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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Landscape Ecology

Losing the best conditions for effective fish spawning habitat in the floodplain due to riparian agriculture and flow regulation, St. Lawrence River, Canada. †

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Abstract:	Context Hydrological and land use changes for human needs, 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 riparian agriculture and water flow regulation have impacted the effectiveness of spawning habitats of northern pike (Esox lucius). Methods Northern pike spawning and nursery habitats were modelled over a 49-years period (1965-2013) to estimate effective spawning areas under four contrasted hydrological conditions. Results These simulations, coupled with land-use analyses, revealed that natural flow conditions usually favourable to fish reproduction have been lost due to human activities. The highest potential for reproduction, usually associated with high and stable water flows, has been lost due to (1) intensive agriculture in the upper floodplain

	that overlaps with suitable habitats for fish, and (2) flow regulation that leads to more frequent drying of spawning grounds. These profound anthropogenic changes have resulted in a significant loss of reproductive potential for northern pike and other fish species that use the floodplain to complete their life cycle. Conclusions This study suggests the need to convert 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 areas for restoration are the most effective and recurrent spawning habitats, ditch and stream networks, and connected managed wetlands.
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Losing the best conditions for effective fish spawning habitat in the floodplain due to riparian agriculture and flow regulation, St. Lawrence River, Canada. †

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Abstract

Context.

Hydrological and land use changes for human needs, 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 riparian agriculture and water flow regulation have impacted the effectiveness of spawning habitats of northern pike (*Esox lucius*).

Methods.

Northern pike spawning and nursery habitats were modelled over a 49-years period (1965-2013) to estimate effective spawning areas under four contrasted hydrological conditions.

Results.

These simulations, coupled with land-use analyses, revealed that natural flow conditions usually favourable to fish reproduction have been lost due to human activities. The highest potential for reproduction, usually associated with high and stable water flows, has been lost due to (1) intensive agriculture in the upper floodplain that overlaps with suitable habitats for fish, and (2) flow regulation that leads to more frequent drying of spawning grounds. These profound anthropogenic changes have resulted in a significant loss of reproductive potential for northern pike and other fish species that use the floodplain to complete their life cycle.

Conclusions.

This study suggests the need to convert 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 areas for restoration are 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 dynamical environments at the interface between aquatic and terrestrial ecosystems. They provide a mosaic of temporary habitats required by a wide number of freshwater fish species to accomplish 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). 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). Quantifying the effects of anthropogenic pressures on the effectiveness of spawning habitats allows the identification of large-scale environmental disturbances that cause widespread recruitment failures (e.g. Goto et al. 2015), an important prerequisite for restoring and managing floodplain ecosystems.

The natural flow regime in floodplains (i.e. magnitude, duration and the periodicity of water levels) is highly variable in space and time, which in turn has a significant driving force on fish habitat surfaces areas and landscape connectivity (Junk et al. 1989; Wiens 2002). Although the flooding of large areas for long periods of time can improve the recruitment success of riverine fish, a rapid decrease in water discharge during early development can suddenly dewater or isolate spawning and nursery habitats, resulting in high egg and larvae 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 the 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 populations (e.g. Farrell et al. 2010; Goto et al. 2015; Mingelbier et al. 2008).

Land-use change is one of the most important factors altering habitats quality and connectivity on floodplains (Tockner and Stanford 2002). The conversion of large areas of natural floodplains to intensive agricultural practices has resulted in a net loss of fish habitat (Baber et al. 2002), a reduction in the abundance of fish eggs and larvae (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 disconnect and isolate a significant portion of the floodplain, reducing access to critical habitats (Blanton and Marcus 2014). In contrast, as fish larvae have limited swimming capacities, passive transport at low water current speeds (Schiemer et al. 2003) and landscape features such as ditch networks (Washitani 2007) can facilitate larval dispersal. Such alternative use of man-made structure can help maintain floodplain connectivity in an anthropized landscape.

In previous work, Foubert et al. (2018) examined spawning and nursery habitats of northern pike (*Esox lucius*) over the past 50 years to investigate how habitat connectivity and hydrological variability interact to alter the distribution of effective spawning habitat in the St. Lawrence River floodplain, Canada. The northern pike was used as a species model because it is an early-spring spawner, archetypal of the floodplain. Pike recruitment is positively influenced by the abundance and quality of spawning habitat, high-water temperature and high-water level maintained for several weeks after egg deposition (Casselman and Lewis 1996; Johnson 1957). Pike abundance has recently declined in several major river systems (Boët et al. 1999; Raat 2001), including the St. Lawrence River (Smith et al. 2007). Foubert et al. (2018) defined *effective spawning habitats* 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 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 the present study, we hypothesised that effective spawning habitats gradually changed during the 20th century, as water flows were regulated and extensive agricultural practices developed. More specifically, in the Lake Saint-Pierre (St. Lawrence River, Canada), we (1) assess the historical loss of potential pike spawning and nursery habitats by riparian agriculture since 1965, (2) test the effects of water flow and land-use changes on connectivity between spawning and nursery habitats under four contrasted hydrological conditions, and (3) estimate the loss of connected habitats due to changes in land-use to identify current effective spawning habitats and the most valuable areas 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 system in the world, in terms of length (~1,200 km), watershed area (1,344,200 km^2) and average annual discharge ((10,270 m3.s-1 at Sorel; Morin and Bouchard 2000). Lake Saint-Pierre and its archipelago were included on UNESCO's Word Heritage Biosphere List in 2000. The shallow depth <3 m, slow lateral slope of the bottom, and low current velocities <0.5 m.s^{-1} contributes to the formation of extensive macrophyte beds (Centre-Saint-Laurent 1998). The annual variability of spring water discharges, ranging between 6,500 and 17,500 m^3.s^{-1} at Sorel, is a key mechanism for maintaining wetland vegetation in floodplains (Morin et al. 2005).

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 of the Moses-Saunders and Beauharnois Power Dams that control the Lake Ontario – St. Lawrence River system in 1958 (Carpentier 2003; Morin and Bouchard 2000). In addition, the development of large urban centres (e.g. Montreal, Trois-Rivières, and Quebec City), intensive agriculture along the river and in the floodplain, and transportation infrastructures along the St. Lawrence River have had a serious impact on fish habitat. Over time, perennial crops (e.g. pasture), which constitute potential fish habitat in the floodplain, have been replaced by annual crops (e.g. corn, soya) with no potential for fish spawning; this phenomenon has accelerated since the early 1990s (de la Chenelière et al. 2014; Fecteau and Poissant 2001). To compensate for the loss of fish habitat, approximately 1,300 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 and are then evacuated in early June to Lake Saint-Pierre.

Data collection

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

Several high spatial resolution hydrodynamic and biological models have been developed in the St. Lawrence River by Environment Canada to simulate the vegetation of the floodplain (e.g. deep marshes, shallow marshes and shrub) in Lake Saint-Pierre under various hydrological conditions (Morin et al. 2000; Morin et al. 2003; Turgeon and Morin 2005). Thus, natural plant succession in the littoral zone could be rebuilt each year for the period 1965 to 2013. As these simulations exclude anthropogenic effects, we used them to estimate the full reproductive habitat potential of northern pike in a natural environment for each year of the 1965-2013 period. Habitat quality indices (HSIs) were developed to map the maximum spawning habitat ($Week_0$: the date varies every year according to water temperature, developed in Mingelbier et al. 2008) and nursery habitat five weeks after the start of the free-swimming stage (HSI $_{nursery}$ at Week$_5$, developed and described in Foubert et al. 2018).

Land-use categories

Land-use in the Lake Saint-Pierre floodplain was described for three reference years: using aerial photographs in 1964 and 1997 (Richard et al. 2011) and satellite images in 2014 (Jobin and Dauphin in prep). In the present study, we interpreted the various types of land-use and assigned six land-use categories, from most suitable to least suitable for pike reproduction habitats: (1) wetlands suitable for spawning and nursery habitats (e.g. wet meadow and marshes), (2) main ditch and stream networks, (3) perennial crops (e.g. pasture and forage crops), (4) unsuitable wetlands and wooded areas (e.g. wooded peat bogs and plantations), (5) roads and urban areas, and finally (6) annual crops (i.e. soya, corn, wheat, vegetable crops, oat, barley and other cereals) (see all land-use types and their associated habitat quality in Online Resource 1). Only treed swamps differed in quality between spawning and nursery habitats. We considered treed swamps being 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: see Fig.1). The next three sections explain the analyses performed, which are illustrated in the conceptual diagram Fig. 1.

Historical habitat losses by agriculture (objective 1)

As annual crops gradually increased between 1964, 1997 and 2014, we conducted a linear interpolation using these three reference years to estimate annual habitat area losses between 1965 and 2013. The loss of spawning and nursery related to annual crops was calculated for each year by superimposing the corresponding land-uses and habitats. Spearman's Rank correlation coefficients were used to assess (1) the relationship between total potential spawning habitat lost due to annual crops and water discharge at spawning ($Week_0$) and (2) the relationship between total potential nursery habitat lost 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 largely varied over the study period (1965-2013), the water discharge between the maximum spawning time ($Week_0$) and the free-swimming stage ($Week_5$) was classified into four distinct 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 spring spawning dynamics (1965, 1973, 1983 and 1998, respectively; Tab.1). Historical 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. Profile recurrences were also calculated for the natural flow regime reconstructed by Morin and Bouchard (2000) for the period 1883-1910 preceding the Ottawa River regulation. During this unregulated period, all profiles were increasing (61%), or stable (39%) between $Week_0$ and $Week_5$ (Le Pichon et al. 2018).

Connectivity estimate

A least-cost approach to modelling movement in landscapes (Adriaensen et al. 2003) was used to quantify connectivity between spawning habitat at $Week_0$ and nursery habitat at $Week_5$. In this model, every landscape element is assigned a 'resistance' value based on its restricting/facilitating effects on animal movements (i.e. Minimal Cumulative Resistance concept) in both upstream and downstream directions (e.g. Caldwell and Gergel 2013; Hanke et al. 2013; Roy and Le Pichon 2017). Foubert et al. (2018) described in detail the method used to measure connectivity between two types of habitats (e.g. flowchart and functional distance examples).

We assigned a resistance value to hydrological and land-use characteristics that simulate different risks of larval mortality (e.g. fast current, dewatering, dense vegetation) or larval dispersion (i.e. passive drift and active swimming) when they leave spawning habitats. First, the environmental characteristics of the landscape sensitive to hydrological variations were considered. The resistance values were adapted from Foubert et al. (2018) and allowed the combined effects of water discharge and current velocities on egg survival and larval dispersal to be assigned to each point (or pixel) of the modelled landscape (see Tab.2). A maximum resistance value preventing any survival or successful dispersal was assigned to dewatered areas (water depth ≤0 cm) and current velocities >10 $cm.s^{-1}$ (Peake 2004). Resistance values <1, reflecting current-assisted larval drift, were assigned to current velocities ranging from 2 to 10 $cm.s^{-1}$. A maximum resistance value has been assigned to dense vegetation (e.g. wet meadows and shrubby swamps in low water depths

<20 cm), since they can act as physical barriers to larval dispersal (see Tab.2). Second, anthropogenic features that restrict (i.e. emerged roads and managed wetland dikes) or facilitate (i.e. ditch and stream networks) dispersion in the contemporary landscape were also examined. We have differentiated submerged roads and managed wetland dikes that influence connectivity. The accuracy of the topographic measurements (every meter) provided by LiDAR and the simulated water depths allowed us to identify submerged and emerged elements for contrasting hydrological conditions in the lake. A maximum resistance value has been assigned to emerged roads and managed wetland dikes (e.g. larvae cannot cross them). In addition, permanent structures (i.e. culverts, water control structures and weirs) allowing larvae to cross roads and managed wetlands dikes have been identified from published material (Mingelbier and Douguet 1999), field observations and GIS analyses. When a road has been cut by a ditch or a stream, a culvert has been considered. A resistance value of 1 that does not involve any restriction or facilitation of movement (i.e. only larval swimming capacity is considered) was assigned to permanent structures, ditches and stream networks (see Tab.2). The types of agricultural crops in the contemporary landscape were not included in connectivity estimates as they are not believed to completely restrict connectivity or cause mortality during larval movement.

After assigning resistance values, we used the open source software *Anaqualand 2.0* (Le Pichon et al. 2006) to generate the functional distance between spawning and nursery habitats (Foubert et al. 2018). The functional distance is defined as the combination of larvae dispersal potential (*i.e.* mobility coefficient (α) defined below) and the sum of the resistance the larvae will encounter along their path. The mobility coefficient (α) is derived from the stage-specific larval swimming capacities and the potential passive transport provided by local currents at the beginning of the free-swimming stage ($Week_5$). The maximal value was set to α =6000 m which corresponds to the maximal 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). Since the functional distance incorporates resistance values, it does not always correspond to a physical instream distance (i.e. minimum distance within the limits of the watercourse).

Connected and disconnected spawning habitats

When the functional distance between a spawning habitat and a nursery was $\leq$ 6000 $m_{functional}$ (i.e. the maximal mobility coefficient), the spawning habitat was considered to be connected (Foubert et al. 2018). However, 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 hydrological and land-use characteristic added successively on connectivity estimate (i.e. water depth, current speed, dense vegetation and roads/managed wetland dikes) were quantified (Tab.3). Direct losses correspond to potential spawning habitats spatially superimposed on restricted landscape features. Technically, spawning habitats were superimposed on landscape features in *ArcGIS 10.1* to estimate (1) spawning habitats lost due to dewatering occurring between $Week_0$ and

Week$_5$ (water depth ≤0, Tab.2), (2) spawning habitats lost due to increased current velocities (>10 cm.s^{-1}), (3) emerged roads, and (4) dense vegetation. Indirect losses are potential spawning habitats that are not connected to a nursery because of limited landscape features that act as physical barriers to larvae dispersal.

Effective spawning habitats (objective 3)

For the four selected hydrological profiles, 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 superimposed on the six land-use categories of the contemporary description (i.e. 2014) in *ArcGIS 10.1*. It 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-use categories (i.e. suitable wetlands, perennial crops and drainage ditches), and (2) ineffective spawning habitat that overlaps with inadequate land-use 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 (i.e. stable-low, stable-high, increasing and decreasing water discharges) were spatially overlaid to identify the most recurrent effective spawning habitats.

Results

Historical habitat losses related to agriculture

With the expansion of intensive agricultural practices, up to 2,446 ha of potential spawning habitats and 1,188 ha of potential nursery habitats have been lost in the Lake Saint-Pierre floodplain between 1965 and 2014 (see Fig. 3). The impacts of agriculture have been particularly severe since 1990, resulting in a total area of spawning habitats of no more than 5,500 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 discharges >12,000 $m^3.s^{-1}$ with the largest losses at discharges >14,000 $m^3.s^{-1}$ (Fig 2).

Habitat availability and connectivity

Potential habitats during contrasting hydrological profiles

The total area of potential spawning and nursery habitats available annually was determined by hydrological conditions (Tab.1, Fig. 4). High spring water discharges resulted in a large area of potential spawning (1998) and nursery habitats (1983), while low water discharges resulted in the smallest areas of potential spawning habitats (1965) and decreasing profile led to the smallest areas of potential nursery habitats (1998). At medium to high water discharges, managed wetlands generated up to 571 ha and 722 ha of potential spawning and nursery habitats respectively, which represent between 10% and 13% of the maximum habitat available in the Lake Saint-Pierre

Connected and disconnected spawning habitats

Due to hydrological variability and anthropogenic landscape characteristics on habitat connectivity, eight to 68% of potential spawning habitats were lost (dewatering or disconnected nurseries; Tab.3). Firstly, 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. Secondly, the increase in water currents above the 10 $cm.s^{-1}$ thresholds after spawning has transformed high-quality habitats into low-quality habitats. These conditions 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. Thirdly, the dense vegetation slightly reduced the total surface of potential spawning habitats (1 %) during the stable-high and decreasing profiles and acted as a physical barrier during the decreasing profile. Fourthly, 2% of potential spawning habitats have disappeared in stable-high and decreasing profiles due to the surface occupied by the 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 $m_{functional}$), connecting potential spawning areas to distant nursery areas (Fig. 5). The overlap between potential spawning and nursery habitats generate large areas of connected spawning habitats, especially when water discharge remains 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 to reach distant nursery habitats when (1) few potential spawning and nursery habitats overlapped, and (2) hydrological conditions maintained large spawning areas during the five first weeks of ontogeny and created large nursery area (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 (α). When fewer spawning habitat areas are available at the beginning of the free-swimming stage ($Week_5$), larval mobility (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 surface of connected spawning habitats by 14% (252 ha) (Online Resource 2). Finally, managed wetlands generated 463 ha (10 %) of total connected spawning habitat areas during the stable-high profile, 439 ha (12 %) during the increasing profile and 216 ha (11 %) during the decreasing profile.

Effective spawning habitats

Considering the latest Lake Saint-Pierre floodplain described (e.g. satellite images taken in 2014; Jobin and Dauphin in prep), from zero to 47% of the connected spawning habitats were not effective due to unsuitable land-use 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 (~11,000 $m^3.s^{-1}$) to high

(~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 surface of connected spawning areas 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-use during the stable-low profile.

Considering contemporary land-use 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, 3,218 ha, corresponding to 70% of the initial potential spawning area, were connected to nursery areas and were not modified by unsuitable land-use (= effective spawning habitats). During the stable-low profile, almost all the potential spawning areas were effective for northern pike recruitment (i.e. 2,549 ha or 91% of potential habitats). During the stable-high profile, similar potential spawning areas remained effective (i.e. 2,463 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-use have already been lost due to hydrological constrains on habitat connectivity. Although only 27% (1,628 ha) of the potential spawning habitats remained effective, only 15% (279 ha) of connected spawning habitats were altered by the land-use. 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 have major effects on the availability and the connectivity of habitats for early life history 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 the regions of the Lake Saint-Pierre most impacted by human alterations. To measure the effects of human pressures, it was first necessary to produce reference conditions representing an unaltered landscape and to assess the intrinsic natural variability of the river, which was accomplished by Foubert et al. (2018). In the present study, the modelling was carried out in a present-day landscape altered by two main human landscape pressures. Results revealed that water flow regulation in the river system and increasing agriculture in the floodplain significantly reduced the spawning habitats effectiveness of species such as northern pike that use the upper littoral zone of a river. Together, these two pressures dramatically reduced the range of natural conditions favourable to fish reproduction in the St. Lawrence River. The highest natural reproductive potential for northern pike, usually associated with high and stable water flows (Casselman and Lewis 1996; Johnson 1957), has been lost due to (1) intensive agricultural practices in the upper floodplain that overlaps with suitable natural habitats for fish, and (2) flow regulation that leads to more frequent drying of spawning grounds and egg mortality. These profound anthropogenic changes in the St. Lawrence River have resulted in a significant loss of reproductive potential for northern pike and other fish species that use the floodplain to complete their life cycle.

In a context of global climate change, where spring water discharge is expected to decrease and extreme hydrological conditions to increase in frequency (Boyer et al. 2010; Mortsch et al. 2000), 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-use changes and potential habitat loss

Changes in land-use have profoundly altered potential fish habitats in productive floodplains (e.g. Baber et al. 2002; Blanton and Marcus 2014; Fernandes et al. 2015). The Lake Saint-Pierre floodplain has been progressively occupied by agriculture. While in 1950 perennial crops dominated (≈ 45% cover, ≈ 21,000 - 22,000 ha) and annual crops accounted for only 10 to 15% of the territory (≈ 5,000 to 7,000 ha), the situation completely reversed in the 1990s since annual crops dominated, occupying 32% of the Lake Saint-Pierre (16,000 ha) compared to 15% (7,000 ha) for perennial crops. Although perennial crops (i.e. pasture and forage crops) can represent potential fish habitat, ploughing annual crops remove vegetation cover and create bare fields without substrate for egg laying in the next spring. The present study has shown that annual crops have negative effects on northern pike habitats especially when the water flow in Sorel 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-use 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 infrastructures (i.e. roads) have had impacts on 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 (3 758 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 larvae 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 9,200 $m^3.s^{-1}$ (Carpentier 2003), has now increased hydrological conditions generating large disconnected spawning areas in Lake Saint-Pierre (e.g. Brodeur et al. 2006). With the regulation of the Ottawa River, the duration of the flood has been shortened by three weeks and the maximum annual water discharge has decreased significantly by nearly 2,500 $m^3.s^{-1}$, a decrease exacerbated by the regulation of Lake Ontario outflows since 1958 (i.e. reduction of 1,020 $m^3.s^{-1}$; 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 (Ospina-Alvarez et al. 2012; Schiemer et al. 2001). 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 speeds in large floodplains favour dispersal of larvae to nurseries (Miehls and Dettmers 2011; Schiemer et al. 2003). 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 because they generate large areas of effective habitats (Gorski et al. 2011; Junk et al. 1989), 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 (4,665 ha), only 47% were effective when land-use was considered. The expansion of intensive agriculture, particularly annual crops, has profoundly altered spawning habitats that were previously connected to nurseries. Historically, 1,517 ha of these habitats were effective for northern pike during favourable hydrological conditions (i.e. stable-high profile represented by 1973). In addition, water flow regulation has dramatically reduced the frequency of these favourable hydrological conditions (see above) (Le Pichon et al. 2018), which have naturally generated large interconnected habitats. As a result, the possibility for stable-high hydrological profiles could produce high potentials for northern pike reproduction was rare and systematically eliminated by intensive agricultural practices, especially since 1990 (Martin and Létourneau 2011).

Under specific hydrological conditions, anthropized floodplains can still generate large effective spawning habitats. In Lake Saint-Pierre, 3,218 ha of effective spawning habitats were 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 habitats generated by medium water discharge were (1) not disconnected by hydrological variability during the increasing profile and (2) not altered by land-use activities in the upper floodplain. In addition, years of low water discharges are the less affected by intensive agriculture since they maintain their full habitat potential, although low. 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 vast potential spawning habitats for northern pike caused by intensive agricultural practices in the floodplain and flow regulation represents a serious constraint, as several fish populations show a significant decline in the St. Lawrence River. This study highlights important new opportunities to improve fish habitat and recruitment in major river systems such as the St. Lawrence River, and identifies the following priority management measures.

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. Gagliardi and Pettigrove 2013; Washitani 2007). Field crop conversions should target areas where large connected habitats are altered by annual crops such as the Saint-Barthélemy Bay (Fig. 2, Fig. 7).

Second, existing structures such as ditches and stream networks should be maintained as they represent effective fish habitats 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 infrastructures (roads) can limit connectivity in floodplains (Blanton and Marcus 2014; Doyle et al. 2008), structures such as culverts have proven to be useful in maintaining connectivity in anthropized floodplains (Douven et al. 2012; Le Pichon et al. 2018).

Third, managed wetland developed in the Lake Saint-Pierre floodplain show great potential for increasing the survival of early-life history 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.

Fourth, 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 rules 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. This type of rules revision 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 known and receive little consideration.

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Table and Figure captions

Tab.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 free-swimming stage (Foubert et al. 2018) in Lake Saint-Pierre (St. Lawrence River, Canada)

Tab.2 Dimensionless resistance values based on the restricting/facilitating effects of hydrological and land-use landscape characteristics on connectivity in downstream or upstream directions. 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)

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

Fig. 1 conceptual diagram that describes the methodological steps (in blue) leading to the main results (in black) of the study

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. Flooding surfaces of three contrasting spring water discharges (low, medium, high) were presented

Fig. 3 Temporal values of northern pike spawning and nursery habitats reconstructed for the period 1965-2013 in the unaltered (without agriculture) and the contemporary landscape (with agriculture) of Lake Saint-Pierre (St. Lawrence River, Canada). Potential spawning and nursery habitat surfaces (left y-axis) in the unaltered landscape have been adapted from Mingelbier et al. (2008) and Foubert et al. (2018) respectively. Remaining spawning and nursery habitat surfaces include losses generated by annual agricultural practices. Water discharge (right y-axis) is measured during the spawning time ($Week_0$) and five weeks later at the beginning free-swimming stage ($Week_5$). Temporal values of habitats (x-axis) were classified according to water discharges (from lowest to highest).

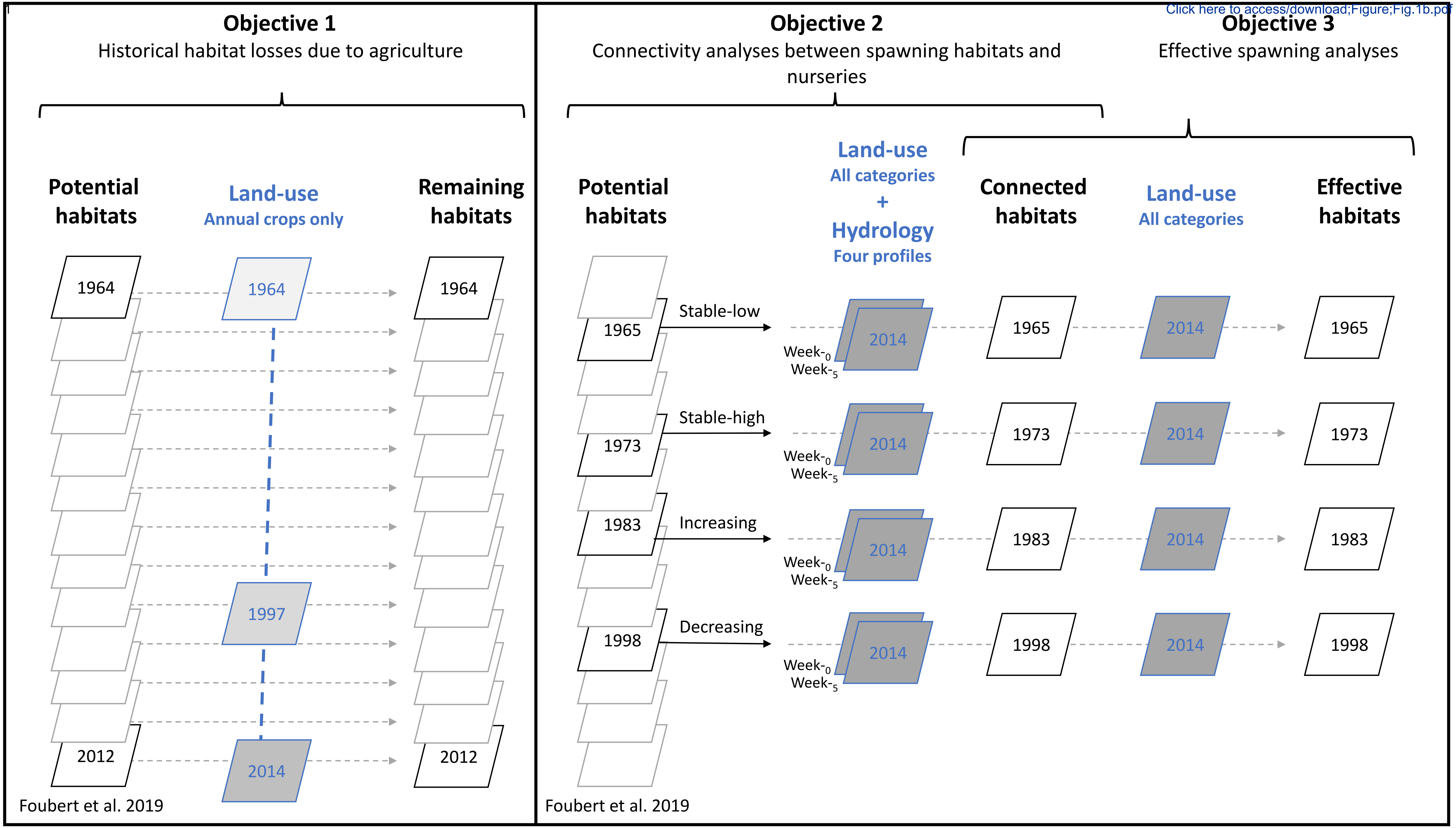
Fig. 4 Map of Lake Saint-Pierre (St. Lawrence River, Canada) showing the potential spawning and nursery habitats of the four hydrological profiles (stable-low, stable-high, increase, decrease). Wetlands managed for fish (black outlines) generated potential habitats when water discharge was medium to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

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 speeds, 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 $\alpha \leq 6000$ m $_{functional}$ (medium blue color), and (3) spawning habitats never connected to a nursery (functional distance > 6000 m $_{functional}$; 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)

Fig. 6 The connected spawning habitats were overlaid to the contemporary land-use 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)

Figure 1



Objective 1
Historical habitat losses due to agriculture
Potential habitats
Land-use
Annual crops only
Remaining habitats
1964
1964
1964
1997
2012
2014
2012
Foubert et al. 2019
Objective 2
Connectivity analyses between spawning habitats and nurseries
Objective 3
Effective spawning analyses
Potential habitats
Land-use
All categories
+
Hydrology
Four profiles
Connected habitats
Land-use
All categories
Effective habitats
1965
Stable-low
1973
Stable-high
1983
Increasing
1998
Decreasing
Week-0
Week-5
2014
1965
1973
1983
1998
Foubert et al. 2019

Figure 2

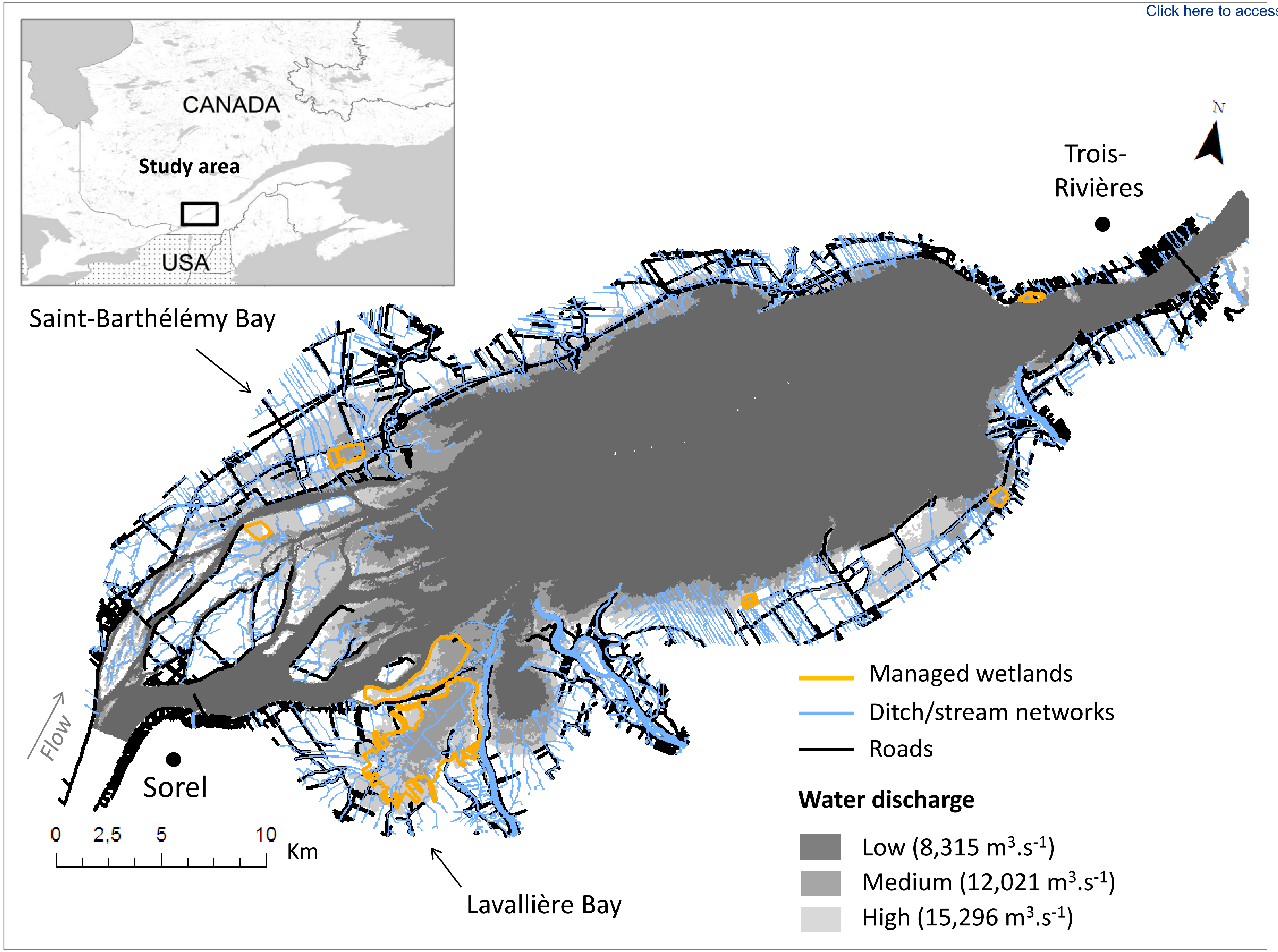

CANADA
Study area
USA
Saint-Barthélémy Bay
Trois-
Rivières
N
Flow
Sorel
0 2,5 5 10
Km
Lavallière Bay
Managed wetlands
Ditch/stream networks
Roads
Water discharge
Low (8,315 m3.s-1)
Medium (12,021 m3.s-1)
High (15,296 m3.s-1)

Figure 3

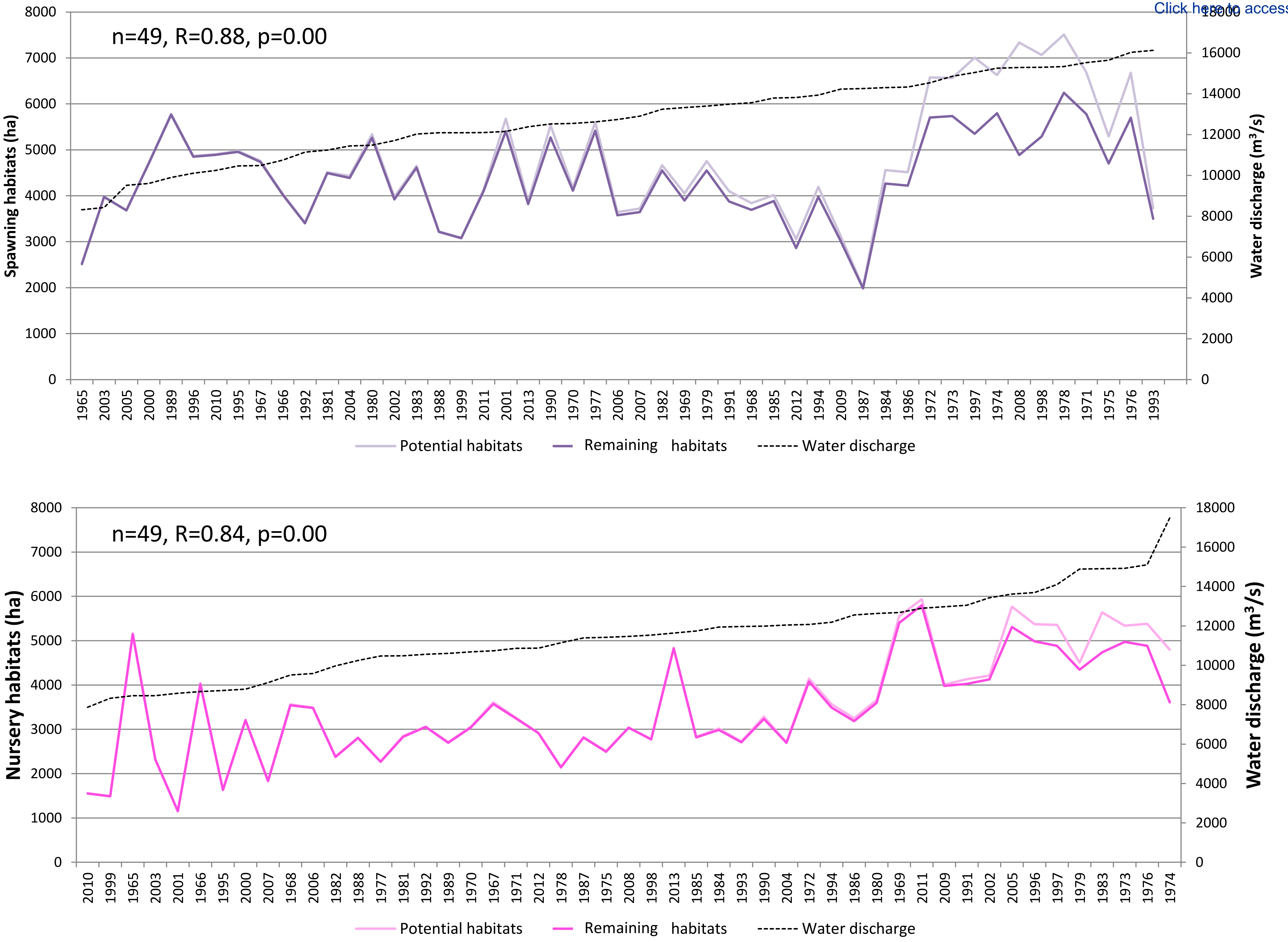
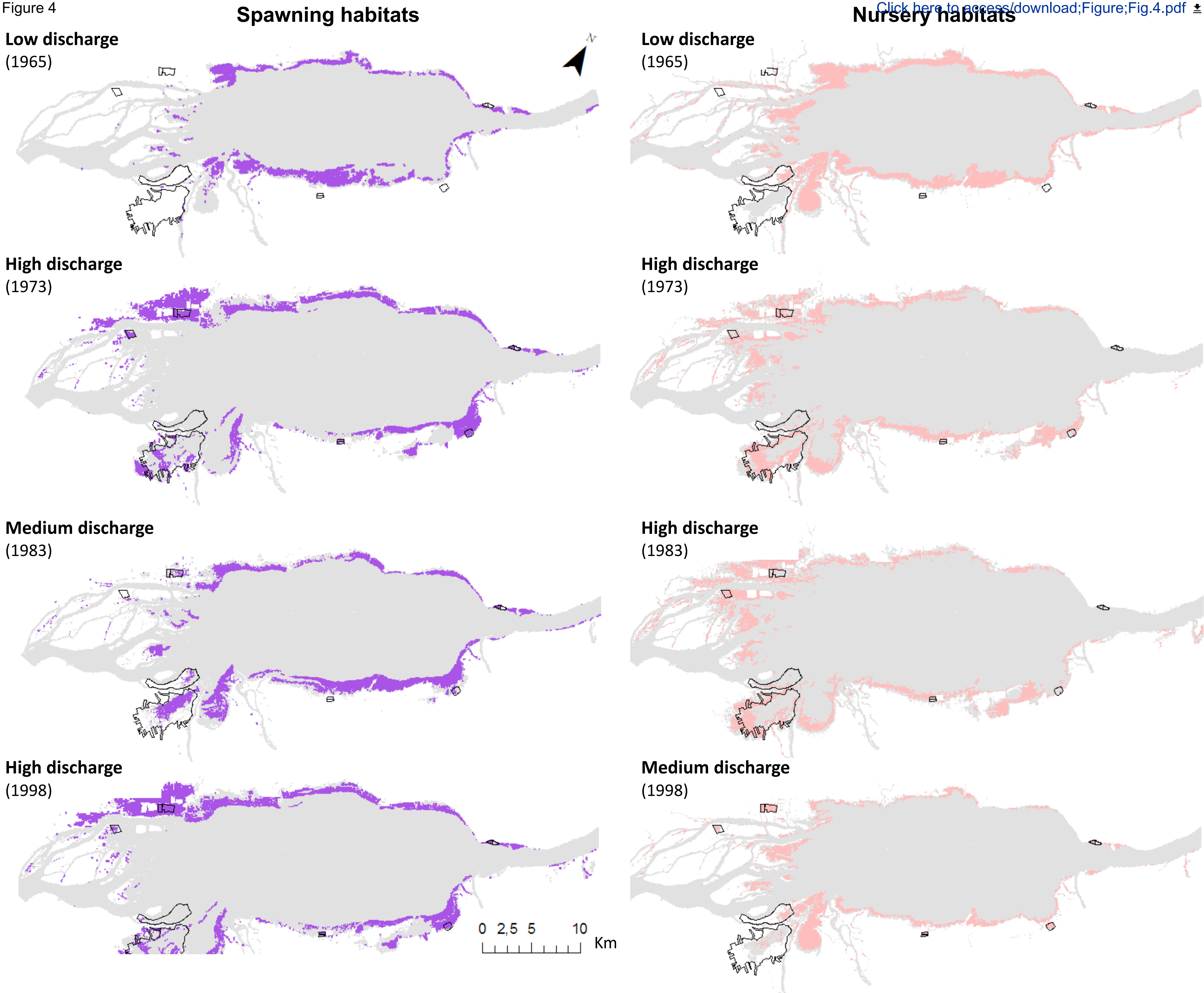

n=49, R=0.88, p=0.00
Spawning habitats (ha)
Water discharge (m³/s)
0 1000 2000 3000 4000 5000 6000 7000 8000
0 2000 4000 6000 8000 10000 12000 14000 16000 18000
1965 2003 2005 2000 1989 1996 2010 1995 1967 1966 1992 1981 2004 1980 2002 1983 1988 1999 2011 2001 2013 1990 1970 1977 2006 2007 1982 1969 1979 1991 1968 1985 2012 1994 2009 1987 1984 1986 1972 1973 1997 1974 2008 1998 1978 1971 1975 1976 1993
Potential habitats
Remaining habitats
Water discharge
n=49, R=0.84, p=0.00
Nursery habitats (ha)
Water discharge (m³/s)
0 1000 2000 3000 4000 5000 6000 7000 8000
0 2000 4000 6000 8000 10000 12000 14000 16000 18000
2010 1999 1965 2003 2001 1966 1995 2000 2007 1968 2006 1982 1988 1977 1981 1992 1989 1970 1967 1971 2012 1978 1987 1975 2008 1998 2013 1985 1984 1993 1990 2004 1972 1994 1986 1980 1969 2011 2009 1991 2002 2005 1996 1997 1979 1983 1973 1976 1974
Potential habitats
Remaining habitats
Water discharge

Figure 4



Spawning habitats
Nursery habitats
Low discharge
(1965)
Low discharge
(1965)
High discharge
(1973)
High discharge
(1973)
Medium discharge
(1983)
High discharge
(1983)
High discharge
(1998)
Medium discharge
(1998)
N
0 2,5 5 10
Km

Figure 5

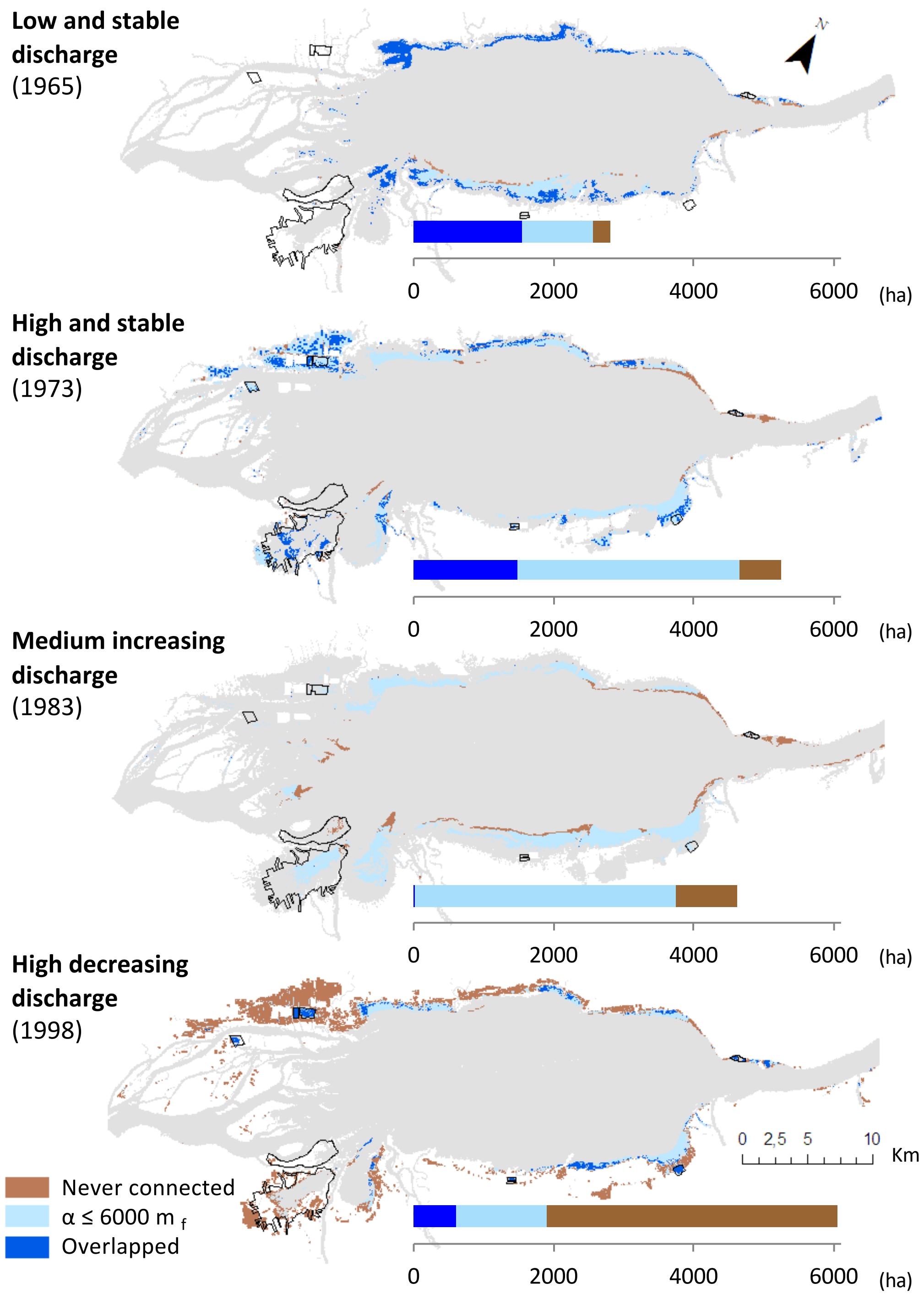

Low and stable discharge (1965)
0
2000
4000
6000
(ha)
High and stable discharge (1973)
0
2000
4000
6000
(ha)
Medium increasing discharge (1983)
0
2000
4000
6000
(ha)
High decreasing discharge (1998)
0 2,5 5 10
Km
Never connected
α ≤ 6000 m f
Overlapped
0
2000
4000
6000
(ha)

Figure 6

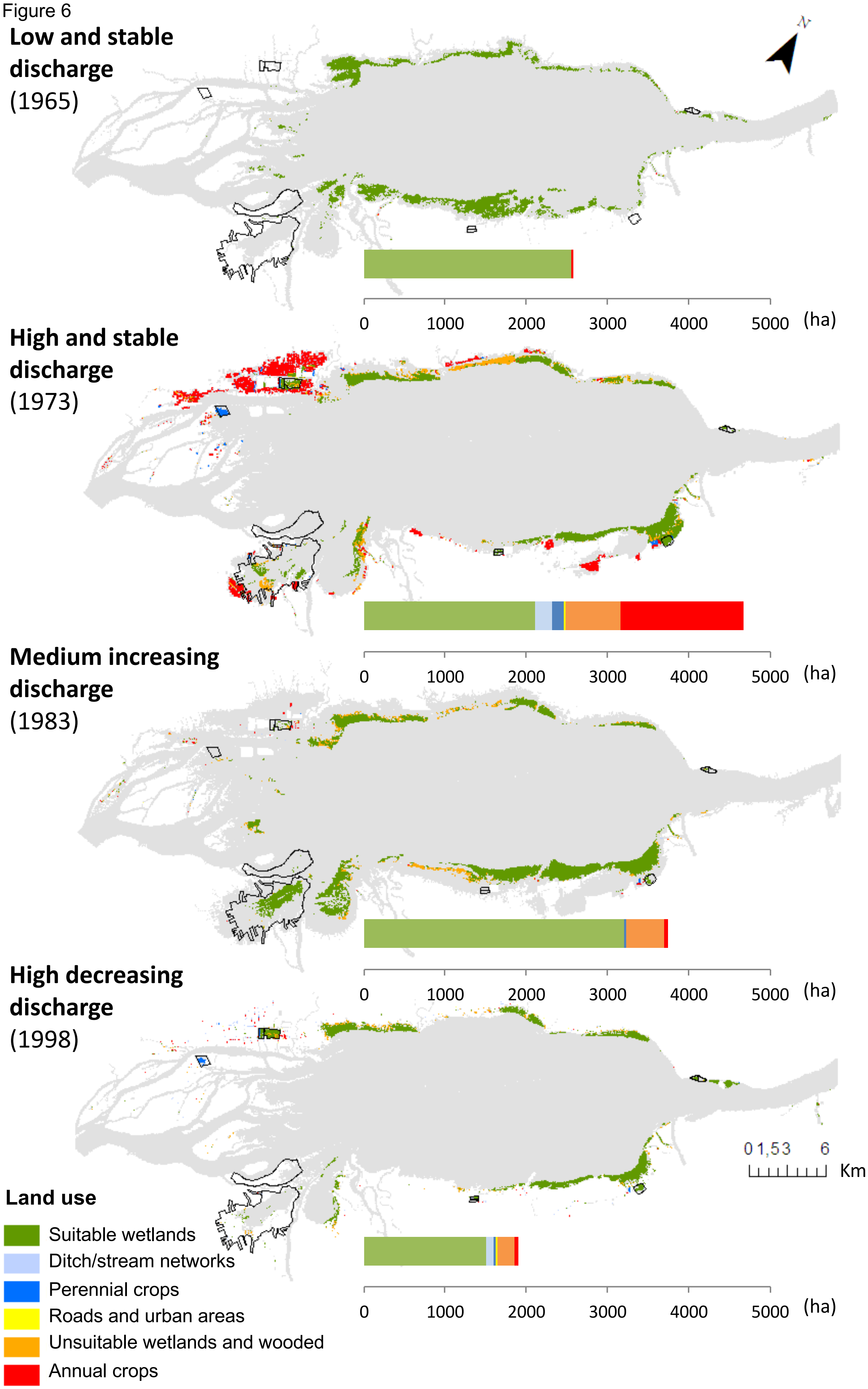
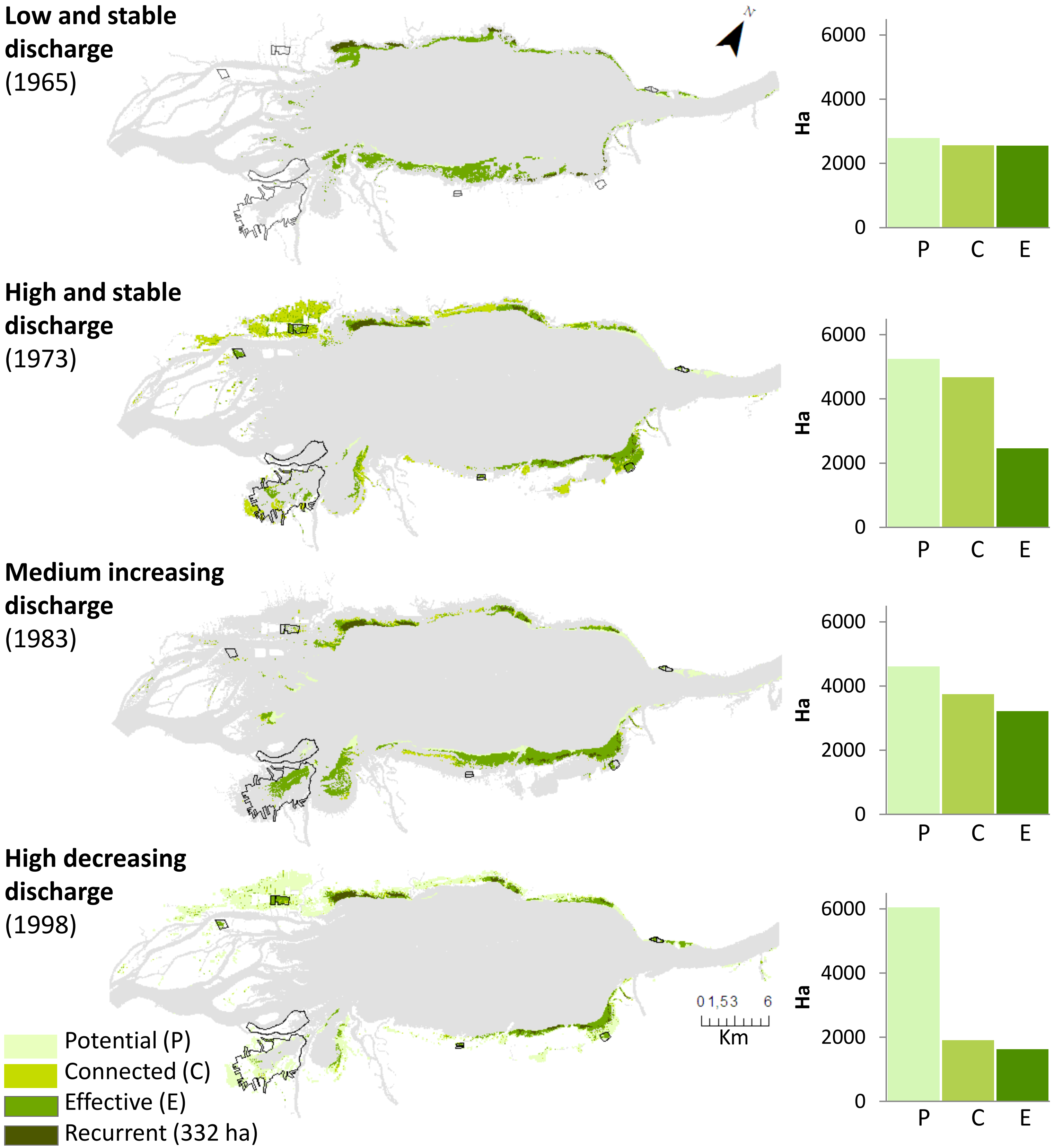

Low and stable discharge (1965)
High and stable discharge (1973)
Medium increasing discharge (1983)
High decreasing discharge (1998)
0
1000
2000
3000
4000
5000
(ha)
0 1,5 3 6
Km
Land use
Suitable wetlands
Ditch/stream networks
Perennial crops
Roads and urban areas
Unsuitable wetlands and wooded
Annual crops

Figure 7


Low and stable discharge
(1965)
High and stable discharge
(1973)
Medium increasing discharge
(1983)
High decreasing discharge
(1998)
Potential (P)
Connected (C)
Effective (E)
Recurrent (332 ha)
0 1,5 3 6
Km
Ha
6000
4000
2000
0
P
C
E

Flow profiles	Water discharge ($m^3.s^{-1}$)	Flooded surface (ha)	Potential habitat surface (ha)
Stable-low (1965)			
Spawning habitats - $Week_0$	Low (8,315)	41,768	**2,794**
Nursery habitats - $Week_5$	Low (8,455)	44,731	**5,107**
Stable-high (1973)			
Spawning habitats - $Week_0$	High (14,853)	57,800	**5,242**
Nursery habitats - $Week_5$	High (14,920)	58,868	**5,047**
Increasing (1983)			
Spawning habitats - $Week_0$	Medium (12,021)	49,455	**4,608**
Nursery habitats - $Week_5$	High (14,905)	62,099	**5,277**
Decreasing (1998)			
Spawning habitats - $Week_0$	High (15,296)	59,407	**6,045**
Nursery habitats - $Week_5$	Medium (11,532)	46,551	**3,019**

Landscape feature		Downstream resistance	Upstream resistance
Water depth ≤ 0 m		10,000	10,000
Current speeds ($cm^3.s^{-1}$)	Speed > 0 ≤ 2	1	1
	Speed > 2 ≤ 4	0.3333	10,000
	Speed > 4 ≤ 6	0.2000	10,000
	Speed > 6 ≤ 8	0.1429	10,000
	Speed > 8 ≤ 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

Table 3

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	**2,794**	4	223	2	0	**229** [8%]	5	0	0	**5** [0.2%]	**2,560**
Stable-high	**5,242**	51	262	100	26	**439** [8%]	110	28	0	**138** [3%]	**4,665**
Increase	**4,608**	2	772	8	0	**782** [17%]	82	0	0	**82** [2%]	**3,744**
Decrease	**6,005**	3,758	61	117	66	**4,002** [66%]	72	0	25	**97** [2%]	**1,906**

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To: **Landscape Ecology**

Dear Editors,

Please find enclosed a paper by Aline Foubert, Frédéric Lecomte, Philippe Brodeur, Céline Le Pichon and Marc Mingelbier entitled "**Losing the best conditions for effective fish spawning habitat in the floodplain due to riparian agriculture and flow regulation, St. Lawrence River, Canada**". This paper presents original findings not published nor being submitted for publication elsewhere. All co-authors have contributed significantly to the present work and agreed for submitting the manuscript to Landscape Ecology. The manuscript was proofread by a colleague who is a native English speaker. We accept to pay for the extra costs for producing the colour figures included in the manuscript.

"Riverscape" ecology, a new emerging concept applying landscape ecology fundamentals to the aquatic realm, proposes to consider the riverine ecosystems as a continuum where spatio-temporal dynamics had to be quantified along its course, including areas impacted by humans. Holistic, spatially explicit approaches are now considered as a prerequisite for defining guiding principles for inland fisheries and watershed management.
The present manuscript quantifies how anthropogenic alterations, such as riparian agriculture and water flow regulation, have impacted the effectiveness of spawning habitats of northern pike (*Esox lucius*) in a large floodplain: the fluvial Lake Saint-Pierre (St. Lawrence River, Canada). Combining GIS-Based habitat modelling covering a 49-years period (1965-2013) to historical land-use analyses and least-cost modelling of the aquatic connectivity allowed the present study to identify a paradigm shift in the relationship between flow conditions and pike recruitment. The highest potential for reproduction, usually associated with high and stable water flows, has been lost due to (1) the intensive agriculture in the upper floodplain that overlaps with suitable spawning habitats and nursery grounds for fish, and (2) the flow regulation that generates more frequent extreme events leading to the complete drying of spawning grounds. Our results convey important implications for fisheries management and conservation; maps identifying the most rewarding areas for restoration are now available for managers. Such information is mandatory for initiating incentive aimed at farmers to convert their use of the floodplain: from cultivating annual crops toward planting perennial crops. Moreover, the present findings stresses the need to update the Lake Ontario – St. Lawrence River flow regulation used by the International Joint Commission (IJC), a commission established between the United States and Canada to regulate water levels of shared water bodies.

Best regards,

Céline Le Pichon

Potential appropriate reviewers

Anne Timm, altimm@fs.fed.us, land use and aquatic habitat connectivity
John Farrell, jmfarrell@esf.edu , pike
Françoise Burel francoise.burel@univ-rennes1.fr, landscape spatial dynamics and permeability to movement
Isabelle Durance, durance@cardiff.ac.uk, role of landscape processes in driving freshwater ecosystems

Current members of the Editorial Board to potentially handle the manuscript.

M. Bélisle, *University of Sherbrooke, Sherbrooke, Canada (connectivity)*
G. Cumming, *James Cook University, Townsville, Australia (aquatic habitat:coral reef)*
S.S. Luque, *National Research Institute of Science and Technology for Environment and Agriculture (IRSTEA), St-Martin d'Hères Cedex, France (GIS-based spatial analysis)*

Supplementary material 1

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Supplementary material
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Supplementary material 2

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