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Spatial behaviour of young-of-the-year northern pike (*Esox lucius* L.) in a temporarily flooded nursery area

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Abstract – Unlike adult northern pike (*Esox lucius*), small-bodied young-of-the-year (YOY) individuals cannot be tracked by conventional telemetry, and virtually no data exist on their spatial behaviour. Here, we monitored 192 individuals released into a nursery area (0.47 ha, subdivided into 253 cells of 4 m × 5 m) that dried out progressively using a portable passive integrated transponder detector. Among them, 66 spent more than 5 days in the nursery area and were localised at least twice, allowing spatial behaviour analyses. The mean radial distance moved averaged 14.3 m (±8.4 SD, range 2.2–41.0) and the average daily movement was 8.0 m·day^{-1} (±5.3 SD, range 0.6–31.1). Pike abundance in a cell significantly correlated with the abundance observed in adjacent cells within 32 m, confirming a patchy distribution. A selective use of the deepest area was measured while no effect of vegetation cover was observed at the cell scale. The existence of YOY pike aggregations and the positive correlation between water depth and their spatial distribution might, however, facilitate predation and/or cannibalism during this critical period. This also suggests that the choice of release habitats requires particular attention during restocking procedures.

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Key words: aggregation; hatchery-reared fish; passive integrated transponder; telemetry; vegetation cover; water depth

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Introduction

Northern pike (*Esox lucius* L.) is a species particularly adapted to shallow freshwater environments (Casselman 1996), and seasonally flooded and vegetated areas are essential spawning and nursery habitats for larvae and juveniles (Souchon 1983; Wright & Shoesmith 1988). When young-of-the-year (YOY) pike hatch in temporarily flooded habitats, they have to cope with the decrease in water level and ultimately total drying out during their first weeks of life, inducing their first key displacements (Craig 2008).

Patterns of individual movements of YOY pike during their first weeks of life in nursery areas are largely unknown, although this might be an issue for recruitment success and restocking programmes. Indeed, the survival rate of YOY pike is usually low (e.g., Lucchetta 1983; Gronkjaer et al. 2004) and high predation rate, cannibalism and food resource shortage have often been reported as possible causes of stocking failure (Lucchetta 1983; Bry et al. 1995; Skov et al. 2003; Gronkjaer et al. 2004). As opposed to adults, conventional telemetry cannot be used for YOY individuals which are a few weeks old. Field investigations are so technically challenging that no data exist on spatial behaviour of YOY pike in nursery habitats.

Recently, passive integrated transponder (PIT) telemetry has emerged as an innovative method to actively monitor small-bodied fish movements in shallow water. The system consists of using a portable detector to locate PIT-tagged fish and recent advances allow accurate detection of 23-mm (e.g., Morhardt et al. 2000; Roussel et al. 2000) and 12-mm PIT tags (e.g., Cucherousset et al. 2005; Keeler et al. 2007) and

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the monitoring of YOY fish movements *in natura*. New issues on fish ecology have been addressed (e.g., Cunjak et al. 2005) and this novel technique has also been used successfully with amphibians (Cucherousset et al. 2008) and crayfish (Bubb et al. 2006).

Investigations on the behaviour of hatchery-reared YOY fish released in the wild are crucial for improving the efficiency of stocking programmes. In a recent paper, Cucherousset et al. (2007a) used PIT telemetry to study the fate (i.e., survival) of 5-week-old hatchery-reared YOY pike after their release into a temporarily flooded nursery area using PIT telemetry with a fairly good detection efficiency (>70%). The present work examines the spatial behaviour of the same PIT-tagged YOY pike to determine how they cope with the progressive drying out of their new habitat. More particularly, we focus on: (1) the mobility of YOY pike in this nursery area, (2) temporal changes in YOY pike spatial distribution and (3) the role of water depth and vegetation cover on YOY pike spatial distribution in the nursery area.

Materials and methods

Study area

The study was carried out in the Brière marsh (north-west France, 47°22′N, 02°11′W), a 7000-ha freshwater marsh composed of a network of permanently flooded canals (144 km covering 206 ha) within a large mosaic of seasonally flooded reed beds (5000 ha) and grasslands (1000 ha; for more details see Cucherousset et al. 2006). Temporary habitats generally flood in winter and dry out progressively during spring and summer as a result of the rainfall regime and water level management. The present study was carried out in spring 2005 (May to June, i.e., when the water level decreases) in a typical grassland located in the heart of the Brière marsh. This grassland was selected because it possesses typical spawning substrate for pike, as well as the characteristics of nursery area for juveniles. Reproduction of wild pike has already been recorded here (Cucherousset et al. 2007b). The 0.47-ha flooded grassland was subdivided into 253 rectangular cells (4 m × 5 m) using transect lines. This area was linked to a pond via a single connection point. A fyke net (5-mm mesh) was set up permanently at this connection point to trap all fish leaving the grassland and it was checked on a daily basis.

Substrate, water depth and vegetation cover were measured in each cell just prior to stocking. The substrate consisted exclusively of compact peat with no soft bottom. Mean water depth was 15.1 cm ± 5.6 SD (range 0–36 cm) at the start of the study (20 May 2005). Vegetation was highly dominated by Poaceae with sparse patches of submerged plants (*Ranunculus* spp. and *Callitriche* spp.) and *Phragmites australis.* On average, vegetation covered 47.2% (± 28.5 SD) of the total area on 20 May. At the beginning of the survey, vegetation cover significantly and negatively correlated with water depth (Pearson correlation, $r = -0.33$, $P < 0.001$, $N = 253$). During the study, the water level of the marsh was recorded daily (source: Parc naturel regional de Brière) making it possible to back calculate temporal changes in water depth in the cells of the nursery area. The vegetation cover was only measured at the beginning of the survey as no significant changes were expected in the course of the study. Water temperature was recorded in one location in the flooded grassland every 15 min throughout the survey using an automatic sensor (Sensor StowAway TidBit; Onset Computer Corporation, Bourne, MA, USA). During the survey, the water level fell continuously until the grassland dried out completely in mid-June, but the water temperature did not follow any particular trend (mean daily value 20.0 °C ± 2.5 SD, Fig. 1). The wet area of the study site was relatively constant until 6 June despite the progressive decline in water level, but afterwards it decreased severely until it dried out totally (Fig. 1).

Fish tagging, stocking and tracking

The YOY pike came from manual fertilisation of gametes of adults collected in the wild. They were hatchery reared and fed with zooplankton. A total of 197 individuals (mean fork length 51.0 mm ± 5.3 SD, min 42, max 65) were anaesthetised with eugenol (0.04 $ml \cdot l^{-1}$). A PIT tag was inserted into the peritoneal cavity using a sterile needle mounted on an injector, and the left pelvic fin was partially clipped to assess tag loss. The PIT tags were 11.5 mm long and 2.1 mm in diameter (Trovan ID 100; EID Aalten B.V., Aalten, The Netherlands); they weighed 0.100 g in air and 0.058 g in water. Initial tag-to-body weight ratio [100 × (tag weight)/fish weight at tagging, in %] ranged from 5.9% to 20.0% (mean 13.3% ± 7.7 SD) in air, and from 3.4% to 11.6% (mean 7.7% ± 2.3 SD) in water. To minimise adverse tagging effects on fish, it has traditionally been suggested that tag-to-body weight ratio should not exceed 2% in air (Winter 1996). This standard is, however, not always supported by empirical data. Recent works demonstrated that this is highly species dependent (Adams et al. 1998; Baras et al. 2000; Knaepkens et al. 2007). For example, using tag-to-body weight ratios ranging from 1.8% to 11.6% in water, Acolas et al. (2007) demonstrated that brown trout (*Salmo trutta*) with tag-to-body weight ratios <3.4% can be PIT tagged with negligible effects on survival and growth, but that this can lead to relatively high tag rejection rates. Although we are not aware of any formal attempt to determine the minimum size at

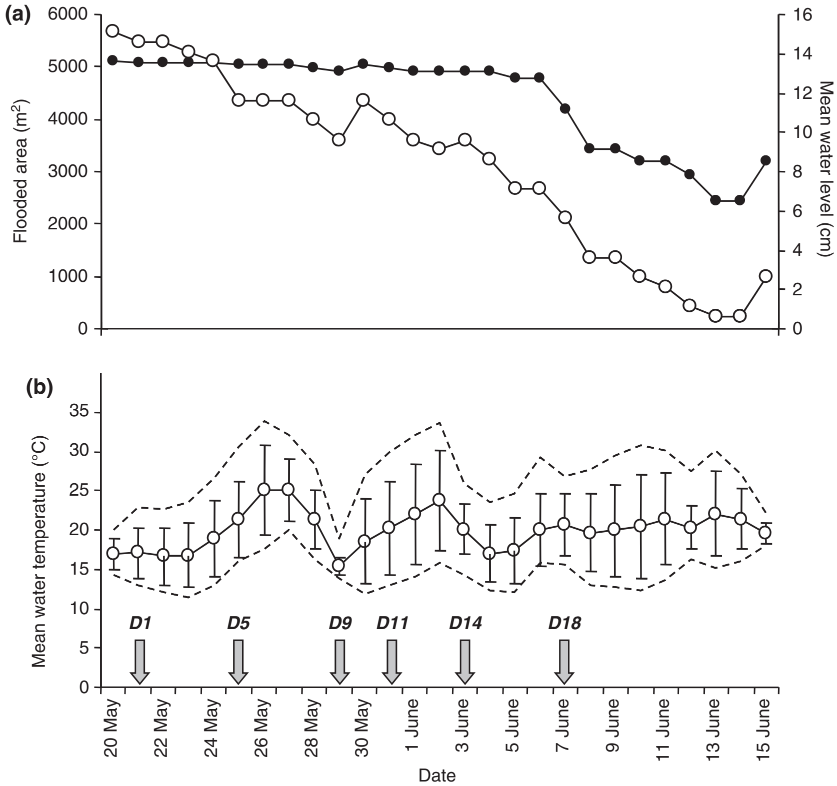

Fig. 1. Daily changes in (a) water level (in cm, black symbols) and extent of flooded area (in m^2, white symbols), and in (b) mean water temperature (in °C) in the nursery area of the Brière marsh (France) from 20 May to 17 June 2005. Vertical bars represent standard deviation errors of water temperature, and upper and lower lines, the maximal and minimal values. Tracking dates of PIT-tagged YOY pike (with abbreviations) are indicated by grey arrows.

PIT tagging of pike, individuals with a relatively high tag-to-body weight ratio were tagged here because of specific characteristics of pike. Indeed, cannibalism is a common feature in this species and it often results in the predation of large-bodied congeners, demonstrating a large elasticity of the peritoneal cavity. Bry et al. (1992) found that the overall mean ratio of pike prey length to pike cannibal length was 66.2% (ranging from 35.0% to 85.4%) in semi-natural conditions, demonstrating that individuals are thus often highly loaded with their food items. For the present data set, the absence of significant difference in mortality rate between PIT-tagged and control YOY pike and the absence of tag loss in recaptured fish strongly suggest that PIT tagging had no significant adverse effects on YOY pike survival (Cucherousset et al. 2007a). Furthermore, no differences in growth performance according to individual body size at tagging were detected, indicating that PIT tagging did not affect the growth of small fish predominantly, as it would have been expected if the effect of tagging on growth was size dependent (Cucherousset et al. 2007a).

Fish were given 6–8 h to recover (five fish died during this period) before being transported to the nursery area in groups of 13–15 individuals, according to local stocking practices to avoid cannibalism during transport. A total of 192 individuals were released randomly at 13 cells into the grassland on 20 May 2005 (D0, Fig. 2). There was no difference in water depth and vegetation cover between the cells where YOY pike were released and the other cells of the nursery area (Mann–Whitney test, $U > 1170$, $P > 0.112$, $N = 253$). During 18 consecutive days (21 May to 7 June), pike trapped in the fyke net were checked for PIT tags before being released into the adjacent pond. During the study period (D1–D18), the position of PIT-tagged pike in the nursery area was recorded every 2–4 days using a portable PIT detector as described in Cucherousset et al. (2007a). The portable PIT detector consisted of one RFID reader (LID 650; EID Aalten B.V.) interfaced with an LCD screen and powered by a 12-V battery. The reader was connected to a waterproof antenna (ANT 612; EID Aalten B.V.) mounted on a 3-m-long aluminium pole. During tracking, the antenna was moved above the water surface by wading between two transects and the entire wet area was scanned in about 8–10 h. When a PIT tag was detected, the tag code was displayed and a piezoelectric buzzer emitted a sound to alert the operator. Although it is possible to localise a fish to the nearest 30 cm, each pike position was plotted relative to one of the 253 rectangular cells. The reason why we did not work at the microhabitat scale is that short fleeing displacements might have occurred when the operator was tracking the study area with the portable antenna, and the size of the cells (4 m × 5 m) was determined according to this consideration. The maximum tag detection distances range from 30 to 36 cm, depending on the orientation of the tag (Cucherousset et al. 2005). Here, this ensured a high detection

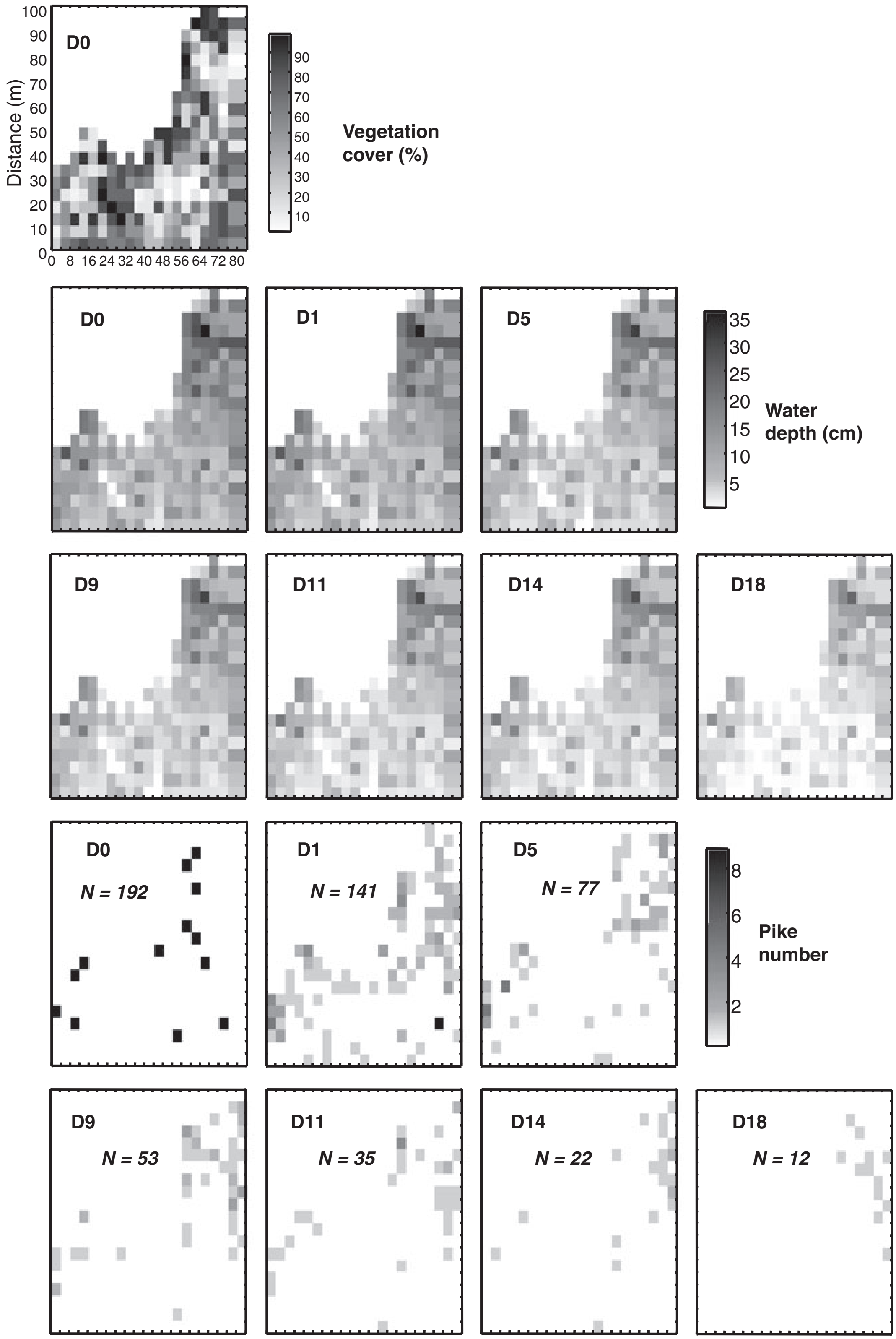

Fig. 2. Vegetation cover (%) at D0 (day 0), and temporal variation in water depth (cm) and spatial distribution of PIT-tagged YOY pike at different tracking dates (expressed in days after stocking) in the nursery area of the Brière marsh (France). The number of fish detected in the flooded grassland is reported at each tracking date (in italics).

efficiency (>70%) as the water depth in the grassland never exceeded the maximal reading distance (Cucherousset et al. 2007a). Furthermore, vegetation did not hamper the operator to move the portable PIT antenna above the water surface. A total of six tracking surveys were made from D1 to D18. On 15 June, two persisting pools in the nursery area (size 40–50 m^2, mean water depth 4.97 cm ± 4.1 SD) were completely disconnected from the adjacent pond; they were electrofished, but no YOY pike were found.

Data analysis

Mortality was high during the 5 days following fish release into the nursery area, and both cannibalism and predation by piscivorous birds were suspected (details in Cucherousset et al. 2007a). For the purpose of the present study, we used data from 66 individuals (mean fork length 51.2 mm ± 4.9 SD, min 44, max 63) that spent more than 5 days in the nursery area and were detected at least twice during the study period. This included data from individuals which were trapped in the fyke net ($N = 31$) or died in the nursery area in the course of the study after the initial 5 days period ($N = 35$). Repeated detections of fish after they had died in the nursery area were cleaned from the data set, following the procedure described in Cucherousset et al. (2007a).

Each YOY pike detected was considered to be at the centre of the cell, and its location was plotted into two-dimensional coordinate values x and y (in m) with respect to the cell size. The arithmetic mean position was calculated for each individual by averaging the x coordinate values of all points ($x_1, x_2, x_3,\ldots$) to obtain $\bar{x}$, and the y coordinate values ($y_1, y_2, y_3,\ldots$) to obtain $\bar{y}$. The arithmetic mean position ($\bar{x}, \bar{y}$) is the point from which the mean-squared distance to all other points ($x_1, y_1; x_2, y_2; x_3, y_3,\ldots$) is minimal (Lair 1987). Radial distances ($d_1, d_2, d_3,\ldots$, expressed in metres) between the arithmetic mean position ($\bar{x}, \bar{y}$) and every location ($x_1, y_1; x_2, y_2; x_3, y_3,\ldots$), and the arithmetic mean radial distance moved ($\bar{d}$) were calculated to provide an estimation of fish dispersal around its arithmetic mean position. Distances between successive positions were calculated and divided by time (in days) to provide a measurement of the average distance travelled per day ($\bar{v}$). Distances moved between the releasing point at D0 and the location at D1 were used to estimate initial dispersion after releasing. For surviving fish, the final distance moved to the fyke net was not considered. Occasionally, an individual was detected twice during a single tracking. When this happened, the first location was used for the calculation.

Geostatistical method was used to examine the spatial structure of YOY pike abundance in the nursery area. Data on YOY pike abundance in each cell and for each tracking were log-transformed to reduce the asymmetry of the frequency distribution. Then, spatial autocorrelation between pike abundance in each cell and that in all other cells was calculated at each tracking date by using Moran's index (I) as a function of spatial distance (see Legendre & Legendre 1998; Legendre et al. 2002; Perry et al. 2002). Moran's index formula is related to Pearson's correlation coefficient (Legendre & Legendre 1998). This index indicates the degree of similarity/dissimilarity of the variable (here pike abundance) in each cell compared with neighbouring locations for various distance classes. The values of this index are reported in a graph (called correlogram) against distance classes. It ranges from −1 (negative spatial autocorrelation) to +1 (positive spatial autocorrelation), 0 being the expected value for random distribution (no spatial autocorrelation). The number of distance classes was calculated following Sturge's rule (Legendre & Legendre 1998) and using the formula:

$$\text{Number of distance classes} = 1 + 3.3\log_{10} m$$

where m is the number of distances in the triangular matrix of geographic distances among cells, the number of distance classes being rounded to the nearest integer. Sixteen distance classes (8 m each) were defined, but only the first 11 classes (i.e., distance up to 88 m) were the most informative and retained for final analysis. The significance of individual autocorrelation coefficients (i.e., for each lag distance) was tested using t-tests, while that of the entire correlogram (11 classes of distance) was tested using a Bonferroni procedure (Rosenberg 2001). The association between pike abundance for each tracking date and each habitat factor measured in the nursery area (water level and vegetation cover) was tested using Pearson's product-moment correlation. When significant spatial correlations were found between pike abundance and habitat descriptors, Moran's I index was recalculated on residuals (i.e., without the effect of this environmental factor). Moran's I statistics and correlograms were computed using PASSAGE software (Rosenberg 2001) and $P \leq 0.05$ was taken as the level of significance.

Results

Mobility of YOY pike

At D1, 141 PIT-tagged YOY pike were detected within the nursery area, then 77 (D5), 53 (D9), 35 (D11), 22 (D14) and 12 (D18). Individuals dispersed rapidly after stocking and exhibited a widespread distribution within the nursery area at D1 (Fig. 2). On average, pike moved 14.3 m (±11.0 SD, ranging from 4.0 to 51.9 m) between D0 and D1. From D5 to D11, the

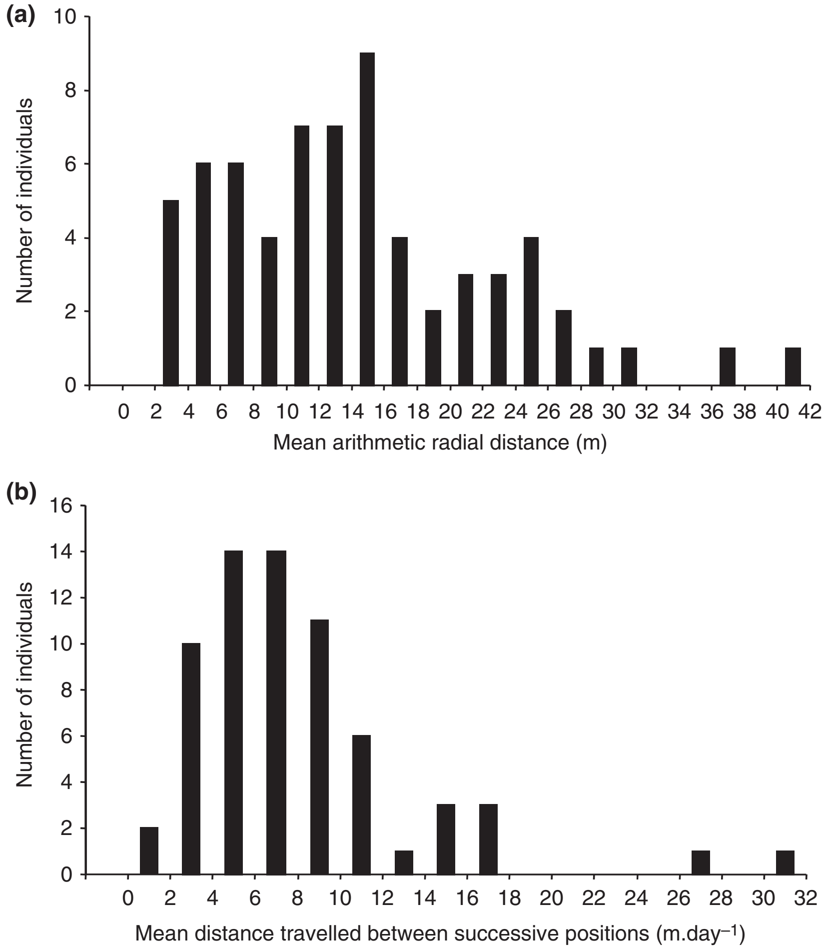

Fig. 3. Frequency distribution of (a) the mean arithmetic radial distance moved ($\bar{d}$, in m) and (b) the average distance travelled per day ($\bar{v}$, in m·day^{-1}) by PIT-tagged YOY pike (N = 66) in the nursery area of the Brière marsh (France) from 21 May to 7 June 2005 (six tracking dates).

major proportion of YOY pike concentrated mainly in two areas of the grassland, corresponding to the deepest areas (Fig. 2). At D18, the fish remaining in the nursery area were located in the deepest area that was still connected to the pond (Fig. 2). On average, fish used for spatial analyses (N = 66) were detected 3.4 times (±1.1 SD, ranging from 2 to 6) over the study period and the average time between two successive detections of the same individual was 4.1 days (±2.1 SD). The mean radial distance moved ($\bar{d}$) averaged 14.3 m (±8.4 SD, ranging from 2.2 to 41.0 m) (Fig. 3a). The average daily movement ($\bar{v}$) was 8.0 m·day^{-1} (±5.3 SD), ranging from 0.6 to 31.1 m·day^{-1} (Fig. 3b). No significant relationships were found between fish size at tagging and $\bar{d}$ and $\bar{v}$ (linear regression, $r^2 < 0.05$, $P > 0.05$, N = 66).

Spatial distribution of YOY pike and relationships with environmental factors

Correlograms were all significant ($P < 0.05$, Fig. 4). Significant and positive autocorrelations of pike abundance were found for the first four distance classes (Moran's I ranging from 0.03 to 0.18, $0.001 < P < 0.05$ except for D18). This means that fish abundance in a cell positively correlated with the abundance observed in adjacent cells within 32 m, confirming the visual appraisal of a patchy distribution of YOY pike within the nursery area (Fig. 2). Spatial distribution of fish abundance positively correlated with water depth in cells at D5, D9 and D11 ($0.27 < r < 0.34$, $P \leq 0.05$), confirming the selective use of the deepest areas by YOY pike within the nursery area (Fig. 2). Conversely, no significant correlations were found with vegetation cover in cells at any dates ($0.07 < r < 0.13$, $P > 0.07$). Significant correlograms were also obtained when calculations were performed on residuals of the regression of YOY pike abundance as a function of water depth, but positive autocorrelations were mainly significant for the first two distance classes (Moran's I ranging from 0.05 to 0.13, $0.001 < P < 0.05$). This indicates that regardless of water depth, individuals tended to distribute themselves in patches of relatively small size (less than 16 m).

Discussion

Studies on early life stages of northern pike have principally focused on growth pattern, survival rate

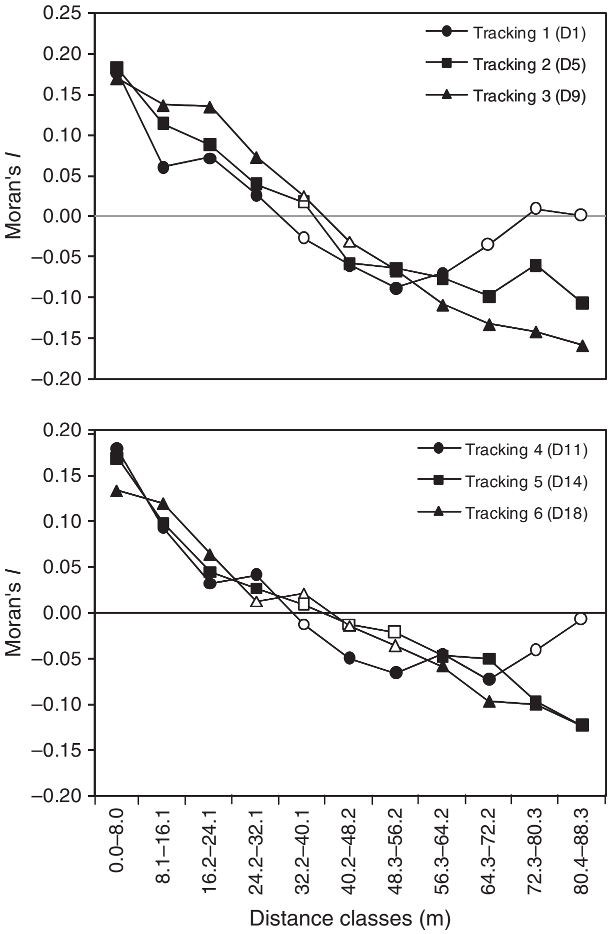

Fig. 4. Spatial correlograms of Moran's *I* for PIT-tagged YOY pike abundance (log transformation) as a function of distance classes (see the text for details on the calculation of distance classes) in the nursery area of the Brière marsh (France) over time (at different tracking dates expressed in days after stocking, D1 = 21 May 2005). Black symbols represent significant values at $P \leq 0.05$ and open symbols not significant values.

(Gronkjaer et al. 2004; Sutela et al. 2004) and to a lesser degree on habitat use, notably with respect to water depth and vegetation cover (Casselman & Lewis 1996; Skov & Berg 1999; Skov et al. 2002). In the present study, first estimations of hatchery-reared YOY pike movements in natural settings have been made thanks to PIT telemetry. In a restricted, shallow and temporarily flooded nursery area of the Brière marsh, we found that YOY pike as small as 44–63 mm fork length at tagging could move 14 m, on average, around their mean focal position during the study period and travel, on average, 8.0 m·day^{-1}. Although the distance travelled per day might be somewhat underestimated because each individual was localised, on average, every 4.1 days, this indicates that fish explored a relatively limited area within the nursery. Significant inter-individual variations in YOY pike mobility have been found, the mean radial distance moved ranging from 2.2 to 41.0 m. However, such variation in mobility among individuals was not related to fish body size at tagging. This indicates that PIT tagging did not affect the displacements of small fish predominantly, as it would have been expected in our experiment if the effect of tagging was size dependent. However, the potential effect of PIT tagging on pike behaviour would deserve for more observations under controlled conditions.

A number of studies support the idea that larvae and early juvenile stages are highly dependent on the presence of vegetation. Fish densities are usually higher in highly vegetated habitats than in open water habitats (Holland & Huston 1984; Skov & Berg 1999). This habitat feature appears to be critical for northern pike during the juvenile period for several reasons. First, habitat complexity as observed in an area with vegetation can enhance the trophic interactions between zooplankton and fish and between forage fish and piscivorous fish (Savino & Stein 1982; Schriver et al. 1995). Experiments have shown that in the presence of prey, YOY pike intensify their use of more structured habitats compared with open water habitats (Skov et al. 2002). Secondly, aquatic vegetation provides concealment and protection for YOY pike against predators (Skov & Berg 1999). However, when the risk of cannibalism is high, the smaller and more vulnerable individuals tend to avoid complex habitats where cannibalistic pike shelter (Skov & Koed 2004). Despite a real predation threat (predation by birds and cannibalism of PIT-tagged pike over the study period reached more than 30%; Cucherousset et al. 2007a), we found that aquatic vegetation did not play a major role in the distribution of fish within the nursery area at the cell scale. However, the absence of a clear relationship between fish abundance and the percentage of vegetation cover at the cell scale do not mean that fish did not shelter in plants at a microhabitat scale, as observed by Casselman & Lewis (1996), and the operator often detected YOY pike holding position in the vegetation during tracking.

However, in highly varying environment such as temporarily flooded grassland, other parameters might act predominantly on YOY pike distribution. Unlike aquatic vegetation, water depth significantly correlated with the spatial distribution of YOY pike within the nursery. Indeed, we found that PIT-tagged YOY pike were more abundant in the two deepest parts of the nursery area (Fig. 2). The patchiness of distribution was relatively constant over time, whatever the abundance of fish still present in the nursery and changes in environmental conditions. Hence, YOY pike tended to aggregate in the deepest areas of the nursery during the period of decreasing water level. We assume that this aggregative distribution was not biased by the stocking design because the cells where

YOY pike were released were environmentally similar to other cells, and because fish moved, on average, 14.3 m within the first day. This suggests that YOY pike have certainly been able to select rapidly the most appropriate habitat in the study area. The aggregation of pike in the deepest areas is in accordance with previous studies that have pointed out the role of water depth on YOY pike distribution (e.g., Vuorinen et al. 1998; Hawkins et al. 2003). This result also corroborates findings by Hawkins et al. (2005), who demonstrated that pike tended to increase the average time spent in deep-water habitat when the density increased. The existence of YOY pike aggregations within the nursery may also suggest that spacing between individuals may decrease during the drying out period, as already reported for this species at the onset of winter (Hawkins et al. 2003). Shallow vegetated nursery areas are beneficial to YOY pike because productivity is high and preys are abundant (Casselman & Lewis 1996; Craig 2008). When the water level decreases, however, the search for the deepest habitats within the nursery probably corresponds to survival behaviour, provided that pools do not disconnect from the main pond or channel. For instance, deepest areas might have been used as refuges against avian predation. In the present study, we did not find any evidence of stranding, suggesting that all fish had left the pools before they disconnected. However, the tendency of YOY pike to gather in the deepest habitat, and the patchy distribution that results, suggest that predation and/or cannibalism might be facilitated during this critical period of the species life cycle.

Decline in the population size of pike has been reported in several places, and although habitat loss is often suspected to be a major cause, restocking is a common management practice for this species (Craig 2008). However, managers often question its efficiency as the survival rate of hatchery-reared YOY is usually low (Lucchetta 1983; Gronkjaer et al. 2004). The juveniles used in the present study came from wild parents and they were reared in hatchery conditions before releasing. Although this might have affected fish behaviour and the results of our study, this is a common practice in restocking programme. The tendency of YOY pike to gather in the deepest areas and the patchy distribution suggest that the choice of release habitats in flooded grassland requires particular attention during restocking procedures to avoid fish stranding during the drying out period following stocking.

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References

Acolas, M.L., Roussel, J.M., Lebel, J.M. & Baglinière, J.L. 2007. Laboratory experiment on survival, growth and tag retention following PIT injection into the body cavity of juvenile brown trout (*Salmo trutta*). Fisheries Research 86: 280–284.

Adams, N.S., Rondorf, D.W., Evans, S.D., Kelly, J.E. & Perry, R.W. 1998. Effects of surgically and gastrically implanted radio transmitters on swimming performance and predator avoidance of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 55: 781–787.

Baras, E., Malbrouck, C., Houbort, M., Kestemant, P. & Helard, C. 2000. The effects of PIT tags on growth and physiology of age-o cultured Eurasian perch fluviatilis of variable size. Aquaculture 185: 159–173.

Bry, C., Basset, E., Rognon, X. & Bonamy, F. 1992. Analysis of sibling cannibalism among pike, *Esox lucius*, juveniles reared under semi-natural conditions. Environmental Biology of Fishes 35: 75–84.

Bry, C., Bonamy, F., Manelphe, J. & Duranthon, B. 1995. Early life characteristics of pike, *Esox lucius*, in rearing ponds: temporal survival pattern and ontogenetic diet shifts. Journal of Fish Biology 46: 99–113.

Bubb, D.H., Thom, J.T. & Lucas, M.C. 2006. Movement patterns of the invasive signal crayfish determined by PIT telemetry. Canadian Journal of Zoology 84: 1202–1209.

Casselman, J.M. 1996. Age, growth and environmental requirements of pike. In: Craig, J.F., ed. Pike: biology and exploitation. London, UK: Chapman & Hall, pp. 69–101.

Casselman, J.M. & Lewis, C.A. 1996. Habitat requirements of northern pike (*Esox lucius*). Canadian Journal of Fisheries and Aquatic Sciences 53: 161–174.

Craig, J.F. 2008. A short review of pike ecology. Hydrobiologia 601: 5–16.

Cucherousset, J., Roussel, J.-M., Keeler, R., Cunjak, R.A. & Stump, R. 2005. The use of two new portable 12-mm PIT tag detectors to track small fish in shallow streams. North American Journal of Fisheries Management 25: 270–274.

Cucherousset, J., Paillisson, J.-M., Carpentier, A., Eybert, M.-C. & Olden, J.D. 2006. Use of an artificial wetland by the invasive catfish *Ameiurus melas*. Ecology of Freshwater Fish 15: 589–596.

Cucherousset, J., Paillisson, J.-M. & Roussel, J.-M. 2007a. Using PIT technology to study the fate of hatchery-reared YOY northern pike released into shallow vegetated areas. Fisheries Research 85: 159–164.

Cucherousset, J., Paillisson, J.M., Carpentier, A. & Chapman, L.J. 2007b. Fish emigration from temporary wetlands during drought: the role of physiological tolerance. Fundamental and Applied Limnology – Archiv für Hydrobiologie 168: 169–178.

Cucherousset, J., Marty, P., Pelozuelo, L. & Roussel, J.-M. 2008. Portable PIT detector as a new tool for non-disruptively locating individually tagged amphibians in the field: a case study with Pyrenean brook salamanders (*Calotriton asper)*. Wildlife Research 35: 780–787.

Cunjak, R.A., Roussel, J.M., Gray, M.A., Dietrich, J.P., Cartwright, D.F., Munkittrick, K.R. & Jardine, T.D. 2005. Using stable isotope analysis with telemetry or mark–recapture data to identify fish movement and foraging. Oecologia 144: 636–646.

Gronkjaer, P., Skov, C. & Berg, S. 2004. Otolith-based analysis of survival and size-selective mortality of stocked 0+ year pike related to time of stocking. Journal of Fish Biology 64: 1625–1637.

Hawkins, L.A., Armstrong, J.D. & Magurran, A.E. 2003. Settlement and habitat use by juvenile pike in early winter. Journal of Fish Biology 63: 174–186.

Hawkins, L.A., Armstrong, J.D. & Magurran, A.E. 2005. Aggregation in juvenile pike (*Esox lucius*): interactions between habitat and density in early winter. Functional Ecology 19: 794–799.

Holland, L.E. & Huston, M.L. 1984. Relationship of Young-of-the-Year northern pike to aquatic vegetation types in backwaters of the upper Mississippi River (U.S.A.). North American Journal of Fisheries Management 4: 514–522.

Keeler, R.A., Breton, A., Peterson, D.P. & Cunjak, R.A. 2007. Apparent survival and detection estimates for PIT-tagged slimy sculpin in five small New Brunswick streams. Transactions of the American Fisheries Society 136: 281–292.

Knaepkens, G., Maerten, E., Tudorache, C., De Boeck, G. & Eens, M. 2007. Evaluation of passive integrated transponder tags for marking the bullhead (*Cottus gobio*), a small benthic freshwater fish: effects on survival, growth and swimming capacity. Ecology of Freshwater Fish 16: 404–409.

Lair, H. 1987. Estimating the location of the focal centre in red squirrel home ranges. Ecology 68: 1092–1101.

Legendre, P. & Legendre, L. 1998. Numerical ecology, second English edition. Amsterdam, The Netherlands: Elsevier.

Legendre, P., Dale, M.R.T., Fortin, M.J., Gurevitch, J., Hohn, M. & Myers, D. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography 25: 601–615.

Lucchetta, J.C. 1983. Utilisation de sites naturels pour le grossissement d'alevins de brochet produit en écloserie. In: Billard, R., ed. Le Brochet: Gestion dans le Milieu Naturel et Elevage. Paris, France: INRA Publication, pp. 199–208.

Morhardt, J.E., Bishir, D., Handlin, C.I. & Mulder, S.D. 2000. A portable system for reading large passive integrated transponder tags from wild trout. North American Journal of Fisheries Management 20: 276–283.

Perry, J.N., Liebhold, A.M., Rosenberg, M.S., Dungan, J., Miriti, M., Jakomulska, A. & Citron-Pousty, S. 2002. Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. Ecography 25: 578–600.

Rosenberg, M.S. 2001. PASSAGE. pattern analysis, spatial statistics, and geographic exegesis. Version 1.0 Tempe, AZ: Department of Biology, Arizona State University.

Roussel, J.M., Haro, A. & Cunjak, R.A. 2000. Field test of a new method for tracking small fishes in rivers using the passive integrated transponder (PIT) technology. Canadian Journal of Fisheries and Aquatic Sciences 57: 326–1329.

Savino, J.F. & Stein, R.A. 1982. Predator–prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Transactions of the American Fisheries Society 111: 255–266.

Schriver, P., Bøgestrand, J., Jeppesen, E. & Søndergaard, M. 1995. Impact of submerged macrophytes on fish–zooplankton–phytoplankton interactions: large-scale enclosure experiments in a shallow eutrophic lake. Freshwater Biology 33: 255–270.

Skov, C. & Berg, S. 1999. Utilization of natural and artificial habitats by YOY pike in a biomanipulated lake. Hydrobiologia 408/409: 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. Journal of Fish Biology 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. Ecology of Freshwater 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. Journal of Fish Biology 62: 311–322.

Souchon, Y. 1983. La reproduction du brochet (*Esox lucius* L., 1758) dans le milieu naturel. In: Billard, R., ed. Le Brochet: Gestion dans le Milieu Naturel et Elevage. Paris, France: INRA Publication, pp. 21–37.

Sutela, T., Korhonen, P. & Nyberg, K. 2004. Stocking success of newly hatched pike evaluated by radioactive strontium (^{85}Sr) marking. Journal of Fish Biology 64: 653–664.

Vuorinen, P.J., Nyberg, K. & Lehtonen, H. 1998. Radioactive strontium (^{85}Sr) in marking newly hatched pike and success of stocking. Journal of Fish Biology 52: 268–280.

Winter, J. 1996. Advances in underwater biotelemetry. In: Murphy, B.R. & Willis, D.W., eds Fisheries techniques, 2nd edn. Bethesda, MD: American Fisheries Society, pp. 555–590.

Wright, R.M. & Shoesmith, E.A. 1988. The reproductive success of pike, *Esox lucius*: aspects of fecundity, egg density and survival. Journal of Fish Biology 33: 623–636.