Long range seasonal movements of northern pike (*Esox lucius* L.) in the barbel zone of the River Ourthe (River Meuse basin, Belgium)

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Abstract

In order to study the annual activity cycle and reproductive ecology of northern pike (*Esox lucius* L.) in the River Ourthe (Belgian Ardenne), 6 fish (579-742 mm FL, 1605-4090 g, 2 females and 4 males) were captured by electric fishing in November 2000 and January 2001. They were surgically implanted with radio-transmitters and tracked for 149 to 349 days in a 30-km river stretch. During the pre-spawning period in winter, most movements were between distinct holding areas spaced from 40 to 550 m. All the pike began the upstream spawning migration between 8 February and 30 March 2001, when the mean water temperature varied from 6.7° C to 8.7° C and the water flow from 52 to 199 m³s⁻¹. The six pike travelled upstream, over distances ranging from 0.75 km to 15.7 km to reach their potential spawning sites. Pike arrived on their potential spawning sites between the 13 February and the 02 April 2001 and remained there from 5 to 25 days when the daily mean water temperature ranged from 2.9 to 10.0 °C. The six pike moved downstream after spawning and showed similar behaviour to those observed prior to spawning, but the distances between holding areas were more extended than during the winter pre-spawning period. When considering the entire tracking period, the longitudinal extension of the activity range varied from 1,421 to 24,798 m (mean 12,050 m). This exploratory study provided original observations on northern pike movements in a barbel zone of the River Meuse basin. Results contrast with the widely established view of pike being a sedentary predator and provide data on its behaviour throughout the annual cycle.

Introduction

As a top predator, northern pike (*Esox lucius* L.) play an important role in the regulation of fish community in rivers and lakes ecosystems (Prejs *et al.*, 1994; Craig, 1996; Berg *et al.*, 1997; Jepsen *et al.*, 2001). They can tolerate a wide range of environmental conditions, but are primarily mesothermal or cool-water fish best adapted to shallow, productive, mesotrophiceutrophic environments (Craig, 1996). Over the past half-century, eutrophication and habitat loss have significantly affected northern pike in Europe and North America (Casselman and Lewis, 1996) and there is an increasing need to conserve and enhance their populations. However, effective management programmes cannot be planned without an understanding of the biological requirements of the species throughout its life cycle.

Biotelemetry studies on the movements of pike have been almost exclusively performed in lakes and reservoirs (Diana *et al.*, 1977; Diana, 1980; Cook and Bergesen, 1988, Rogers and Bergesen; 1995, Jepsen *et al.*, 2001). Strangely, investigations in rivers ecosystems have been limited. Masters *et al.* (2002) studied the habitat utilisation during winter floods in an English river and a study on the movements of a single pike in an Irish canal was performed by Donnely *et al.* (1998). Currently, the established view of pike is of a largely solitary predator (Raat, 1988; Maitland and Campbell, 1993 in Rosell and MacOscar, 2002), migrating only in spawning season, and being relatively sedentary at other times. According to Lucas and Baras (2001) Esocids tend to display limited migration, altough local movement may be of key significance for population maintenance.

In order to study the seasonal activity cycle of *E. lucius* in the barbel zone of the River Ourthe (River Meuse basin), six individuals were radio-tracked during an annual cycle.

Materials and methods

Study site

The River Ourthe is the main sub-basin of the River Meuse in Southern Belgium. It runs through the Belgian Ardenne where it meets tributaries such as the Amblève and Aisne streams (Fig. 1). This section contains small weirs, of less than 3 m in height, which may sometimes inter-

fere with the free movement of some species of fish (synthesis in Ovidio and Philippart, 2002). In the study area, the River Ourthe has a mean slope of 0.12%, a mean width and flow in summer of 25 m and 32 m 3 s⁻¹, respectively. River Ourthe is typical of the barbel and grayling rivers and hosts a mixed cyprinid-salmonid fish assemblage (31 indigenous species) of which the main constituents are: the barbel, *Barbus barbus* (L.), chub *Leuciscus cephalus* (L.), nase *Chondrostoma nasus* (L.), grayling *Thymallus thymallus* (L.) and brown trout *Salmo trutta* (L.). The water temperature in the River Ourthe varies over the annual cycle, from 0 °C to 26 °C (mean: 10.5 °C, data from 1990 to 2000).

Fish tagging and environmental records

Six pike were captured by electric fishing (DEKA, 2.5 kVA) in an area situated in the vil-

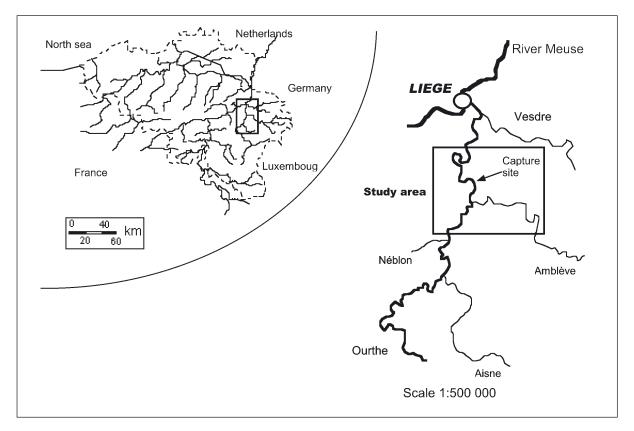


Fig. 1 – Location of the study area in Belgium and in the River Ourthe sub-basin (River Meuse basin)

lage of Poulseur (Fig.1). This area is characterised by the presence of two secondary river branches that contain immersed vegetation and that are commonly used by pike for reproduction since several years (Philippart et. al., unpublished results). Three pike were captured in a river branch and the three others in the main course of the River Ourthe in November 2000 and in January 2001 (Table 1). Pike were anaesthetised in a 0.2mll⁻¹ solution of 2phenoxy ethanol then placed ventral side up into a v-shaped support adjusted to their morphology. A mid-ventral incision was made between the pelvic girdle and the anus and an alcohol-sterilised transmitter (ATS Inc., 40 MHz, internal coiled antenna, 20 g) was inserted into the body cavity. The incision was closed by three separate stitches, using sterile plain vicryl sutures. Fish were released at their capture site as soon as they had recovered

Table 1 - Characteristics of the six tracked pike

limnimetric scales installed near the temperature loggers. Water flow was recorded continuously about 10 km downstream from the capture site (data from SETHY-MET).

Tracking

Fish were located once a week from 21 November 2000 to 29 January 2001. From the 30 January to the 1 April 2001, fish were located 6 times/week. From 2 April to 6 June 2001 they were located 3 times/week and then once every 10 days after 6 June 2001. Locations were made by triangulation from markers on the rivers' banks, using a mobile FieldMaster radio receiver and a loop antenna (ATS Inc.). Most locations were made during daytime, with accuracy between 5 to 20 m², depending on the distance between the fish and the observer and the

Fish N°	Fork length	Body weight	Tag Ratio	Sex	Date of capture	Date of last location	Tracking duration
	(FL, mm)	(g)	(%)				(days)
1	598	1 605	1.25	М	21 Nov. 2000	04 June 2001	196
2	607	2 170	0.92	F	21 Nov. 2000	01 June 2001	194
3	742	4 090	0.49	F	24 Jan. 2001	07 Jan. 2002	349
4	660	2 482	0.81	Μ	24 Jan. 2001	21 June 2001	149
5	662	2 310	0.87	Μ	24 Jan. 2001	13 Dec. 2001	324
6	579	1 630	1.23	Μ	24 Jan. 2001	07 Jan. 2002	349

posture and spontaneous swimming (about 10 min after surgery). This methodology minimises the possible biases originating from long term postoperative care. The sex of the pike was determined by visual inspection of the gonads through the incision, except for Pike 1 that was sexed after its recapture during the study. All the females were potentially mature and presented eggs under development in the ovaries.

Temperature in the River Ourthe and in the secondary branches was logged every 30 min using data loggers (TidBit Onset Corp.) installed in Poulseur with an accuracy of 0.16 °C. Water levels were measured daily in the River Ourthe and in the secondary branch with an accuracy of 1 cm, on width of the river. During the migration, distances between two locations were determined to the nearest 20 m using a decametre on the field or topographical map (1:5 000). The longitudinal extension of the activity range during distinct periods (pre- and post-spawning) was defined by the distance separating the most upstream and the most downstream location of each pike.

Results

Pre-spawning movements

During the winter pre-spawning period, pike demonstrated quite similar patterns of movements

(Figs. 2 and 3). Most movements were between resting-places 40 to 550 m apart. They usually moved upstream and downstream but the distances travelled between two locations rarely exceeded 300 m. Pike 1 travelled frequently between two resting-places situated in a secondary river branch and in the main course of the River Ourthe (Fig. 3). The resting-places of the other pike were essentially located either in the main course or in the secondary river branches.

Spawning migration

Pike began their spawning migration between 8 February and 30 March 2001 (Fig. 2). Individuals 1 and 3 started their migration on the same day (15 March). Migrations started when the mean water temperature was between 6.7 °C to 8.7 °C and the water flow between 51.6 and 199 m³s⁻¹ (mean flow the first day of migration: 124 m³s⁻¹; mean annual flow in 2001: 54.3 m³s⁻¹, Fig.3). Fish travelled upstream, over distances ranging from 0.75 km to 15.7 km to reach their potential spawning sites (Figs. 2 and 3). Some individuals migrated directly to the spawning sites whilst other moved discontinuously. Pike 5 moved 11.3 km upstream in 4 days, but, in contrast, pike 3 achieved a 4.5-km migration in 13 days (Fig. 2). Pike 2, 5 and 6 sometimes travelled more than 3.0 km upstream from one day to another in high water flow conditions (±100 m³s⁻¹). On 8 March 2001 between 16:25 hours and 17:25 hours (7.7 °C and 79 m³s⁻¹), pike 5 travelled 1.05 km upstream. This corresponds to a movement of 0.44 body lengths⁻¹. During it's 15.7 km upstream migration, pike 6 moved past three obstacles (Fig. 2).

Each pike used a different spawning site (Fig. 4). Pike 2 and 6 entered into the Amblève, a tributary of the River Ourthe. The four other individuals stayed in the main course of the River Ourthe or in a secondary branch for reproduction. The potential spawning areas were characterised by shallow (10-60 cm depth) and calm water and the presence of aquatic vegetation (*Ranunculus* sp., *Potamogeton* sp., *Carex* sp., *Scirpus* sp.) or immersed terrestrial vegetation (Gramineae). Pike 2 and 5 probably spawned in a secondary river branch. The other pike spawned in areas located along the banks of the Ourthe or Amblève.

Pike arrived on their potential spawning sites between the 13 February and the 02 April 2001 and stayed there 5 to 25 days (mean 11.2 ± 7.8 days). During this period, the daily mean water temperature ranged from 2.9 to 10.0 °C (mean: 6.97 ± 1.75 °C) and the water flow from 41.4 to 259.0 m³s⁻¹ (mean: 99.8 ± 55.7 m³s⁻¹) (Fig. 3). They left the spawning sites between 10 March and 13 April 2001.

In order to test if the pike effectively moved upstream to the spawning site, electric fishing was performed in June 2001 on habitats where pike 2 and 5 had migrated (Figs. 2 and 4). Juveniles were captured in the two sites, indicating their suitability for the pike's reproduction. Electric fishing was also achieved on the original capture sites of the six pike (Fig. 4) and juveniles were also observed at these places.

Downstream migration

The six pike moved downstream after reproduction (Figs. 2 and 4). Pike 1 returned to a previous resting-place used before the spawning migration. Pike 2 and 4 rapidly returned in a few days in an earlier resting-place, but several days later, they respectively moved 20 and 8 km downstream on 20 March and 10 May 2001. After it's downstream migration, pike 3 was located 800 m upstream of it's capture place, but never reintegrated the original resting-place. Pike 5 and 6 were located 10 and 3 km upstream of their capture and tagging site after the downstream migration.

During it's downstream migration fish 6 was confronted for the second time with the weirs of the Amblève, but in the direction of the water flow. The pike stopped its migration three days just upstream of each weir, indicating that the obstruction may interfere with the movement of pike in both directions (Fig. 2).

Post reproduction behaviour

After the downstream migration and until the end of the intensive tracking period (late June), pike

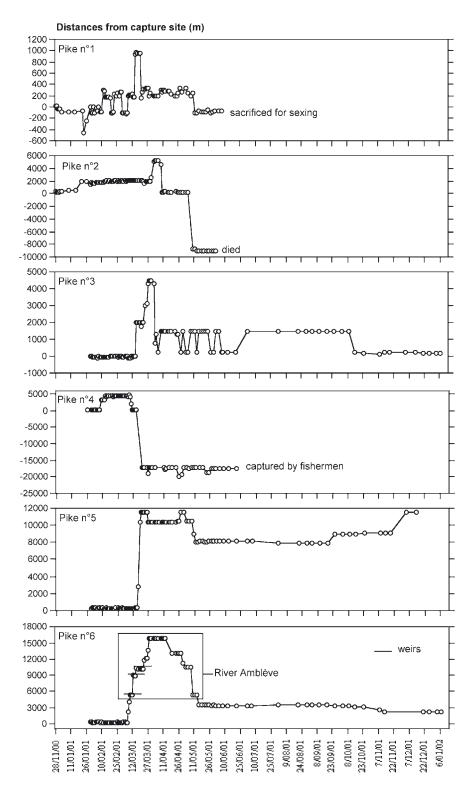


Fig. 2 - Movements in meters of the six pike radio-tracked in the river Ourthe sub-basin with reference to capture site.

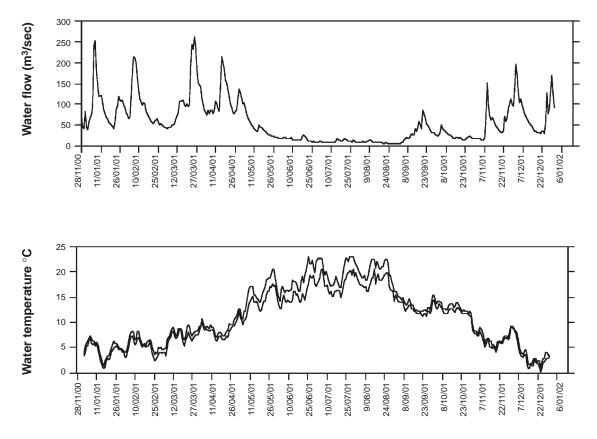


Fig. 3 - Variation of water level and water temperature (daily min. and max.) in the River Ourthe during the study.

showed similar behaviour to those observed prior to spawning, but the distances travelled between two resting-places sometimes exceeded 1.2 km (pike 3 and 4).

In June, three fish were no longer followed. Pike 1 was captured by electric fishing on 7 June 2001. It was covered by biting and fighting injuries (suggesting its participation to spawning activity) and was sacrificed for sexing. Pike 2 probably died as no movements were detected during the last days of tracking. Its transmitter was finally found in the water. A fisherman captured pike 4 and affirmed that the fish was in very good health and exempt of injuries.

Pike 3, 5 and 6 were followed less intensively after June 2001. Interestingly, pike 5 returned to the spawning site previously utilised in March 2001 in early December 2001 (Figs. 2 and 4), but the transmitter failed two days later. Pikes 3 and 6 stayed in the same sites until the end of the battery life of their transmitters.

Longitudinal extension of the activity range

Table 2 shows the longitudinal extension of the activity range of the pike before, and after the spawning migration as well as during the entire tracking period. Kruskal-Wallis test indicated significant differences between the 3 groups (p<0.005; H=11.275) suggesting an heterogeneity in the extension of movements from winter to summer. The longitudinal extension of the activity range is significantly longer after the spawning migration than before (Mann-Whitney; P<0.05; Z=-2.082). The longitudinal extension of the activity range was not correlated with the characteristics of the individuals (length, weight).

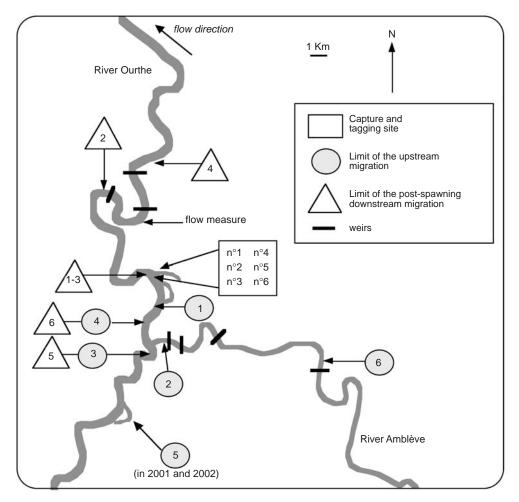


Fig. 4 – Geographical representation of the dispersion of the six radio-tagged pike before, during and after spawning.

Table 2 – Longitudinal extension of the activity range (m) of the six radio-tagged pike during three different periods.

Pike n°	Before spawning migration (m)	After spawning migration (m)	Total (m)
1	754	295	1 421
2	1 895	9 342	14 295
3	119	1 267	4 609
4	171	2 788	24 798
5	176	1 280	11 446
6	167	1 410	15 732

Discussion

This exploratory study provided original observations on northern pike movements in a barbel river. Results contrast with the widely established view of pike being a sedentary predator and bring data on its biological cycle and behavioural tactics throughout the annual cycle. Because the number of tracked fish was limited, results remain preliminary. But, by both the duration and the accuracy of the locations our study provides a better understanding of the behavioural ecology of northern pike in river ecosystems and constitutes a precious tool to improve the management of their populations.

Pike were tagged using surgical implantation. This method has several advantages over external attachment, including avoidance of vegetation entanglement, as well as less interference with swimming behaviour and speed (Winter, 1983; Mellas and Haynes, 1985; Herke and Moring, 1999). However, this tagging technique can be disadvantageous when tagging females just before spawning (Herke and Moring, 1999), but has been found to have no or very little adverse long-term effect on the growth and survival of pike (Jepsen and Aarestrup, 1999). In order to minimise this problem, fish were captured and tagged from three to two months before spawning, using transmitters representing a very low ratio of the fish body weight (<1.25% for the males and <0.92% for the females).

Annual movements

In the River Ourthe, pike were relatively mobile. The movements were more important during the spring upstream and downstream migration, but the pike still moved frequently outside the spawning periods. During the winter and summer seasons, the pike moved between distinct holding areas >1500 m apart. In an Irish canal a single radio-tracked pike moved in between different resting-places spaced out from up to 8 km. In the Lake Ste. Anne, Diana et al. (1977) found no differences in the level of movements between summer and winter, although during the winter, the tagged pike moved longer distances (>1000 m) more frequently than in the summer. In a Colorado reservoir, Cook and Bergesen (1988) found a small increase in number of pike movements, but a decrease in distance moved during winter. Rogers and Bergesen (1995) found no change in the level of pike movement from August to December despite drastic changes in temperature over the period.

Migration

Indirect proofs given by season, temperature, maturity of females during tagging, juvenile occurrence at the end of the spring and the characteristics of the potential spawning sites suggested that migration of pike were related to reproductive events.

Migrations started from 8 February to 30 March and ranged from 0.75 to 15.7 km. In the river "aux Pins" (Québec), Massé *et al.* (1991) performed factorial analysis after a capture-tagging-recapture study, and suggested that the spawning movements were facilitated by the river cues. In the River Ourthe, pike began their migrations during important flow conditions and during increasing water temperatures, ranging from 6.7 to 8.7 °C (mean daily temperature). From an ecological point of view, these cues may stimulate pike to migrate during thermal conditions that allow a sufficient swimming capacity and under high flows conditions associated with immersion of the terrestrial vegetation.

Two individuals entered in a tributary of the River Ourthe, and the others stayed in the main watercourse or in branches. Similar biotelemetry studies in rivers do not exist. Craig (1996) affirmed that northern pike living in rivers are rather sedentary but they have to migrate to reach the spawning grounds. A migration of 15 km (exceptionally 78 km) was reported by Carbine and Applegate (1948, in Craig, 1996) using capture-tagging-recapture methods. In our study, pike arrived on their spawning sites between 13 February and 02 April 2001 and stayed there 5 to 25 days (mean 11.2 ± 7.8 days). During the spawning period, the mean water temperature ranged from 2.9 to 10.0 °C (mean: 6.97 \pm 1.75 °C). Others studies reported that the spawners are present on the spawning grounds when water temperature is in the range 1-4 °C (Franklin and Smith, 1963; Dumont et al., 1980) and even 0 °C (Clark, 1950). In lake Windermere, spawning takes place at temperature range 6-14 °C (Forst and Kipling, 1967). Sukhanova (1979) observed pike spawning at temperature of 3.8-4.5 °C, but they were more active in the afternoon after 17:00 at 5-8 °C. In our study, potential spawning areas were located in shallow waters and were characterised by the presence of aquatic or immersed terrestrial vegetation, as it was already observed by several authors (synthesis in Craig, 1996).

Despite the fact that the tracked fish were captured and released near verified pike spawning areas, they all migrated upstream to spawn in distinct sites of the river basin. The first hypothesis is the existence of spawning site fidelity, expressed by the return of adults to previous years spawning areas. In our study, after its post-spawning downstream migration in April 2001 and a period of stability from April to November, pike 5 returned to the same spawning site in early December. This movement may correspond to the expression of spawning site fidelity. Spawning site fidelity has been shown in a number of esocids populations, including northern pike Esox lucius (Carbine and Applegate, 1948; Frost and Kipling, 1967; Bregazzi and Kennedy 1980; Karas and Lethonen, 1993) and muskellunge Esox masquinongy (Crossman, 1990). Rosell and MacOscar (2002) showed a high degree of specificity of return of individual fish to particular spawning areas, with 18 of 36 spawning season recaptures being found within 500 m of their previous years spawning site. Five were recorded at exactly the same spawning site. Individual returns, sometimes on many occasions, to spawning areas have been described before (Kipling and Lecren, 1984; Karas and Lehtonen, 1993). But the spawning site fidelity can also be the expression of natal-site fidelity. In order to verify this hypothesis in the future, we pit-tagged 150 young of the year pike in distinct spawning site in order to study their dispersal and possible return as adults to their natal site (homing behaviour). Another way to provide evidence of natal-site fidelity is to show genetic differences among spawning populations, which would result from reproductive isolation in cases of both natal-site and spawning site fidelity (Miller et al., 2001). Miller et al. (2001) showed significant differences between two spawning populations of northern pike in a single large reservoir by comparison of allele frequencies at five polymorphic microsatellites markers. The reproductive isolation suggested by these genetic differences could not occur if fish chose their initial spawning site randomly, even if they subsequently returned to those sites.

Dispersion of genitors during reproduction could also correspond to an adaptation strategy of the species that warrants a multiplication of the reproduction sites and allows a sufficient recruitment in case of problem (pollution, important diminution of the water level in the spawning site, predation) or to avoid genetic isolation.

During the spawning migration, one pike was confronted with several physical obstacles. This underlines the importance of considering the situation of northern pike in the different restoration programs in allowing the free movements of fish in rivers (Ovidio and Philippart, 2002).

Post spawning movements

After spawning, the tracked pike moved downstream. Some individuals returned to their initial capture site, even though some stayed between the capture site and the spawning area and others moved downstream of their capture site.

Similar upstream and downstream movements were observed by Koed et al. (2000) in adult pikeperch (Stizostedion lucioperca) in a Danish lowland river. Authors suggested that the pikeperch make a feeding migration during autumn and winter from upper reach to the lower reach and the estuary of the river Gudenaa, and an upstream spawning migration during the spring. The total distance annually travelled by pikeperch ranged from 47 to 226 km. In our study, distances travelled by fish were less important and the environmental conditions in the upper and lower limits of the pike's locations were not different. This suggests that in the River Ourthe sub-basin, the meaning of the post-spawning downstream migration could be partially or totally different. For a spawner, this downstream post-reproductive migration can be a way to avoid cannibalism on its own progeny or to return to a well-known river section that can be optimally exploited.

Longitudinal extension of activity range

The longitudinal extension of the activity range of the tracked pike was variable among individuals and period of the year. When considering the entire tracking period, including the spawning migration, the stretch of the river occupied by pike varied from about 1.5 km and 25 km. In an Irish canal, Donnely *et al.* (1998) tracked a single northern pike (81 cm FL, 3400 g) from January to June that occupied a longitudinal home range of about 9 km.

In artificial or natural lakes, contrasting results were collected on the extension of northern pike home-range. In Lake Ste. Anne (Alberta), Diana et al. (1977) affirmed that ultrasonic tagged northern pike did not have a well-defined home range, but rather appeared to move at random throughout a relatively narrow zone around the edge of the Lake. Several authors suggested that home range among pike is not very restricted (Bregazzi and Kennedy, 1980; Chapman and Mackay, 1984; Cook and Bergesen, 1988). Malinin (1969; 1970; 1971) found that pike are relatively sedentary with a home range of 50 to 150 m in diameter where the bottom is flat. Other studies revealed restricted movements among pike (Alessio, 1986; Karas and Lethonen 1993; Grimm and Klinge, 1996; Eklöv, 1997). Jepsen et al. (2001) observed different kinds of space utilisation between a lake and a reservoir in Denmark. In the lake, pike did not occupy restricted home ranges over long periods, but utilised most of the lake during the year. In the reservoir, pike showed three types of behaviour: i) staying in a restricted area, ii) moving between two or three "favourite areas" and iii) utilising larger habitats with frequent habitat shifts. Mann (1980) suggested that pike population is constituted of two groups of individuals. One group, mainly females, occupies restricted home range, and, the second group moves extensively.

In our study, six of the pike showed types of behaviour which, in our opinion, may not be placed in separate categories. We consider that dividing pike populations into "migrant" and "sedentary" fractions is too reductionist. It is probably a direct consequence of data-collecting methodologies likely to highlight extreme situations but not always suitable in accounting for tactics of intermediate resource utilisation. As in the case of the common trout *Salmo trutta* (Ovidio, 1999), pike seems capable of developing a multitude of behavioural tactics.

Acknowledgements

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References

- Alessio, G. 1986. Breeding of pike, *Esox lucius* L., in spring waters: migratory movements and interspecific recognition. *Rivista di Idrobiologia*, 25: 1-3.
- Berg, S., Jeppesen, E. & Søndergaard, M. 1997. Pike (*Esox lucius* L.) stocking as a biomanipulation tool. 1. Effects on the fish population in lake Lyng (Denmark). *Hydrobiologia*, 342/343: 311-318.
- Bregazzi, P.R. & Kennedy, C.R. 1980. The biology of pike, *Esox lucius* L., in a southern eutrophic lake. *J. Fish. Biol.*, 17: 91-112.
- Carbine, W.F. & Applegate, V.C. 1948. The movement and growth of marked northern pike (*Esox lucius* L.) in Houghton lake and Muskegon River. *Trans. Am. Fish. Soc.*, 32: 215-238.
- Casselman, J.M. & Lewis, C.A. 1996. Habitat requirement of northern pike (*Esox lucius*). Can. J. Fish. Aquat. Sci., 53: 161-174.
- Chapman, C.A. & Mackay, W.C. 1984. Versatility in habitat use by a top aquatic predator, *Esox lucius* L. J. Fish. Biol., 25: 109-115.
- Clark, C.F. 1950. Observation on the spawning habits of northern pike, *Esox lucius*, in northwestern Ohio. *Copeia*, 1950: 258-288.
- Cook, M.F. & Bergesen, E.P. 1988. Movements, habitat selection and activity periods of Northern pike in Eleven mile Reservoir, Colorado. *Trans. Am. Fish. Soc.*, 117: 495-502.
- Craig, J.F. 1996. Pike, biology and exploitation. London, Chapman & Hall, Fish and Fisheries Series 19: 298 pp.
- Crossman, E.J. 1990. Reproductive homing in muskellunge, *Esox masquinongy. Can. J. Fish. Aquat. Sci.*, 47: 1803-1842.

- Diana, J.S., 1980. Diel activity patterns and swimming speeds of northern pike (*Esox lucius*) in Lac Ste. Anne, Alberta. *Can. J. Fish. Aquat. Sci.*, 37: 1454-1458.
- 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.
- Donnely, R.E., Caffrey, J.M. & Tierney, D.M. 1998. Movement of bream (*Abramis brama* (L.)), rudd X bream hybrid, tench (*Tinca tinca* (L.)) and pike (*Esox lucius*) in an Irish canal habitat. *Hydrobiologia*, 371/372: 305-308.
- Dumont, P., Fortin, R. & Fournier, H. (1980). Certain aspects of the reproduction of upper Richelieu and Mississipi Bay northern pike, *Esox lucius* L. Rap. Rech. Faun., Minist. Loisir, Chasse, Pêche, Dir. rech. Faun. (Québec, Canada), 52: 231-48.
- Eklöv, P. 1997. Effects of habitat complexity and prey abundance on the spatial and temporal distribution of perch (*Perca fluviatilis*) and pike (*Esox lucius*). Can. J. Fish. Aquat. Sci., 54: 1520-1531.
- Franklin, D.R. & Smith, L.L. Jr. 1963. Early life history of the northern pike (*Esox lucius* L.) with special reference to the factors influencing the numerical strength of year classes. *Trans. Am. Fish. Soc.*, 92: 91-110.
- Frost, W.E. & Kipling, C. 1967. A study of reproduction early life, weight-length relationship, and growth of pike, *Esox lucius* L., in Windermere. J. Anim. Ecol., 36: 651-693.
- Grimm, M.P. & Klinge, M. 1996. Pike and some aspects of its dependence on vegetation. *In* Craig, J.F., ed. *Pike: biology and exploitation*. 125-126 pp. London, Chapman & Hall, Fish and Fisheries Series 19, 298 pp.
- Herke, S.W & Moring, J.R. 1999. "Soft" harness for external attachment of large radio transmitters to northern pike (*Esox lucius*). *Fish. Res.*, 39: 305-312.
- Jepsen, N. & Aarestrup, K. 1999. A comparison of the growth of radio-tagged and dye-marked pike. J. *Fish Biol.*, 55: 880-883.
- 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 (1): 26-34.
- Karas, P. & Lethonen, H. 1993. Patterns of movement and migration of pike (*Esox lucius*) in the Baltic Sea. *Nordic J. Fish.*, 68: 72-79.
- Kipling, C. & LeCren, E.D. 1984. Mark recapture experiments on pike in Windermere, 1943-1982. *J. Fish. Biol.*, 24: 395-414.

- Koed, A., Mejlhede, P., Balleby, K. & Aarestrup, K. 2000. Annual movement and migration of adult pikeperch in a lowland river. J. Fish. Biol., 57: 1266-1279.
- Lucas, M. & Baras, E. 2001. *Migration of Freshwater Fish*, Blackwell Science Ltd., 392 pp.
- Maitland, P.S. & Campbell, R.N. 1993. Freshwater Fishes. London, Collins, 338 pp.
- Malinin, L.K. 1969. Home range and homing instinct of fish. *Fish. Res. B. Can. Transl. Ser.* 2282.
- Malinin, L.K. 1970. Use of ultrasonic transmitters for the marking of bream and pike. *Fish. Res. B. Can. Transl. Ser.*, 2146: 75-78.
- Malinin, L.K. 1971. Home range and actual paths of fish in the river pool of the Rybinsk reservoir. *Fish. Res. B. Can. Transl. Ser.*, 2282: 158-166.
- Mann, R.H. 1980. The numbers and production of pike (*Esox lucius*) in two dorset rivers. J. Anim. Ecol., 49: 899-915.
- Massé, G., Dumont, P., Ferraris, J. & Fortin, R. 1991. Influence des régimes hydrologiques et thermiques de la rivière aux Pins (Québec) sur les migrations de fraie du grand Brochet et sur l'avalaison des jeunes brochets de l'année. Aquat. Living Resour., 4: 275-287.
- 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 (1-3): 185-191.
- Mellas, E.J. & Haynes, J.M. 1985. Swimming performance and behaviour of rainbow trout (*Salmo* gairdneri) and white perch (*Morone americana*): effects of attaching telemetry transmitters. Can. J. Fish. Aquat. Sci., 42: 488-493.
- Miller, L.M., Kallemeyn, L. & Senanan, W. 2001. Spawning site fidelity by northern pike in a large lake: Mark-recapture and Genetic Evidence. *Trans. Am. Fish. Soc.*, 130: 307-316.
- Ovidio, M. 1999. Cycle annuel d'activité de la truite commune (*Salmo trutta* L.) adulte: étude par radio-pistage dans un cours d'eau de l'Ardenne belge. *Bull. Fr. Pêche Piscic.*, 352: 1-18.
- Ovidio, M. & Philippart, J.C. 2002. The impact of small physical obstacles on upstream movements of six species of fish. Synthesis of a five years telemetry study in the River Meuse Basin. *Hydrobiologia*, 483 (1-3): 55-69.
- Prejs, A., Martyniak, A., Boron, S., Hliwa, P. & Koperski, P. 1994. Food web manipulation in a small eutrophic Lake Wirbel, Poland: effects on

stocking with juvenile pike on planktivorous fish. *Hydrobiologia*, 275/276: 65-70.

- Raat, A, J, P. 1988. Synopsis of biological data on the northern pike *Esox lucius* Linneaus 1758. FAO *Fish. Syn.*, 30: 188 pp.
- Rogers, K.B. & Bergersen, E.P. 1995. Effects of a fall Drawdown on Movement of Adult Northern Pike and Largemouth Bass. N. Am. J. Fish. Mgmt., 15: 596-600.
- Rosell, R.S. & MacOscar, K.C. 2002. Movements of pike, *Esox lucius*, in lower Lough Erne, deter-

mined by mark recapture between 1994 and 2000. *Fish. Mgmt. Ecol.*, 9:189-196.

- Sukhanova, A.I. 1979. The spawning and fecundity of the pike *Esox lucius*, in Vilyuy reservoir, *J. Ichtyol.*, 19: 74-79.
- Winter, J.D. 1983.Underwater biotelemetry. In L.A., Nielsen & Johnson, D.L. eds. Fisheries techniques, 371-395 pp. Bethesda, MD, American Fisheries Society, 496 pp.