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Differences in movements of northern pike inhabiting rivers with contrasting flow regimes

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ABSTRACT

Little is known about the effect of short-term flow changes on the movement of northern pike (*Esox lucius* L.). We conducted a comparative study in two rivers with different flow regimes (i.e. one regulated and one unregulated) to evaluate the extent to which adult northern pike movement is influenced by short-term river flow conditions. Data on northern pike hourly movement were collected in northeastern Ontario on 40 individuals in the Mississagi River, a river subjected to extreme daily flow variations associated with hydro-electric operations (i.e. hydropeaking), and the Aubinadong River, an unregulated river. Using manual tracking by radio-telemetry, we found that northern pike moved at a higher rate in the river subjected to short-term changes in river flow than in the unregulated river. Results also show that the relationship between movement of northern pike and flow can vary among rivers. In the Mississagi River, flow had a significant positive effect on northern pike activity, while the effect of flow in the Aubinadong River depended on water temperature. Moreover, fish in the Mississagi River utilized a restricted river section and travelled more laterally in comparison to fish inhabiting the Aubinadong River, where longer upstream-downstream movements were more common. The present study contributes to our understanding of the effects of short-term changes in flow on fish movement. This constitutes the first step towards assessing the effect of flow on fish habitat use, and eventually developing flow management strategies to mitigate impacts on fish. Copyright © 2016 John Wiley & Sons, Ltd.

KEY WORDS fish movement; flow; telemetry; northern pike

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INTRODUCTION

Fish movement is one of the most important behaviours and determines habitat selection, foraging efficiency, and predator avoidance (Schreck *et al.*, 1997; Kahler *et al.*, 2001). Fish movement is the individual displacements over short distances between resting, hiding, and foraging habitats, happening within the fish home range (McMahon and Matter, 2006; Jacobson and Peres-Neto, 2010). Movement therefore acts as a key mechanism by which fish maximize fitness endpoints such as growth, survival, and reproductive success (Scherer, 1992; Schreck *et al.*, 1997; Barton *et al.*, 2002).

Short-term (i.e. minutes to hours) flow changes in rivers lead to dynamic environmental conditions that have long been known to modify fish habitats (Valentin *et al.*, 1996; Scruton *et al.*, 2003; Hillyard and Keeley, 2012). Fish have been hypothesized to cope with these short-term flow changes by moving rapidly from an original habitat to a relocated habitat of a presumed similar suitability, thereby increasing their travel rate as flow fluctuates (Taylor *et al.*, 2014*a*). Studies that attempted to test the effect of short-term flow changes on fish movement, hereafter referred to as the 'mobility hypothesis', reached different conclusions. Movement of adult striped bass (*Morone saxatilis*) in the tailwater of a hydroelectric facility was significantly increased during elevated flow (Young and Isely, 2007), and bull trout (*Salvelinus confluentus*) swimming muscle activity was significantly related to the hourly mean flows ranging from 0 to $1770\,\mathrm{m}^3\cdot\mathrm{s}^{-1}$ (Taylor *et al.*, 2014*b*). In contrast, Enders *et al.* (2008) and Robertson *et al.* (2004) found no such relationship for Atlantic salmon (*Salmo salar*) in rivers where flow ranged from 0.3 to $7.9\,\mathrm{m}^3\cdot\mathrm{s}^{-1}$, and from 1.3 to $5.2\,\mathrm{m}^3\cdot\mathrm{s}^{-1}$ respectively. A number of elements (e.g. fish species or life-stage, sampling scale, river geomorphology, and flow regime) may explain the range of conclusions reached by different studies. It has also been shown that flow can affect fish movement patterns. The home range of European grayling (*Thymallus thymallus*) increased with elevated flow in a Czech Republic river (Horká *et al.*, 2015),

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and lateral movements performed by the whole fish community of an Australian stream happened mainly during flow increases (Lyon *et al.*, 2010). One element common to most studies is that they fail to include non-regulated 'control' rivers, which makes the among-river comparisons challenging (Taylor and Cooke, 2012).

Northern pike (*Esox lucius* L.) is a common freshwater top predator found in lakes, rivers, and brackish marine waters of the northern hemisphere (Craig, 2008). Northern pike prefer to use slow water velocity habitat where they can ambush their prey and capture them using brief anaerobic bursts (Raat, 1988; Savino and Stein, 1989). For that reason, pike can be more sensitive to flow fluctuations than species that prefer faster water velocities (Hontela *et al.*, 1997). In accordance with the recognized sensitivity of pike to flow, the few studies that investigated the effect of flow on pike's seasonal and daily movement suggest that hourly movement could be affected by hourly flow changes. Masters *et al.* (2003) observed that extensive upstream movement of two tagged pike in the river Frome, UK, coincided with a three-fold increase in river flow, and Pauwels *et al.* (2014) found that the daily distances travelled by males were significantly and negatively affected by river flow.

Flow regime of regulated rivers characterized by short term (i.e. hourly) and drastic (e.g. 20-fold increase) flow changes affect a long suite of environmental variables such as dissolved oxygen (Calles *et al.*, 2007), water temperature regime (Hillyard and Keeley, 2012), wetted width, water depth and velocity (Zhong and Power, 1996), substrate composition and distribution (via different erosion and sedimentation patterns; Osmundson *et al.*, 2002), and aquatic plant diversity and abundance (Aronsuu *et al.*, 1999). A number of these environmental variables and their interactions, all related to the flow regime, may affect fish movement in rivers. It is therefore impossible to isolate the effect of a single variable on fish movement among rivers that differ in flow regimes. However, it is possible to assess the extent to which fish movement may vary between rivers possessing different flow regimes. Radio-telemetry is now a common tool in fisheries assessment and management (Cooke *et al.*, 2016) and provides opportunity for tracking the spatial ecology of wild fish in riverine systems (Cooke *et al.*, 2013). Consequently, the objectives of the present study, focusing on adult pike during the summer, were: (1) to examine the inter-river differences in distance travelled by northern pike ($m \cdot h^{-1}$) in two rivers with different flow regimes; (2) to assess the 'mobility hypothesis' in these two rivers by examining the intra-river relationships between flow and the distance travelled by northern pike; (3) to compare the longitudinal range, the preferred movement type (longitudinal or lateral), and the lateral travel rate performed by northern pike in the two study rivers. The present study is unique because it compares fish movements in a regulated river to fish movements in an unregulated river located nearby.

MATERIAL AND METHODS

Study rivers

The study was conducted in the Mississagi River and the Aubinadong River of northeastern Ontario, Canada (Figure 1). The study area (46°54′N, 83°16′W) on the Mississagi River is a 2 km river portion (width range: 80–180 m), located 5 km downstream of a hydroelectric facility (Aubrey Falls Dam, average daily flow = $38\,m^3 \cdot s^{-1}$) built in 1969. The hourly flow in this study area can vary drastically within 3–4 h (range: 6 – $307\,m^3 \cdot s^{-1}$; Harvey-Lavoie, S., unpublished data). Such important and sudden flow changes related to hydropower production are referred to as 'hydropeaking'. Hourly flow data (from 2004 to 2014; Brookfield Renewable Power, Ontario) has shown that, for this period of time, the operation strategy has been consistently hydropeaking, with minor seasonal differences. The Aubinadong River (46° 55′N, 83° 26′W) is an unregulated river that flows into the Mississagi River 13 km downstream of Aubrey Falls Dam (Figure 1). The study area in the Aubinadong River is an 18 km river portion (width range: 20–115 m) that has an average daily flow of $15\,m^3 \cdot s^{-1}$ (range: 2–$120\,m^3 \cdot s^{-1}$). The two study areas, one on the Mississagi River and one on the Aubinadong River, were selected based on their accessibility by canoe and their similar altitude, morphology, fish density (Table I), and fish community (14 species being present in the Aubinadong River and 13 in the Mississagi River, with only blacknose dace [*Rhinichthys atratulus*] being absent from the latter; Macnaughton *et al.*, 2015). Both study areas have natural habitats in terms of riverbanks (i.e. presence of natural substrate, aquatic plants, and logs), natural sinuosity, and highly variable depths and flow velocities, both spatially and temporally. There are also numerous side channels, side pools, riffle and run sequences, and small bays, in addition to the main channel. Fish captures on the Aubinadong River were situated at least 3 km upstream from its junction with the Mississagi River, thus minimizing the probability that our data include fish travelling between both rivers. During the study period, the average hourly flow was 2.4 times higher in the Mississagi River (11.8–$258.6\,m^3 \cdot s^{-1}$; average $42.7\,m^3 \cdot s^{-1}$) than in the Aubinadong River (9–$24\,m^3 \cdot s^{-1}$; average $17.9\,m^3 \cdot s^{-1}$). In the former, flow was overall low in the morning (11.8 to $13.0\,m^3 \cdot s^{-1}$; average $11.9\,m^3 \cdot s^{-1}$; 9:00 to 12:00 h) and higher at night (14.6 to $258.55\,m^3 \cdot s^{-1}$; average $87.2\,m^3 \cdot s^{-1}$; 17:00 to 21:00 h); a pattern absent from the Aubinadong River (Figure 2). Water temperatures of the studied rivers were very similar during the tracking period (Mississagi River: average 18.6 °C, range 12 – 25 °C; Aubinadong River: average 18.8 °C, range 13 – 26 °C).

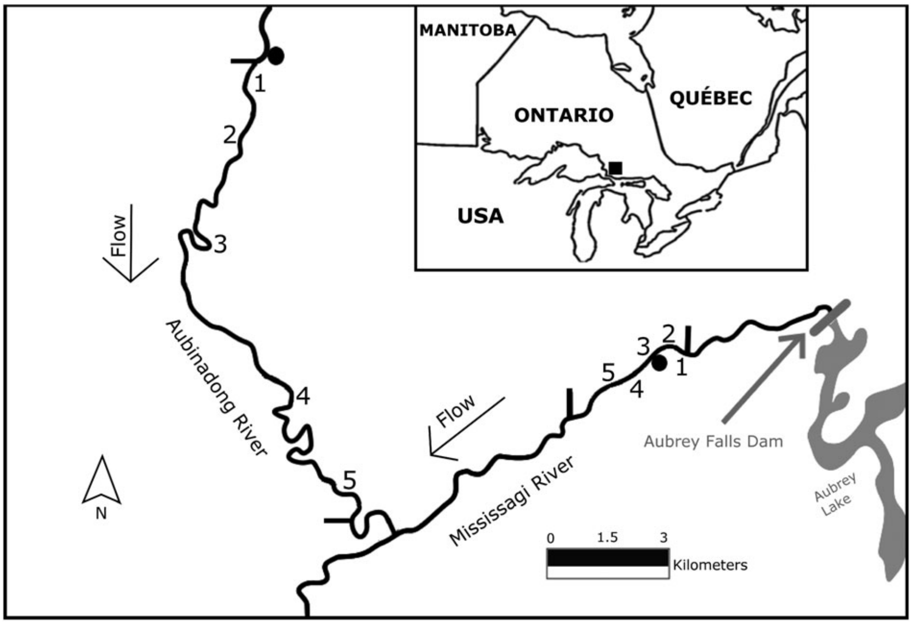

Figure 1. Map of the study rivers (the Mississagi and Aubinadong rivers; Northeastern Ontario, Canada). The black square on the inset map represents the location of the rivers in Canada. The filled black circles on the large map are the flow gauges, and the river portion in-between the two dashes, on each river, represent the area where fish tracking took place. The numbers corresponds to pike catch location on each river in Table II.

Table I. Watershed area, altitude, hydrology, morphology, and fish density of the unregulated river (Aubinadong River) and the regulated hydropeaking river (Mississagi River) at two levels: watershed and study reach.

Level		River and regulation type	
		Mississagi Hydropeaking	**Aubinadong Unregulated**
Watershed	Drainage basin area (km^2)	4152.2	1580.5
	Drainage density (km/km^2)	0.1088	0.1317
	Median basin elevation (meters above sea level)	455	484
	Maximum basin elevation (meters above sea level)	590	607
	Basin slope (mean; %)	5.7	8.9
	Basin slope (SD)	4.2	5.8
	Total precipitation (1961–1990; mm/year)	906	973
Study reach	Fish density (fish/m^2)	0.1370	0.1755
	Mean daily flow (m^{3}s^{-1})	38	15
	Slope (m/m)	0.0007	0.0009
	Width (range in m)	80–180	20–115
	Mean annual flood (m^{3}s^{-1}; months of April and May)	29	38

Fish capture and tagging

Fish capture and tagging took place between 12 June and 6 July 2013 (Table II). We collected 91 northern pike (Mississagi River = 56, Aubinadong River = 35) by angling, from a canoe or from the shore, using barbless artificial lures and nylon lines (4.5 kg test; Figure 1). Fish were reeled in, captured using a dip net, and placed in an insulated container (990 × 480 × 480 mm) filled with well-aerated river water. The lure was removed while fish remained in the water, thus ensuring minimal handling stress and a quick recovery (Arlinghaus *et al.*, 2009). Total length can have a positive effect on pike movement (Vehanen *et al.*, 2006), and in order to minimize this effect, 40 adult fish with a total length of 440–655 mm were kept for the radio-telemetry. The remaining 51 fish were used to develop a length–weight relationship. Total fish mass (g wet blotted weight), total length (TL, in mm), and sex (Casselman, 1974) were recorded. Movements were quantified by radio-telemetry, using externally attached individually coded transmitters (3.2 g in air, 25 × 13 × 6 mm, 120 mm antenna, battery life 6 months, 3 s pulse interval; Model PD-2, Holohil Systems Inc., Carp,

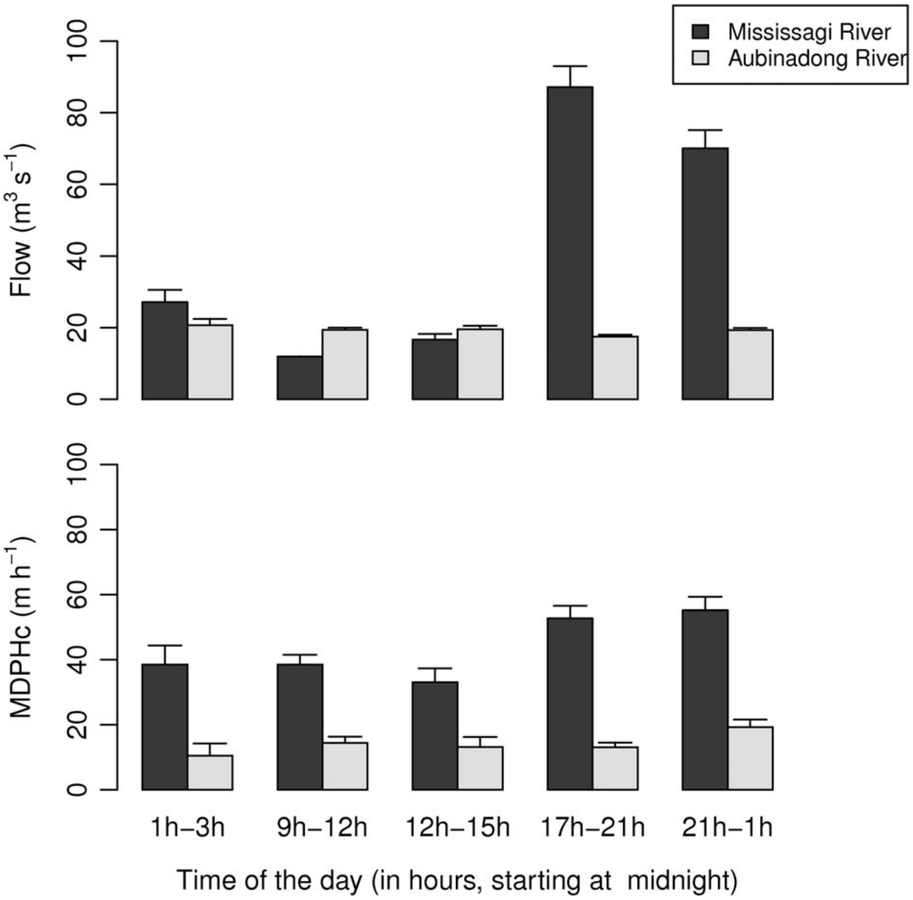

Figure 2. The flow (mean + standard error; $m^3 \cdot s^{-1}$) and the $MDPH_C$ (mean + standard error; $m \cdot h^{-1}$) of northern pike in the Mississagi River (hydropeaking) and the Aubinadong River (unregulated), with respect to the time of the day.

ON, Canada), following the method described by Arlinghaus *et al.* (2009). The external attachment method was rapid (few minutes) and does not require the use of anaesthetics, which necessitates a long recovery and clearing period (i.e. few hours; Cooke, 2003). External tagging is a suitable and commonly used method for esocids (Arlinghaus *et al.*, 2009; Landsman *et al.*, 2011; Colotelo *et al.*, 2013) in short-term studies (few months). The relative mass of the transmitters was ≤0.6% of fish body mass. Fish were released within 5–10 min of capture.

Fish tracking

Fish were tracked between 10 July and 16 August 2013, alternating between the two rivers on a daily basis. There was therefore at least 4 days between the tagging (12 June to 6 July 2013; Table II) and the onset of tracking. A study by Arlinghaus *et al.* (2009) showed that, following a capture by angling, pike recovered and resumed their normal behaviour within 24 h post-release. In addition, a study by Cooke (2003) showed that the attachment of external radio-transmitters did not affect the 1 h or 24 h post tagging parental care behaviour of rock bass (*Ambloplites rupestris*). Given these findings, the time interval of a minimum of 4 days between tagging and tracking was deemed sufficient for fish to recuperate and resume their normal behaviour. Tracking was performed at two different time periods by two different teams: in the morning (05:00 to14:00) and at night (17:00 to 02:00). Individual fish positions were therefore estimated at approximately 8-h intervals. This strategy was adopted because flow variations in the study rivers did not present noticeable short-term periodicities (1 h to few hours) during the day (9:00–17:00). However, in Mississagi River, because of hydropeaking happening at night (17:00–1:00), flow was consistently at its lowest at *ca* 09:00 and at its highest at *ca* 21:00. No such periodicities were noticeable in Aubinadong River. An 8-h interval to assess fish positions was therefore considered sufficient to achieve our objective to assess the effect of flow variations on fish movement. Teams were assigned to either the morning or night shifts, and switched halfway through the sampling period (*ca* two weeks), thereby minimizing potential team bias. Fish positions were determined using a portable radio-receiver equipped with a three-element Yagi antenna (Lotek SRX

Table II. Fish ID code, longitudinal range, sex, mass, length, date tagged, catch location, number of all observations, mean of $MDPH_C$ for all observations, number of observations for travel time ≤ 24 h, and mean of $MDPH_C$ for travel time ≤ 24 h for every fish from both the hydropeaking Mississagi River and the unregulated Aubinadong River.

River	Fish ID	Longitudinal range (m)	Sex	Mass (g)	Length (mm)	Date tagged (all in 2013)	Catch location (Figure 1)	Number of all observations	$MDPH_C$ all observations mean (range)	Number of observations for travel time ≤ 24 h	$MDPH_C$ for travel time ≤ 24 h mean (range)
Aubinadong	A1	5660	Male	756	512	14-Jun	1	26	21.3 (1–99)	16	15 (2–36)
	A2	971	Female	689	511	14-Jun	1	30	8.8 (1–43)	19	9.4 (1–19)
	A3	1053	Female	670	499	14-Jun	1	22	5.8 (1–17)	13	6.7 (1–17)
	A4	942	Female	763	523	15-Jun	1	28	12.8 (1–115)	18	7.8 (1–60)
	A5	193	Female	670	494	15-Jun	1	30	7.5 (1–29)	19	8.6 (1–27)
	A6	1041	Male	959	562	21-Jun	3	27	32.0 (1–115)	16	17.3 (2–71)
	A7	704	Male	1420	614	22-Jun	4	3	31.3 (6–51)	2	21.5 (6–37)
	A8	1182	Female	1296	645	22-Jun	4	8	14.8 (5–42)	3	9.7 (5–17)
	A9	136	Female	1244	570	24-Jun	1	30	10.7 (1–26)	19	13.8 (3–26)
	A10	7292	Female	1313	610	24-Jun	5	21	26.7 (2–117)	14	15.3 (2–51)
	A11	1420	Female	619	463	25-Jun	2	24	23.6 (2–57)	15	25.8 (2–54)
	A12	5626	Male	1631	655	25-Jun	4	2	66.5 (11–122)	1	11 (–)
	A13	Missing	Male	1581	655	03-Jul	4	0	—	0	—
	A14	2353	Female	760	489	03-Jul	4	10	40.4 (4–165)	6	22.7 (4–37)
	A15	Missing	Male	1142	553	04-Jul	5	0	—	0	—
	A16	486	Female	1126	578	04-Jul	5	11	32.8 (8–71)	5	40.2 (8–71)
	A17	Missing	Male	702	482	04-Jul	5	0	—	0	—
	A18	Missing	Male	1205	563	04-Jul	5	0	—	0	—
	A19	6199	Female	750	475	05-Jul	5	6	34.7 (8–70)	4	23.5 (8–55)
	A20	7939	Male	950	578	06-Jul	1	27	21.1 (2–75)	18	16.6 (2–35)
Mississagi	M1	689	Male	1101	556	12-Jun	2	29	60.4 (11–261)	18	53.8 (11–145)
	M2	489	Female	1532	635	12-Jun	1	27	50.4 (4–188)	15	52.5 (15–126)
	M3	413	Male	1419	610	12-Jun	5	31	57.0 (6–317)	19	57.0 (6–317)
	M4	672	Male	1199	581	12-Jun	5	31	64.1 (2–203)	19	64.1 (3–177)
	M5	305	Female	1228	593	13-Jun	2	27	53. 9 (4–171)	16	57.8 (4–171)
	M6	273	Male	1169	598	13-Jun	3	31	55.3 (13–120)	19	55.5 (13–120)
	M7	397	Male	1298	622	13-Jun	5	30	48.2 (4–144)	18	54 (11–144)
	M8	232	Female	1204	573	13-Jun	1	28	46.4 (11–141)	16	46.4 (11–141)
	M9	611	Female	526	440	15-Jun	2	9	42.3 (6–103)	4	30.5 (16–51)
	M10	559	Female	588	467	09-Jul	1	29	36.3 (5–179)	17	31.5 (5–94)
	M11	205	Female	677	481	16-Jun	2	31	34.7 (4–91)	19	38.8 (6–91)
	M12	293	Female	659	474	17-Jun	2	27	47.1 (8–137)	15	40.9 (9–137)
	M13	305	Male	1325	609	17-Jun	3	31	50.5 (3–169)	19	53.2 (3–169)
	M14	342	Male	631	471	17-Jun	4	27	35.6 (3–100)	15	41.4 (10–100)
	M15	800	Female	677	483	17-Jun	1	23	70.4 (3–155)	13	67.2 (5–155)
	M16	521	Female	1232	577	19-Jun	3	28	76 (4–210)	16	61.1 (4–210)
	M17	523	Male	1474	613	19-Jun	5	27	65.9 (9–135)	16	58.3 (10–135)
	M18	436	Female	595	475	20-Jun	2	33	22.8 (2–52)	21	23.5 (2–49)
	M19	133	Male	1349	574	20-Jun	3	28	44.8 (3–162)	19	49.1 (4–162)
	M20	176	Female	1199	586	20-Jun	1	26	20.4 (5–54)	15	24.6 (7–54)

400 Telemetry Receiver, Lotek, Ontario, Canada). Pike were tracked from a canoe using the successive gain reduction technique, which consists in beginning with an elevated receiver gain and gradually decreasing it while approaching the source of the signal to pinpoint the location of the fish (Taylor *et al.*, 2014a). Using this technique, pike could be approached within 2 m without inducing a fleeing response, a distance also reported by Klefoth *et al.* (2008) and Kobler *et al.* (2008). Repeated tracking of hidden transmitters placed at different locations in the river revealed a precision of our tracking method of ±5 m. The geographic coordinates of fish positions were recorded using a handheld GPS instrument (Garmin 76sc, USA) with a precision of ±5 m. Water temperature (°C; Traceable thermometer, ThermoFisher Scientific, USA), date, and time were also recorded at each fish position. Hourly flow was recorded by a gauging station (Figure 1) in the Mississagi River ($\text{m}^3 \cdot \text{s}^{-1}$; Harvey-Lavoie, S., unpublished data) and the Aubinadong River (Survey of Canada, http://wateroffice.ec.gc.ca/). All fish tagged in the Mississagi River remained in the study area, but four of the fish tagged in the Aubinadong River were never located (Table II). The 36 fish were located 0–2 times every session, which resulted in 0–4 positions per fish per day, and 2–33 positions per fish over the complete duration of the study (Table II). A total of 858 fish positions were obtained (Mississagi: 553 positions; Aubinadong: 305 positions). The tendency of fish from the Aubinadong River to occupy more distant positions in the river, and to preferentially perform longitudinal movements is consistent with the loss of four tagged fish, and the small number of observations in this river.

Data exploration and analyses

The distance travelled per hour was estimated using the minimum distance (m) between two consecutive positions of the same fish. We assessed the shape of the relationship between the distance travelled and the time elapsed between two consecutive observations performed on the same fish. The time elapsed between consecutive fish observations was highly variable (from 3 to 105 h); therefore, the distance travelled had to be standardized with respect to travel time (e.g. in $\text{m} \cdot \text{h}^{-1}$). Because the relationship must have an intercept of 0 (travelled distance must be exactly 0 when the travel time is exactly 0), and in order to account for the possibility of a non-linear relationship, we modelled the relationship between travelled distance (D; m) and travel time (ΔT; h) as a power relationship with constants a and b as:

$$D = a \cdot \Delta T^b. \tag{1}$$

The parameters of this relationship were estimated independently for each river, to account for potential inter-river differences in fish behaviour. From the parameters a and b, the relationship between the standardized distances (D_{std}; m) and the standardized travel time (ΔT_{std}; h) was obtained as:

$$D_{std} = a \cdot \Delta T_{std}^b. \tag{2}$$

The values of D_{std} and ΔT_{std} were estimated using a rule of three (Reist, 1986; Guénard *et al.*, 2010), a method previously used in the context of morphological analysis, as follows:

$$\frac{D_{std}}{D} = \frac{a \cdot \Delta T_{std}^b}{a \cdot \Delta T^b}. \tag{3}$$

We used a standard travel time ΔT_{std} of 1 h, and defined the resulting D_{std} as a corrected version of the Minimal Distance travelled Per Hour (MDPH_C; $\text{m} \cdot \text{h}^{-1}$), which, after simplification of Equation 3, was calculated as follows:

$$MDPH_C = D \cdot \left(\frac{1}{\Delta T}\right)^b. \tag{4}$$

Three explanatory models of MDPH_C were developed. The first model, referred to as the 'Inter-river Model', uses pooled data from both rivers, and is aimed towards reaching our first objective. The second and third models are river-specific models referred to as the 'Aubinadong intra-river Model' and the 'Mississagi intra-river Model'. They are aimed towards reaching our second objective. Our third objective was achieved using three descriptors of pike movement: the longitudinal range, the preferred movement type, and the lateral travel rate. The longitudinal range was calculated for every individual fish as the distance (in km) between the most upstream and the most downstream position (Clapp *et al.*, 1990; Bettinger and Bettoli, 2002). Every MDPH_C corresponds to a Euclidean vector with an x component (i.e. perpendicular to shore) and a y component (i.e. parallel to shore), which form mutually perpendicular reference axes. In the case where x is longer than y, MDPH_C was classified as being lateral. In the reverse situation, MDPH_C was classified as being longitudinal. The preferred movement type is the most frequent type of movement performed by a fish, and was estimated by summing, for each individual fish, the occurrence of MDPH_C classified as either longitudinal or lateral and taking the type having the largest sum as the preferred one. The lateral travel rate (in $\text{m} \cdot \text{h}^{-1}$) corresponds to the mean of all MDPH_C described as lateral, for all fish from the same river pooled together. The lateral travel rate indicates that fish followed the lateral direction (i.e. get closer to the shore) over a short time interval (number of meters travelled laterally during

1 h; lateral $\mathrm{MDPH_C}$). Because the mean channel width of the Mississagi River is larger than that of the Aubinadong River, we divided each of the lateral travel rates observed in the Mississagi River (i.e. the $\mathrm{MDPH_C}$) by a factor of 1.926 (i.e. the mean river width of the Mississagi River, 130 m, divided by the mean river width of the Aubinadong River, 67.5 m) to standardize them. Only fish movements with a travel time $\leq$ 24 h (sub-daily movements; 517 observations; Table II) were used to develop generalized linear mixed-effects models (GLMM), and to estimate the preferred movement type and the lateral travel rate. This leads to some individual fish with a very small number of observations (i.e. one observation for fish A12 and two observations for fish A7); however, it is acceptable to develop GLMM with only one observation per group, for some of the groups (Gelman and Hill, 2007).

Inter- and intra-river effects of flow on $\mathrm{MDPH_C}$ were analysed using GLMM, because observations performed on the same fish could not be taken as statistically independent (Zuur *et al*., 2009). GLMM used fish identity (fish ID) as a qualitative variable having a random effect, whereas flow ($\mathrm{m^3 \cdot s^{-1}}$), water temperature (°C), time of the day (h), sex (male or female), and total length (mm) were modelled as having fixed effects, on $\mathrm{MDPH_C}$. We also included a categorical variable representing the river inhabited by each individual fish in the fixed effects of the Inter-river Model, hereafter referred to as the river effect. We used the Poisson GLMM because our $\mathrm{MDPH_C}$ are counts during a standardized time interval (number of meters per hour), with a small occurrence of elevated counts and a high occurrence of small counts (Johnson *et al*., 2005). All GLMM were developed by backward elimination, and selected based on the smallest Akaike's Information Criterion (AIC; Zuur *et al*., 2009). The initial models included all the explanatory variables and the interaction terms that, based on our ecological knowledge, were likely to have a significant effect on $\mathrm{MPDH_C}$: (1) flow and water temperature, and (2) water temperature and time of the day. Generalized additive mixed modeling (GAMM) was considered in our selection of modeling methods but was not retained because there was no clear pattern in the plots of residuals against fitted values, and residuals against each explanatory variable for every GLMM developed. The presence of clear patterns in these plots is an indication of the need for GAMM modeling (Zuur *et al*., 2009). Our results show that the relationships between $\mathrm{MDPH_C}$ and explanatory variables are linear. We achieved our first objective by pooling observations from the two rivers, and removing the most extreme values of flow (i.e. $\geq 24\,\mathrm{m^3 \cdot s^{-1}}$) to obtain a similar range for the explanatory variables in the two rivers. Goodness of fit of the models was analysed using the marginal R^2 (R^2_m; the variance explained by the fixed factors) and the conditional R^2 (R^2_c; the variance explained by the entire model) described by Nakagawa and Schielzeth (2013). Inter-river variations in the longitudinal range and lateral travel rate were tested using Kruskal–Wallis rank sum tests and the preferred movement type was tested using Fisher's exact test. A linear model (LM) was developed between the log-transformed response variable fish weight and two explanatory variables: the log-transformed fish length and a categorical variable representing the two rivers. The inter-river difference in fish conditions was assessed by an analysis of variance conducted on the results of the LM. All statistical analyses were conducted with R (R Core Team, 2014).

RESULTS

We found no inter-river difference in the length (Mississagi range: 440–635 mm TL; Aubinadong range: 463–655 mm TL) or the mass (Mississagi range: 526–1532 g blotted wet mass; Aubinadong range: 619–1631 g blotted wet mass) of tagged fish (Table II; Kruskal–Wallis rank sum tests; length: $p = 0.98$; weight: $p = 0.70$). The fish length significantly explained the fish weight ($F = 607.92$, $p < 0.0001$), but we found no inter-river difference in pike condition ($F = 0.10$, $p = 0.75$).

Inter-river model

The $\mathrm{MDPH_C}$ ranged from 1 to 317 $\mathrm{m \cdot h^{-1}}$, and were higher in the Mississagi River than in the Aubinadong River for all flows (Figure 3). GLMM indicated that time of the day ($z = 10.16$, $p < 0.0001$), water temperature ($z = 4.62$, $p < 0.0001$), flow ($z = 3.435$, $p < 0.0001$), river ($z = 8.45$, $p < 0.0001$), and the interaction between flow and water temperature ($z = -3.276$, $p < 0.001$) had a statistically significant effect on $\mathrm{MDPH_C}$ (Table III). These variables explained 59% of the variation of $\mathrm{MDPH_C}$, and the random

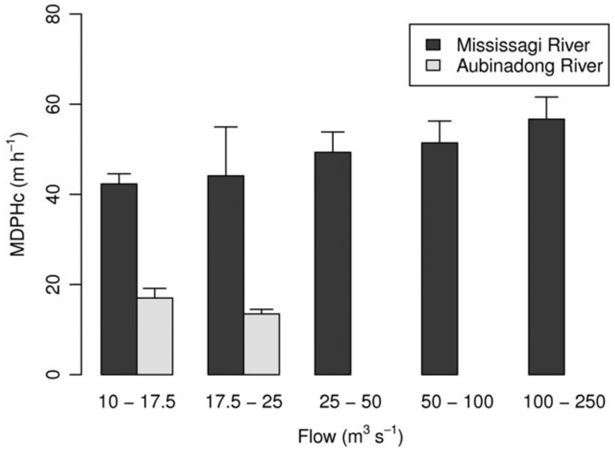

Figure 3. The $\mathrm{MDPH_C}$ (mean + standard error; $\mathrm{m \cdot h^{-1}}$) of northern pike at different flows (mean + standard error; $\mathrm{m^3 \cdot s^{-1}}$) in the Mississagi River (hydropeaking) and the Aubinadong River (unregulated). The maximum flow value observed in Aubinadong River was 24 $\mathrm{m^3 \cdot s^{-1}}$.

factor (fish ID) explained an additional 33%, for a total explanatory power of 92%. Sex had no effect on movements ($z = 0.603$, $p = 0.55$), nor did total body length ($z = 1.209$, $p = 0.23$). The latter may be related to the small size range used in our study (450 mm < total length < 650 mm). These results meant that, at the same water temperature, flow, and time of the day, a fish travelling at a rate of $11.7\,\mathrm{m \cdot h^{-1}}$ in the Aubinadong River would be travelling at $38.2\,\mathrm{m \cdot h^{-1}}$ (3.26 times faster) in the Mississagi River.

Mississagi intra-river model

$\mathrm{MDPH_C}$ in the Mississagi River ranged from 2 to $317\,\mathrm{m \cdot h^{-1}}$. The GLMM developed specifically for this river indicated that the variables time of the day ($z = -6.733$, $p < 0.0001$), water temperature ($z = -0.063$, $p < 0.0001$), flow (GLMM, $z = 6.341$, $p < 0.0001$), the interaction between time of the day and water temperature ($z = -4.138$, $p < 0.0001$), and total body length ($z = 2.984$, $p = 0.003$) had statistically significant effects on $\mathrm{MDPH_C}$ (Table III). Sex had no effect on movement (GLMM, $z = 1.9$, $p = 0.06$). The $\mathrm{MDPH_C}$ of the Mississagi River peaked at night from 21:00 to 1:00, following the hydropeaking schedule (Figure 2). According to the GLMM, a 55 cm fish observed at 20:00, in a water temperature of 23 °C, would have a $\mathrm{MDPH_C}$ of $49.7\,\mathrm{m \cdot h^{-1}}$ at a flow of $10\,\mathrm{m^3 \cdot s^{-1}}$, but a $\mathrm{MDPH_C}$ of $62.8\,\mathrm{m \cdot h^{-1}}$ at a flow of $250\,\mathrm{m^3 \cdot s^{-1}}$ (an increase of 26% in $\mathrm{MDPH_C}$ for a 25-fold increase in flow). The interaction between time of the day and water temperature indicated that the effect of the time of the day on $\mathrm{MDPH_C}$ tended to diminish as water temperature increased. That GLMM explained a total of 84% of $\mathrm{MDPH_C}$ variation in the Mississagi River, with 38% being associated to the environmental conditions and 46% to the random effect (fish ID).

Aubinadong intra-river model

$\mathrm{MDPH_C}$ in the Aubinadong River ranged from 1 to $165\,\mathrm{m \cdot h^{-1}}$. The GLMM developed for the Aubinadong River indicated that water temperature ($z = 4.58$, $p < 0.0001$), flow ($z = 4.79$, $p < 0.0001$), the interaction between flow and water temperature ($z = -4.138$, $p < 0.0001$), and time of the day ($z = 2.65$, $p = 0.008$) had a statistically significant effect on $\mathrm{MDPH_C}$ (Table III). Neither sex ($z = 0.488$, $p = 0.63$) nor body mass ($z = -0.31$, $p = 0.75$) had a statistically significant effect on the $\mathrm{MDPH_C}$. The effect of flow on $\mathrm{MDPH_C}$ depended on water temperature: the relationship was positive below 16.9 °C and negative above 16.9 °C. Hence, a 55 cm fish observed at 12:00 at a flow of $20\,\mathrm{m^3 \cdot s^{-1}}$ would have a $\mathrm{MDPH_C}$ of $16.6\,\mathrm{m \cdot h^{-1}}$ at a water temperature of 13 °C, but a $\mathrm{MDPH_C}$ of $6.0\,\mathrm{m \cdot h^{-1}}$ at a water temperature of 26 °C (a decrease of 64% in $\mathrm{MDPH_C}$ for a twofold increase in water temperature). While the GLMM explained a total of 79% of $\mathrm{MDPH_C}$ variation in the Aubinadong River, 72%

Table III. Estimate, standard error (SE), Wald statistic (z), probability associated to z ($\Pr(>|z|)$) of the Log-linear (Poisson) GLMM of the three models: inter-river Model, Mississagi, and Aubinadong intra-river models, all calculated on $\mathrm{MDPH_C}$ with the random effect being fish IDs. R^2_m is the marginal R^2 (variance explained by the fixed factors) and R^2_c is the conditional R^2 (total variance explained by the fixed and the random factors). Variable separated by colon punctuation mark designed interaction.

Parameter	Estimate	SE	z	$\Pr(>\|z\|)$	R^2_m	R^2_c
Inter-river model						
Intercept	0.254	0.498	0.509	0.610	0.59	0.92
River Mississagi	1.186	0.140	8.452	<0.0001		
River Aubinadong	Ref	—	—	—		
Time of the day (h)	0.020	0.002	10.155	<0.0001		
Flow ($\mathrm{m^3/s}$)	0.110	0.032	3.435	<0.0001		
Water temperature (°C)	0.101	0.024	4.169	<0.0001		
Flow: Water temperature	−0.005	0.002	−3.276	0.001		
Mississagi intra-river model						
Intercept	3.2244	0.5769	5.589	<0.001	0.38	0.84
Time of the day (h)	−0.106	0.016	−6.733	<0.001		
Water temperature (°C)	−0.063	0.015	−4.138	<0.001		
Total body length (mm)	0.027	0.009	2.984	0.003		
Flow ($\mathrm{m^3/s}$)	0.001	0.000	6.341	<0.001		
Time of the day: water temperature	0.006	0.001	7.482	<0.001		
Aubinadong intra-river model						
Intercept	0.125	0.672	0.187	0.852	0.07	0.79
Time of the day (h)	0.009	0.003	2.654	0.008		
Water temperature (°C)	0.142	0.031	4.582	<0.001		
Flow ($\mathrm{m^3/s}$)	0.186	0.039	4.787	<0.001		
Flow: Water temperature	−0.011	0.002	−5.575	<0.001		

was associated to the random effect (fish ID), and only 7% of the variation was associated to environmental conditions.

Longitudinal range, preferred movement type, and lateral travel rate

The longitudinal range of fish was significantly smaller in the Mississagi River (mean: 419 m; range: 133–800 m) than in the Aubinadong River (mean: 2700 m; range: 136–7939 m; $\chi^2 = 13.1733$, $p < 0.001$).The relative frequency for fish longitudinal and lateral preference was statistically different between the Mississagi River and the Aubinadong River (Fisher test, $p = 0.03$), an equal number of fish preferred to move longitudinally (10 fish) as laterally (10 fish) in the former, while fish preferred to move longitudinally in the latter (preferred movement type of 14 out of 16 fish; Figure 4). The lateral travel rates in the Mississagi River were, on average, $18\,\mathrm{m \cdot h^{-1}}$ (range: $3–30\,\mathrm{m \cdot h^{-1}}$), and were significantly higher than the average of $7\,\mathrm{m \cdot h^{-1}}$ observed in the Aubinadong River (range: $3–22\,\mathrm{m \cdot h^{-1}}$, $\chi^2 = 81.98$, $p < 0.001$).

DISCUSSION

The distance travelled by fish per hour ($\mathrm{MDPH_C}$; $\mathrm{m \cdot h^{-1}}$) in the Mississagi River was significantly higher than in the Aubinadong River. This finding is consistent with the 'mobility hypothesis' that suggests that fish can cope with increasing or decreasing flow by either remaining still, or changing their positions in order to find new suitable environmental conditions. Because the tendency to either hold a position or to move is related with the studied species' preference for velocity conditions, it is possible that pike moved to habitat with slower water velocity as flow changed in the Mississagi River. This pattern was not observed in the Aubinadong River, and thus leads to significantly greater $\mathrm{MDPH_C}$ in the former. Electromyogram telemetry revealed that bull trout maintain similar focal velocities across flows ranging from 0 to $920\,\mathrm{m^3 \cdot s^{-1}}$ in a hydropeaking river (Taylor *et al.*, 2014*b*). Bull trout held a position using fine-scale adjustments, yet it is unclear if non-salmonids are able to do the same. While understanding the tendency to preferably hold a position or to preferably move as flow increases, it is also important to consider the experience of fish to previous fluctuating flows (Scruton *et al.*, 2003). The Mississagi River pike in this study were exposed to daily flow fluctuations for a prolonged period of time (near continuously since 1969).

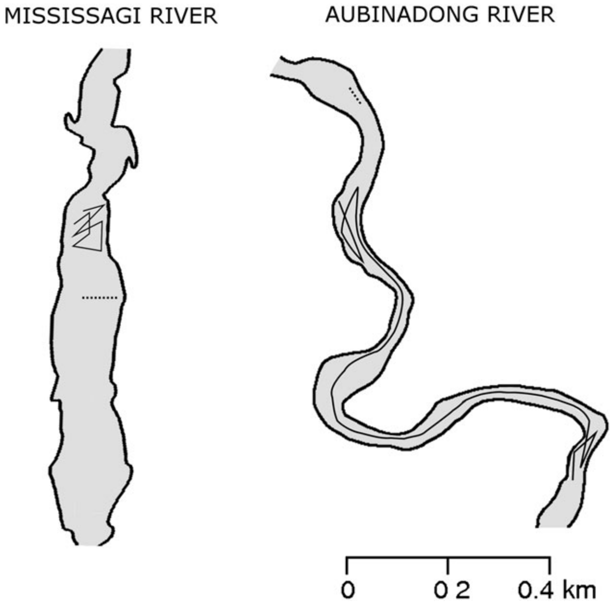

Figure 4. The northern pike movement patterns in the Mississagi River and the Aubinadong River. The single dashed line in each river represent the mean MDPHc (Mississagi River = 48 m/h; Aubinadong River = 15 m/h) of the preferred movement type in Aubinadong River (i.e. lateral) and the movement type preferred by half of the pike in Mississagi River (i.e. longitudinal). The solid line in each river is a 4 consecutive days track of the fish M14 and the fish A11. It is important to note that the tracks are raw data and not MDPHc; the solid lines cannot be taken as a measure of movement rate.

One of the main concerns about short-term changes in river flow is the additional energetic cost for fish to frequently find alternate locations with suitable environmental conditions (Scruton *et al.*, 2005). Fish need to obtain energy reserves during the summer to grow and withstand or survive the winter period of diminished food availability (Johnson and Evans, 1991; Miranda and Hubbard, 1994). For Mississagi River pike, the energy loss associated with the extra cost of activity can be roughly estimated using fish mass and swimming speed in calculations of the net energetic costs of routine swimming (Boisclair and Tang, 1993). The total net energetic cost associated to routine swimming for a 5 months period (1 May to 31 September) and a 1000 g pike were estimated at 336 kJ for a fish travelling half the time (12 h by day) at $42.6\,\mathrm{m\,h^{-1}}$ (mean $\mathrm{MDPH_C}$ at low flow: $\leq 24\,\mathrm{m^3 \cdot s^{-1}}$) and half the time at $52.7\,\mathrm{m \cdot h^{-1}}$ (mean $\mathrm{MDPH_C}$ at high flow: $>24\,\mathrm{m^3 \cdot s^{-1}}$) in the Mississagi River, and at 92 kJ for a fish travelling all the time at $14.7\,\mathrm{m \cdot h^{-1}}$ (mean $\mathrm{MDPH_C}$ at low flow $< 24\,\mathrm{m^3 \cdot s^{-1}}$, as high flows were absent) in the Aubinadong River. Based on the work of Diana (1979), we were able to approximate the among-river difference in the net energy available for growth and reproduction of a fish swimming in a water temperature of 19 °C (Diana, 1983); an increase in the swimming of the Mississagi River fish led to a decrease of 16% in the net energy available. This is a rough estimate and it is, by no means, the exact net energy available to pike in the study rivers. This estimate nevertheless suggests that Mississagi River pike could be losing a significant amount of energy (16%) by travelling more than fish in the Aubinadong River. However, our length–weight relationships suggest that there is no inter-river difference in pike conditions, thus indicating that another mechanism (e.g. increased food intake), or a combination of mechanisms, may allow pike to overcome the increased activity in Mississagi River. One hypothesis is that the water mixing, created by flow fluctuations in the Mississagi River, could have made food more available to pike. While our data does not allow us to substantiate this idea, it is tempting to speculate that the potential increase of prey catchability in the regulated river may help to explain the lack of difference in pike condition between the regulated and the unregulated rivers. Growth limitations were not assessed herein and further research is needed to assess whether increased activity levels could be detrimental to the growth of non-salmonid fishes.

A meta-analysis on the effect of flow on fish movement has revealed that a 40-fold flow increase (2–332 $m^3 \cdot s^{-1}$) had a significant positive effect on the distance travelled by fish (Taylor and Cooke, 2012), which is consistent with the results of the Mississagi intra-river Model. However, our results suggest that findings from regulated rivers studies do not apply to unregulated rivers. The effect of flow on movement in the Aubinadong River depended on water temperature, with no discernible effect of flow when the water temperature reached 17 °C, which are close to the temperatures associated with pike optimal activity (19–20 °C; Casselman, 1978). The differences in the effect of flow between the intra-river models indicate that the interaction of water temperature with flow could potentially only take place at conditions of low flow (<24 $m^3 \cdot s^{-1}$). In the Mississagi River, the flow can increase 22-fold in 3–4 h, while the range of flow observed in the Aubinadong River was 9.7 – 24.0 $m^3 \cdot s^{-1}$, with a maximum daily fluctuation of 2 $m^3 \cdot s^{-1}$. The absence of an interaction between flow and water temperature in the Mississagi River suggests that high flows (24–258.6 $m^3 \cdot s^{-1}$) trigger pike movement, irrespective of water temperature, and that high flows in an unregulated river caused, for instance, by storms or spring floods, could also affect $MDPH_C$ (e.g. 26% increase). However, only 7% of the variation was explained by environmental conditions in the Aubinadong River, which could indicate that fish moved in a more 'random walk' fashion in this river than in the Mississagi River (Codling *et al*., 2008).

We found the longitudinal range for Mississagi River fish to be sixfold smaller than that of Aubinadong River fish. Such a difference in pike's longitudinal range was unexpected because studies on pike movement have reported mostly sedentary behaviour during the summer period (Koed *et al*., 2006; Vehanen *et al*., 2006). This had a major influence on the sampling design of our study: in order to locate every fish (or try locating) at every session, the river portion covered in the Aubinadong River during the tracking session needed to be longer (18 km) than anticipated. In comparison, pike from the Mississagi River stayed in a longitudinal segment of 2 km. The length of the river surveyed should not be taken as a bias of our survey design, but as a result of fish behaviour. The general tendency of pike to be mostly sedentary during summer is consistent with the results from Mississagi River, but not with that of Aubinadong River.

A study by Jepsen *et al*. (2001) found intra-specific heterogeneity in the dispersion of pike populations; they had a larger home range in a clear water lake than in a turbid reservoir. They also found prey density differences between the lake and the reservoir that could have caused the dissimilarity in home ranges. However, fish density, which may be taken as a proxy for prey density, is almost equivalent in the Mississagi and Aubinadong rivers (Table I). This minimizes the potential role of prey density in the between-river movement differences observed in the present study. For salmonids species, Hillyard and Keeley (2012) found that the total distance (m) moved per week by Bonneville cutthroat trout (*Oncorhynchus clarki utah*) during the summer in a regulated river (average of 701 m; sedentary) was 11-fold smaller than in an unregulated river (average of 7964 m; mobile); a movement pattern also observed in the Mississagi and Aubinadong rivers. Hillyard and Keeley (2012) attributed the difference in mobility to small, infrequent, and widely distributed hospitable patches of cold water during warm summer months in the regulated river. Water temperatures exceeded the upper thermal limit of the Bonneville cutthroat trout (24.2 °C; Johnstone and Rahel, 2003) in the study by Hillyard and Keeley (2012). However, this situation was not observed in either the Mississagi River (water temperature range: 12 – 25 °C) or the Aubinadong River (water temperature range: 13 – 26 °C), because the upper thermal limit of the pike is 29.4 °C (Casselman, 1978). It is therefore unlikely that the difference in pike longitudinal range could be attributed to the water temperature of spatially variable, hospitable habitat patches. Lee and Berejikian (2008) have found that juvenile steelhead (*Oncorhynchus mykiss*) reared in stable environmental conditions were more inclined to have an exploratory behaviour than fish held in unstable environments where structures (rocks and plants) in aquaria were repositioned every 2–3 days. The environment in the Mississagi River can be characterized as unstable, where 22-fold daily flow changes affect velocity conditions and water depth, thus leading to losses or gains in habitats. The habitat changes in the Aubinadong River happen on a longer time-lapse (2 $m^3 \cdot s^{-1}$ maximum daily flow fluctuations during the tracking period), making it more stable on a daily basis. Rodríguez (2002) demonstrated that intra-specific heterogeneity exists in the length of river sections used by salmonids. The present study demonstrates that intra-specific behaviour heterogeneity also exists for non-salmonids fishes, and that the stability of flow conditions in which juvenile pike were reared is the most probable explanation of the difference observed in the longitudinal range of fish inhabiting both rivers.

In addition, fish preference for lateral movement and fish lateral travel rate were both higher in the Mississagi River than in the Aubinadong River. This behaviour may help fish to avoid high flow velocities by reaching flow refuges (off-channel habitats like floodplains, tributaries, inundated grassland, side channels, and backwaters; Cucherousset *et al.*, 2007; DeGrandchamp *et al.*, 2008; Nunn *et al.*, 2010; Gardner *et al.*, 2013; Gorski *et al.*, 2014). The increased preference for lateral movement for fish subjected to elevated discharge in the Mississagi River is consistent with findings from Kwak (1988), where the number of fish per day that travelled laterally to a floodplain was positively correlated to mean daily flow. As flow increases, fish can move either longitudinally (i.e. upstream or downstream) or laterally (towards the shoreline). Because no extended downstream movement was observed in the Mississagi River, pike could have been moving laterally because the other remaining choice in the type of movement (i.e. moving upstream against an increasing flow) would correspond to a high-energy demand upon the fish.

Our results demonstrate that pike respond to short-term changes and elevated flows ($>24\,\mathrm{m}^3\cdot\mathrm{s}^{-1}$) by increasing the $\mathrm{MDPH_C}$ in the regulated river. Under natural flow conditions and low flows ($<24\,\mathrm{m}^3\cdot\mathrm{s}^{-1}$), the importance of the flow on the $\mathrm{MDPH_C}$ depended on the water temperature. Therefore, the way that $\mathrm{MDPH_C}$ varied with flow depended on the river itself, because flow regulation was completely different between the study rivers (regulated vs. unregulated river). This emphasizes the need for further work on net energy available for growth and reproduction in rivers subjected to short-term changes in flow. Differences in pike movement patterns were observed between the Mississagi and Aubinadong rivers. The flow regime affects many environmental conditions that could be the cause of such differences and identifying the sole environmental condition responsible of these differences was beyond the scope of the present study. Moreover, our findings only apply to the size class of pike studied (440 to 655 mm TL), to summer months (July and August at a latitude of 46° north), and to movement performed over a temporal scale of approximately 8 h (i.e. the average time between two consecutive fish positions included in all the analyses, except for the longitudinal range, were 8.36 h in Mississagi River and 8.35 h in Aubinadong River). To date, most studies on the effect of short-term flow changes on fish behaviour were conducted on single systems (e.g. Piper *et al.*, 2013; Tripp *et al.*, 2013; Gorski *et al.*, 2014; Pauwels *et al.*, 2014; Taylor *et al.*, 2014a), thus making it difficult to assess the indirect effects of flow regulation on fish populations. The approach chosen in the present study, which allows among-river comparisons of fish movement, enhances our understanding of the potentially adverse effects of flow regulations on fish.

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