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# Habitat use and preference of adult pike (*Esox lucius* L.) in an anthropogenically impacted lowland river

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ABSTRACT

To efficiently manage northern pike (*Esox lucius*), information is needed on its habitat use and preference. However, knowledge gaps still exist, especially on pike habitat use and preference in rivers characterised by artificial environments. We investigated the use of the main river, tributaries and side arms at the macro-scale, and the use and preference of riparian habitats by adult pike at the meso-scale in an anthropogenically impacted river basin. Adult pike were followed in winter and spring by radio telemetry. At the macro-scale pike intensively used the main river in winter and spring, but also frequented specific side arms in winter and specific tributaries in spring, which may indicate the importance of these habitats to adult pike. At the meso-scale, reedy semi-natural banks were used the most, irrespective of any assumption on habitat availability or use. The findings underline the value of protecting the least impacted, (semi)natural habitats for adult pike in an anthropogenically impacted river system. The large behavioural differences in habitat use between individuals at both habitat scales further underline the importance of habitat heterogeneity. The results also provide insight into the impact of riparian habitat restoration on adult pike and may be used to more efficiently manage pike rivers, e.g. by enhancing the lateral connectivity with river side arms or by reconstructing natural riparian habitats.

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## 1. Introduction

Loss of natural habitat by channelization, water pollution and migration barriers caused pike (*Esox lucius* Linnaeus 1758) population declines and impedes successful restoration programmes (Chapman and Mackay, 1984a; Ovidio and Philippart, 2003; Radomski and Goeman, 2001). Indeed, pike requires natural habitats to successfully survive and reproduce, such as shallow areas with submerged vegetation to spawn and areas with emergent vegetation to hunt for prey and hide from larger cannibalistic pike (Bry, 1996; Casselman and Lewis, 1996; Grimm and Klinge, 1996). Adult pike choose habitat according to intrinsic fitness gradients, equalizing their fitness across habitats (Haugen et al., 2006). They are versatile in their habitat use, depending on availability of prey and meteorological factors (Chapman and Mackay, 1984b). Although they use the open water as well as vegetated areas, they are more often observed in the proximity of vegetated areas than would be expected if they were choosing the habitat randomly (Chapman and

Mackay, 1984a). Studies on the impact of river and lake management on pike have mainly focused on juvenile and spawning habitat requirements (Cooper et al., 2008; Engstrom-Ost et al., 2005; Farrell et al., 1996; Hawkins et al., 2003; Miller et al., 2001; Skov and Berg, 1999; Skov et al., 2002, 2003).

The studies that revealed adult pike behaviour were mainly conducted in natural to semi-natural lake (Chapman and Mackay, 1984b; Cook and Bergersen, 1988; Diana et al., 1977; Haugen et al., 2006; Kobler et al., 2008) and river (Masters et al., 2002; Vehanen et al., 2006) systems. However, a gap still exists for river systems characterised by an artificial environment, such as for instance partly channelized rivers. Large pike may use the whole river or lake, including the most impacted areas, or restrict their home range to the least impacted areas. Furthermore, they may use artificial riparian habitats. The only study that compared an impacted habitat to a less impacted habitat was conducted in a reservoir and a lake (Jepsen et al., 2001). Although large behavioural differences were observed between the reservoir and the lake, the study revealed more variation between individuals within each population. Insight into the required physical and ecological habitat conditions of adult pike in a modified river system can further improve the effectiveness of river conservation and restoration plans.

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Therefore, the aim of this study is to investigate adult pike habitat use and preference in a river characterised by an artificial environment. Specifically, radio telemetry was applied to evaluate which river parts are used at the macro-scale and which riparian habitat types are used and preferred at the meso-scale.

## 2. Materials and methods

### 2.1. Study area

Pike were studied in the 1101 km<sup>2</sup> drainage area of the 44 km long Belgian part of the river Yser (Fig. 1). The river has a rainfall-dominated hydrology with an average annual flow of 1.44 m<sup>3</sup> s<sup>-1</sup>, a peak flow of 5.7 m<sup>3</sup> s<sup>-1</sup> and a base flow of 0.8 m<sup>3</sup> s<sup>-1</sup> (Mouton et al., 2012). The river is navigable and a tidal sluice at the estuary prevents tidal water level fluctuation and inflow of salt water. Directly upstream of the tidal sluice the river flows in a 370 × 1000 m wide basin with a depth of 7 m. There is no migration barrier in the main river, and pike can freely move between the main river and most of its tributaries. Average water depth is 2.5 m (Mouton et al., 2012) with the river thalweg varying in depth from 2.8 to 5 m. Near the French border, the river is 8 to 10 m wide, at the mouth it is 25 m wide (Mouton et al., 2012). In the river Yser, 58% of the river banks were originally artificially embanked, because a significant area of the floodplain lies below sea level. Due to this channelization, depth, substrate and flow velocity are distributed relatively uniformly. To restore the riparian habitat and the associated fish populations, the river managers constructed several artificial foreshores and river side arms between 2002 and 2005.

The water quality of the river Yser varies little throughout the year (Flemish Environment Agency, [www.vmm.be](http://www.vmm.be)). The conductivity averages 0.75 mS cm<sup>-1</sup> but can exceed 1 mS cm<sup>-1</sup> in extremely dry periods. The fish fauna in the study area consists of 24 species, however not all 24 species are present everywhere in the study area. The most dominant species, occurring everywhere in the study area and being dominant in numbers and biomass are white bream (*Blicca bjoerkna* L.), roach (*Rutilus rutilus* L.), European eel (*Anguilla* L.), freshwater bream (*Abramis brama* L.) and common carp (*Cyprinus carpio* L.). Two dominant predators beside pike are European perch (*Perca fluviatilis* L.) and pikeperch (*Sander lucioperca* L.; see Research Institute for Nature and Forest, [www.vis.inbo.be](http://www.vis.inbo.be), for the full species list). Fisheries legislation prohibits fishing from March 1st to May 31st in the tributaries of the river Yser, however, on the main river fish can be caught throughout the year. All fish have to be released immediately after they were caught.

In this study we investigated pike habitat use and preference at the meso- and macro-scale. At the meso-scale, eight different riparian habitat types were defined based on a combination of the vegetation types and river bank types. The riparian vegetation in the study area can be classified as bare (B), reedy (R) and woody (W) vegetation. Three river bank types, characterised by a different degree of anthropogenic disruption, are present in the study area: artificial vertical banks (AVs; high disruption), artificial foreshores (AFs; moderate disruption) and semi-natural banks (SNBs; low disruption). AVs are vertically straightened and reinforced with concrete, while AFs consist of a row of 0.2 m diameter wooden posts that are positioned in the river channel between 0.7 m and 2.5 m from the river bank. The posts are placed at 0.05–0.2 m distance from each other to protect the riparian habitats from shipping wave action. Vegetation in the zone between the posts and the river bank consists mainly of reed and vegetation cover ranges from 0 to 100%. SNBs are highly heterogeneous and characterised by varied bank vegetation such as trees, reed and other emergent vegetation (Mouton et al., 2012). The combination of the different vegetation and river bank types led to eight different riparian habitat types

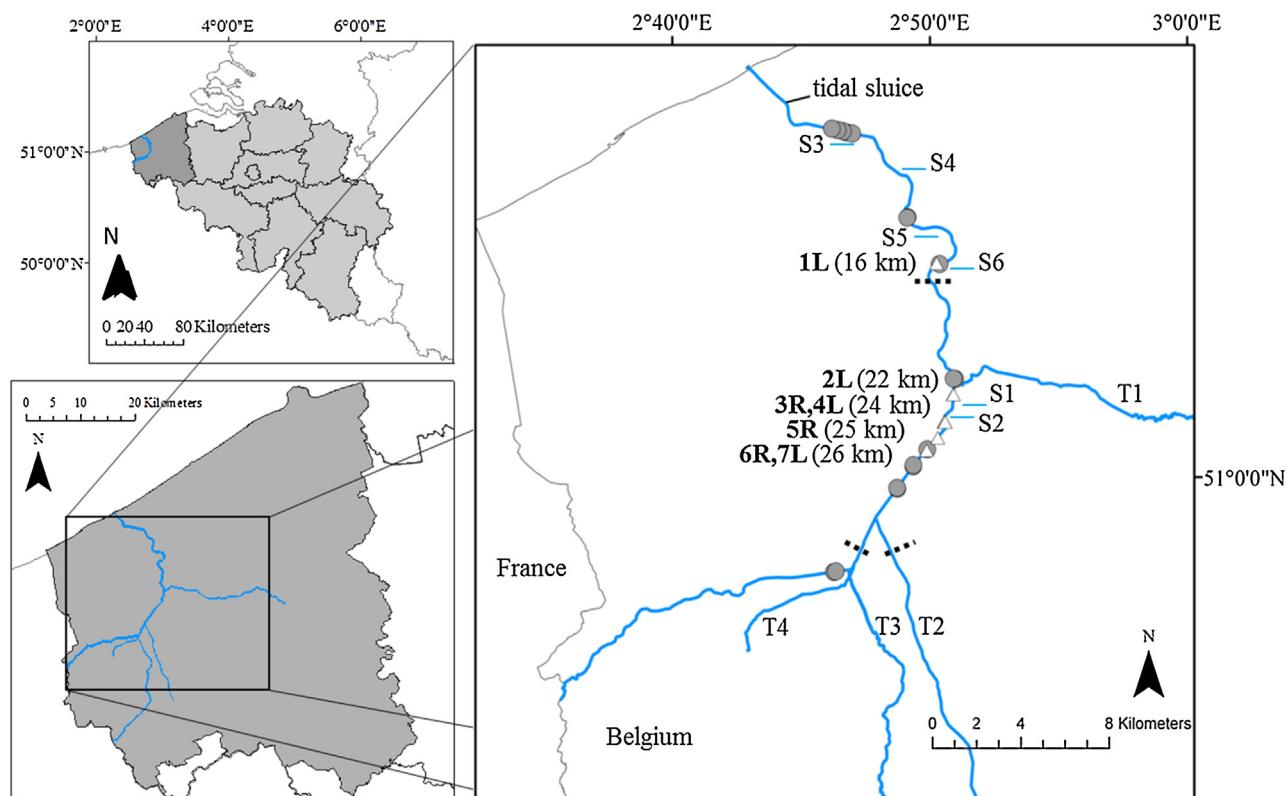
in the study area: bare, reedy and woody artificial vertical banks (B:AVs, R:AVs and W:AVs, respectively), bare, reedy and woody semi-natural banks (B:SNBs, R:SNBs and W:SNBs, respectively) and bare and reedy artificial foreshores (B:AFs and R:AFs, respectively; Fig. 2).

The smallest scale at which variation in the defined riparian habitat types occurred was 20 m. Consequently, the riparian habitat use and preference was assessed by dividing the banks of the main river, the tributaries and side arms in segments of 20 m length. For segments consisting of more than one riparian habitat type, the habitat type that covered more than 50% of the segment was selected. The riparian habitat type within each segment was determined based on riparian habitat data retrieved from a digital map (Research Institute for Nature and Forest, unpublished data) in ArcMap (ArcGIS 10, ESRI BeLux). Riparian habitat use and availability were defined as the number of segments used and available, respectively (Fig. S6).

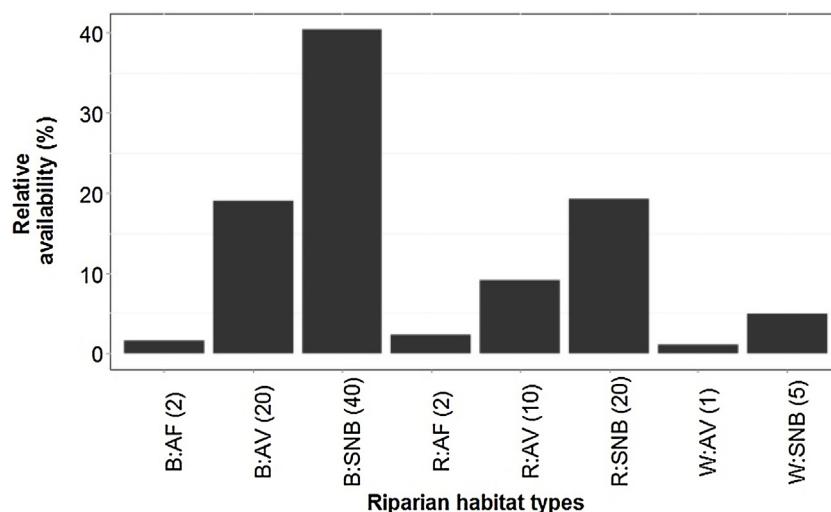
At the macro-scale, five different habitat types were distinguished: the main river, the large and small tributaries and the artificial and natural side arms. The main difference between the large and small tributaries is their width and depth. The two largest tributaries of the river Yser (the Handzamevaart (T1) and the Ieper-Yser Canal (T2; Fig. 1) are 10 to 15 m wide and 1 to 2.5 m deep, whereas the small tributaries are 4 to 10 m wide and maximally 2 m deep. Two small tributaries that were used by tagged pike are the Landdijkgracht (T3) and the Boezingegracht (T4; Fig. 1). Side arms are shallow (0.5 to 1.5 m deep) and stagnant, with banks that are dominated by tall herbs and reed, and are connected to the main river. Two of the six side arms in the study area are natural (S1 to S2; Fig. 1) and four are artificial (S3 and S6; Fig. 1). The artificial side arms were created between 2002 and 2005 to restore the riparian habitat in the river Yser. Although they are relatively young, the reed vegetation is similar to the reed vegetation in the natural side arms. All side arms in the study area are between 150 and 500 m long and between 10 and 20 m wide. All meso-scale riparian habitat types are present in the main river. The two largest tributaries are characterised by B:SNBs, R:SNBs and W:SNBs, except the most downstream part of T1 in the city of Diksmuide that consists of B:AVs and R:AVs. The riparian habitat types in the small tributaries are B:SNBs, R:SNBs and (less abundant) B:AVs.

### 2.2. Fish capture and tagging

Although historical evidence of a high-density (estimate based on historical angling reports of 26 kg ha<sup>-1</sup>) population of pike in the river Yser exists, densities have been low since the first standardised observations in 1996 (Research Institute for Nature and Forest, [www.vis.inbo.be](http://www.vis.inbo.be)). For the tracking study, pike were sampled at 15 different locations in the river between 3 and 32 km upstream of the tidal sluice (Fig. 1) by fyke sampling during nine events between November 24th and December 13th 2010. At each sampling location, two double fykes were placed in the river for 48 h. In total, nine females and six males were caught at five of the 15 different locations during seven of the nine different sampling events (Table 1). The pike were anaesthetised immediately in a 1:9:10000 clove oil:ethanol:water solution (C8392, Sigma, Bornem, Belgium), measured, weighed and tagged with a 68 mm long and 18 mm wide body implant radio transmitter (Model: F1230, coil antenna, Advanced Telemetry Systems Inc., Isanti, MN, USA; weight: 23 g in air and 6 g in water, battery life: 502 days). Each transmitter had a different frequency between 40000 and 41000 MHz. The minimal, median and maximal female and male mass and length were 1057, 3700 and 8750, and 1100, 5540 and 8150 g, and 55, 78 and 99, and 67, 83 and 97 cm, respectively. Thus, the transmitters never exceeded 2% of the body mass (Jepsen et al., 2002; Table 1). The transmitters were inserted into the body cavity through a ventral



**Fig. 1.** The Belgian part of the River Yser, in Flanders (Belgium) and the fyke locations. Capture locations are described by an index (1–7), the position of the fyke near the left (L) or right (R) bank and the distance to the tidal sluice at the river mouth (km). Locations where temperature was logged are marked by a dotted line (T1 = Handzamevaart, T2 = Canal from the city of Ieper to the River Yser, T3 = Landdijkgracht, T4 = Boezingegracht; white triangles = pike caught for tagging, gray dots = no pike caught by fykes, horizontal lines = locations of river side arms: S1–S2 = natural river side arms and S3–S6 = artificial river side arms).



**Fig. 2.** Relative availability of the riparian habitat types in the river Yser in Belgium (B:AV = bare artificial vertical bank, R:AV = reedy artificial vertical bank, W:AV = woody artificial vertical bank, B:SNB = bare semi-natural bank, R:SNB = reedy semi-natural bank, W:SNB = woody semi-natural bank, B:AF = bare artificial foreshore, R:AF = reedy artificial foreshore).

20–25 mm incision between the pelvic girdle and the anal fin, which was then closed with three sutures. The sex was determined during surgery by gonad inspection. The duration of the operations ranged from 5 to 10 min, and the pike needed about 10 min to recover. One hour after recovery the pike were released at their catch location.

Additionally, the presence of young-of-the-year pike (YOY) was evaluated by an electro and fyke fishing campaign in the river side arms and the tributaries in the study area in May and June 2011. Electrofishing and fyke net sampling efforts in previous research

showed that juvenile pike density was very low in the main river (Mouton et al., 2012). Therefore, we focused on the side arms and tributaries. In total 26 locations were fished, of which five were located in river side arms, 13 in tributaries and eight in tributaries of tributaries. The locations were strategically chosen to cover the potential spawning habitats in the study area. Three locations had been visited by tagged adult pike and eight locations were within 500 m of a pike observation. Each location was subjected to sampling by using one-pass electrofishing with a generator and

**Table 1**

Overview of the biometric data of 15 pike in the Belgian part of the river Yser (M=male, F=female). Data of pike that were lost before half February (\*) were omitted from spring analyses, and was observed less than 25 times (\*\*) was omitted from all statistical analyses.

Sex	Time of tagging	Length at tagging (cm)	Mass at tagging (g)	Fish ID (Freq. in MHz)	Catch location (Fig. 1)	Number of observations
F	13/12/2010	60	1057	40.600	3	62
M	1/12/2010	97	8150	40.611	3	66
F	26/11/2010	55	1124	40.620	3	63
M	10/12/2010	68	2350	40.630	2	67
F	2/12/2010	99	8750	40.651	2	72
M	2/12/2010	67	1100	40.671	5	62
F	24/11/2010	70	2927	40.681	3	59
F	2/12/2010	85	5600	40.781	2	69
M	10/12/2010	82	5010	40.801	2	58
F	6/12/2010	59	1700	40.811	4	55
M	1/12/2010	83	6070	40.820	3	63
F	24/11/2010	78	3700	40.841	1	59
F	1/12/2010	78	4430	40.661 *	5	29
M	1/12/2010	89	6310	40.771 *	3	30
F	10/12/2010	96	7340	40.831 **	2	17

a control box (DECA 3000) that converted a 230 V alternating current into a 200 V direct current, while a 0.1 m diameter anode was applied to sample the fish. Previous research has shown that juvenile fish are caught more efficiently with this small anode (Baras and Nindaba, 1999; Copp, 1992; Mouton et al., 2012). At each location, the habitat was gently approached by wading and three times 10 randomly selected points were sampled within three different 100 m stretches. Thus, at each location 30 randomly selected points were sampled following the point abundance methodology (Copp, 1990). To compensate for potential low catch efficiency, each location was additionally sampled for 48 h by a fyke of  $0.5 \times 0.5 \times 1$  m.

### 2.3. Tracking

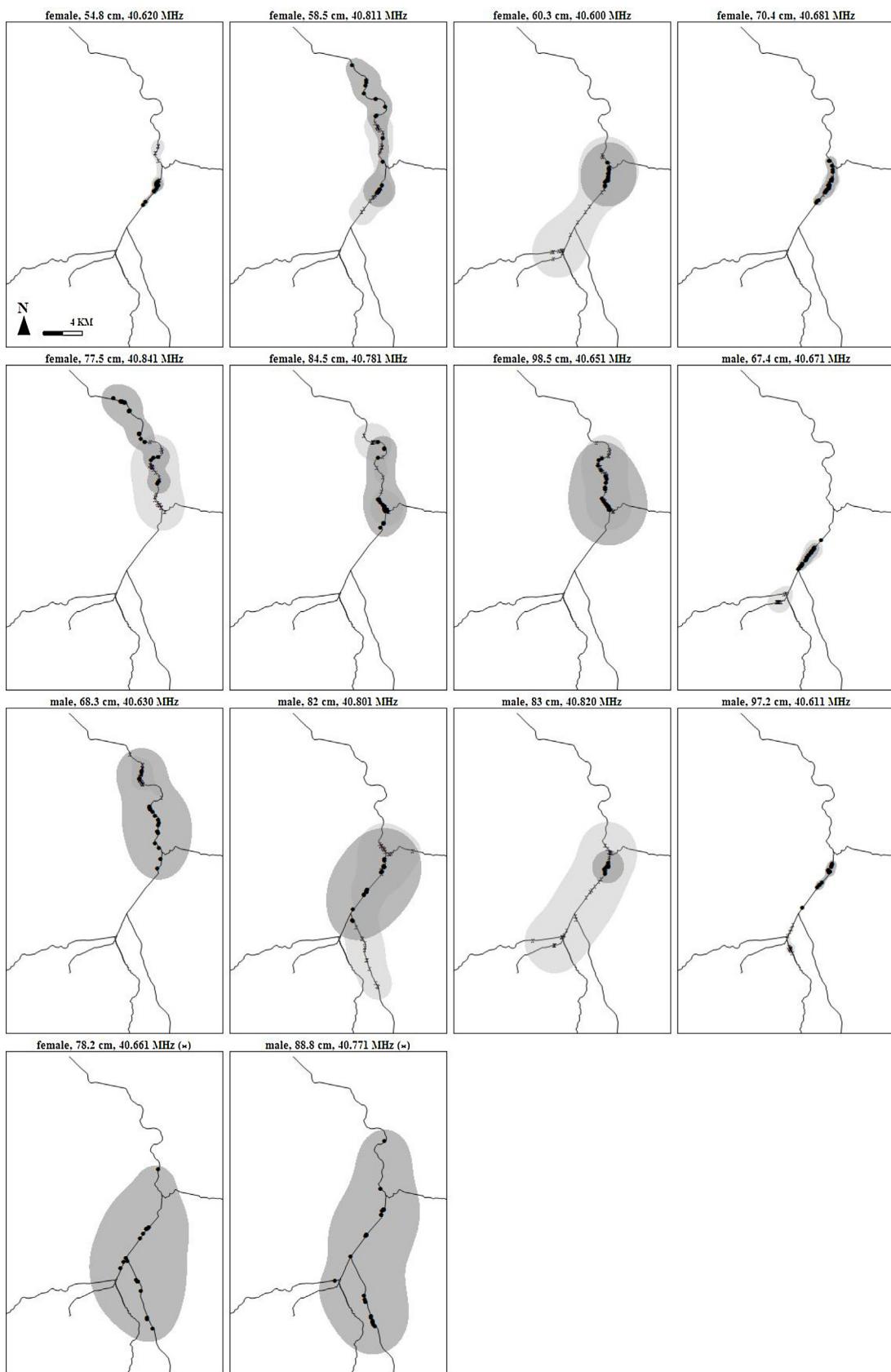
Pike observations were obtained by radio tracking manually from land with a magnetic dipole antenna (Advanced Telemetry Systems Inc., Isanti, MN, USA) to firstly track the pike at a precision of  $2000 \text{ m}^2$ . Subsequently, a low frequency loop antenna (Advanced Telemetry Systems Inc., Isanti, MN, USA) was used to localise the pike by triangulation (Diana et al., 1977; Jepsen et al., 2001). The theoretical precision parallel to the river banks was determined as minimally 20 m at a potential, maximal bearing error of  $10^\circ$  (White and Garrot, 1990), a maximal distance between the two triangulation locations of 60 m in this study and a maximal distance of 27 m between a tagged pike and the observer. Accidental tracking of a dead fish at 8 m from the river bank for four weeks, however, revealed a tracking precision of  $\pm 4$  m. The tracking precision diminished at conductivities of  $1 \text{ mS cm}^{-1}$  and higher. However, such conductivities were not observed during the tracking period from November 2010 till May 2011. The antennas were connected to a R2000 receiver (Advanced Telemetry Systems Inc., Isanti, MN, USA) that searched each frequency at 4 s intervals. The exact pike position was recorded on a 1:500 map of the study area.

Pike were tracked between November 2010 and May 2011. Routine monitoring consisted of tracking the pike every two days. During two periods this tracking frequency was increased to daily trackings: immediately after each pike was tagged until January 1st, to avoid loss of pike due to potentially higher activity after tagging, and in February and March, which is generally recognised as the spawning period (Craig, 1996) when higher pike activity may occur. During each tracking campaign pike were tracked along 47 km of the main river, tributaries and side arms. When pike were missing, they were searched in the small tributaries. Data of two pike that were lost before half February were omitted from spring analyses, and data of one that was relocated less than 25 times was omitted from all analyses. Consequently, during the study period 814 pike

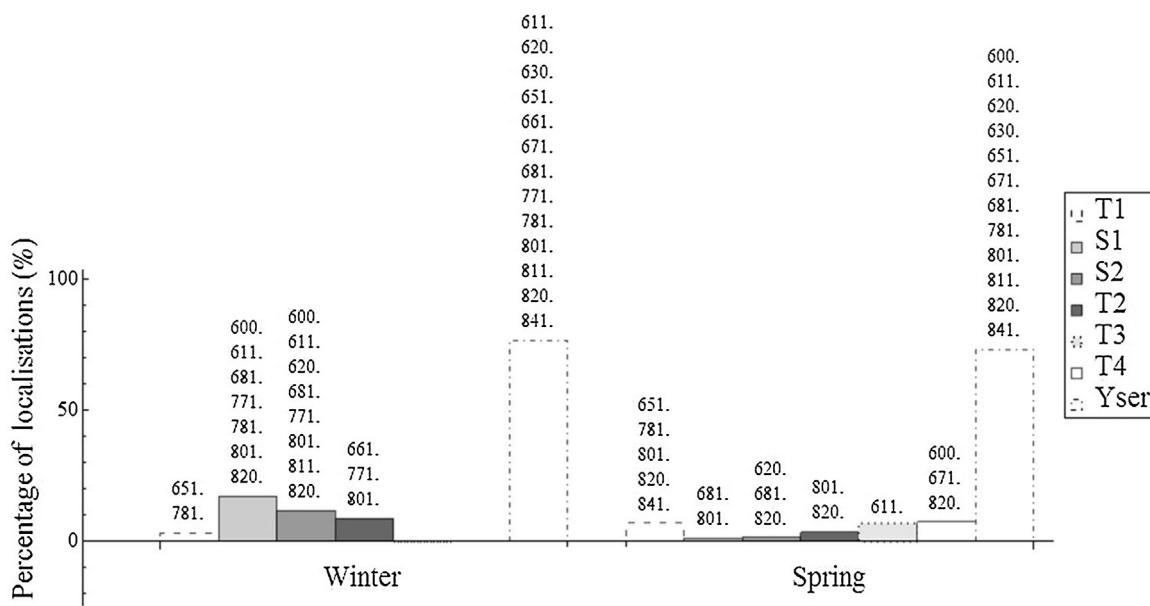
observations were collected of 14 pike (14 in winter, 12 in spring) that were each observed between 29 and 72 times (Table 1).

### 2.4. Data exploration and analysis

Habitat use at the macro-scale was evaluated by counting the pike observations in the river, tributaries and side arms. At the meso-scale, the compositional analysis as proposed by Aebischer et al. (1993) was applied to find evidence for riparian habitat selection and to investigate riparian habitat use. The analysis is carried out in two steps: first significance of habitat selection is tested using a Wilks' lambda. Significant habitat selection means that the habitat is used more or less than expected from its availability. Second, a ranking matrix is built to determine whether a riparian habitat type is significantly used more or less than the other riparian habitat types (further named relative habitat use). We refer to Aebischer et al. (1993) for a detailed description on the methodology. Habitat use and selection was evaluated at three levels of habitat selection (further named orders of habitat selection according to Johnson, 1980) to exclude potential effects of territoriality (Skov and Koed, 2004) and different habitat availability per individual pike (Aebischer et al., 1993). The three orders differed in the quantification of used and available habitat. In the first order analysis the used and available habitats in the whole study area were considered. The second order analysis considered the used habitat in the home ranges and the available habitats in the whole study area, whereas the third order analysis analysed the used and available habitats within each pike home range (Aebischer et al., 1993). Consequently, comparison of the first and third with the second order analysis allows evaluating a different definition of habitat use (here pike observations versus pike home ranges), whereas the comparison of the first and second order analysis with the third order analysis allows evaluating a different definition of habitat availability (here availability in the whole study area versus availability within the home range). To investigate habitat use the riparian habitat types were ranked according to their relative use, from 'most used' (top) to 'least used' (bottom). Ranking the riparian habitat types overcomes the problem of dependence between habitat types (Aebischer et al., 1993). Home ranges were calculated using the Brownian Bridge Kernel (BBK; Horne et al., 2007; Fig. 3). The Kernel Brownian Bridge Home Range function (kernelbb; part of the ADEhabitat package in R) was used to estimate areas in which there is at least a 95% chance of finding the studied pike (further named home ranges). The home ranges were calculated for winter and spring and all home ranges were stable. The Kernel Brownian Bridge Home Range estimation relies on two smoothing parameters. The first smoothing parameter relates to the speed of the



**Fig. 3.** Home ranges and observations of 14 pike in winter (dark grey polygon and black dots, respectively) and 12 pike in spring (light grey polygon and black x, respectively). Home ranges are 95% Brownian Bridge Kernel (BBK) home ranges. Sex, body length and pike ID are indicated on top of each graph. The two graphs at the bottom of the figure illustrate the home ranges of the pike that were lost before spring (Table 1).



**Fig. 4.** Percentage of pike observations in the river Yser, its tributaries and river side arms in winter and spring (T1 = Handzamevaart, T2 = Canal from the city of Ieper to the River Yser, T3 = Landdijkgracht, T4 = Boezingegegracht, S1-S2 = natural river side arms). Data of winter are based on the observations of 14 pike and data of spring on the observations of 12 pike. Fish IDs (Table 1) above each bar indicate the observed individuals.

animal. It describes how far a given animal can distance itself from the line linking two successive relocations in one second. The “liker” function in the ADEhabitat R package was employed to estimate this value using the maximum likelihood approach as described by Horne et al. (2007). The second smoothing relates to position uncertainty (Le Pichon et al., 2014). In this study we defined the second parameter by the standard deviation of the average minimal distance travelled per day per season.

Although the aforementioned analysis (Aebischer et al., 1993) allows testing the occurrence of riparian habitat selection and the relative habitat use, no absolute preference per riparian habitat type is calculated. Therefore, we calculated selection ratios and their associated Bonferroni-adjusted 95% confidence intervals (CIs) as proposed by Manly et al. (2002) in addition to the analysis proposed by Aebischer et al. (1993). The selection ratio pools observations from all fish in the sample, but takes variation in resource selection from individual fish into account (Manly et al., 2002). When a selection ratio and accompanying CI is higher than 1.0, habitat preference is considered significant (Hobbs and Bowden, 1982; Manly et al., 2002; Rogers and White, 1990). The selection ratios and CIs were calculated for the population ( $\hat{w}_i$ ). The selection ratio was calculated as follows:

$$\hat{w}_i = \frac{u_{i+}}{(\pi_i u_{++})},$$

where  $u_{i+}$  is the number of segments of habitat type  $i$  used by all fish,  $u_{++}$  is the total number of segments used (all riparian habitat types by all pike) and  $\pi_i$  is the availability of riparian habitat type  $i$  defined as the ratio between the number of segments of habitat  $i$  and the total number of segments in the study area between the most upstream and most downstream pike observation (Manly et al., 2002). Conditional on known values for  $\pi_i$ , the variance of  $\hat{w}_i$  was estimated as:

$$\text{var}(\hat{w}_i) = \frac{n}{U_{++}^2} \sum_{j=1}^n \left( \frac{u_{ij}}{\pi_i} - \hat{w}_i U_{+j} \right)^2,$$

where  $n$  is the number of pike,  $u_{ij}$  is the number of segments of habitat type  $i$  used by pike  $j$  and  $U_{+j}$  is the total number of segments used by pike  $j$ . Simultaneous Bonferroni confidence intervals for popu-

lation selection ratios were constructed with an overall confidence level of approximately  $100(1 - \alpha)\%$  so that the probability of all the intervals containing the true value is approximately  $(1 - \alpha)$ . These intervals are of the form

$$\hat{w}_i \pm Z_{\frac{\alpha}{I}} SE(\hat{w}_i),$$

where  $I$  is the number of habitat types (Manly et al., 2002).

To statistically test for individual differences in riparian habitat preference, the log-likelihood test statistic ( $\chi^2_{L1}$ ) was used:

$$\chi^2_{L1} = 2 \sum_{j=1}^n \sum_{i=1}^I u_{ij} \log_e \left[ \frac{u_{ij}}{(u_{i+} u_{+j} / u_{++})} \right].$$

If the value of  $\chi^2_{L1}$  is sufficiently large with  $(I - 1)(n - 1)$  degrees of freedom, there is evidence that pike riparian habitat preference differs between individuals (Rogers and White, 1990).

All statistical analyses were conducted for winter and spring. Water temperature regimes were used to divide the study period into winter (water temperature below 5 °C, November 26th to February 4th) and spring (water temperature between 5 and 15 °C, February 5th to April 19th). This division was based on the findings that pike start spawning migration around 5–6 °C (Ovidio and Philippart, 2003), spawn at water temperatures between 6 and 14 °C (Raaij, 1988) and tend to decrease their activity around 0 °C (Vehanen et al., 2006). Water temperature was logged every 30 min at three locations in the study area by Tidbit temperature loggers (Onset) with an accuracy of 0.01 °C (Fig. 1). All analyses were performed in R (R, 2010) and the package adehabitat 0.3.8 (Calenge, 2006) was used to perform the test for habitat selection and the compositional analysis, calculate the selection ratios and estimate the home ranges.

### 3. Results

#### 3.1. Habitat use at the macro-scale

The use of the main river was similar in winter and spring, whereas the use of the tributaries and side arms differed substantially. In winter, 77% of all pike observations were located in the

main river. The river was used by all pike and two pike were even always observed there. The other twelve pike were observed there between 25 and 95% of the observations and regularly moved in and out of the main river (Fig. 4). Although six side arms were available in the study area, only S1 and S2 were used (Fig. 1) and thus pike did not use any of the four artificial side arms. Six pike used both side arms, one used only S1 and two used only S2. Based on all observations in winter, pike used the side arms relatively more (29% of the observations) than the tributaries (T1 and T2, 11% of the observations) and the side arms were used by more individuals (9) than the tributaries (5).

In spring, 73% of all observations were located in the main river. All pike used the main river and two individuals were never observed outside the main river. Again only the two natural side arms were used. Some pike also used two small tributaries upstream in the study area (T3 and T4, in total 15% of the observations), beside the larger tributaries (T1 and T2). In contrast to winter, the large tributaries (T1 and T2) were used more intensely (10% of the observations) than the two natural side arms (S1 and S2; 3% of the observations). In line with winter, the artificial side arms were not used in spring. The lower use of the side arms in spring was due to six individuals that moved to the tributaries (Fig. 4).

One individual migrated to a small tributary (T3) through a temporally opened flap gate and appeared to be locked in the tributary. All pike that used T4 had returned to the river by the end of April. The only locations in the study area where YOY were observed were T3 and T4 and specifically the tributaries of T3 and T4, which are between 0.20 and 0.40 m deep and vegetated.

At the macro-scale, the use of the river, tributaries and side arms substantially differed between individuals. Throughout winter and spring, one pike never used tributaries and side arms, another never used side arms and one fish never used tributaries. Four fish used the main river, the large tributaries and the natural side arms and only one fish used the main river, the large and small tributaries and the natural side arms (Fig. 4).

### 3.2. Habitat use and preference at the meso-scale

In winter, pike used reedy and bare semi-natural banks the most and significantly more than other riparian habitats at the first and third order (Table 2). At the second order, reedy semi-natural banks and artificial vertical banks were used significantly more than other riparian habitat types (Table 2).

Habitat selection in winter was significant at the first ( $\lambda = 0.1115$ ,  $p\text{-value} = 0.0001$ ), second ( $\lambda = 0.2718$ ,  $p\text{-value} = 0.0109$ ) and third ( $\lambda = 0.1158$ ,  $p\text{-value} = 0.0380$ ) order of habitat selection. The selection ratios and accompanying CIs revealed that pike significantly preferred reedy semi-natural banks in winter at the first and second order of habitat selection (Fig. 5). In contrast to their relative high use, bare semi-natural banks were not preferred (Fig. 5). Based on the selection ratios, the absence of a significant preference for artificial vertical banks and artificial foreshores is in line with the relative low use of these riparian habitat types at the first order of habitat selection. At the second order, pike preferred woody artificial vertical banks although the use of this habitat type was relatively low compared to the other riparian habitat types.

In spring, pike used reedy semi-natural banks significantly most, followed by bare semi-natural banks in all orders of analysis. Bare artificial vertical banks were significantly used more than other riparian habitats at the first and third order analysis, but not at the second order (Table 2). Similar to winter, the use of artificial foreshores was relatively low.

Habitat selection in spring was significant at the first ( $\lambda = 0.1170$ ,  $p\text{-value} = 0.0006$ ) and the second order ( $\lambda = 0.0737$ ,  $p\text{-value} = 0.0001$ ), but not at the third order

**Table 2**

Rank of the riparian habitat types according to their relative use from most used (top) to less used (bottom) in winter and spring in three orders of habitat selection (Aebischer et al., 1993; Johnson 1980). Bold text indicates significance and asterisks represent the number of habitat types that are significantly less used than the corresponding habitat type. Results of winter are based on 14 pike, results of spring are based on 12 pike (Table 1; B:AV = bare artificial vertical bank, R:AV = reedy artificial vertical bank, W:AV = woody artificial vertical bank, B:SNB = bare semi-natural bank, R:SNB = reedy semi-natural bank, W:SNB = woody semi-natural bank, B:AF = bare artificial foreshore, R:AF = reedy artificial foreshore).

First order	Second order	Third order
Winter		
R:SNB *****	R:SNB **	R:SNB ***
B:SNB ***	R:AV ***	B:SNB ***
B:AV *	W:SNB	B:AV ***
W:SNB	B:SNB	R:AF
R:AF	W:AV	W:SNB
R:AV	B:AV	R:AV
W:AV	R:AF	W:AV
B:AF	B:AF	B:AF
Spring		
R:SNB ***	R:SNB *	R:SNB ***
B:SNB ***	B:SNB	B:SNB **
B:AV **	R:AV	B:AV **
W:SNB	B:AV	W:SNB
R:AV	W:SNB	R:AV
W:AV	W:AV	W:AV
B:AF	R:AF	B:AF
R:AF	B:AF	R:AF

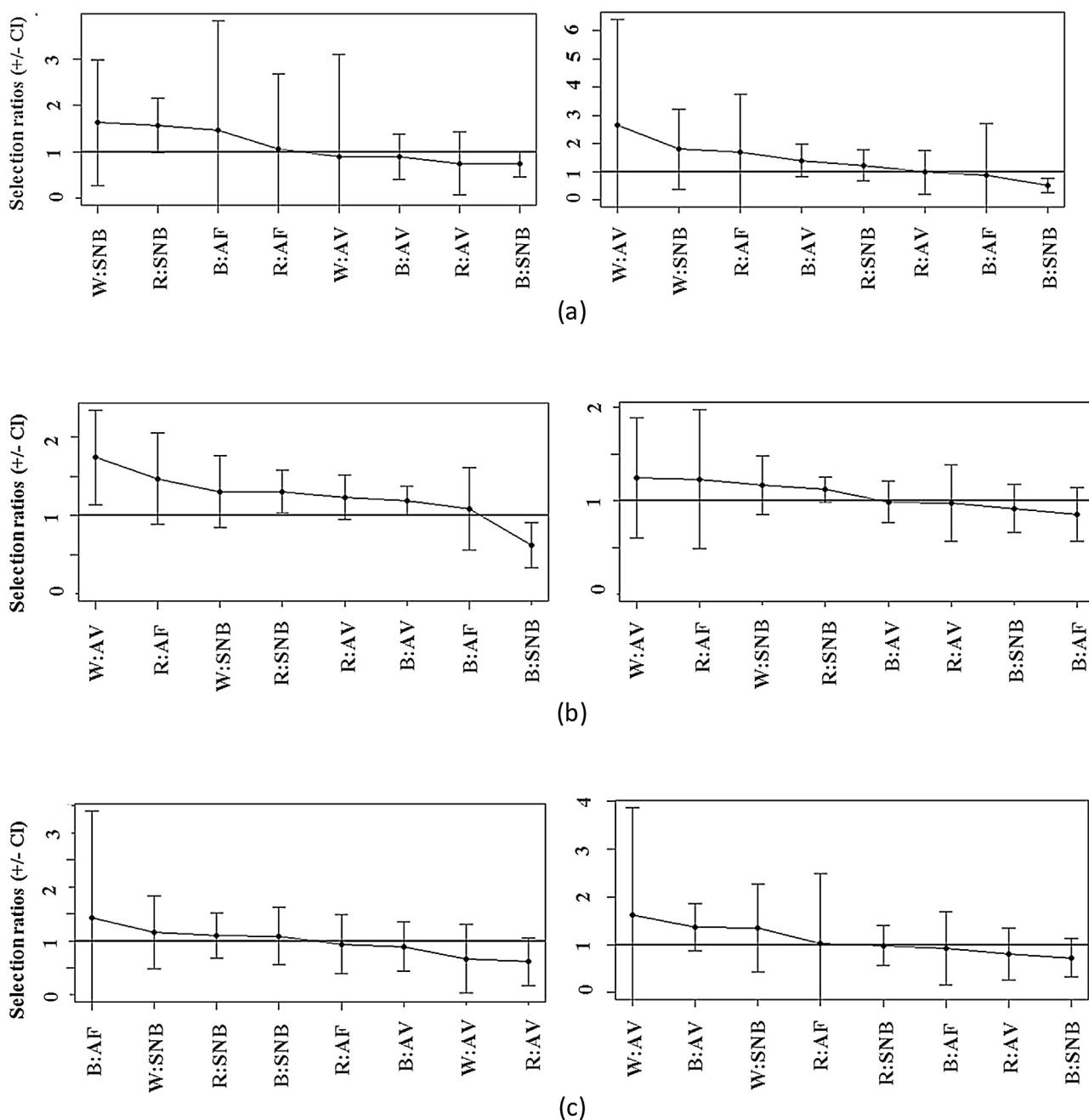
analysis ( $\lambda = 0.1426$ ,  $p\text{-value} = 0.1500$ ). The selection ratios and accompanying CIs revealed that pike did not significantly prefer a riparian habitat type in spring at the first order of habitat selection. In contrast to the significant high use of reedy semi-natural banks, no significant preference for this riparian habitat type was observed. Only in the second order of habitat selection the preference was nearly significant (Fig. 5).

At the meso-scale, the preference for the riparian habitat (calculated at the first order) differed significantly between individuals in both winter ( $\chi^2_{L1} = 130.01$ , df: 84,  $p\text{-value}: 0.0010$ ) and spring ( $\chi^2_{L1} = 135.63$ , df: 84,  $p\text{-value}: 0.0000$ ). The individual variation was the largest for those habitat types that were least available, such as woody semi-natural banks and bare and reedy artificial foreshores in winter (Fig. 5) and the woody habitats (woody artificial vertical banks and woody semi-natural banks), and artificial foreshores in spring (Fig. 5).

## 4. Discussion

### 4.1. Habitat use at the macro-scale

The analysis of the macrohabitat use demonstrates that in a lowland river characterised by an artificial environment pike not only intensively use the main river, but also river side arms and tributaries. Given the large home range of eight of the 12 studied pike in winter and spring, it is not surprising that pike also used side arms and tributaries beside the main river. However, the observation that they frequented specific tributaries and side arms may suggest that these tributaries and side arms are important. Seven pike collectively used two side arms in the centre of the study area in winter, although it is known that the foraging success of pike, which is a solitary sit-and-wait predator (Craig, 1996), decreases with an increasing density of conspecifics (Eklöv, 1992). One hypothesis explaining why pike used the side arms and probably gave up their potential territorial behaviour (Skov and Koed, 2004) is that pike look for areas of slower flowing to stagnant water to shelter from high flow. Although this hypothesis was not further investigated here, it could be supported by our analysis of the movement behaviour of pike, which revealed lower activity at high



**Fig. 5.** Selection ratios  $\pm$  95% confidence intervals (CIs, black lines) for the riparian habitat types in the river Yser in Belgium at the first (a), second (b) and third (c) order of habitat selection in winter (left) and spring (right); B:AV = bare artificial vertical bank, R:AV = reedy artificial vertical bank, W:AV = woody artificial vertical bank, B:SNB = bare semi-natural bank, R:SNB = reedy semi-natural bank, W:SNB = woody semi-natural bank, B:AF = bare artificial foreshore, R:AF = reedy artificial foreshore). Notice that the order of the riparian habitat types on the x-axis differs from Figs. 2 and 6 because they are ordered from highest to lowest selection ratio.

flow (Pauwels et al., 2014). The analysis of the movement behaviour was based on the same data as the analysis described here. Another hypothesis is that pike would leave the main river to exploit higher prey abundances. Masters et al. (2002) for instance revealed pike exploiting their prey in flooded fields and ditches in winter.

In spring, a large proportion of the observations outside the main river were situated in the small T3 and T4 tributaries upstream. Although pike spawning was not explicitly observed there, the observation of YOY indicates that spawning occurred in or near these tributaries. The YOY pike were found in tributaries of T3 and T4. These tributaries were shallower and fully covered with emergent and submerged vegetation and thus more in line with the spawning habitat requirements of pike than the habitat in T3

and T4 (Casselman and Lewis, 1996; Craig, 1996). Since four tagged pike invest energy in migrating 10 km upstream to these tributaries (Pauwels et al., 2014) in an energy demanding period (Diana, 1983), this may indicate the importance of these tributaries' habitat. However, another explanation could be homing behaviour of pike to the natal site. These observations are also supported by the observations of Koed et al. (2006) in a natural river system, demonstrating that despite suitable spawning grounds available near the areas where pike resided most of the year, several pike, mainly females, migrated to distant locations during spring.

The fact that two pike were always observed in the main river in spring could indicate that this habitat is suitable for spawning, or for pre-mature pike that have not spawned during the study

period. Since spawning was not observed in our study, further research could clarify this. The observation of juvenile pike in one side arm and in one artificial foreshore in the main river in a previous study might be an indication that spawning in the main river occurs (Mouton et al., 2012).

The high individual variation in use of the river, tributaries and side arms emphasizes the high importance of macrohabitat heterogeneity for adult pike. Our analysis at the macro-scale suggests that protection and creation of habitat heterogeneity by conservation and accessibility of existing tributaries and side arms might be more beneficial for the adult pike population than creation of new side arms.

#### 4.2. Habitat use and preference at the meso-scale

The analysis on the relative use of the riparian habitats revealed that irrespective of any assumption on habitat availability or use, reedy semi-natural banks were used most and significantly more than the other riparian habitat types in both winter and spring. The higher use of reedy semi-natural banks in winter observed in this study is in line with Kobler et al. (2008), who found a stronger association of adult pike with reed in winter than in summer. He suggests that pike follow their prey, which are less active and stay in refuges close to shore in winter. Based on literature it is also expected that pike would prefer riparian habitats that are least impacted and characterised by vegetation like reedy semi-natural banks (Grimm and Klinge, 1996). In contrast to the semi-natural banks, artificial foreshores were never significantly used. This suggests that pike might benefit more from conservation of existing semi-natural banks than from creation of artificial foreshores.

The analyses of habitat selection revealed significant selection for riparian habitat types at all orders of habitat selection in winter, and the first and second order in spring. This means that if we assume that adult pike were able to freely choose the habitat in the whole study area, without limitations like territoriality or migration barriers (Haugen et al., 2006), they significantly select one or more riparian habitat types. The absence of significant habitat preference in the third order analysis in spring means that no riparian habitat selection occurred within the home ranges. This might indicate that pike were free to choose their home range, which is further supported by the similar rank of the riparian habitat types in the first and third order analyses.

The selection ratios revealed that pike significantly preferred reedy semi-natural banks in winter and at the second order also in spring. These riparian habitat types were indeed also relatively often used, which might thus reflect the preference of pike for these riparian habitat types. In contrast, pike did not prefer bare semi-natural banks although they often used it. Potentially pike used the latter relatively often following the relative high and patchy availability. The preference for reedy semi-natural banks in winter is in line with Kobler et al. (2008), as mentioned earlier. Although no significant preference for woody semi-natural and artificial vertical banks was observed, the preference of woody artificial vertical banks and the higher proportion of woody semi-natural banks in the winter home ranges supports their potential importance for some adult pike. These results are further in line with Casselman and Lewis (1996), who indicated the importance of the boundary zone between stands of aquatic vegetation and the open water, providing an important edge affording ambush hunting sites (Casselman and Lewis, 1996; Chapman and Mackay, 1984a; Inskip, 1982). This might also support the observed preference for woody habitats beside reedy habitats, providing an edge for ambush hunting as well. Large individual differences in selection ratios were also observed, especially for the riparian habitat types that were ranked lower in the habitat use analysis (Aebischer et al., 1993) such as the woody riparian habitats. This is in line with

previously observed differences in preference between individuals (Chapman and Mackay, 1984b), but can also result from an unequal availability of these riparian habitat types to each individual due to an overall low availability in the study area.

The conclusions following from these results are similar to those from the macrohabitat analysis. The high variability in individual mesohabitat preference indicates that mesohabitat heterogeneity may be much more important for the population's welfare than previously expected and pike may benefit more from conservation of existing semi-natural banks than from restoration of artificial vertical banks.

Since the number of fish that could be tracked using radio telemetry in a large study area at daily time intervals is never substantially large (Koed et al., 2006; Ovidio and Philippart 2003; Vehanen et al., 2006 and references therein), it is necessary to question the representativeness of the number of studied fish for the population. Further research could indicate how representative 12 studied pike are for the pike population in the river Yser by precise estimates of the population size. However, the low catch frequency during regular fish samplings of the Research Institute for Nature and Forest in the river Yser from 1996 to 2012 ([www.vis.inbo.be](http://www.vis.inbo.be)), and the effort needed in this study to catch 15 adult pike already indicate a small population size. Regarding the statistical analysis, a sample size of 12 individuals is sufficient. Aebischer et al. (1993) indicated that 6 individuals is the absolute minimal sampling size necessary to correctly test for habitat preference and recommended 10 individuals (however, preferably >30) as a minimum to adequately represent a population. At the start of our study we caught and tagged 15 adult pike because this number was regarded the maximal number feasible to daily track by radio telemetry in this study area, which consists of more than 60 km of connected waterways. However, two pike were lost before half February and one was relocated less than 25 times. The resulting sample size of 12 pike is comparable to previous pike radio telemetry studies (Cook and Bergersen 1988; Kobler et al., 2008; Vehanen et al., 2006 and references therein). In two of these studies more than 15 pike were studied (Cook and Bergersen, 1988; Kobler et al., 2008).

The results of this study indicate the importance of habitat heterogeneity both at the macro- and meso-scale. River managers could focus on the lateral connectivity between the main river and its tributaries and side arms to conserve and optimize the heterogeneity at the macro-scale and could protect and restore riparian habitats that enables growth of emergent reed and of woody vegetation like trees and shrubs on the banks. Despite river restoration efforts, our findings underline the value of least impacted, (semi)natural habitats in an anthropogenically impacted river system. Loss of these remaining suitable habitats might threaten pike populations in artificial environments. Therefore, the precautionary principle should be applied while managing such river systems.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.limno.2016.10.001>.

## References

- Aebischer, N.J., Robertson, P.A., Kenward, R.E., 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74, 1313–1325.
- Baras, E., Nindaba, J., 1999. Seasonal and diel utilisation of inshore microhabitats by larvae and juveniles of *Leuciscus cephalus* and *Leuciscus leuciscus*. *Environ. Biol. Fish.* 56, 183–197.
- Bry, C., 1996. Role of vegetation in the life cycle of pike. In: Craig, J.F. (Ed.), *Pike: Biology and Exploitation*. Chapman & Hall, London, pp. 45–67.
- Calenge, C., 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* 197, 516–519.
- Casselman, J.M., Lewis, C.A., 1996. Habitat requirements of northern pike (*Esox lucius*). *Can. J. Fish. Aquat. Sci.* 53, 161–174.
- Chapman, C.A., Mackay, W.C., 1984a. Direct observation of habitat utilization by northern pike. *Copeia* 1984, 255–258.
- Chapman, C.A., Mackay, W.C., 1984b. Versatility in habitat use by a top aquatic predator, *Esox lucius* L. *J. Fish Biol.* 25, 109–115.
- Cook, M.F., Bergersen, E.P., 1988. Movements, habitat selection, and activity periods of northern pike in 11 mile reservoir, Colorado. *Trans. Am. Fish Soc.* 117, 495–502.
- Cooper, J.B., Mead, J.V., Farrell, J.M., Werner, R.G., 2008. Potential effects of spawning habitat changes on the segregation of northern pike (*Esox lucius*) and muskellunge (*E. masquinongy*) in the Upper St. Lawrence River. *Hydrobiologia* 601, 41–53.
- Copp, G.H., 1990. Effect of regulation on 0+ recruitment in the Great Ouse, a lowland river. *Regul. River* 5, 251–263.
- Copp, G.H., 1992. Comparative microhabitat use of cyprinid larvae and juveniles in a lotic floodplain channel. *Environ. Biol. Fish.* 33, 181–193.
- Craig, J.F., 1996. *Pike: Biology and Exploitation*. Chapman & Hall, London, UK.
- Diana, J.S., Mackay, W.C., Ehrman, M., 1977. Movements and Habitat Preference of Northern Pike (*Esox-Lucius*) in Lac Ste Anne, Alberta. *Trans. Am. Fish Soc.* 106, 560–565.
- Diana, J.S., 1983. An energy budget for northern pike (*Esox lucius*). *Can. J. Zool.* 61, 1968–1975.
- Eklöv, P., 1992. Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns. *Anim. Behav.* 44, 313–326.
- Engstrom-Ost, J., Lehtiniemi, M., Jonasdottir, S.H., Viitasalo, M., 2005. Growth of pike larvae (*Esox lucius*) under different conditions of food quality and salinity. *Ecol. Freshw. Fish* 14, 385–393.
- Farrell, J.M., Werner, R.G., LaPan, S.R., Claypoole, K.A., 1996. Egg distribution and spawning habitat of northern pike and muskellunge in a St Lawrence River Marsh, New York. *Trans. Am. Fish Soc.* 125, 127–131.
- Grimm, M.P., Klinge, M., 1996. Pike and some aspects of its dependence on vegetation. In: Craig, J.F. (Ed.), *Pike: Biology and Exploitation*. Chapman & Hall, London, UK.
- Haugen, T.O., Winfield, I.J., Vollestad, L.A., Fletcher, J.M., James, J.B., Stenseth, N.C., 2006. The ideal free pike: 50 years of fitness-maximizing dispersal in Windermere. *Proc. R. Soc. B* 273, 2917–2924.
- Hawkins, L.A., Armstrong, J.D., Magurran, A.E., 2003. Settlement and habitat use by juvenile pike in early winter. *J. Fish Biol.* 63, 174–186.
- Hobbs, N.T., Bowden, D.C., 1982. Confidence-Intervals on food preference indexes. *J. Wildl. Manage.* 46, 505–507.
- Horne, J.S., Garton, E.O., Krone, S.M., Lewis, J.S., 2007. Analyzing animal movements using Brownian bridges. *Ecology* 88, 2354–2363.
- Inskip, P.D., 1982. Habitat suitability index models: northern pike. U.S. department of the interior. *Fish. Wildl. Serv.*
- Jepsen, N., Beck, S., Skov, C., Koed, A., 2001. Behavior of pike (*Esox lucius* L.) > 50 cm in a turbid reservoir and in a clearwater lake. *Ecol. Freshw. Fish* 10, 26–34.
- Jepsen, N., Koed, A., Thorstad, E.B., Baras, E., 2002. Surgical implantation of telemetry transmitters in fish: how much have we learned? *Hydrobiologia* 483, 239–248.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71.
- Kobler, A., Klefoth, T., Wolter, C., Fredrich, F., Arlinghaus, R., 2008. Contrasting pike (*Esox lucius* L.) movement and habitat choice between summer and winter in a small lake. *Hydrobiologia* 601, 17–27.
- Koed, A., Balleby, K., Mejlihede, P., Aarestrup, K., 2006. Annual movement of adult pike (*Esox lucius* L.) in a lowland river. *Ecol. Freshw. Fish* 15, 191–199.
- Le Pichon, C., Trancart, T., Lambert, P., Daverat, F., Rochard, E., 2014. Summer habitat use and movements of late juvenile European flounder (*Platichthys flesus*) in tidal freshwaters: results from an acoustic telemetry study. *J. Exp. Mar. Biol. Ecol.* 461, 441–448.
- Manly, B.F., McDonald, L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Kluwer Academic Publishers, Dordrecht.
- Masters, J.E.G., Welton, J.S., Beaumont, W.R.C., Hodder, K.H., Pinder, A.C., Gozlan, R.E., Ladle, M., 2002. Habitat utilisation by pike *Esox lucius* L. during winter floods in a southern English chalk river. *Hydrobiologia* 483, 185–191.
- Miller, L.M., Kallemeij, L., Senanan, W., 2001. Spawning-site and natal-site fidelity by northern pike in a large lake: mark-recapture and genetic evidence. *Trans. Am. Fish Soc.* 130, 307–316.
- Mouton, A.M., Buysse, D., Stevens, M., Van den Neucker, T., Coeck, J., 2012. Evaluation of riparian habitat restoration in a lowland river. *River Res. Appl.* 28, 845–857.
- Ovidio, M., Philippart, J.C., 2003. Long range seasonal movements of northern pike (*Esox lucius* L.) in the barbel zone of the river ourthe (River meuse basin, Belgium). In: fifth conference on fish telemetry held in europe, ustica, Italy, 9–13 june 2003. vol aquatic telemetry. *Adv. Appl.*, 191–202.
- Pauwels, I.S., Goethals, P.L.M., Coeck, J., Mouton, A.M., 2014. Movement patterns of adult pike (*Esox Lucius* L.) in a Belgian lowland river. *Ecol. Freshw. Fish* 23, 373–382.
- R, d. c. t., 2010. *R: a Language and Environment for Statistical Computing*. R foundation for statistical computing, Vienna, Austria.
- Raat, A.J.P., 1988. Synopsis of biological data on the northern pike (*Esox lucius Linnaeus, 1758*). Review 2, FAO, vol 30. FAO Fisheries Synopsis, Rome, Italy.
- Radomski, P., Goeman, T.J., 2001. Consequences of human lakeshore development on emergent and floating-leaf vegetation abundance. *North Am. J. Fish. Manage.* 21, 46–61.
- Rogers, K.B., White, G.C., 1990. Analysis of movement and habitat use from telemetry data. In: White, G.C., Garrott, R.A. (Eds.), *Analysis of Wildlife Radio-Tracking Data*. Academic Press 1990, pp. 625–676.
- Skov, C., Berg, S., 1999. Utilization of natural and artificial habitats by YOY pike in a biomaniupulated lake. *Hydrobiologia* 408, 115–122.
- Skov, C., Koed, A., 2004. Habitat use of 0+ year pike in experimental ponds in relation to cannibalism, zooplankton, water transparency and habitat complexity. *J. Fish Biol.* 64, 448–459.
- Skov, C., Berg, S., Jacobsen, L., Jepsen, N., 2002. Habitat use and foraging success of 0+ pike (*Esox lucius* L.) in experimental ponds related to prey fish, water transparency and light intensity. *Ecol. Freshw. Fish* 11, 65–73.
- Skov, C., Jacobsen, L., Berg, S., 2003. Post-stocking survival of 0+ year pike in ponds as a function of water transparency, habitat complexity, prey availability and size heterogeneity. *J. Fish Biol.* 62, 311–322.
- Vehanen, T., Hyvarinen, P., Johansson, K., Laaksonen, T., 2006. Patterns of movement of adult northern pike (*Esox lucius* L.) in a regulated river. *Ecol. Freshw. Fish* 15, 154–160.
- White, G.C., Garrott, R.A., 1990. *Analysis of Wildlife Radio-Tracking Data*. Academic Press inc, San Diego, California.

## Web references

<http://www.vmm.be>, July 9th 2013, Flemish Environment Agency (VMM).

<http://www.vis.inbo.be>, November 4th 2013, Research Institute for Nature and Forest (INBO).