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Movement patterns of adult pike (*Esox lucius* L.) in a Belgian lowland river

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Abstract – Northern pike, *Esox lucius*, needs different habitats to survive and reproduce and thus depends on the availability and accessibility of these habitats. To efficiently manage pike, information is needed on its spatial and temporal patterns of migration. In this study, we investigated the occurrence of adult pike migration and which environmental variables influenced migration. From December 2010, we followed 15 pike for 1 year by use of radio telemetry in the River Yser, a typical lowland river characterised by anthropogenic impacts such as artificial embankments. Pike migrated most in February and March, which could indicate they frequented spawning habitat in this period. Four environmental variables significantly affected pike migration, ranging from the location where pike were observed (strongest effect), over water temperature and flow to diel water temperature change (weakest effect). The relation between migration and the location where pike were observed could demonstrate that pike preferred specific regions in the river. Increasing water temperature triggered migration for both sexes, and males started migrating at lower temperatures than females, which suggests that males start migrating earlier. This was the only substantial difference observed between male and female pike migration. The results suggest that migration was inhibited by high flow, as no migration was observed at high flow. River managers can use this information to efficiently manage their pike populations, for example, by removing or temporarily opening hydraulic structures like valves, weirs and sluices. This may facilitate access to suitable habitats at moments pike needs these habitats to fulfil its life cycle.

Key words: northern pike (*Esox lucius*); patterns of movement; radio telemetry; river management; fisheries management

Introduction

Loss of natural habitat by canalisation, water pollution and migration barriers causes pike (*Esox lucius* Linnaeus 1758) population declines and impedes successful restoration programmes (Chapman & Mackay 1984; Radomski & Goeman 2001; Ovidio & Philippart 2003). Indeed pike requires diverse habitats to successfully survive and reproduce, and therefore regularly migrates, specifically during the spawning season (Casselman & Lewis 1996; Ovidio & Philippart 2003; Koed et al. 2006; Vehanen et al. 2006; Craig 2008; Knight et al. 2008). Consequently, insight into pike migration and the environmental variables that affect migration is needed for effective conservation and restoration of the species.

Fish migration was defined as those movements that result in an alteration between two or more separate habitats, occurring with a regular periodicity (sometimes annual but certainly within the lifespan of an individual) and involving a large fraction of the population. It is predominantly directional and mostly occurs to and away from the feeding habitat, for instance to suitable spawning habitat (Northcote 1978). As the feeding and spawning habitat rarely overlap, migration mostly equals movement over a longer distance. In contrast, displacement is regarded as the daily movement between resting, hiding and foraging habitat and is therefore short distance and less directional. Most of the studies that have been devoted to pike movement thus far analysed patterns of displacement (Diana 1980; Cook & Bergersen 1988; Burkholder & Bernard 1994; Jepsen et al. 2001; Kobler et al. 2008). The few studies on pike migration have focused on sedentary versus active behaviour and have evaluated the periodicity of

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migration (Masters et al. 2003; Koed et al. 2006; Vehanen et al. 2006).

Thus far, little is known about the environmental factors influencing migration (Ovidio & Philippart 2003; Koed et al. 2006). It is assumed that migration to spawning grounds is initiated by high flows after ice-out (Craig 1996) and is triggered by an increase in water temperature (Ovidio & Philippart 2003). Nothing is known about the effect of diel temperature change on migration and a potential time lag between migration and water temperature or flow. Furthermore, it is possible that these effects differ between latitudes. This study is unique in the sense that it investigates the relation between diel water temperature change and migration and that it accounts for potential effects of the location where the pike were observed. Besides Masters et al. (2003), this is the only study investigating this in a lowland river at a latitude of 51°N. In addition to Masters et al. (2003), this river is characterised by anthropogenic impacts.

The aim of this study was to identify the occurrence of adult pike migration and which environmental variables influenced migration. Therefore, we firstly described the pattern of pike movement during 1 year and evaluated when migration occurred. Further, the effect of temperature, diel temperature change, flow and photoperiod on migration was analysed, taking into account sex, length and mass differences and potential dependence on the location in the river. If certain thresholds of, for example, temperature and flow could be identified at which pike starts migrating towards spawning areas, river managers can use this information, for instance, to temporarily open migration barriers in the river by adjusted barrier management.

Materials and methods

Study area

Pike were studied in the 44-km-long Belgian part of the River Yser and its tributaries (Fig. 1). The drainage area is 1101 km^2, and it has a rainfall-dominated hydrology with an average annual flow of 1.44 $m^3 \cdot s^{-1}$, a peak flow of 5.7 $m^3 \cdot s^{-1}$ and a base flow of 0.8 $m^3 \cdot s^{-1}$ (Mouton et al. 2012). The River Yser is a navigable waterway. A tidal sluice at the estuary prevents tidal-water-level fluctuation and inflow of salt water. Upstream of the sluice, 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

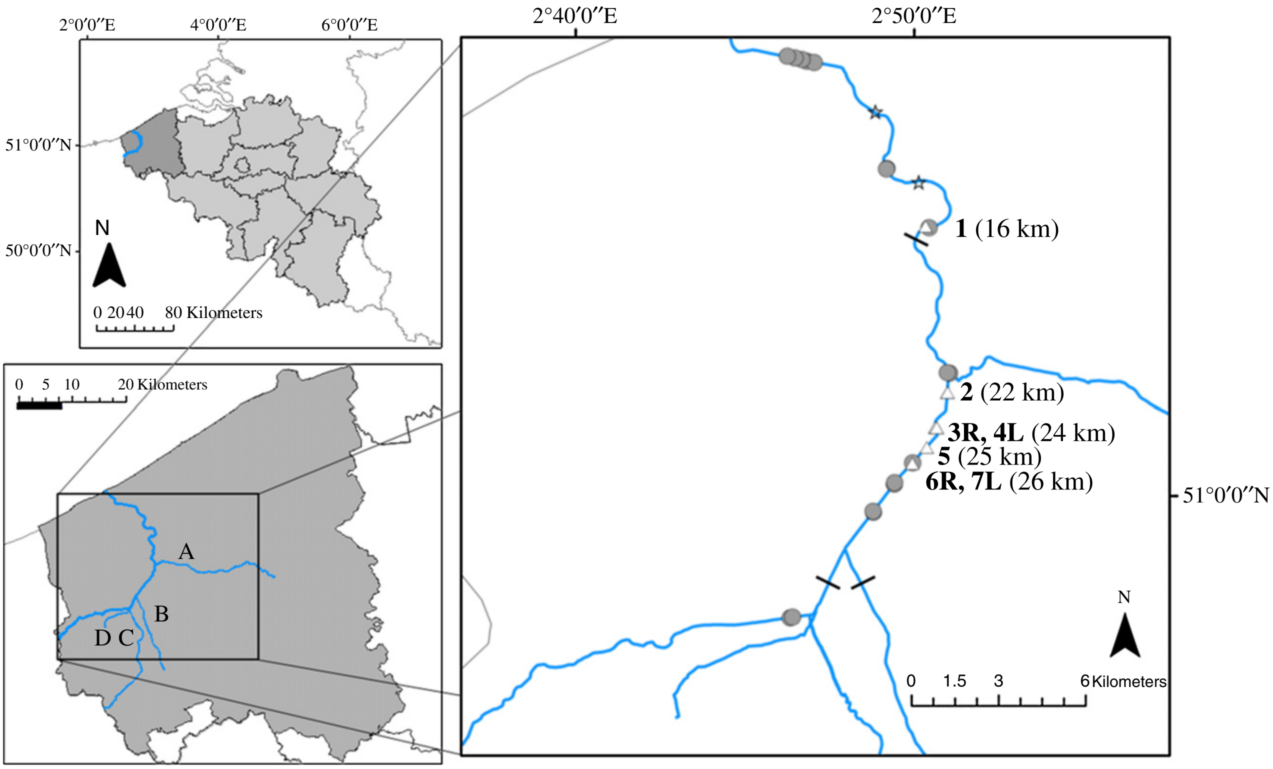

Fig. 1. The Belgian part of the River Yser, in Flanders (Belgium), and the fyke locations. Capture locations are described by an index (1–7), the position of the fyke near the left (L) or right (R) bank and the distance to the tidal sluice at the river mouth (km). Locations where temperature was logged are marked by a vertical line. (A = Handzamevaart, B = canal from the city of Ieper to the River Yser, C = Kemmelbeek, D = Boezingegracht; white triangles = pike caught for tagging, grey dots = no pike caught by fykes).

et al. 2012). Near the French border, the river is 8–10 m wide, and at the mouth, it is 25 m wide (Mouton et al. 2012). Due to canalisation, depth, substrate and flow velocity are distributed relatively uniformly. The water quality of the River Yser varies little throughout the year (Flemish Environment Agency, www.vmm.be). The conductivity averages 0.75 $mS \cdot cm^{-1}$, but can exceed 1 $mS \cdot cm^{-1}$ in extremely dry periods. In the study area, different river-bank types can be distinguished: artificial banks, foreshores, spawning grounds and seminatural banks (Mouton et al. 2012). Seminatural banks and spawning grounds are the most natural riparian habitats in the study area. 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. Daily flow data (±0.01 $m^3 \cdot s^{-1}$) were provided by the Hydrographic Information Centre (HIC, www.waterstanden.be).

Fish capture and tagging

Although historical evidence of a high-density population of pike in the River Yser exists, densities have been low since the first standardised observations in 1996 (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 24 November and 13 December 2010. At each sampling, two double fykes were placed in the river for 48 h. To maximise catch likelihood, locations were chosen such that they maximally covered the study area. In total, nine females and six males were caught at five different locations during seven 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, battery life: 502 days). Each transmitter had a different frequency between 40,000 and 41,000 MHz. The average female and male mass and length were 4213 ± 2889 and 4832 ± 2640 g, and 75 ± 16 and 81 ± 12 cm, respectively. Thus, the transmitters never exceeded 2% of the body mass (Jepsen et al. 2002). The transmitters were inserted into the body cavity through a ventral 20- to 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.

Tracking

Radio tracking was performed 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 m² and with a low-frequency loop antenna (Advanced Telemetry Systems Inc., Isanti, MN, USA) to subsequently localise the pike by triangulation (Diana et al. 1977; Rogers & Bergersen 1996; Rogers 1998; Jepsen et al. 2001) at a precision of 1–4 m² depending on the distance between the pike and the observer. The antennas were connected to a R2000 receiver (Advanced Telemetry Systems Inc., Isanti, MN, USA) that searched each frequency at 4-s intervals. The precise

Table 1. Overview of the biometric data of 15 pike in the Belgian part of the River Yser.

Sex	Tim'e of tagging	Length at tagging (cm)	Weight at tagging (g)	Number of observations	Fish ID (Freq. in MHz)	Catch location (Fig. 1)	Mean MDD (STDEV) ($m \cdot day^{-1}$)	Total observed movement (m)
F	13/12/2010	60	1057	79	40.600	3	658 (1230)	87170
M	1/12/2010	97	8150	91	40.611	3	114 (171)	25155
F	26/11/2010	55	1124	71	40.620	3	155 (210)	22600
M	10/12/2010	68	2350	69	40.630	2	640 (1051)	74116
F	2/12/2010	99	8750	74	40.651	2	1171 (1447)	107094
M	2/12/2010	67	1100	84	40.671	5	212 (384)	43159
F	24/11/2010	70	2927	61	40.681	3	273 (324)	28781
F	2/12/2010	85	5600	75	40.781	2	428 (734)	64502
M	10/12/2010	82	5010	77	40.801	2	605 (957)	109764
F	6/12/2010	59	1700	82	40.811	4	434 (639)	66588
M	1/12/2010	83	6070	83	40.820	3	569 (1034)	110585
F	24/11/2010	78	3700	60	40.841	1	786 (1001)	85256
F	1/12/2010	78	4430	29	40.661*	5	1734 (2044)	79262
M	1/12/2010	89	6310	30	40.771*	3	1187 (2202)	73526
F	10/12/2010	96	7340	17	40.831**	2	491 (440)	43119

Data of pike that were lost before half February (*) or were relocated less than 25 times (**) were omitted from statistical analyses.

positions of every tracked pike were directly recorded on a 1:500 map.

Pike were followed between November 2010 and December 2011. During the weeks immediately after their release, they were tracked daily. However, when the distance between consecutive observations was less than 500 m for more than 2 weeks, we started tracking less intensively (e.g., from 2/3 days to weekly), whereas tracking was intensified when increased activity was observed and when behaviour was less predictable such as at the expected start of spawning migration (i.e., when the distance between two consecutive observations exceeded 500 m when we were tracking weekly, and when the distance between the first and last of five consecutive observations exceeded 500 m when we tracked with 2/3 day intervals). During each tracking campaign, pike were tracked along 47 km of the river and tributaries by car. When pike were missing, they were searched by foot in the small tributaries. Except the three individuals that were omitted from data analysis, no fish were often missing.

Additionally, the occurrence of young-of-the-year pike (YOY) was evaluated by an electro- and fyke fishing campaign for YOY in the (artificial) spawning grounds and the tributaries in the study area in May and June 2011. In total, 26 locations were fished, of which five were located in spawning grounds, 13 in tributaries and eight in tributaries of tributaries. Two locations were situated in the same tributary. Three locations had been visited by tagged adult pike, and eight locations were within 500 m of a pike relocation.

Data exploration and analysis

Pike movement was quantified by the minimum average daily distance moved (MDD). The MDD was defined as the distance along the midline of the river between the positions of two consecutive observations of the same fish divided by the number of days between the observations. Data of two pike that were missing before half February and of one that was relocated too little were omitted from the analyses (Table 1). One (fish # 661; Table 1) of the two pike that were lost before half February lost his tag. The other pike (fish # 771; Table 1) could have been caught by anglers or could have migrated far upstream to spawn. We lost the animal on the 3rd of February 2011. We evaluated whether this fish had a different spawning location than the remaining fish during the days following this date by checking all accessible small tributaries, potential spawning grounds and the River Yser in the area till 12 km upstream of the study area. Nonetheless, it is possible that we missed this pike. Data from the first 2 weeks after tagging were deleted, to avoid potential distortion of results following tag implantation (Beaumont et al. 2002).

To evaluate the movement patterns of the pike and identify when migration occurred, we analysed the observations from December 2010 to December 2011. The analysis on the environmental variables affecting migration only included data from December 2010 to May 2011. MDD values were not normally distributed (Shapiro–Wilk *P*-value: 2.62156×10^{-39}) and were $\log(x + 1)$-transformed.

We analysed the impact of eight different variables on pike migration: the water temperature, which is the average of 1 day at three locations in the study area (Fig. 1), the diel (24 h) water temperature change, which is the difference in temperature between consecutive days, flow, the location in the study area where pike were observed, the photoperiod, mass, length and sex. However, initial data exploration (following Zuur et al. 2009) showed strong collinearity based on the variance inflation factor (VIF) between length and mass and between photoperiod and water temperature (Table 2), and length and photoperiod were thus omitted from further analysis. To avoid loss of information by removing length, we evaluated a potential effect of pike length, but no significant effect was found during backward selection in the GAM (*t*-value = 1.35, $P = 0.18$).

To investigate the impact of temperature and flow on migration, these variables were included in the analysis, but we also evaluated whether a time lag

Table 2. *P*-values of the *F*-statistic for two linear regression models: one model with all nine covariates (initial model) and one model without the covariates having a high collinearity (reduced model) and the variance inflation factor (VIF) values for the initial model. In the initial model, pike minimal average daily distance moved (MDD) is modelled as a function of the covariates listed in the first column. Sex is not included because this is a discrete covariate. In the second and third columns, the *P*-values and VIF values for the initial model are presented (note that no covariates have been removed yet). In the fourth column, *P*-values are presented for the model after collinearity has been removed by sequentially deleting each covariate for which the VIF value was highest until all remaining VIFs were below 3. The initial and reduced model differed significantly (*P*-value: 0.012).

Covariate	*P*-value (initial model)	VIF	*P*-value (collinearity removed)
Water temperature	0.308	38.645	0.311
Water temperature with time lag	0.008	40.429	Removed 1st
Diel water temperature change	0.838	2.638	0.054
Flow	0.012	8.413	0.035
Flow with time lag	0.097	8.824	Removed 3rd
Pike mass	0.339	26.081	0.332
Pike length	0.115	26.184	Removed 2nd
Photoperiod	0.068	7.475	Removed 4th
Location where pike were observed	0.000	1.038	7.833×10^{-5}

existed between peaks in pike migration, defined as the MDDs exceeding the 85% percentile of the MDDs per individual, and peaks in water temperature and flow. Specifically, we analysed the impact of temperature and flow on time lags of 1–5 days by defining the cumulative temperature and flow over these time lags. As these variables were highly correlated with the water temperature and flow (Table 2), we did not include the cumulative temperature and flow in the further analysis.

Because a full model with the remaining six covariates and all their interactions would still be too complex, we first evaluated whether all covariates and interactions are expected to have a significant effect on the MDD (Zuur et al. 2009). We found that pike mass did not significantly explain the remaining variance in the residuals of a LM containing all selected covariates besides mass, while other covariates did ($F = 1.77$, d.f. = 1, $P = 0.18$). Therefore, we omitted mass from further statistical analysis. Based on our ecological knowledge and interest, we evaluated whether the effect of temperature and flow on MDD differed between sexes, whether the effect of temperature on MDD depended on flow and *vice versa* and whether the effects of temperature and flow differed according to the location of the individual in the study area. Consequently, we started model development with five covariates and five-two-way interactions in the basic full model F1:

$$\begin{aligned}\text{LogMDD}_i = \alpha &+ \beta_{1i} * \text{water temperature}_i + \beta_{2i} \\ &* \text{diel water temperature change}_i \\ &+ \beta_{3i} * \text{flow}_i + \beta_{4i} * \text{location}_i + \beta_{5i} \\ &* \text{sex}_i + \beta_{6i} * \text{water temperature}_i \\ &* \text{sex}_i + \beta_{7i} * \text{flow}_i * \text{sex}_i + \beta_{8i} \\ &* \text{water temperature}_i * \text{flow}_i + \beta_{9i} \\ &* \text{water temperature}_i * \text{location}_i \\ &+ \beta_{10i} * \text{flow}_i * \text{location}_i + \varepsilon_i\end{aligned}$$

where α is the intercept, β_{ji} are the covariate coefficients, j is the index of the covariate and i is the ith record in the data set. To investigate how these variables and interactions affected pike migration, different models were fitted to the data: a linear model (LM), a general additive model (GAM), a general linear mixed model (GLMM) and a general additive mixed model (GAMM). Models were compared using the Aikake information criterion (AIC), and autocorrelation was evaluated using the autocorrelation function (ACF). All analyses were conducted using the nlme and mgcv libraries in R (Hastie & Tibshirani 1990; Wood 2006).

Starting from the full model (F1), we firstly investigated the addition of a random part to F1. We analysed the effect of adding individual pike as a random intercept and extended this with random slopes for temperature, diel temperature change, flow and location. Adding individual pike as random intercept substantially reduced the autocorrelation between consecutive observations. Specifically, in the LM (M1 in Table 3), autocorrelation was found between 10 consecutive observations, whereas this was reduced to correlation between only three consecutive observations when individual pike was added as a random intercept (M2 in Table 3). The GLMM with individual pike as random intercept and water temperature as random slope performed best.

Further exploration of the GLMM residuals indicated the need for nonparametric smooth functions to better describe the effects of the numerical covariates. The GLMM was therefore extended to a GAMM (M6 in Table 3), and similarly, the LM was extended to a GAM (M3 in Table 3). In both models (M6 and M3), a model selection was performed that led to M4 and M7, respectively. The difference existed in the smoothing function on water temperature and flow that contained two smoothers (one for each sex) in the GAM (M4 in Table 3), whereas this was only one for temperature and none for flow in the GAMM (M7 in Table 3). Although the autocorrelation between consecutive observations in the GAM was higher, it had a lower AIC than the corresponding GAMM (Table 3). Therefore, the GAM (M4, Table 3) was selected as the final model.

Table 3. Comparison of alternative models describing the effect of water temperature, flow, diel water temperature change, the location where pike were observed and their interaction with sex, on pike minimum average daily distance moved (MDD).

Model	Model description	−log-lik	d.f.	AIC
M1	LM on F1	−1530.822	12	3085.644
M2	GLMM on F1 with individual as random intercept and water temperature as random slope	−1487.852	15	3005.704
M3	GAM on F1	–	31	2860.367
M4	GAM on reduced F1, two smoothers on water temperature, two on flow and two on location	–	27	2854.239
M5	GAM on reduced F1, one smoother on water temperature, none on flow and one on location	–	16	2868.262
M6	GAMM on F1 with random part of M2	−1455.660	15	2941.320
M7	GAMM on reduced F1 with random part of M2, one smoother on water temperature, one on flow and one on location	−1428.292	11	2878.584

Models were compared using the Aikake information criterion (AIC). All analyses were conducted using the nlme and mgcv library in R (Hastie & Tibshirani 1990; Wood 2006). −log-lik, log-likelihood ratio; d.f., degrees of freedom.

$$\begin{aligned}\text{LogMDD}_i = \alpha &+ f_{1i}(\text{water temperature}_i * \text{sex}_i)\\ &+ \beta_{2i} * \text{diel temperature change}_i\\ &+ f_{2i}(\text{flow}_i * \text{sex}_i)\\ &+ f_{3i}(\text{location}_i * \text{sex}_i) + \varepsilon_i\end{aligned} \quad \text{(M4)}$$

Results

Annual movement

The estimated MDDs differed significantly between different months ($F = 12.5$, d.f. = 11, $P = 2.2 \times 10^{-16}$). Specifically, the MDD (minimum average daily distance moved) was highest during February and March (Fig. 2). Overall, pike migrated less than 500 m·day^{-1} for most of the time (75%) and only sporadically moved distances up to 2000 and 4000 m·day^{-1} (Fig. 2 and Figure S1, Table 1).

Migration

About 75% of the distances longer than 2000 m·day^{-1} were travelled during February and March. Two female pike and one male never swam more than 1000 m·day^{-1} (Table 1, Figure S1B, C and G in the Supporting information).

During February and March, eight pike migrated to locations that were distinct from the locations where they resided most of the year in the river (Figures S1 and S2 in the Supporting information). At least three of these migrated to two smaller upstream tributaries where YOY pike were found during the YOY fishing campaign. The male pike that never moved farther than 1000 m·day^{-1} was one of these. This indicates that migration to a spawning area does not necessarily entail a longer distance (Figures S1 and S2 in the Supporting information).

Triggers for pike migration

Four environmental variables significantly affected pike migration, ranging from the location where pike were observed (strongest effect), over water temperature and flow to diel water temperature change (weakest effect). The MDD increased when the water temperature rose to 9–10 °C, above which it tended to decrease again (Fig. 3). Specifically, male pike MDD increased with rising water temperatures between 0 °C and 8 °C, whereas female pike MDD only increased at temperatures above 5–6 °C, till 10 °C (M4: $F_{\text{females}} = 3.21$, $P_{\text{females}} = 0.003$, $F_{\text{males}} = 5.97$, $P_{\text{males}} = 0.000$, Fig. 3). The relation between the MDD and the diel temperature change was positive (M4: estimated coefficient = 0.27 ± 0.11, $t = 2.56$, $P = 0.011$). Furthermore, the MDD slightly decreased with increasing flow. The male pike MDD decreased slightly more with rising flow than the female pike MDD (M4: $F_{\text{females}} = 1.20$, $P_{\text{females}} = 0.308$, $F_{\text{males}} = 13.23$, $P_{\text{males}} = 0.000$, Fig. 3). Our initial data exploration indicated that this correlation was even more negative above flows of 20 m^3·s^{-1}. This was not found after model selection, which indicated a linear relationship between MDD and flow. The MDD was also significantly related to the location in the study area, being low between 22 and 25 km upstream and higher both upstream and downstream of this location (M4:

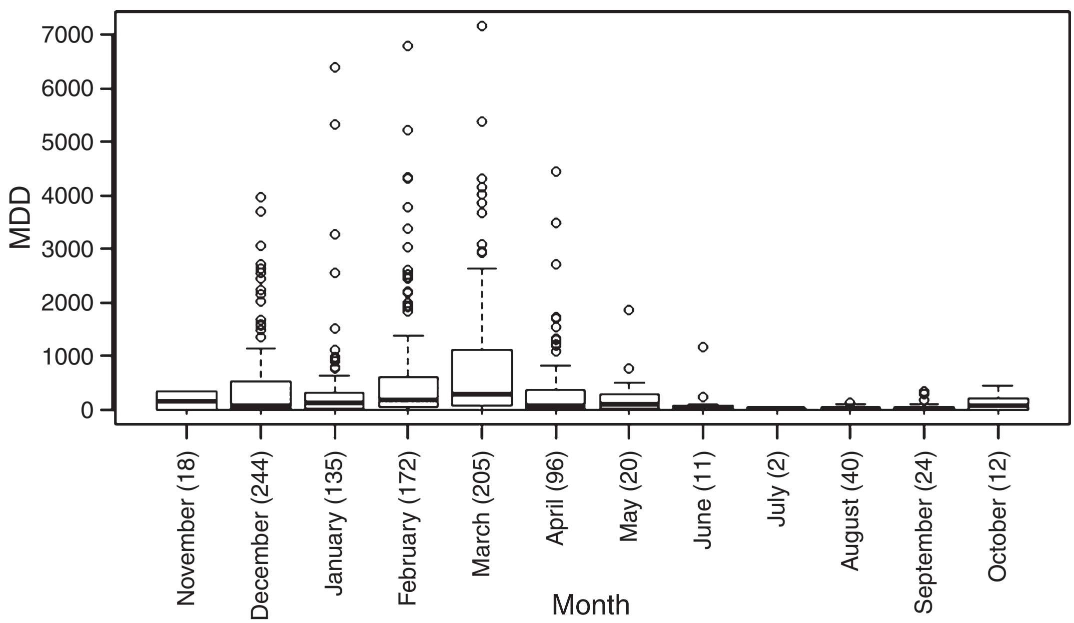

Fig. 2. Box plots of the minimum average daily distance moved (MDD) for 12 pike per month. The numbers in the *x*-axis indicate the number of pike observations per month. (bold vertical line: average, whisker: minimum and maximum without outliers, circle: outlier).

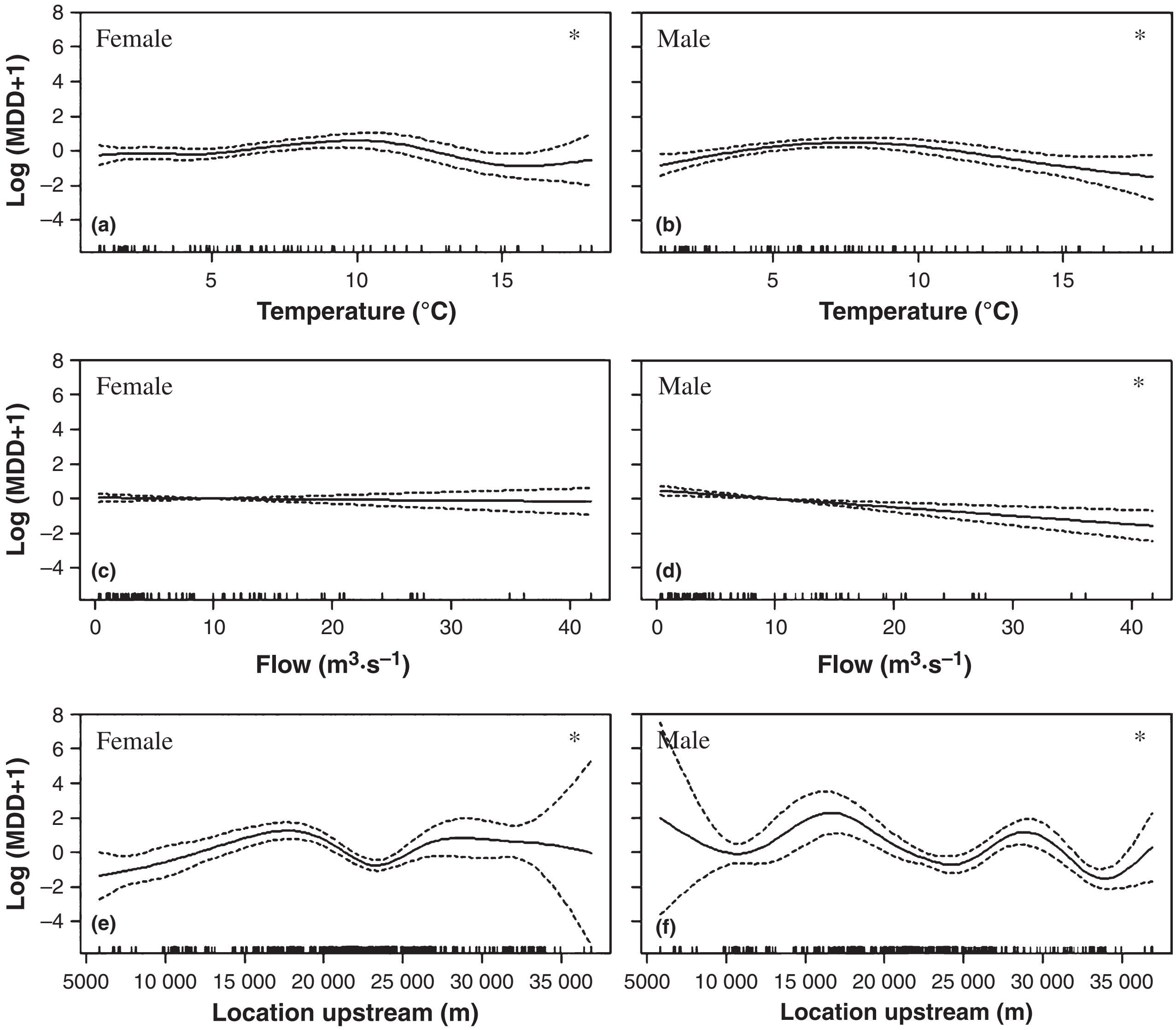

Fig. 3. Smoothers and 95% pointwise confidence intervals from model M4 (a to f), illustrating the nonlinear relations between log (MDD+1) and water temperature (a, b), flow (c, d) and location in the study area (e, f) for each sex. Significant relations are marked by asterics. (a: P = 0.0034, b: P = 0.0001, c: P = 0.3079, d: P = 0.0003, e: $P = 3.62 \times 10^{-10}$, f: $P = 2.46 \times 10^{-9}$).

$F_{females} = 8.53$, $P_{females} = 3.62 \times 10^{-10}$, $F_{males} = 7.17$, $P_{males} = 2.46 \times 10^{-9}$, Fig. 3).

Model selection revealed that the interactions between the environmental variables and location in the study area were insignificant. Specifically, the significant relationship between pike MDD and location in the study area does not mean that the pike's reaction to temperature and flow depended on their location. Although the location in the study area appeared to have the strongest impact on MDD, this does not imply that location is triggering migration.

Discussion

Pike MDDs were highest between December and May with a peak in February and March. Higher MDDs from December to February could be explained by a high competition for food during these months (Chapman 1968; Dawson et al. 1991; Knight et al. 2008), whereas higher MDDs between February and May could coincide with the spawning migration, which is often observed to encompass longer distances compared with the distances moved during the rest of the year (Ovidio & Philippart 2003; Koed et al. 2006). The higher MDDs in February and March correspond with earlier observations by Koed et al. (2006) and Knight et al. (2008). Cook & Bergersen (1988) reported a higher pike activity during April and May and the lowest activity during October. In contrast, Kobler et al. (2008) and Vehanen et al. (2006) both reported a higher pike activity from the beginning of June to September and a lower pike activity from December to March and from October to April, respectively, whereas Baktoft et al. (2012) observed no consistent seasonal trend in pike activity.

Our analysis on the relation between environmental variables and migration revealed that four environmental variables significantly affected pike migration, ranging from the location where pike were observed (strongest effect), over water temperature and flow to the diel water temperature change (weakest effect). Specifically, the relation between the location where pike were observed and the MDD revealed a lower MDD in an area between 22 and 25 km upstream of the tidal sluice. This may suggest a preference of pike for this specific area or habitat type. The area is characterised by a seminatural riparian habitat, which is assumed to be the most suitable habitat type available. Other characteristics such as river morphology and prey densities may also affect the low MDDs in this area, but this was not further investigated in this study. Despite the significant relation between the location where pike were observed and the MDD, this location had no significant influence on the relations between temperature and MDD, and flow and MDD.

The relation between water temperature and MDD showed an increase in MDD with rising temperatures until a maximum of 10 °C, above which MDD decreased again. This corresponds with the assumption that pike spawning migration is stimulated by rising temperatures (Craig 1996; Lucas et al. 2001; Ovidio & Philippart 2003) and is in line with the analysis of Lucas (1992), who found highest daily pike movement between 8 and 10 °C. In the study of Ovidio & Philippart (2003), pike started the upstream migration at temperatures between 6.7 and 8.7 °C. We hypothesise that 9–10 °C is a threshold level for migration in our study, as the activity was highest at ca. 9 °C, and there was only a 1-day time lag between migration peaks and temperature peaks exceeding 10 °C. The decrease in MDD at temperatures above 10 °C could indicate that pike have arrived at their spawning area by then. Although we could not observe spawning after migration, the occurrence of YOY pike at two locations visited by tagged pike suggests that at least some tagged pike visited habitats that are most likely to be suitable for spawning.

The different effects of water temperature on MDD of male versus female pike found in our study indicate that male pike are triggered to migrate at lower temperatures than female pike. Male pike MDDs increased when temperature exceeded 0 °C, while female pike MDDs only increased when temperature exceeded 5–6 °C. Craig (1996) also reported that males started spawning migration earlier than females.

The relation between diel water temperature change and MDD was linear and indicated that the MDD slightly increased with increasing diel water temperature change. This relation was, however, less significant than the relation between MDD and water temperature, which may indicate that water temperature more strongly affects pike migration than the diel temperature change.

Although Craig (1996) demonstrated that migration was triggered by increased flow, we observed a negative relation between MDD and flow. This discrepancy may be because the water velocity in the River Yser often exceeded the critical velocity that inhibits pike movement during the study period (Jones et al. 1974).

Sex had no significant effect on pike MDD and only affected the relations between MDD and water temperature, flow and the location where pike were observed. The insignificant relation between sex and MDD is in line with the study of Burkholder & Bernard (1994), but contrasts with the observation of sex-dependent movement rates by Lucas (1992) and Koed et al. (2006). Lucas (1992) observed a higher activity of males, whereas Koed et al. (2006) found a higher activity of females. The dissimilarity of the discussed studies is notable and was also observed in studies on pike's diurnal activity, on the grouping of pike into sedentary and active animals and on the pike length–movement rate relation. As Kobler et al. (2008) and Jepsen et al. (2001) already stated, these differences might reflect not only variation in pike behaviour among different ecosystems, but also differences in method and study design.

In this respect, we suggest the most important differences between our study and the aforementioned pike telemetry studies are the shape (lake versus river) and the length of the study area, besides the statistical method applied compared with the migration studies. Compared with the aforementioned studies, we also studied between 5 and 40 pike. We tracked the pike for 1 year at different sampling intervals, which is comparable with the protocols of the aforementioned studies on pike in rivers (Ovidio & Philippart 2003; Koed et al. 2006; Vehanen et al. 2006), but contrasts with most of the studies in lakes, specifically with those of Diana (1980) and Baktoft et al. (2012), in which pike were tracked at equal, short time intervals over 50 days and 2 years, respectively. Apparently, the tracking protocols in radio telemetry are highly dependent on the shape and extent of the study area. Continuous monitoring of tagged fish to a few metres precisely using acoustic telemetry and stationary radio receivers is only possible in a small lake. Consequently, the sampling intervals are larger and more variable in telemetry studies on rivers, specifically on large river systems.

The study of Baktoft et al. (2012) indicated that long sampling intervals may entail a great sampling error. This is also applicable to our study, even though this sampling error was minimised by only lowering the tracking frequency when reduced activity was observed. For instance, pike were observed to be less active from May to November, so sampling error is expected to be relatively low in this period, even though our tracking frequency was lowered (Cook & Bergersen 1988; Koed et al. 2006; Knight et al. 2008). Our study area entailed >60 km of accessible river channels, whereas this was between 2 and 30 km in other studies (Masters et al. 2002, 2003; Ovidio & Philippart 2003; Koed et al. 2006; Vehanen et al. 2006). In a study area of this size, it is practically impossible to track more than 15 pike at equal small (daily) sampling intervals for more than one season. This is further evidenced by Koed et al. (2006), who studied 10 pike, and Ovidio & Philippart (2003), who studied six pike. We suggest that studies with a similar approach therefore combine periods of high (daily) tracking frequency with periods of low (weekly) tracking frequency or apply more sophisticated approaches to allow detailed tagging of a high number of pike in a large study area.

The lack of complete certainty on the occurrence of spawning after migration was encountered as a limitation here to exclusively investigate the triggers for spawning migration. To overcome this problem, future research on the triggers of migration could be expanded by an identification of the true purpose of each migration. For instance, accelerated failure time or Cox regression (Castro-Santos & Haro 2003) could be applied to analyse the triggers for spawning migration. Besides, it could reveal how many individuals of the population spawn and migrate to spawn and how many spawning migrations occur per individual during one spawning period.

Based on our results, river managers could consider the impact of water temperature on pike migration to facilitate accessibility of small tributaries and spawning grounds, for example, by opening valves at water temperatures between 0 and 12 °C. The apparent inhibition of pike migration at high flows suggests that pike could benefit from the buffering of peak flows, for example, by restoring floodplains and increasing lateral connectivity. Our study not only provides further insight into pike migration, but also presents a statistically underpinned approach to analyse the complex nonlinear relation between environmental variables and fish migration in general. This information may be crucial for effective conservation worldwide and to evaluate management actions, such as the restoration of connectivity to spawning habitat.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Water temperature and flow versus minimum average daily distance moved (MDD) of 12 pike (A to L).

Figure S2. Location where pike were observed versus water temperature and flow of 12 pike (A to L).