The Lower St. Lawrence River (hereafter LSLR) lake sturgeon *Acipenser fulvescens* population is the largest in Canada and supports an important commercial fishery of 80,000 kg yr^{-1} in addition to a recreational fishery (Dumont and Mailhot, 2013). The abundance of this population is currently estimated to be high, with an increasing trend (COSEWIC, 2017). Until a few decades ago, information on the location and use of lake sturgeon spawning sites outside of the Montréal area was lacking (La Haye et al., 1992; Dumont et al., 2011). Efforts have been made by the provincial government and its partners to characterize lake sturgeon spawning sites in the LSLR and its tributaries, resulting in a significant increase in knowledge. Projects to improve lake sturgeon habitat have also been conducted in the LSLR, with spawning areas expanded or artificially created as part of compensatory habitat mitigation projects (Dumont et al., 2011; Dumont and Mailhot, 2013; Thiem et al., 2013; Baril et al., 2018).

Although lake sturgeon were once considered abundant in the Ottawa River (hereafter OR), the largest tributary of the LSLR, their numbers declined significantly in the early 20th century, primarily due to exploitation (Haxton and Findlay, 2008; COSEWIC, 2017). Most populations in various segments of the OR are considered to have low abundances and declining trajectories, with the exception of three contiguous, unimpounded mid-river reaches, where populations are considered to be robust and stable or increasing (COSEWIC, 2017). The management and conservation of OR lake sturgeon is shared between the provinces of Québec and Ontario. Information on lake sturgeon spawning sites in the OR is scattered among organizations and only partially published. Given that recruitment appears to be impaired in many impounded reaches of the OR, in part due to poor spawning habitat (Haxton and Findlay, 2008; OMNRF and MFFP, 2018), there is a need to review all available knowledge on lake sturgeon spawning sites in this system.

Since the industrial era, the LSLR and OR have been subjected to several human pressures that threaten various fish species and their habitats. Among other things, these large river systems have been harnessed and their flow regulated, particularly the OR, whose flow regime was strongly modified in 1911 (Morin and Bouchard, 2000). These modifications led to losses of connectivity and profound alterations in the natural hydrological flow regimes of their watersheds. The effects of these major perturbations are still felt today; they include a reduction of flood magnitude and a change in flood timing, hydrodynamics, and sediment dynamics, resulting in important changes in fish habitat characteristics over large areas (Foubert et al., 2020). Sturgeon are sensitive to these factors, which influence the timing of spawning and the characteristics of spawning habitats (Nilo et al., 2006). In addition, since the early 1850s, extensive excavation to build a shipping lane has greatly transformed the bed of the LSLR and now forces sturgeon to coexist with daily boat traffic. Sturgeon are exposed to many pressures in this large system, thus it is all the more important to document the spawning habitats as accurately as possible to protect early life stages.

The aim of this paper is to make important information regarding lake sturgeon spawning grounds in the LSLR and the OR systems available to the scientific community. To achieve this, articles, reports, and unpublished observations were reviewed to synthesize available information on (1) the location of known lake sturgeon spawning sites in the LSLR and OR systems, including their main tributaries; (2) the level of spawning activity for each site; and (3) the methodologies used for spawning site assessments and to confirm reproduction and spawning runs. In addition, information on (4) artificially created or enhanced spawning sites was reviewed to assess whether these habitats were used by lake sturgeon. This review should help future management and recovery decisions regarding lake sturgeon in large systems.

Methods

Study site

The St. Lawrence River, located at the outflow of the Great Lakes, is one of world's largest rivers in terms of length (~1,200 km), watershed area (1,344,200 km^2), and average annual discharge (10,270 m^3/s at Sorel; Morin and Bouchard, 2000). The LSLR is defined here as the ~ 350 km stretch of river located between the Beauharnois–Les Cèdres hydroelectric complex (just upstream of Montréal) and the middle estuary of the St. Lawrence River located downstream of Québec City. This section includes Lac des Deux Montagnes, which is the outlet of the OR (downstream of the Carillon Dam; Fig. 1). The LSLR has many tributaries, most of which have dams or natural obstacles in their lower reaches that are impassable barriers for lake sturgeon.

The OR is a large and highly fragmented river system. The river extends 1,130 km from its source at Lake Capitmitchigama (Québec) to its confluence with the St. Lawrence River in the Montréal area (Haxton and Findlay, 2008). Nine reaches of the OR are separated by either natural rapids or hydroelectric generating stations, including (from upstream to downstream) lakes Témis-

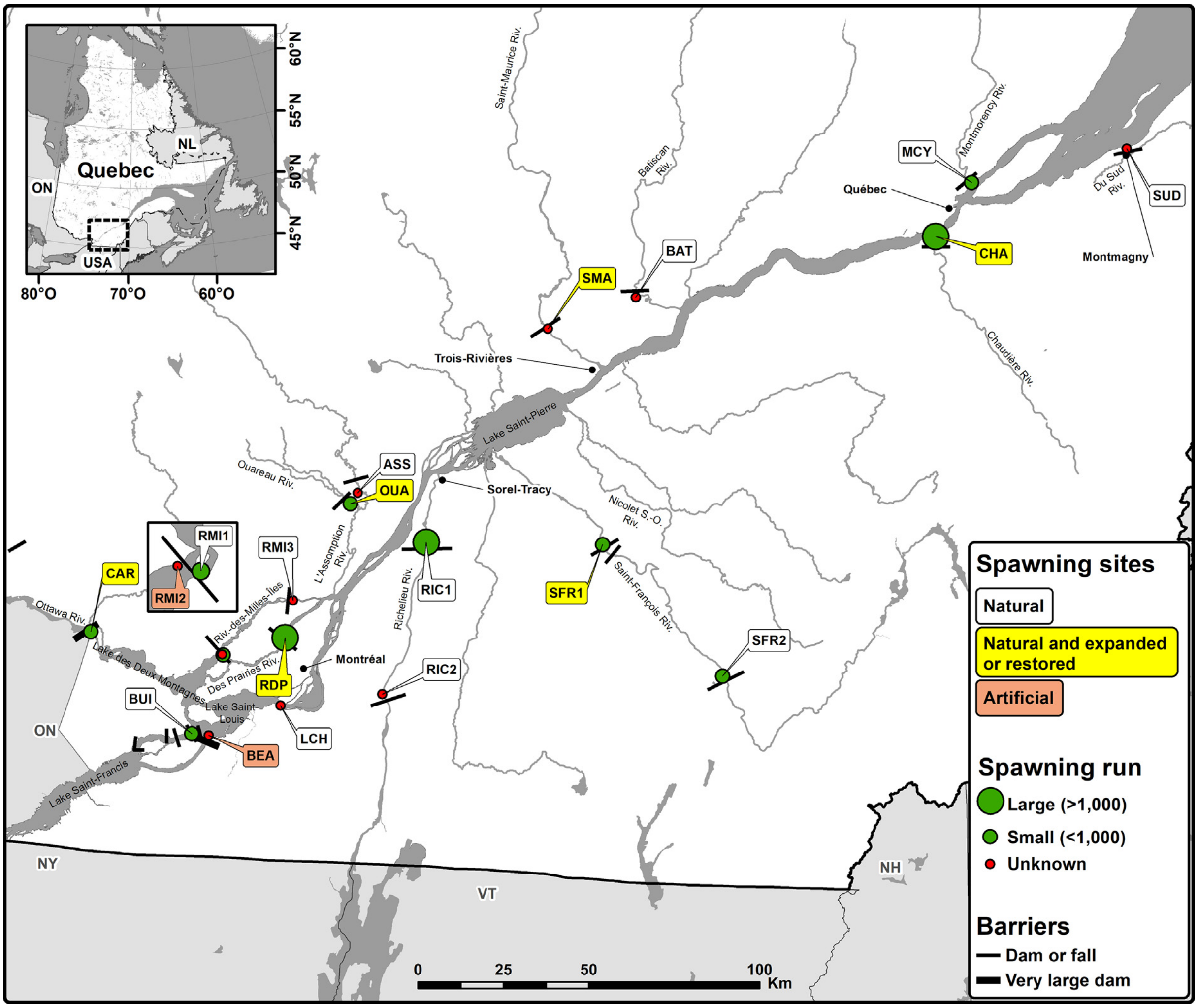

Fig. 1. Lake sturgeon spawning sites in the Lower St. Lawrence River system. See Table 1 for spawning site characteristics. ASS: L'Assomption River; BAT: Batiscan River; BEA: Beauharnois generating station, St. Lawrence River; BUI: Pointe-du-Buisson dam, St. Lawrence River; CAR: Carillon generating station, lac des Deux Montagnes (Ottawa River outlet); CHA: Chaudière River; MCY: Montmorency River; LCH: Lachine rapids, St. Lawrence River; Montmorency River; OUA: Ouareau River; RDP: Des Prairies River; RIC1: Richelieu River, spawning ground 1; RIC2: Richelieu River, spawning ground 2; RMI1: des Milles-Iles River, spawning ground 1; RMI2: des Milles-Iles River, spawning ground 2; RMI3: des Milles-Iles River, spawning ground 3; SFR1: Saint-François River, spawning ground 1; SFR2: Saint-François River, spawning ground 2; SMA: Saint-Maurice River; SUD: du Sud River.

camingue, la Cave, Holden, Allumette, Coulonge, du Rocher Fendu, des Chats, Deschênes, and Dollard des Ormeaux (Haxton and Findlay, 2008; OMNRF and MFFP, 2018; Fig. 2). For the OR, our review only includes lake sturgeon spawning sites in the section between Lake Témiscamingue and Carillon Dam (Figs. 1, 2).

Description of spawning sites

To gather information on the location, use, and characteristics of lake sturgeon spawning sites in the LSLR and OR systems, 90 reports and articles as well as 28 unpublished sources were reviewed (Electronic Supplementary Material (ESM) Table S1, Appendix S1). Most of the unpublished information was collected from biologists working in various regional offices of the Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP; Table S1). All documented spawning sites were classified into one of three categories reflecting their origin: (1) natural or not intentionally created (e.g., possibly created during dam construction; included with the term "natural" in the rest of the text); (2) natural and expanded (i.e., spawning ground enhancement in sites where lake sturgeon spawning activities were previously observed); or (3) artificial (i.e., spawning grounds created in sites where no lake sturgeon spawning activities had previously been observed). To assess whether the spawning sites were used by lake sturgeon, we collected all available information on the presence of lake sturgeon spawners, egg deposition, and larval drift as well as the year of monitoring and the sampling methods (ESM Table S1). For each spawning site, we estimated the run size (number of adult sturgeon aggregating during the spawning season) and divided them into three categories: (1) large (>1,000 spawners); (2) small (<1,000 spawners); or (3) unknown. Spawning run size was generally estimated from gill-net samplings and mark–recapture experiments. The presence of an obstacle to migration within a 5 km river stretch upstream from the spawning site was coded as follows: (1) presence of a dam; (2) presence of a natural waterfall; or (3) no obstacles. The locations of the spawning grounds, the sizes of spawning runs, and the presence of natural (waterfalls) and artificial (dams) obstacles were mapped (Figs. 1, 2). Finally, all other available information regarding spawning site characteristics (e.g., surface area, characteristics of artificially created or enhanced spawning sites, presence of other fish species) were compiled. Because the collection of detailed information on habitat

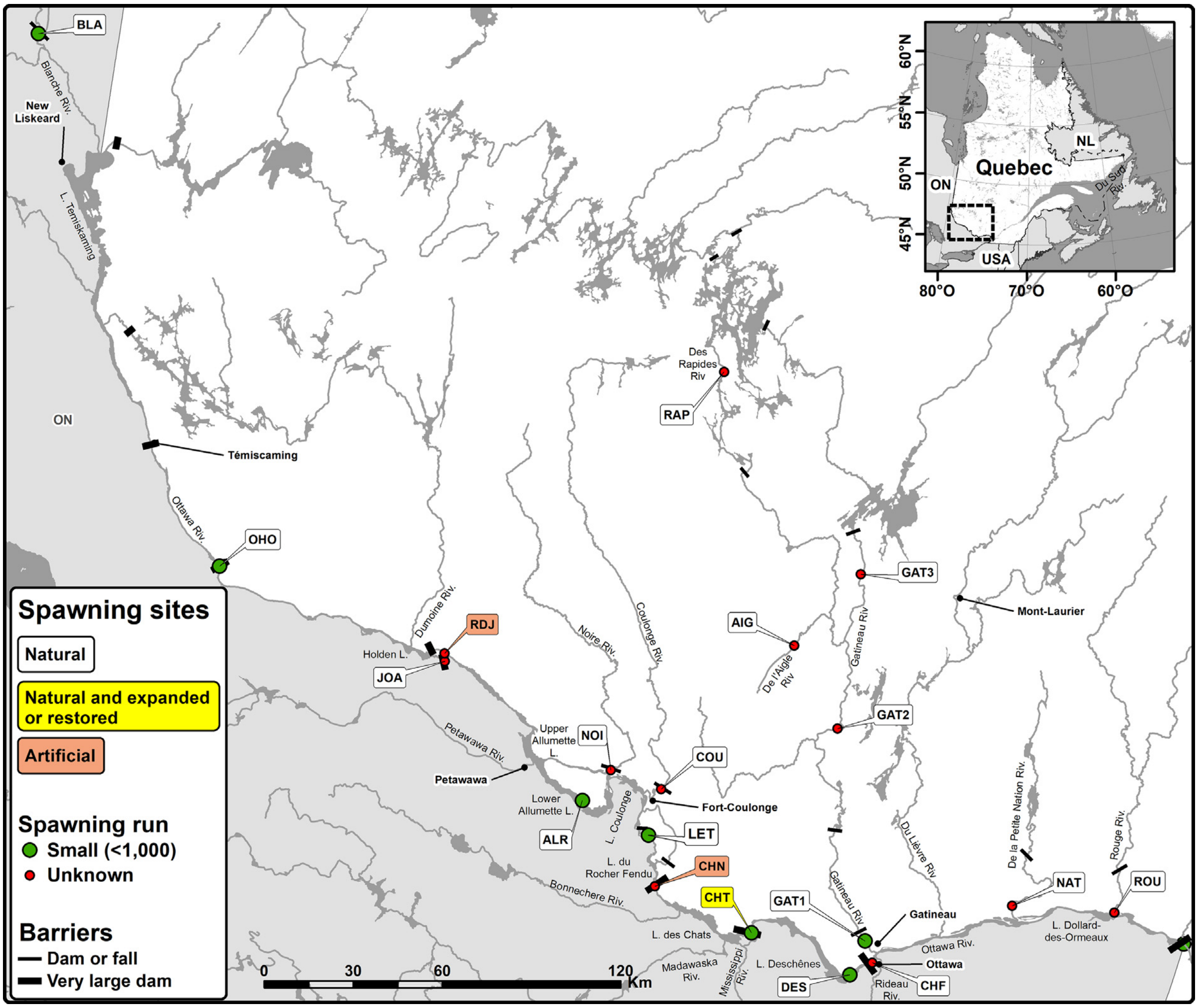

Fig. 2. Lake sturgeon spawning sites in the Ottawa River system. See Table 2 for spawning site characteristics. AIG: de l'Aigle River; ALR: Allumette Rapids, Ottawa River; BLA: Blanche River; CHF: Chaudière Falls, Ottawa River; CHN: Chenaux generating station, Ottawa River; CHT: Chats Falls generating station, Ottawa River; COU: Coulonge River; DES: Deschênes Rapids, Ottawa River; GAT1: Gatineau River, spawning ground 1; GAT2; Gatineau River, spawning ground 2; GAT3: Gatineau River, spawning ground 3; JOA: Des Joachims generating station, Ottawa River; LET: Baie de Letts, Ottawa River; NAT: de la Petite Nation River; NOI: Noire River; OHO: Otto Holden generating station, Ottawa River; RAP: des Rapides River. RDJ: Rapides-des-Joachims, Ottawa River; ROU: mouth of the Rouge River, Ottawa River.

characteristics (e.g., depth, flow velocities, water temperature, substrate) is inconsistent among studies and lacking for most spawning sites in the LSLR and OR, this information was not compiled. A comprehensive review of available information on habitat characteristics of lake sturgeon spawning sites was published by Baril et al. (2018).

Results

This review revealed a total of 38 lake sturgeon spawning sites in the LSLR and OR systems (Tables 1, 2). Of these, 27 were natural spawning sites where no specific enhancement or restoration had been conducted, and 11 were either enhanced (i.e., expanded / restored) or artificially created for lake sturgeon. Our review revealed that 15 different sampling methods were used to investigate spawning activities (ESM Table S1), the most common being drift nets, gill nets, and egg mats (Fig. 3), and most spawning sites were investigated using multiple sampling techniques (Fig. 3, ESM Table S1). Spawners, eggs, and larvae were observed at 95 %, 79 %, and 37 % of the sites, respectively (Tables 1, 2).

Lower St. Lawrence River

In the LSLR, 19 lake sturgeon spawning grounds were identified, with most spawning sites located in tributaries (Table 1, Fig. 1). Of these, 17 were natural lake sturgeon spawning grounds, and six of them had been expanded as part of compensatory habitat mitigation projects (Table 1, Fig. 1). Two additional spawning grounds were artificially created specifically for lake sturgeon (RMI2 and BEA; Fig. 1). Overall, 17 LSLR spawning sites had confirmed lake sturgeon spawning activities, including at least three sites with large spawning runs (>1,000 spawners) and seven sites with smaller spawning runs (<1,000 spawners; Table 1, Fig. 1). Spawning activities have been confirmed at all natural and expanded spawning grounds, although only sporadically for the Ouareau River site (OUA; Table 1, Fig. 1). One spawning site on a reach of the Saint-François River (SFR2) has been cut off from the St. Lawrence River since 1919 (Fig. 1) and thus may be considered an isolated group of lake sturgeon. To date, use of the artificially created spawning sites near Beauharnois (BEA; Fig. 1) and in des Milles-Iles River (RMI2; Fig. 1) by lake sturgeon has not been confirmed, although these sites have been monitored for several years (Table 1).

Table 1
Locations and descriptions of lake sturgeon spawning sites in the Lower St. Lawrence River and its main tributaries. Site identification (Site ID; see Fig. 1 for acronyms) and river name, type of spawning ground (N: natural; E: expanded or restored; A: artificial), presence of an obstacle to migration upstream of the spawning site (D: dam; F: waterfall; No: no obstacle), years of site assessment (first and last assessment years are presented when multi-year surveys were conducted) and number of spawning run assessments (NA: no assessment), surface area of the spawning ground, documented (confirmed) spawning activities (Obs.; S: spawners; E: eggs; L: larval drift), confirmed spawning activities (yes or no), and estimated spawning run size are presented for each lake sturgeon site.

Site ID (water body)	Type	Upstream obstacle	Assessment years (number of spawning run assessments)	Area (ha)	Obs.	Conf. activity	Estimated spawning run
ASS (L'Assomption Riv.)	N	F	1986–2003 (NA)	0.22	S, E, L	yes	Unknown
BAT (Batiscan Riv.)	N	F	1951–2021 (NA)	Unknown	S, E, L	yes	Unknown
BEA (St. Lawrence Riv.)	A	D	1998–2002 (NA)	0.30	S[a]	no	Unknown
BUI (St. Lawrence Riv.)	N	D	1986–2004 (1)	Unknown	S, E	yes	<1,000
CAR (lac des Deux Montagnes)	N, E	D	1983; 2020 (2)	Unknown	S, E	yes	<1,000
CHA (Chaudière Riv.)	N, E	F	1951–2013 (6)	Unknown	S, E	yes	>1,000
LCH (St. Lawrence Riv.)	N	No	2001–2021 (NA)	6.00	S, E, L	yes	Unknown
MCY (Montmorency Riv.)	N	F	2010–2013 (3)	5.50	S, E	yes	<1,000
OUA (Ouareau Riv.)	N, E	D	1985–2011 (6)	0.26 (N) 0.30 (E)	S, E, L	yes	<1,000
RDP (Des Prairies Riv.)	N, E	D	1982–2011 (10)	2.00	S, E, L	yes	>1,000
RIC1 (Richelieu Riv.)	N	D	2005–2011 (1)	5.3	S, E	yes	>1,000
RIC2 (Richelieu Riv.)	N	D	1975–2008 (NA)	Unknown	S	yes	Unknown
RMI1 (des Milles-Iles Riv.)	N	D	2012–2016 (1)	Unknown	S, E	yes	<1,000
RMI2 (des Milles-Iles Riv.)	A	No	2012–2016 (NA)	0.43	S	no	Unknown
RMI3 (des Milles-Iles Riv.)	N	D	1982, 1984 (NA)	Unknown	E, L	yes	Unknown
SFR1 (Saint-François Riv.)	N, E	D	1947–2018 (5)	0.34	S, E, L	yes	<1,000
SFR2 (Saint-François Riv.)	N	D	2014, 2015 (2)	Unknown	S, E	yes	<1,000
SMA (Saint-Maurice Riv.)	N, E	D	1988–2000 (NA)	1.00	S, E	yes	Unknown
SUD (du Sud Riv.)	N	D	2011–2014 (NA)	Unknown	S	yes	Unknown

[a] Observed nearby.

Table 2
Locations and descriptions of lake sturgeon spawning sites in the Ottawa River and its main tributaries. Site identification (Site ID; see Fig. 2 for acronyms) and river name, type of spawning ground (N: natural; E: expanded or restored; A: artificial), presence of an obstacle to migration upstream of the spawning site (D: dam; F: waterfall; No: no obstacle), years of site assessment (first and last assessment years are presented when multi-year surveys were conducted) and number of spawning run assessments (NA: no assessment), surface area of the spawning ground, documented spawning activities (Obs.; S: spawners; E: eggs; L: larval drift; NA: information not available), confirmed spawning activities (yes or no), and estimated spawning run size are presented for each lake sturgeon site.

Site ID (water body)	Type	Upstream obstacle	Assessment year (number of spawning run assessments)	Area (ha)	Obs.	Conf. activity	Estimatedspawning run
AIG (de l'Aigle Riv.)	N	No	1997 (NA)	1.54	NA	yes	Unknown
ALR (Ottawa Riv.)	N	No	2001–2007 (3)	47.0	S	yes	<1,000
BLA (Blanche Riv.)	N	F	2009–2018 (NA[a])	0.4	S, E, L	yes	<1,000
CHF (Ottawa Riv.)	N	D	1989 (NA)	0.25	E	yes	Unknown
CHN (Ottawa Riv.)	A	D	2007–2020 (NA[a])	1.1	S, L	yes	<1,000
CHT (Ottawa Riv.)	N, E	D	1949–2004 (4)	5.9	S, L	yes	<1,000
COU (Coulonge Riv.)	N	No	1994–2021 (NA)	0.2–0.54	S, E, L	yes	Unknown
DES (Ottawa Riv.)	N	No	2010 (1)	0.34	S	yes	<1,000
GAT1 (Gatineau Riv.)	N	D	1994–2021 (1)	13.76	S, E	yes	<1,000
GAT2 (Gatineau Riv.)	N	No	1973–1994 (NA)	1.39	S, E	yes	Unknown
GAT3 (Gatineau Riv.)	N	F	1950 (NA)	0.06	NA	yes	Unknown
JOA (Ottawa Riv.)	N	D	2008 (NA)	0.59	NA	yes	Unknown
LET (Ottawa Riv.)	N	F	2008 (NA)	0.58	NA	yes	Unknown
NAT (de la Petite Nation Riv.)	N	F	1989 (NA)	Unknown	E	yes	Unknown
NOI (Noire Riv.)	N	D	1994–2006 (NA)	1.39	E	yes	Unknown
OHO (Ottawa Riv.)	N	D	2003, 2006 (2)	1.3	S	yes	<1,000
RAP (des Rapides Riv.)	N	No	1950 (NA)	0.17	NA	yes	Unknown
RDJ (Ottawa Riv.)	A	D	2008–2021 (NA)	7.42	NA	no	Unknown
ROU (Ottawa Riv./Rouge Riv.)	N	F	1989–2000 (NA)	3.90	E	yes	Unknown

[a] The exact assessment years of the spawning run is unknown.

Ottawa River

In the OR, 19 lake sturgeon spawning sites were identified (Fig. 2). Eighteen of these sites had confirmed lake sturgeon spawning activities (Table 2). Two sites, located in the Gatineau (GAT3) and des Rapides (RAP) rivers, had confirmed spawning activity in 1950 (Table 2), but recent information is not available. Two historical spawning sites (Hawkesbury and the Chenaux Islands) were extensively flooded after impoundment and are no longer used for lake sturgeon spawning; these sites were not considered in this review. Two sites downstream of the Chats Falls GS (CHT) and Chenaux GS (CHN) hydroelectric dams have been enlarged (CHT) or artificially created (CHN) by the addition of rock rubble. Four spawning sites, those in the de l'Aigle (AIG), Gatineau (GAT2, GAT3), and des Rapides (RAP; Fig. 2) rivers, are in tributaries that have been cut off from the OR since the 1930 s and therefore probably do not contribute to its population. The level of spawning activity in the OR system is mostly unknown (Table 2, Fig. 2).

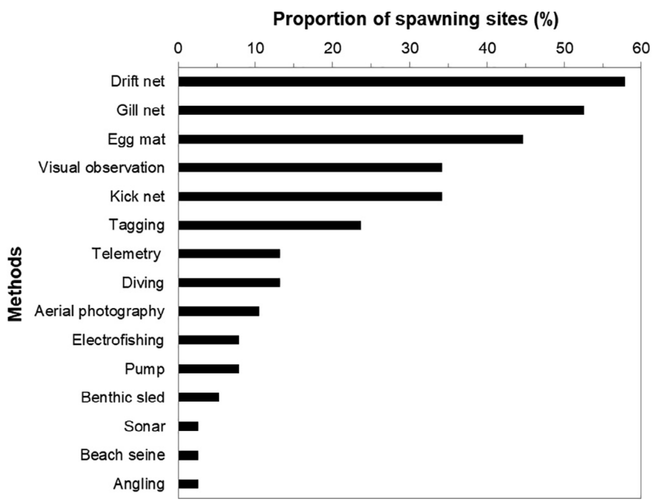

Fig. 3. Sampling methods used to investigate lake sturgeon spawning activities in the Lower St. Lawrence and Ottawa river systems.

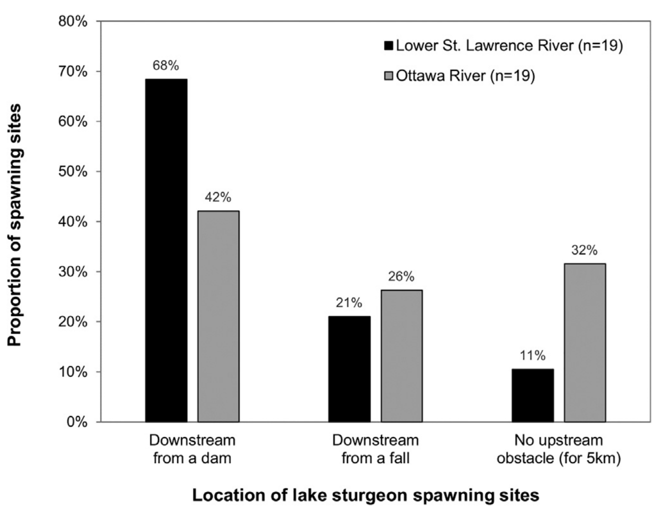

Fig. 4. Lake sturgeon spawning site locations within the Lower St. Lawrence and Ottawa river systems. The proportion of spawning sites located downstream of a barrier is shown.

Observations from both systems

The surface areas of spawning sites identified in the LSLR and OR systems ranged from 0.06 to 47 ha (Tables 1, 2). Lake sturgeon spawning sites have also been used for reproduction by several species listed under Québec's Act as threatened or vulnerable species, including American shad *Alosa sapidissima*, river redhorse *Moxostoma carinatum*, copper redhorse *Moxostoma hubbsi*, and channel darter *Percina copelandi*. Overall, breeding was documented for at least 32 species of fish from many families, including Catostomidae, Centrarchidae, Clupeidea, Cottidae, Cyprinidae, Esocidae, Hiodontidae, Moronidae, Osmeridae, Percidae, Percopsidae, Petromyzontidae, and Sciaenidae, indicating that most of these habitats were multi-species spawning grounds (ESM Table S1).

In the LSLR, most of the 19 lake sturgeon spawning sites were located within 5 km downstream of a migration barrier, either a dam (68 %) or a natural waterfall (21 %; Table 1, Figs. 1, 4). Known lake sturgeon spawning sites in the OR system were also predominantly located within 5 km downstream of a migration barrier (47 % downstream from a dam and 29 % downstream from a waterfall), but 35 % of spawning sites were not associated with a migration barrier (Table 2, Figs. 2, 4).

In the LSLR and OR systems, projects to create or expand spawning sites were conducted between 1979 and 2017. For those sites with available data, created spawning areas ranged from approximately 420 m^2 to 10,700 m^2. Available data suggest that substrates up to 800 mm were used to build spawning grounds and that boulders were carefully positioned to provide low flow velocity fish refuges at several spawning sites. Characteristics of the expanded (or restored) and newly created habitats in the LSLR and OR systems are summarized in ESM Table S1.

Discussion

The LSLR lake sturgeon population differs from most other lake sturgeon populations in many ways. In this section of the Great Lakes watershed, except for Lac des Deux Montagnes, lake sturgeon are abundant and support the last commercial lake sturgeon fishery in North America (Dumont and Mailhot, 2013; Mailhot et al., 2011). The number of lake sturgeon spawning sites in this large system is high: at least three of the 19 sites have spawning runs of over 1,000 individuals. The LSLR lake sturgeon population is probably the largest in North America (COSEWIC, 2017), due in part to a long stretch of the river and some of its tributaries that provide lake sturgeon with access to multiple highly productive and well-connected spawning, rearing, and nursery habitats (Dumont and Mailhot, 2013; Mailhot et al., 2011; Nilo et al., 2006). In addition, lake sturgeon spawning activity has recently been confirmed in previously unknown, poorly documented, or historically degraded spawning sites, suggesting that the population is expanding. Around 2010, the LSLR lake sturgeon population was thought to be primarily supported by the Des Prairies River spawning ground (RDP; Fig. 1; Dumont et al., 2011). However, new knowledge on the extent and number of lake sturgeon spawning sites in the St. Lawrence River and its tributaries now suggests that this population relies on multiple spawning sites within the system. This knowledge is valuable to recovery efforts for other sturgeon populations or species. Multiple spawning shoals within the LSLR—and probably the OR—may have contributed to the robustness of the resident population in terms of early survival and recruitment. Environmental conditions at a specific spawning site may vary among years, so these sites may not be suitable each year for lake sturgeon spawning or the survival of young life stages. The occurrence of diverse spawning locations within a system may ensure that at least some sites with favourable conditions are available each year.

Creating artificial spawning sites or expanding existing spawning grounds is a common strategy that has been used for lake sturgeon recovery (Roseman et al., 2011; Thiem et al., 2013; Fischer et al., 2018, McAdam et al., 2018). However, lake sturgeon habitat restoration has proved to be a major challenge with mixed levels of success (Dumont et al., 2011; Roseman et al., 2011; Fischer et al., 2018) and failure (Baril et al., 2019). Although there is not sufficient information to clearly identify key success and failure factors of restored and newly created spawning sites in the LSLR, a few general observations can be made. The expansion of existing spawning grounds with appropriate substrate (see McAdam et al., 2018) can significantly improve lake sturgeon reproductive success when problems related to egg overcrowding or poor-quality substrate are encountered. In fact, after expansion of the Des Prairies River (RDP) spawning ground, a strong increase in larval production was observed, even though high-quality spawning habitats were already available (Dumont et al., 2011). Prior to habitat enhancement, egg overcrowding was observed on this spawning ground (Dumont et al., 2011).

In contrast, creating a new spawning ground in an inappropriate location can be unsuccessful. For example, the artificial spawning ground created in the tailrace of the Beauharnois hydroelectric generating station (BEA) was not successful despite the presence of spawners nearby. Periphyton quickly colonized the enhanced substrate because of the pronounced water transparency (Dumont et al., 2011). A similar issue occurred in the upper reach of the St. Lawrence River (120 km upstream of Beauharnois), where lake sturgeon quickly abandoned the artificially created spawning ground after periphyton developed on spawning substrate (Johnson et al., 2006).

Sites to be developed must also exhibit conditions conducive to spawning (i.e., flow velocities and depth conditions; see Baril et al., 2018, and McAdam et al., 2018), as well as areas in which substrate size and quality can be increased to allow egg and embryo retention (Dumont et al., 2011; Fischer et al., 2018). Prior knowledge of long-term fluvial and geomorphological processes, hydraulic conditions (McAdam et al., 2018), and spawners' movements in relation to water flow is also a definite asset (Dumont et al., 2011). Successful habitat restoration requires multidisciplinary input, including knowledge of the hydrogeomorphology and the use of 2D and 3D numerical models, prior to installation of instream structures (Baril et al., 2019; Fischer et al., 2020).

Although expanding existing spawning sites in the LSLR system was more successful than creating new artificial spawning sites, the latter technique should still be considered as a potentially efficient strategy for lake sturgeon since it has been used successfully in other systems (Roseman et al., 2011; Bouckaert et al., 2014; OR system in this study). Moreover, spawning habitat conditions may not be the only factors limiting lake sturgeon recruitment, so knowledge of the system is essential prior to extensive and potentially unnecessary rehabilitation (Haxton and Findlay, 2009).

In the OR system, lake sturgeon are known to occur in all nine major reaches from Lake Témiscamingue to Carillon, although recruitment is minimal in several areas (Haxton and Findlay, 2008; COSEWIC, 2017; OMNRF and MFFP, 2018). In most reaches, spawning is thought to occur downstream of most hydroelectric generating stations (Haxton, 2008; OMNRF and MFFP, 2018). Some of these sites were likely historical since most dams were built on existing natural rapids (Haxton and Chubbuck, 2002). However, dams fragmented habitats and obstructed access, or drastically altered historical spawning areas by flooding them or altering habitat to facilitate water flow. In the OR system, improved knowledge of lake sturgeon spawning locations over the past decade has not resulted in any major breakthroughs in terms of knowledge about the level of spawning activities or the efficiency of habitat restoration projects. For most OR spawning sites, spawning size runs are small (<1,000) or unknown. There are at least two other suspected spawning areas in the OR system where adult lake sturgeons have been observed congregating in May–June, but these areas have never been assessed. There are also numerous potential spawning sites in the upper Gatineau River system (including the de l'Aigle and Désert rivers) which have not been confirmed (Barth et al., 2018). In addition, several potential or confirmed lake sturgeon spawning sites are known upstream of Lake Témiscamingue, where the OR is highly fragmented by hydroelectric development (J.-P. Hamel and M. Bélanger, MFFP, unpublished results, 2020). The main known spawning area for Lake Témiscamingue is located 55 km upstream of a small tributary in Ontario (L. McDonald and T. Haxton, OMNRF, personal communication, 2020). Historically, spawning occurred upstream of the Première-Chute Generating Station, which fragments the Ottawa River and prevents lake sturgeon access to spawning areas. Nearly half of the known spawning areas in the OR are immediately downstream of a dam where historical habitat or flow conditions have been altered. Subsequently, these are areas where recruitment is impeded while populations are relatively robust when spawning does not occur near a man-made barrier (Haxton and Findlay, 2008; Haxton, 2011; OMNRF and MFFP, 2018). Efforts have been made to remedy this situation. Two spawning sites, Chenaux GS (CHN) and Rapides-des-Joachims (RDJ), were artificially created, but only one (CHN) has confirmed lake sturgeon spawning activities. Ontario Power Generation added rock rubble to the downstream areas of Chenaux GS (CHN) in 2008 and 2013, while Rapide-des-Joachims (RDJ) was created in 2017. Although signs of lake sturgeon spawning have been observed at Chenaux GS (spawners, larvae), spawning run size is unknown.

Even though dams form barriers to migratory species and may limit access to historical spawning areas (Birstein, 1993; DeVore et al., 1995; Wei et al., 1997), lake sturgeon often spawn immediately downstream from dams (Auer, 1996; Haxton and Findlay, 2008; Dumont et al., 2011; Thiem et al., 2013; Baril et al., 2018). This may give the perception that the population is faring well given the longevity and spawning fidelity of the species (i.e., observed annually at the foot of dams) while recruitment may rather be impeded (DeVore et al., 1995; Haxton et al., 2015) and only detected after the population has dramatically declined. Therefore, it is essential to assess the availability and use of other types of habitats necessary for the species to complete its life cycle in river systems under multiple human pressures.

Conclusions

The LSLR, OR, and their tributaries are large river systems where connections between different habitats—which are crucial for migratory fish species like lake sturgeon—have been interrupted by major artificial barriers. Documenting the locations and characteristics of lake sturgeon spawning sites should allow for better protection of these critical habitats in river systems under multiple human pressures. Moreover, recording spawning intensity and reproductive success is also vital for understanding the contribution of these sites to overall population recruitment and for assessing the need for enhancement of these habitats where they are a limiting factor. For the LSLR and OR systems, further research should focus on assessing the contribution of individual spawning sites to the larger metapopulation of the LSLR and unimpounded sections of the OR. This could provide invaluable insight and knowledge on the importance of different spawning sites within these large river basins and identify sites that could benefit from a habitat enhancement project. Finally, in the context of climate change, it would be beneficial to project changes in environmental conditions at each spawning ground identified in this review. Understanding the possible impacts of climate change on spawning sites could help to prioritize future enhancements on sites considered suitable for lake sturgeon over the long term.

CRediT authorship contribution statement

Yves Paradis: Conceptualization, Investigation, Writing – original draft, Visualization, Supervision. **Simon Bernatchez:** Investigation, Writing – original draft, Visualization. **Éliane Valiquette:** Validation, Investigation, Writing – review & editing, Visualization. **Marc Mingelbier:** Writing – review & editing. **Daniel Hatin:** Validation, Investigation, Writing – review & editing. **Philippe Brodeur:** Validation, Investigation, Writing – review & editing. **Émilie Paquin:** Validation, Investigation, Writing – review & editing. **Chantal Côté:** Validation, Investigation, Writing – review & editing. **Léon L'Italien:** Validation, Investigation, Writing – review & editing. **Thierry Calvé:** Validation, Investigation, Writing – review & editing. **Jean-Pierre Hamel:** Validation, Investigation, Writing – review & editing. **Martin Bélanger:** Validation, Investigation, Writing – review & editing. **Tim J. Haxton:** Validation, Investigation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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