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RESEARCH ARTICLE

How intensive agricultural practices and flow regulation are threatening fish spawning habitats and their connectivity in the St. Lawrence River floodplain, Canada

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Abstract
Context Hydrological and land use changes for human purposes, have resulted in the increased fragmentation of river landscapes and the loss of aquatic habitats, leading to profound changes in fish diversity and productivity.
Objectives In the fluvial Lake Saint-Pierre (St. Lawrence River, Canada), we studied how agricultural practices and water-flow regulation have impacted the area and connectivity of spawning habitats of northern pike (*Esox lucius*).
Methods Northern pike spawning and nursery habitats were modelled over a 49-year period (1965–2013) to estimate effective spawning area under four contrasting hydrological conditions.
Results Simulations coupled with land cover analyses revealed that natural flow conditions historically favourable for fish reproduction (high and stable water flows) have been lost due to human activities. The highest potential for reproduction and habitat connectivity have been lost due to (1) intensive agriculture and ploughing of natural vegetation in the upper floodplain that overlaps suitable spawning areas for northern pike, and (2) flow regulation that has lowered and shortened spring floods and dried spawning grounds more frequently.

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Conclusions To restore the St. Lawrence River functions, we propose to reconvert the portion of the floodplains that is vital to fish, but is currently used by intensive agriculture, into natural wetlands or perennial crops and to restore a more natural flow regime by extending the duration of floods between spawning and nursery periods. The highest priority for habitat restoration should target the most effective and recurrent spawning habitats, ditch and stream networks, and connected managed wetlands.

Keywords Northern pike reproduction · Habitat modelling · Connectivity modelling · Agricultural landscape · Water regulation

Introduction

In unaltered rivers, floodplains are highly productive and dynamic environments at the interface between aquatic and terrestrial ecosystems. They provide a mosaic of temporary habitats required by a large number of freshwater fish species to complete their life cycle. Given the high mortality rate in the early life stages of fishes, quality spawning and nursery habitats are crucial for fish recruitment (Bayler 1991; Gorski et al. 2011). However, floodplains are under increasing anthropogenic pressure around the world (Tockner and Stanford 2002) and their connectivity level highly affects their response to human disturbances (Wohl 2017). Impacts of water flow regulation and agricultural expansion are major threats to floodplain ecosystems (Beesley et al. 2014; Fernandes et al. 2015), where potential spawning habitats can turn into mortality traps (e.g. Jeffres and Moyle 2012; Sheaves et al. 2014) and lead to significant fish recruitment failures (e.g. Goto et al. 2015).

The natural flow regime in floodplains (i.e. magnitude, duration and periodicity of water levels) is highly variable in space and time, which impacts fish habitat area and connectivity (Junk et al. 1989; Wiens 2002). Although the flooding of large areas for extended periods of time can improve recruitment success of riverine fish, a rapid decrease in water discharge during early development can suddenly isolate spawning and nursery habitats, resulting in high egg and larval mortality (Bayler 1991; Gorski et al. 2011). In addition, water-flow regulation has significantly altered natural flow regimes in many river systems around the world, which can be critical for overall fish production (Nilsson et al. 2005). Reduction in spring water discharges has limited the duration of floods and their inter-annual variability, which has affected the quality of river habitat and resulted in a decline in fish abundance (e.g. Mingelbier et al. 2008; Farrell et al. 2010; Goto et al. 2015).

Land cover change is one of the most important factors altering habitat quality and connectivity of floodplains (Tockner and Stanford 2002). The conversion of large areas of natural floodplains to intensive agriculture has resulted in a net loss of fish habitat (Baber et al. 2002), a reduction in overall productivity (Matsuzaki et al. 2011), and threatened the long-term persistence of several fish species (Fernandes et al. 2015). In addition, transportation infrastructure, such as roads along rivers, can isolate portions of the floodplain, reducing access to critical habitats (Van der Ree et al. 2011; Blanton and Marcus 2014). Alternatively, landscape features such as ditch networks (Washitani 2007) can facilitate larval dispersal via passive transport at low water velocities (Schiemer et al. 2003). Such alternative use of man-made structure can help maintain floodplain connectivity in an anthropized landscape.

The northern pike (*Esox lucius*) has often been used as a model species because it is an early-spring spawner and is typical of the floodplain (Casselman and Lewis 1996; Mingelbier et al 2008; Farrell et al 2010). Pike recruitment is positively influenced by the abundance and quality of spawning habitat, defined by high water temperatures and high water levels maintained for several weeks after egg deposition on favourable types of vegetation (Johnson 1957; Casselman and Lewis 1996). Pike abundance has been declining in several major river systems for decades (Boët et al. 1999; Raat 2001), including the St. Lawrence River (Smith et al. 2007). Spawning habitats and nursery habitats of northern pike have been studied over the past 50 years in the floodplain of the St. Lawrence River (Canada) to determine how habitat connectivity and hydrological variability interact to modify the distribution of effective spawning habitats (Foubert et al. 2018). The *effective spawning habitats* of northern pike was defined as habitats that permit survival of eggs and larvae, while affording larvae access to nursery areas that are essential for successful recruitment to the adult population. As the simulations in Foubert et al. (2018) were carried out in a reconstructed “unaltered” landscape to measure the intrinsic natural variability of the river, they provided a way to compare a simulated pristine environment with a present-day landscape altered by human activities.

In this study, we hypothesised that effective spawning habitat for northern pike gradually changed over the twentieth century, as water flows were regulated and extensive agricultural practices developed. More specifically, in Lake Saint-Pierre (St. Lawrence River, Canada), we will first assess the changes in pike spawning and nursery habitats since 1965 with changes in local agriculture practices, secondly we will test the effects of water flow and land cover changes on connectivity between spawning and nursery habitats under four contrasting hydrological conditions, and thirdly, we will estimate the loss of connected habitat due to changes in land cover to identify current effective spawning habitat and the areas most valuable to protect and restore. These three objectives are represented in a conceptual diagram that describes the methodological steps leading to the main results of the study (Fig. 1).

Method

Study Area

Lake Saint-Pierre is the largest fluvial lake of the St. Lawrence River (Fig. 2), one of the largest river systems in the world in terms of length (~ 1200 km), watershed area (1,344,200 km^2), and average annual discharge (10,270 m^3 s^{-1} at Sorel; Morin and Bouchard 2000). Since the beginning of the industrial era, cumulative anthropogenic pressures have altered the Lake Saint-Pierre ecosystem. The gradual excavation of the navigation channel (now 11.3 m deep and ~ 250 m wide) between Montreal and Quebec City began around 1840 and was completed in 1998. Water regulation in the St. Lawrence River began in 1911 with the harnessing of the Ottawa River, its main tributary, for hydroelectric power generation, flood control, and navigation purposes. The regulation of the St. Lawrence River was further enhanced by the construction in 1958 of the Moses-Saunders and Beauharnois Power Dams that control the Lake Ontario—St. Lawrence River system (Morin and Bouchard 2000; Carpentier 2003). In addition, the

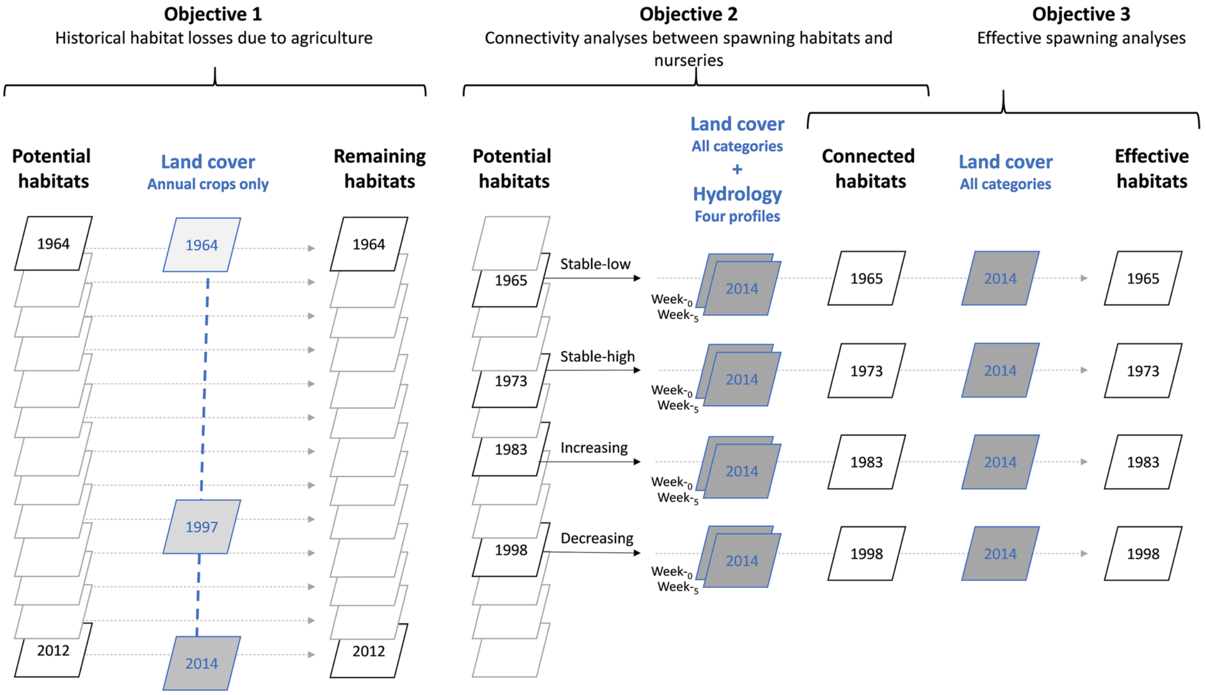

Fig. 1 conceptual diagram that describes the methodological steps (in blue) leading to the main results (in black) of the study. Potential habitats were used from Foubert et al. (2018)

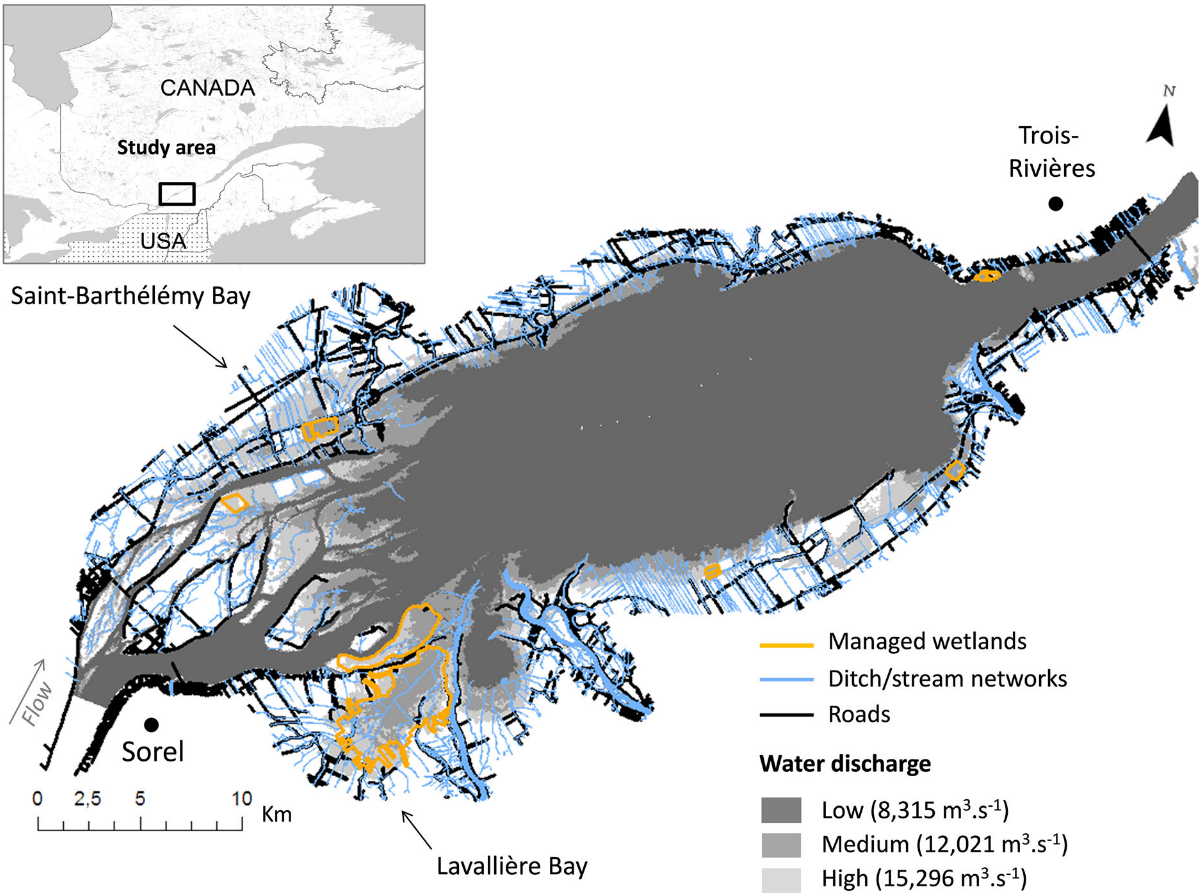

Fig. 2 Map showing the largest fluvial lake in the St. Lawrence River: Lake Saint-Pierre and its archipelago (Québec, Canada). Fish managed wetlands, ditch and stream networks, and roads on the floodplain have been located. Water extent for three contrasting spring modelled water discharges were indicated: the water extent at low water discharges are represented in dark grey, then the areas that are added for medium (medium grey) and high (light grey) water discharges are represented

development of large urban centres (e.g. Montréal, Trois-Rivières, and Québec City), intensive agriculture along the river and in the floodplain, and transportation infrastructure along the St. Lawrence River have had serious impacts on fish habitat availability and quality. Over time, perennial cover (e.g. pasture), which constitutes potential fish habitat in the floodplain, has been replaced by annual crops (e.g. corn, soy beans) with no potential for fish spawning; this phenomenon has accelerated since the early 1990s (Fecteau and Poissant 2001; de la Chenelière et al. 2014). To compensate for the loss of fish habitat, approximately 1300 ha of the Lake Saint-Pierre floodplain have been managed since the 1980s (Mingelbier and Douguet 1999). Managed wetlands are surrounded by dikes and partially controlled to maintain high and stable water levels, extend the duration of spring floods, and accelerate water warming. During spring floods, fish use these managed wetlands to spawn. They are subsequently drained in early June to Lake Saint-Pierre.

Lake Saint-Pierre and its archipelago were included on UNESCO's World Heritage Biosphere List in 2000. The shallow depth (< 3 m), slow lateral slope, and low current velocity (< 0.5 m s^{-1}) contributes to the formation of extensive macrophyte beds (Centre Saint-Laurent 1998). The annual variability of spring water discharge, ranging between 6500 and 17,500 m^3 s^{-1} at Sorel, is a key mechanism for maintaining wetland vegetation in floodplains (Morin et al. 2005).

Data collection

Potential habitat modelling in an unaltered floodplain (1965–2013)

Several high resolution hydrodynamic and biological models have been developed in the St. Lawrence River by Environment Canada to simulate the vegetation composition of the floodplain (e.g. deep marshes, shallow marshes and shrub) in Lake Saint-Pierre under various hydrological conditions (Morin et al. 2000, 2003; Turgeon and Morin 2005). As a result, natural plant succession in the littoral zone can be reconstructed annually for the period 1965 to 2013. As these simulations exclude anthropogenic effects, we used them to estimate the full spawning or nursery habitat potential of northern pike in a natural environment annually for the period 1965 to 2013. Habitat suitability indices (HSIs) were developed to map the maximum spawning habitat (i.e., Week_0: the date varies every year according to water temperature, see Mingelbier et al. 2008) and nursery habitat 5 weeks after the start of the free-swimming stage ($\text{HSI}_{\text{nursery}}$ at Week_5, see Foubert et al. 2018).

Land cover categories

Land cover in the Lake Saint-Pierre floodplain was described for three reference years using aerial photographs taken in 1964 and 1997 (Richard et al. 2011), and satellite images from 2014 (ECCC and MDDELCC 2018). Land cover classes distinguish landscape features such as lakes, streams, pastures, soybeans, corns, roads, forests, marshes, swamps, bare ground etc. (see detailed land cover classes in ECCC and MDDELCC 2018). In the present study, land cover classes were aggregated in six categories for the Lake Saint-Pierre floodplain, from most suitable to least suitable for pike spawning: (1) suitable wetlands (e.g. wet meadows, swamps and marshes), (2) ditch and stream networks, (3) perennial cover (e.g. pasture and forage crops), (4) unsuitable wetlands and wooded areas (e.g. peatlands and coniferous stand), (5) roads and urban areas, and (6) annual crops (i.e. soybeans, corn, wheat, vegetables, oats, barley and other grains; see land cover categories and their associated land cover classes in Online Resource 1). Only tree swamps differed in quality between spawning and nursery habitats. We considered tree swamps were suitable for nurseries (e.g. food supply) but unsuitable for spawning due to the lack of appropriate substrate for egg deposition. In addition, the managed wetlands were included in the analysis because they are used by pike and other fish species during their early stages of development (Mingelbier and Douguet 1999 updated with field observations).

The next three sections explain the analyses performed (Fig. 1).

Historical habitat changes related to agriculture practices (objective 1)

As annual crop production gradually increased between 1964, 1997, and 2014, we conducted a linear interpolation using these three reference years to estimate annual habitat area changes between 1965 and 2013. The spawning and nursery habitat changes related to annual crop production was calculated for each year by overlaying the corresponding land uses and potential habitats modelled in a reconstructed "unaltered" landscape. Spearman's Rank correlation coefficients were used to assess: (1) the relationship between total potential spawning habitat change due to annual crop production and water discharge at spawning (Week_0), and (2) the relationship between total potential nursery habitat change due to annual crops and water discharge when larvae became free-swimming (Week_5).

Habitat connectivity for four hydrological profiles (objective 2)

Selected hydrological profiles

Since the flow regime of the Lake Saint-Pierre floodplain varied over the study period (1965–2013), the evolution of water discharge between the maximum spawning time (Week_0) and the free-swimming stage (Week_5) was classified into four distinct hydrological profiles: (1) stable-low, (2) stable-high, (3) increasing, and (4) decreasing. Four years of the 1965–2013 period were chosen to represent the four profiles to assess their influence on pike habitats (1965, 1973, 1983, and 1998, respectively; Table1). An analysis covering the 1965–2013 period revealed that the profile recurrences were 16% for stable-low, 16% for stable-high, 14% for increasing and 53% for decreasing discharges. During the unregulated period

Table 1 The total surface of potential habitats for the four hydrological profiles (stable-low, stable-high, increase, decrease) was calculated for potential spawning habitats at maximal spawning time (developed in Mingelbier et al. 2008) and nursery habitats five weeks later at the beginning of the free-swimming stage (Foubert et al. 2018) in Lake Saint-Pierre (St. Lawrence River, Canada)

Flow profiles	Water discharge (m^3 s^{-1})	Flooded surface (ha)	Potential habitat surface (ha)
Stable-low (1965)			
Spawning habitats—Week$_0$	Low (8315)	41,768	2794
Nursery habitats—Week$_5$	Low (8455)	44,731	5107
Stable-high (1973)			
Spawning habitats—Week$_0$	High (14,853)	57,800	5242
Nursery habitats—Week$_5$	High (14,920)	58,868	5047
Increasing (1983)			
Spawning habitats—Week$_0$	Medium (12,021)	49,455	4608
Nursery habitats—Week$_5$	High (14,905)	62,099	5277
Decreasing (1998)			
Spawning habitats—Week$_0$	High (15,296)	59,407	6045
Nursery habitats—Week$_5$	Medium (11,532)	46,551	3019

of 1883–1910, preceding the Ottawa River regulation, profiles were only increasing (61%) or stable (39%) (Le Pichon et al. 2018; Morin and Bouchard 2000).

Connectivity estimate

A least-cost approach to modelling movement across landscapes (Adriaensen et al. 2003) was used to quantify connectivity between spawning habitat at Week$_0$ and nursery habitat at Week$_5$. Using this model, every landscape element was assigned a 'resistance' value based on its restricting/facilitating effects on animal movements and functional distances were calculated using the Minimal Cumulative Resistance concept in both upstream and downstream directions (Le Pichon et al. 2006a; Caldwell and Gergel 2013; Hanke et al. 2013; Roy and Le Pichon 2017).

We assigned resistance values to landscape features that affect larval dispersal capacities or mortality when they leave spawning habitats. Factors driving floodplain permeability were water depth, current velocities and hydro-resistance of some land cover types (e.g. "dense vegetation" which was defined as marshes, -wet meadows and swamps in shallow water depths $<$ 20 cm). Resistance values ranged from 0.1 to 10,000 depending on whether they facilitate ($R < 1$), are neutral ($R = 1$) or impede movement and decrease survival ($R > 1$). Downstream resistance values < 1 were assigned to classes of current velocities ranging from 2 to 10 cm s^{-1}, which reflected habitats with current-assisted drift. Rx were calculated as inversely proportional to the mean current velocity of each class ($Rx = 1/Vx$, Table 2). A neutral resistance value of 1 was assigned to (1) ditches and stream networks, (2) permanent structures such as culverts and water control structures allowing larvae to cross roads and managed wetlands dikes, and (3) current velocities below 2 cm s^{-1} in both directions. Maximum resistance values, acting as non-passable barriers ($R = 10{,}000$), were assigned to (1) dewatered areas (water depth ≤ 0 cm), (2) current velocities > 10 cm s^{-1} in downstream direction (Peake 2004) and > 2 cm s^{-1} in upstream direction (larval are not able to swim against current), (3) emerged roads and managed wetland dikes and (4) "dense vegetation", which inhibit larval dispersal (Table 2). Emerged roads and "dense vegetation" for contrasting hydrological conditions in the lake were identified using simulated water depths and 1-m resolution topography provided by LiDAR data (Fortin et al. 2002). Agricultural crop types in the contemporary landscape (i.e. 2014) were not included in connectivity estimates as they are not believed to restrict connectivity or cause mortality during larval movement.

Functional distance maps between spawning and nursery habitats were performed using the freeware *Anaqualand 2.0* (Le Pichon et al. 2006b). The

Table 2 Dimensionless resistance values based on the restricting/facilitating effects of hydrological and land cover landscape characteristics on connectivity in downstream or upstream directions

Landscape feature	Downstream resistance value	Upstream resistance value
Water depth ≤ 0 m	10,000	10,000
Current speeds (cm^3 s^{-1})		
Speed $> 0 \leq 2$	1	1
Speed $> 2 \leq 4$	0.3333	10,000
Speed $> 4 \leq 6$	0.2000	10,000
Speed $> 6 \leq 8$	0.1429	10,000
Speed $> 8 \leq 10$	0.1111	10,000
Speed > 10	10,000	10,000
Ditch and stream networks	1	1
Emerged roads and dikes	10,000	10,000
Dense vegetation	10,000	10,000

Water depth, current speed, ditch and stream networks, emerged roads and dense vegetation are simulated at the beginning of free-swimming stage ($Week_5$). Water depth corresponds to the dewatering between the spawning time ($Week_0$) and the free-swimming stage ($Week_5$) in Lake Saint-Pierre (St. Lawrence River, Canada)

functional distance is defined as the sum of the resistance*distance the larvae will encounter along their path. Since the functional distance incorporates resistance values, it could be lower or higher than the physical instream distance for the same path (i.e. minimum distance within the limits of the watercourse).

Connected and disconnected spawning habitats

The mobility coefficient is derived from the stage-specific larval swimming capacities and the potential passive transport facilitated by local currents at the beginning of the free-swimming stage ($Week_5$). The maximal value was set to $\alpha = 6000$ m which corresponds to the maximum distance travelled at 1 cm s^{-1} by a neutral particle in the water column over a one-week period in the St. Lawrence River (see sensitivity analyses in Online Resource 2). When the functional distance between a spawning habitat and a nursery was $\leq 6000\ m_{functional}$ (i.e. the maximal α), the spawning habitat was considered to be connected (Foubert et al. 2018); whereas, when the functional distance exceeded $6000\ m_{functional}$, the spawning habitat was considered disconnected. Connected and disconnected spawning habitats were mapped in *ArcGIS 10.1* and their surfaces were quantified (surface expressed in ha) for the four selected hydrological profiles (1965, 1973, 1983, and 1998).

In addition, the effects of each hydrologic and land cover characteristics added successively on connectivity estimate (i.e. water depth, current speed, dense vegetation, and roads/managed wetland dikes) were quantified (Table 3). Direct losses correspond to potential spawning habitats spatially overlaid on restricted landscape features. Technically, spawning habitats were overlaid on landscape features in *ArcGIS 10.1* to estimate spawning habitat loss due to: (1) dewatering occurring between $Week_0$ and $Week_5$ (water depth ≤ 0, Table 2), (2) increased current velocities (> 10 cm s^{-1}), (3) emerged roads, and (4) dense vegetation. Indirect losses were considered as potential spawning habitats that were not connected to a nursery because of limited landscape features that act as physical barriers to larval dispersal.

Effective spawning habitats (objective 3)

For the four selected hydrological profiles (stable-low, stable-high, increasing and decreasing water discharges), the total area of connected spawning habitats (i.e. including the effects of water depth, current velocity, dense vegetation, ditch and stream networks, and emerged roads/managed wetland dikes) was overlaid on the six land cover categories of the

Table 3 Effects of landscape features that limit connectivity (i.e. water depth, current speed, roads and dense vegetation) on potential spawning habitat losses for the four hydrological profiles (stable-low, stable-high, increase, decrease) in Lake Saint-Pierre (St. Lawrence River, Canada)

Flow profile	Potential spawning habitats (ha)	Direct losses (i.e. transform high to low habitat quality)					Indirect losses (i.e. act as physical barriers)				Connected spawning habitats (ha)
		Dewatered areas	High speeds (> 10 cm s^{-1})	Roads	Dense wetlands	Total (ha) [%]	High speeds (> 10 cm s^{-1})	Roads	Dense wetlands	Total (ha) [%]	
Stable-low	2794	4	223	2	0	229 [8]	5	0	0	5 [0.2]	2560
Stable-high	5242	51	262	100	26	439 [8]	110	28	0	138 [3]	4665
Increase	4608	2	772	8	0	782 [17]	82	0	0	82 [2]	3744
Decrease	6005	3758	61	117	66	4002 [66]	72	0	25	97 [2]	1906

The connected spawning habitat area is the result of a subtraction between the potential spawning habitat area (Habitat Suitability Indices) and total habitat losses

contemporary description (i.e. 2014, see Online Resource 1) in *ArcGIS 10.1*. This allowed us to quantify and differentiate the area of (1) effective spawning habitat, which corresponds to the overlap of connected spawning habitats with suitable land cover categories (i.e. suitable wetlands, perennial crops and drainage ditches), and (2) ineffective spawning habitat that overlaps with inadequate land cover categories (i.e. unsuitable wetlands and wooded, annual crops, and roads and urban areas). Finally, the effective spawning habitat areas obtained for the four hydrological profiles were spatially overlaid to identify the most recurrent effective spawning habitats.

Results

Historical habitat changes related to agriculture practices

With the expansion of annual crops, up to 2446 ha of potential spawning habitat and 1188 ha of potential nursery habitat have been lost in the Lake Saint-Pierre floodplain between 1965 and 2014 (Fig. 3). The impacts of agriculture have been particularly severe since 1990, from when the total spawning habitat area did not exceed 5500 ha. The total loss of both spawning and nursery habitats was positively correlated with water discharges at Week_0 and at Week_5, respectively ($P < 0.05$, Spearman's rank correlation). The impact of agriculture on potential spawning and nursery habitats occurred at modelled discharges $> 12{,}000$ m^3 s^{-1} with the largest losses at discharges $> 14{,}000$ m^3 s^{-1} (Fig. 3).

Habitat availability and connectivity

Potential habitats during contrasting hydrological profiles

The total area of potential spawning and nursery habitats available annually was determined based on hydrological conditions (Table 1, Fig. 4). High spring water discharges resulted in a large area of potential spawning (1998) and nursery habitats (1983), while low water discharge resulted in the smallest areas of potential spawning habitat (1965), and a decreasing profile led to the smallest areas of potential nursery habitats (1998). At medium to high water discharge,

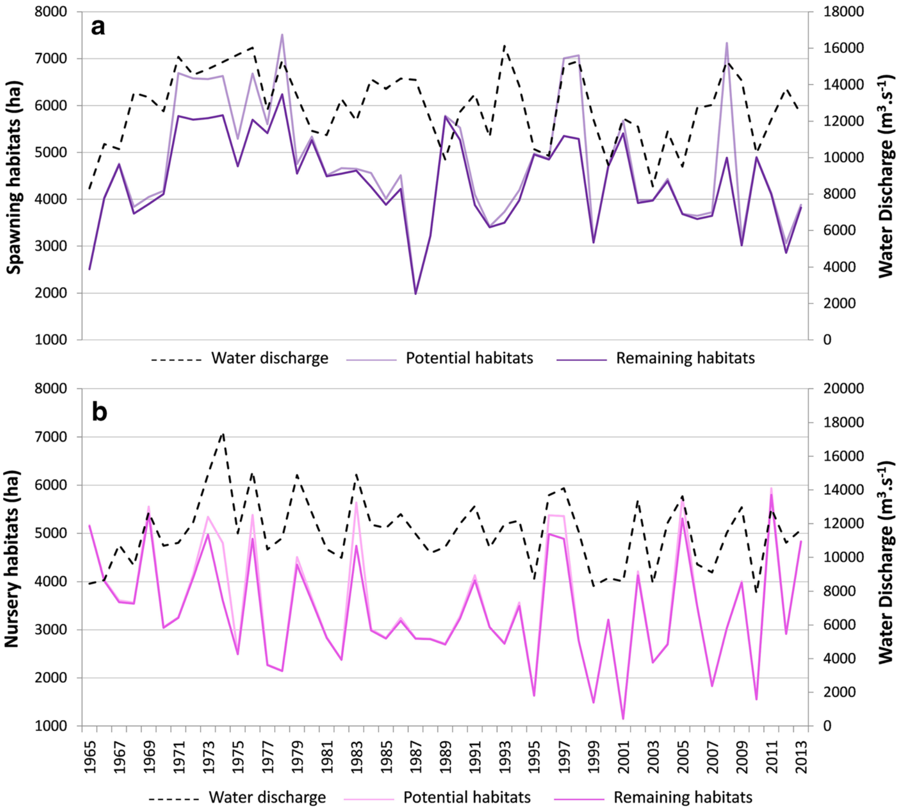

Fig. 3 Reconstitution of northern pike **a** spawning and **b** nursery areas for the period 1965–2013 in the unaltered (without agriculture) and the contemporary landscape (with agriculture) of Lake Saint-Pierre (St. Lawrence River, Canada). **a** Potential spawning (light purple) and **b** nursery (light pink) habitat areas (left y-axis) in the unaltered landscape have been adapted from Mingelbier et al. (2008) and Foubert et al. (2018) respectively. Remaining a spawning (dark purple) and b nursery (dark pink) habitat areas include land cover changes, specifically the annual crops extension. Water discharge (right y-axis, dashed line) is measured during the spawning time (Week$_0$) and 5 weeks later at the beginning free-swimming stage (Week$_5$)

managed wetlands generated up to 571 ha and 722 ha of potential spawning and nursery habitats, respectively, which represented between 10 and 13% of the maximum habitat available in Lake Saint-Pierre.

Connected and disconnected spawning habitats

Due to the impact of hydrological variability and anthropogenic landscape characteristics on habitat connectivity, 8–68% of potential spawning habitat was lost (dewatering or disconnected nurseries; Table 3). First, the largest disconnected spawning areas appeared during the decreasing profile between the maximum spawning time (Week$_0$) and the free-swimming stage (Week$_5$) due to the dewatering of 62% of potential spawning areas. Second, the increase in water currents above the 10 cm s^{-1} thresholds after spawning has transformed high-quality habitats into low-quality habitat and appeared frequently during the increasing profile. These fast water currents acting as physical barriers prevented access to 2% of spawning habitats during the increasing profile. Third, the dense vegetation slightly reduced the total area of potential spawning habitats (1%) during the stable-high and decreasing profiles and acted as a physical barrier during the decreasing profile. Finally, 2% of potential spawning habitat disappeared in stable-high and decreasing profiles due to the surface occupied by emerged roads. Although spawning habitat losses were small, emerged roads also served as physical barriers during stable-high profiles.

The largest area of connected spawning habitat occurred during the stable-high profile, one-third resulting from the overlap between potential spawning and nursery habitats, and two-thirds related to the larval mobility coefficient (α = 6000 m$_{\text{functional}}$),

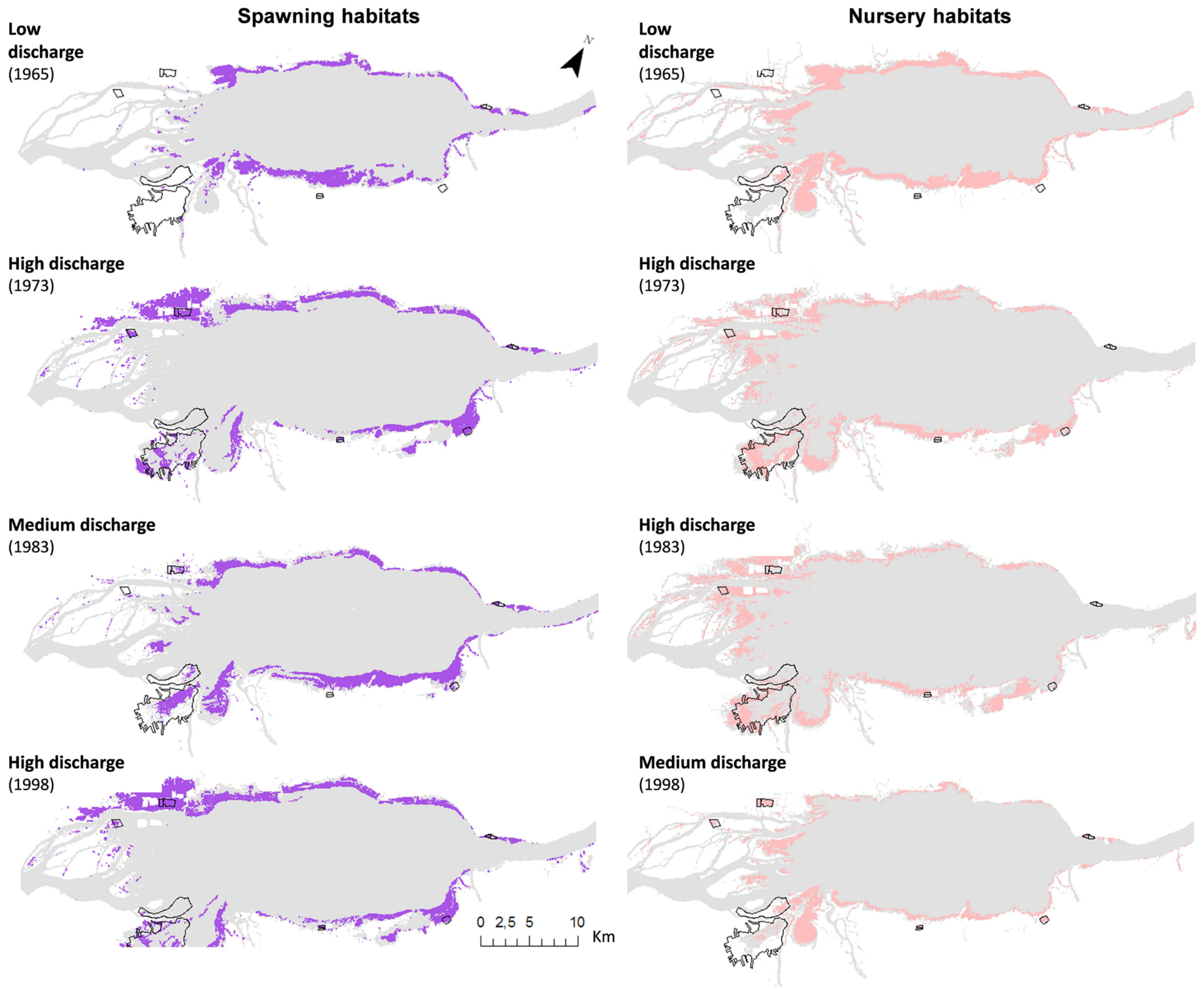

Fig. 4 Map of Lake Saint-Pierre (St. Lawrence River, Canada) showing the potential spawning (purple) and nursery (pink) habitats of the four hydrological profiles (stable-low, stable-high, increase, decrease). Wetlands managed for fish (black outlines) generated potential habitats when water discharge was medium to high

connecting potential spawning areas to distant nursery areas (Fig. 5). The overlap between potential spawning and nursery habitats generated large areas of connected spawning habitats, especially when water discharge remained stable between Week$_0$ and Week$_5$. The overlapping habitat areas reached 55% of the total connected spawning area in the stable-low profile, 28% in the stable-high profile, 0.2% in the increasing profile and 10% in the decreasing profile (see dark blue in Fig. 5). Moreover, larval mobility (α) allowed attaining distant nursery habitats (1) where potential spawning and nursery habitats overlapped, and (2) when hydrological conditions did not dewater spawning areas and created large nursery habitats (Fig. 5). The total area of connected spawning habitat increased by 61% in the stable-high profile and by 81% in the increasing profile due to larval mobility. When fewer spawning habitat areas were available at the beginning of the free-swimming stage (Week$_5$), α increased the surface of connected spawning habitat by 36% (stable-low profile) and by 21% (decreasing profile). During the decreasing profile, ditch and stream networks in dewatered areas further increased the area of connected spawning habitats by 14% (252 ha) (Online Resource 2). Finally, managed wetlands generated 463 ha (10%) of total connected spawning habitat during the stable-high profile, 439 ha (12%) during the increasing profile and 216 ha (11%) during the decreasing profile.

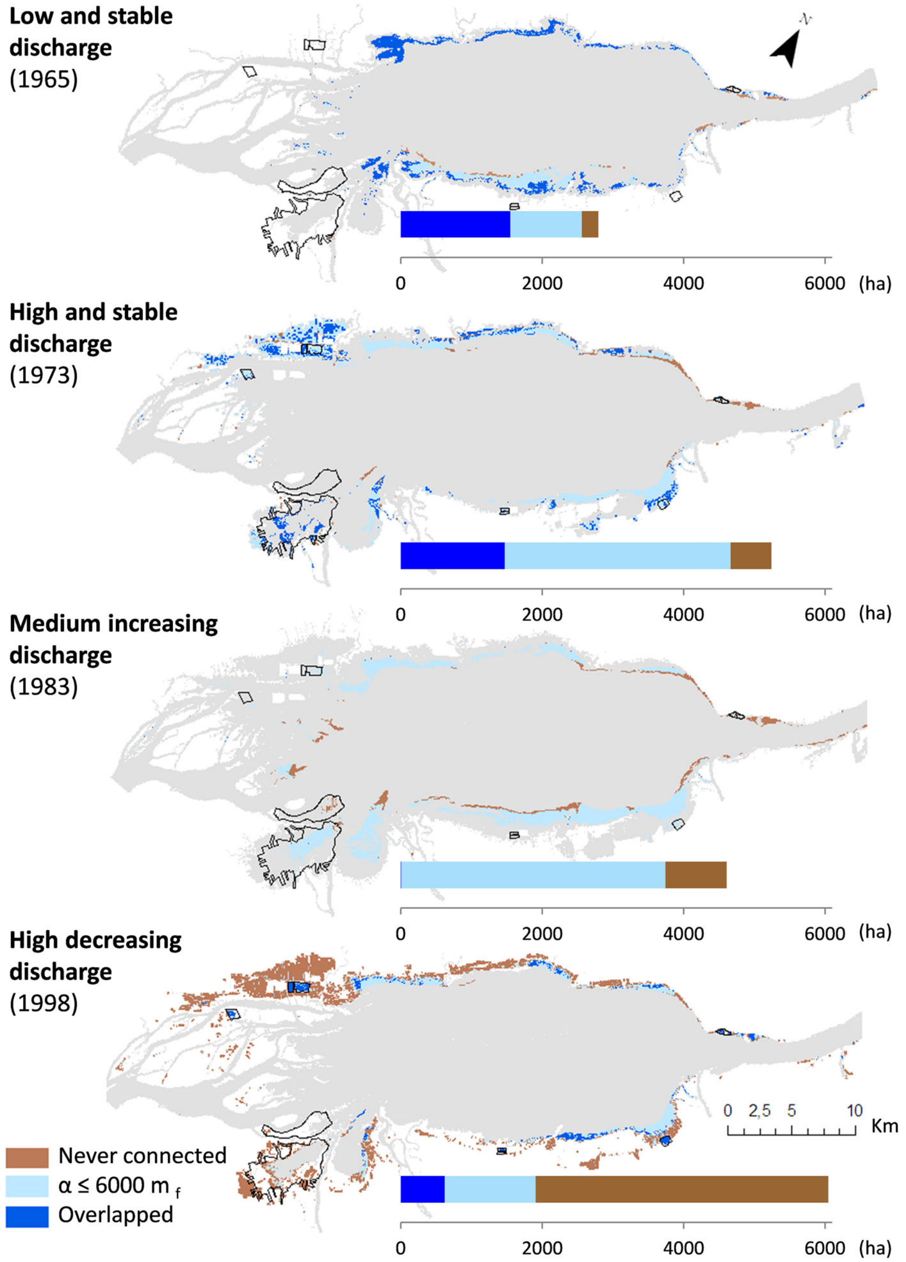

Fig. 5 Map of Lake Saint-Pierre (St. Lawrence River, Canada) showing the spawning habitats disconnected and connected for the four hydrological profiles (stable-low, stable-high, increase, decrease) taking into account the hydrological and anthropogenic characteristics of the landscape (i.e. water depth, current velocities, ditch and stream networks, roads, dense wetlands). The connectivity values correspond to three classes: (1) spawning habitats overlapping nurseries (dark blue color), (2) spawning habitats connected when $\alpha \leq 6000\ \text{m}_{\text{functional}}$ (medium blue color), and (3) spawning habitats never connected to a nursery (functional distance $> 6000\ \text{m}_{\text{functional}}$; brown color). Since α is a distance integrating the minimal cumulative resistance (i.e. functional distance), the α unit is not equivalent to the distance in the watercourse (i.e. international metric system)

Effective spawning habitats

Considering the most recent description of the Lake Saint-Pierre floodplain (e.g. satellite images taken in 2014; ECCC and MDDELCC 2018), 0–47% of the [potential] connected spawning habitats were not effective for egg deposition due to unsuitable land cover categories (Fig. 6). The largest loss of connected spawning habitat was observed for the stable-high profile with 32% of non-effective surfaces related to agricultural practices, mostly used for corn and soybean production. When water discharges reached average ($\sim$ 11,000 $m^3\ s^{-1}$) to high ($\sim$ 15,000 $m^3\ s^{-1}$) discharges during the first five weeks of ontogeny (i.e. in 1973, 1983 and 1998), unsuitable wetlands and wooded areas reduced the area of connected spawning habitat by 11% to 14%. Less than 1% of connected spawning area was lost due to the presence of submerged roads and urban areas in the four hydrologic profiles. Finally, only 0.4% of connected spawning area was affected by land cover during the stable-low profile.

Considering contemporary land cover changes in connected spawning habitats, the increase in water discharge between the maximum spawning time ($Week_0$) and the free-swimming stage ($Week_5$), which ranges from medium to high, was found to be the most favourable hydrological conditions for northern pike habitats in Lake Saint-Pierre (increasing profile in Fig. 7). In this case, 3218 ha, corresponding to 70% of the initial potential spawning area, were connected to nursery areas and were not modified by unsuitable land cover (= effective spawning habitats). During the stable-low profile, almost all the potential spawning areas were effective for northern pike recruitment (i.e. 2549 ha or 91% of potential habitats). During the stable-high profile, similar potential spawning areas remained effective (i.e. 2463 ha), but represent only 47% of the potential spawning area. This significant decrease is due to agricultural practices. During the decreasing profile, potential habitats altered by the land cover had already been lost due to hydrological constrains on habitat connectivity. Although 27% (1628 ha) of the potential spawning habitats remained effective, only 15% (279 ha) of connected spawning habitats were altered by the land cover. Finally, 332 ha of effective spawning habitats were spatially recurrent over the four contrasting hydrological profiles (dark green in Fig. 7).

Discussion

This study shows that anthropogenic alterations to the floodplain and hydrological regime can have major effects on the availability and the connectivity of habitats for early life stages of fishes. The various habitat and connectivity models, carried out under highly contrasting hydrological conditions over the past 50 years and combined with a description of land use for several reference periods, have proven to be very effective in identifying regions of Lake Saint-Pierre most impacted by human alterations. In the present study, the modelling was carried out in a recent landscape (2014) altered by two main anthropogenic pressures that have dramatically reduced the range of natural conditions favourable to fish reproduction in the St. Lawrence River. First, intensive agriculture in the floodplain (annual crops) overlapping with suitable natural habitats for fish, is leading to destruction of natural vegetation by ploughing. Such intensive agriculture has increased over time with significant reduction of spawning habitat and its connectivity for species such as northern pike and other fish species that use the floodplain to complete their life cycle. Second, the highest natural reproductive potential for northern pike, usually associated with high and stable water flows (Johnson 1957; Casselman and Lewis 1996), has been lost due to flow regulation that leads to lower and shorter spring floods and more frequent drying of spawning grounds resulting in egg mortality.

In a context of global climate change, where spring water discharge is expected to decrease and extreme hydrological conditions to increase in frequency (Mortsch et al. 2000; Boyer et al. 2010), effective spawning habitats in Lake Saint-Pierre could be further reduced, which could make it impossible to maintain fish abundance at their past levels. Hence, restoring habitat quality and connectivity in floodplains coupled with better flow regime management will play an important role in conserving biodiversity and maintaining sustainable populations.

Land cover changes and potential habitat loss

Land cover changes have profoundly altered fish habitat abundance and distribution in productive floodplains (e.g. Baber et al. 2002; Blanton and Marcus 2014; Fernandes et al. 2015), including the

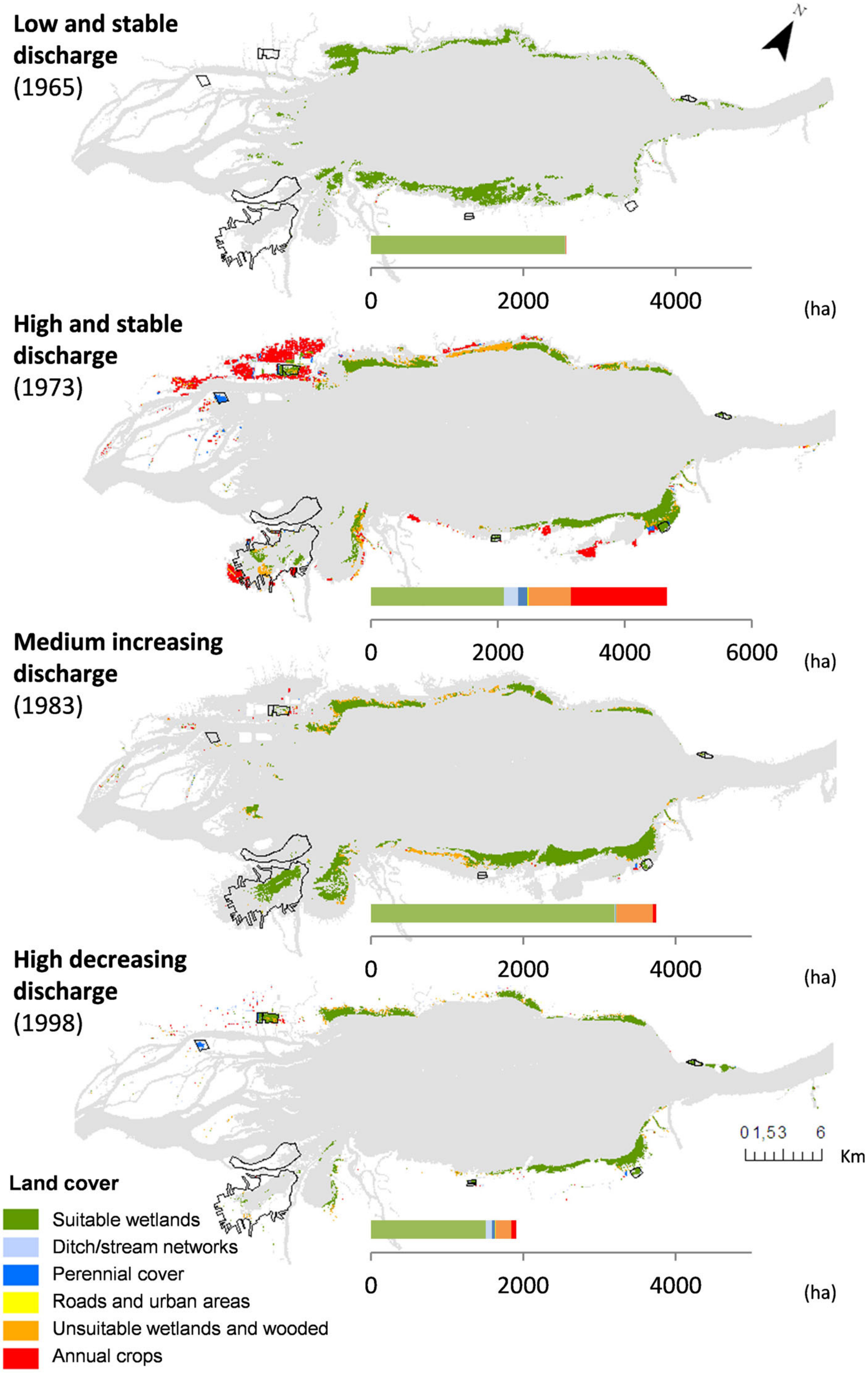

Fig. 6 The connected spawning habitats were overlaid to the contemporary land cover of Lake Saint-Pierre (description 2014′) to identify effective (green and blue colors) and ineffective (yellow, orange and red colors) spawning habitats for the four hydrological profiles (stable-low, stable-high, increase, decrease)

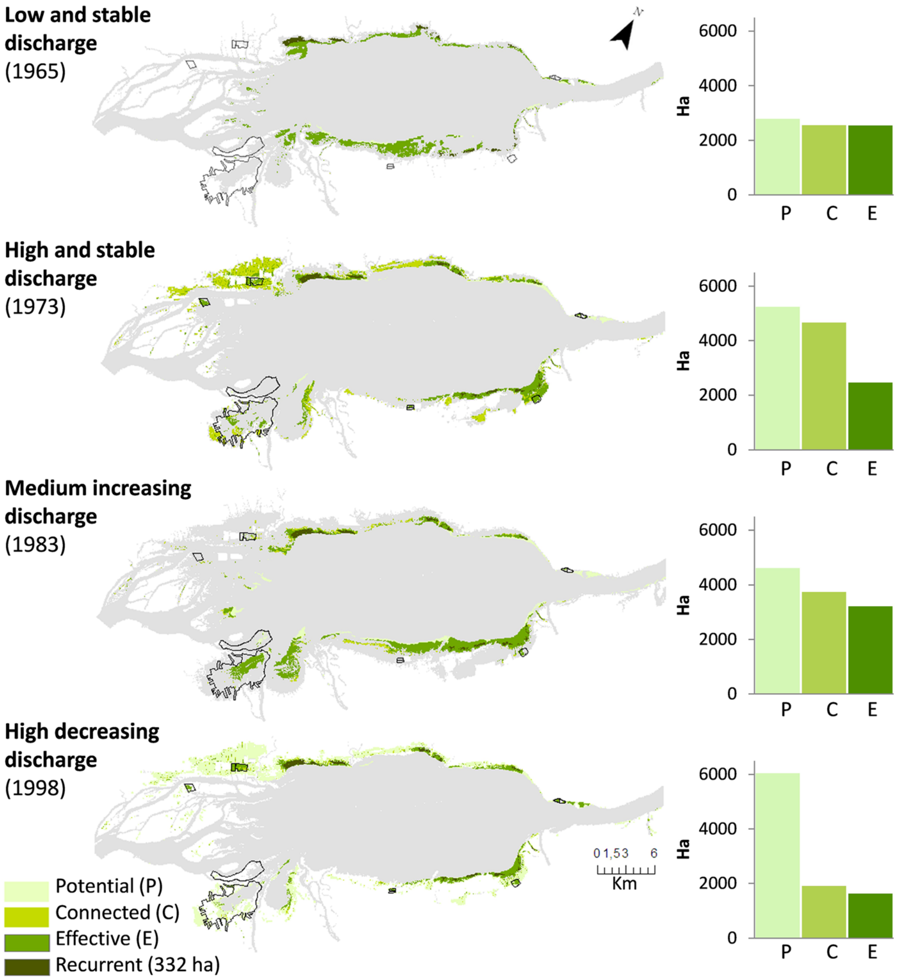

Fig. 7 Spawning habitat area as (1) potential, (2) connected, (3) effective and (4) recurrent in the Lake Saint-Pierre floodplain (St. Lawrence River, Canada). Recurrent habitats are effective spawning habitats located at the same location during the four hydrological profiles (stable-low, stable-high, increase, decrease)

Lake Saint-Pierre floodplain, which has been progressively occupied by agricultural practices. While perennial crops dominated the landscape (≈ 45% cover, ≈ 21,000–22,000 ha) and annual crops accounted for only 10 to 15% of the territory (≈ 5000 to 7000 ha) in 1950, the situation completely reversed in the 1990s. More recently, annual crops have dominated the landscape, occupying 32% of the Lake Saint-Pierre (16,000 ha) compared to 15% (7000 ha) for perennial crops. Although perennial crops (i.e. pasture and forage crops) can represent potential fish habitat, ploughing annual crops removes vegetation cover and creates bare fields without substrate for egg laying in the next spring. Based on the results of our models, annual crops have negative effects on northern pike habitat especially when the water flow exceeds 14,000 m^3 s^{-1}, which happens very often in the spring (annually or biannually; Morin and Bouchard 2000). Indeed, large potential habitat losses were observed during high water discharges because fish habitats overlapped with unsuitable land cover due to agricultural practices that are mainly located in the upper part of the floodplain.

Habitat connectivity

In large floodplains, not all potential spawning habitats are connected to a nursery area, and therefore become mortality traps (Jeffres and Moyle 2012; Sheaves et al. 2014). Although transportation infrastructure (i.e. roads) has impacted habitat connectivity in the Lake Saint-Pierre floodplain (Le Pichon et al. 2018), rapid dewatering during the five first weeks of ontogeny appears to be the main factor limiting connectivity between northern pike spawning and nursery habitats (Foubert et al. 2018). Rapid dewatering after pike eggs were laid revealed large areas of spawning habitat in mortality traps (3758 ha or 62% of potential habitats). In addition, a decreasing profile can transform moderately dense vegetation associated with high quality spawning and nursery habitats (Casselman and Lewis 1996; Timm and Pierce 2015) into very dense low oxygen macrophyte beds (Casselman 1978; Holland and Huston 1984). Although only increasing (61% of all years) or stable (39%) hydrological profiles were observed before water-flow regulation (1883–1910; Le Pichon et al. 2018), the most recurrent condition since 1965 has been a steadily decreasing profile between the spawning time (Week$_0$) and the larval free-swimming period (Week$_5$). The regulation of the Ottawa River, considered the main tributary of the St. Lawrence River with a water discharge ranging from 570 to 9200 m^3 s^{-1} (Carpentier 2003), has now generated large disconnected spawning areas in Lake Saint-Pierre (e.g. Brodeur et al. 2006). Indeed, the duration of the flood has been shortened by three weeks and the maximum annual water discharge has decreased significantly by nearly 2500 m^3 s^{-1}, a decrease exacerbated by the regulation of Lake Ontario outflows since 1958 (i.e. reduction of 1020 m^3 s^{-1}; Morin and Bouchard 2000).

In large floodplains characterized by recurrent dewatering profiles where intensive agricultural practices are covering large expanse of the landscape, managed wetlands and ditch/stream networks appear to be key landscape features facilitating habitat connectivity due to their permanent aquatic characteristic (e.g. Washitani 2007). Our results highlighted the role of these two anthropogenic landscape features in maintaining connected spawning habitats in the upper part of the Lake Saint-Pierre floodplain, where potentially flooded areas have become vulnerable to dewatering and agricultural expansion (e.g. in 1998 and 1973 in Saint-Barthélemy Bay). Although managed wetlands are accessible only at medium to high water discharges (Brodeur et al. 2004), they promote spatial overlap of spawning and nursery habitats that improve larval growth and survival (Schiemer et al. 2001; Ospina-Alvarez et al. 2012). In addition, when spawning and nursery habitats are spatially separated, ditch and stream networks can be used by mobile individuals to connect nursery habitats (e.g. Ishiyama et al. 2014). Although young pike larvae have limited swimming capacities, low current velocities in large floodplains favour dispersal of larvae to nurseries (Schiemer et al. 2003; Miehls and Dettmers 2011). Several independent observations in Lake Saint-Pierre confirmed the presence of northern pike larvae in ditch and stream networks and managed wetlands considered effective spawning and nursery habitats in this study (Brodeur et al. 2016).

Effective spawning habitats

Natural hydrological conditions, that are favourable for fluvial fish recruitment in large unaltered floodplains (Junk et al. 1989; Gorski et al. 2011) have lost their benefits due to anthropogenic pressures. Although a stable-high hydrological profile ($> 14{,}000$ m^3 s^{-1}) in Lake Saint-Pierre generated large areas of potential spawning habitats connected to nurseries (4665 ha), only 47% were effective when land cover was considered. The expansion of intensive agriculture, particularly annual crops, has profoundly altered spawning habitat that were previously connected to nurseries. Historically, 1517 ha of these habitats were effective for northern pike during favourable hydrological conditions (i.e. stable-high profile represented by 1973). Furthermore, water-flow regulation has dramatically reduced the frequency of these favourable hydrological conditions (Le Pichon et al. 2018), which have naturally generated large interconnected habitats. As a result, the possibility for stable-high hydrological profiles that could produce high potentials for northern pike reproduction was rare and the habitats in the upper floodplain systematically eliminated by intensive agricultural practices, especially since 1990 (Martin and Létourneau 2011).

Under specific hydrological conditions, human-altered floodplains can still generate large effective spawning habitat for freshwater fishes. In Lake Saint-Pierre, 3218 ha of effective spawning habitat was estimated during the increasing profile—i.e. when the water discharge increased from medium to high between the maximum spawning time (Week$_0$) and the free-swimming stage (Week$_5$). Potential spawning habitat generated by medium water discharge were not disconnected by hydrological variability during the increasing profile and not altered by land cover activities in the upper floodplain. In addition, in years of low water discharges, fish habitat, which is small in area, is less affected by intensive agriculture because it is located lower in the uncultivated floodplain. Nevertheless, the increasing profile and the stable profile, which produce the largest effective spawning habitat areas in the anthropised floodplain of Lake Saint-Pierre, has been greatly reduced by the regulation of water flow (Le Pichon et al. 2018).

Management implications

In conclusion, the loss of conditions favouring the formation of spawning habitats for northern pike caused by intensive agricultural practices in the floodplain and flow regulation can be critical to recruitment success, as several fish populations show a significant decline in the St. Lawrence River. This study highlights important new opportunities to improve fish habitat and connectivity in major river systems such as the St. Lawrence River, and identifies the following priority management measures (Wohl et al. 2015).

First, to regain production potential in years with high water flows, the priority would be to convert large intensive annual crops located in the floodplain to natural wetlands, or at least to perennial crops that represent potential fish habitat. Such actions are much needed for improving the health of the St. Lawrence River ecosystem (e.g. Washitani 2007; Gagliardi and Pettigrove 2013) and for increasing the species dispersal in landscape dominated by agriculture (e.g. Volk et al. 2018). Field crop conversions should target areas where large connected habitats are altered by annual crops such as the Saint-Barthélemy Bay (Figs. 2, 7).

Second, existing structures such as ditches and stream networks should be maintained as they represent effective fish habitat and contribute to habitat connectivity (Beier and Noss 1998). In some particular cases, additional structures could be installed if required by local needs. Although transportation infrastructure (roads) can limit connectivity in floodplains (Doyle et al. 2008; Blanton and Marcus 2014), structures such as culverts have proven to be useful in maintaining connectivity in human-altered floodplains (Douven et al. 2012; Le Pichon et al. 2018).

Third, managed wetlands created in the Lake Saint-Pierre floodplain show great potential to increase the survival of early-life stages of fishes. Indeed, these managed marshes are surrounded by dikes that could extend the duration of the flood, as was the case during the non-regularized period of the St. Lawrence system, while maintaining connectivity between spawning and nursery habitats, which is also positive for the survival of young fish. Our findings indicate that protected areas provide valuable frameworks for maintain and enhancing habitat connectivity (such as in Bishop-Taylor et al. 2015).

Finally, the water discharge regulation of the Ottawa River since 1911 has altered the natural flow regime of the St. Lawrence River, decreasing the average water level of spring floods in Lake Saint-Pierre by ~ 0.75 m and reducing its duration by about 3 weeks (Morin and Bouchard 2000). Our simulations suggest that a revision of flow management guidelines in the Ottawa River to restore a more natural spring flow regime could benefit species that use the floodplains of the St. Lawrence River, for example by extending the duration of spring floods to ensure better connectivity between spawning and nursery habitats. Similar revision of guideleines was conducted in the Lake Ontario-St. Lawrence River basin by the International Joint Commission (IJC), established under the 1909 Boundary Waters Treaty Act between the United States and Canada, which approved a new management plan in 2016 that allowed for more natural water level variations. In comparison, the changes induced by the regulation of the Ottawa River are much less well known and receive little consideration.

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