Spedicato, M.T.; Lembo, G.; Marmulla, G. (eds.)
Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe. Ustica, Italy, 9-13 June 2003.
Rome, FAO/COISPA. 2005. 295p.

Spatial behaviour of pike *Esox lucius* L. in the River Frome, UK

J. E. G. Masters, K. H. Hodder, W. R.C. Beaumont*, R. E. Gozlan, A. C. Pinder, R. E. Kenward, J. S. Welton

Centre for Ecology and Hydrology, Winfrith Technology Centre, Winfrith Newburgh, Dorchester, Dorset, DT2 8ZD, United Kingdom, Phone: +44 (0) 1305 213500, fax: +44 (0) 1305 213600.
**Corresponding Author, e-mail:wrb@ceh.ac.uk.*

Key words: Pike, *Esox lucius*, spatial behaviour, static, mobile.

Abstract

Fifteen pike *Esox lucius* L. were radio tracked in the River Frome, UK, for between 8 and 25 months. Examination of the locations of seasonally determined cluster polygon home ranges, together with positional fixes recorded throughout the year, revealed that spatial behaviours could not be grouped into the simple 'static' and 'mobile' categories that had previously been proposed for the species. Rather, a continuum of spatial behaviours existed, from individuals that always remained within the same few hundred metres of river, to individuals that made repeated journeys over several kilometres on a broadly seasonal basis. Relocations were also observed, whereby pike moved to a distinctly different location to that which they had formerly occupied.

Introduction

The pike *Esox lucius* L. is a piscivorous fish, occurring in lakes and rivers in temperate and arctic regions of the northern hemisphere (Raat, 1988).

The spatial behaviour of pike in lakes has been well studied, and is known to be highly variable, both within and between populations with some individuals staying within a restricted area, whilst others move between two or three favoured areas, or wander more freely throughout the lake (e.g. Diana *et al*., 1977; Diana, 1980; Mackay and Craig, 1983; Chapman and Mackay, 1984; Cook and Bergersen, 1988; Lucas *et al*., 1991; Jepsen *et a*l., 2001).

Pike in rivers have received comparatively little attention. Riverine pike have been shown to be capable of extensive movements, with mean upstream spawning migrations of 7.7 km reported for pike in the Ourthe and Amblève rivers (Ovidio and Philippart, 2002). Movements >100 km, between summer and winter locations, occurred in an Alaskan wetland area (Burkholder and Bernard, 1994). These reports contrast with the results of a mark-recapture study, based in the River Frome, UK, during which most jaw tagged pike appeared to remain within the 3 km of study area after release, although some pike dispersed more widely, leading to the proposal that the pike population consisted of both static and mobile components, with the former comprising ca. 74% of the population (Mann, 1980). Gerlier and Luquet (1999) reported radio tagged pike occupying between 400 m and 12260 m of the River Ill, France, although interpretation of the results, in terms of static and mobile fish, is complicated by differences in release strategy and track duration.

Classic studies, which described limited movement (e.g. Mann, 1980), together with the adaptations of pike for fast-start swimming (Helfman *et al*., 1997) and the species preference for areas of slack water in rivers (Lamouroux *et al*., 1999), have led to reports of extensive movements being viewed as paradoxical (Ovidio and Philippart, 2002).

The present study aimed to describe the long-term spatial behaviour of riverine pike by referring to the locations of seasonally determined home ranges for radio tagged individuals and by interval tracking of these same fish throughout the year, including during the spawning period, which occurs in spring (Raat, 1988). Specifically, the

hypothesis that pike populations comprise both static and mobile individuals (Mann, 1980) was to be examined.

Materials and methods

Study area

This study was based in the River Frome, Dorset, UK, a largely unmodified groundwater fed chalk stream in southern England. The river had a meandering main channel and was free to burst its banks under high flows, when water inundated the surrounding meadows. The main study area (SY 8686 and SY 8768), consisted of > 2000 m of river channel (mean width=14 m), flowing west to east, with adjoining drainage ditches and a millstream, this being the same area of river in which pike were marked and recaptured by Mann (1980) (Fig. 1). Whilst the East Stoke gauging weir, at the head of the weirpool (Fig. 1) formed a potential barrier to movement, there were no barriers downstream of the main study area. Submerged vegetation in the river consisted mainly of *Ranunculus* spp. and *Potamogeton* spp. Emergent vegetation (*Phragmites australis* (Cav.) and *Glyceria maxima* (Hartm.)) was rare and mainly confined to the banks. The majority of the river lay within areas of grazed pasture and there was little outstream shade. Discharge data (courtesy of the Environment Agency) and water temperature were recorded every fifteen minutes at the East Stoke gauging weir.

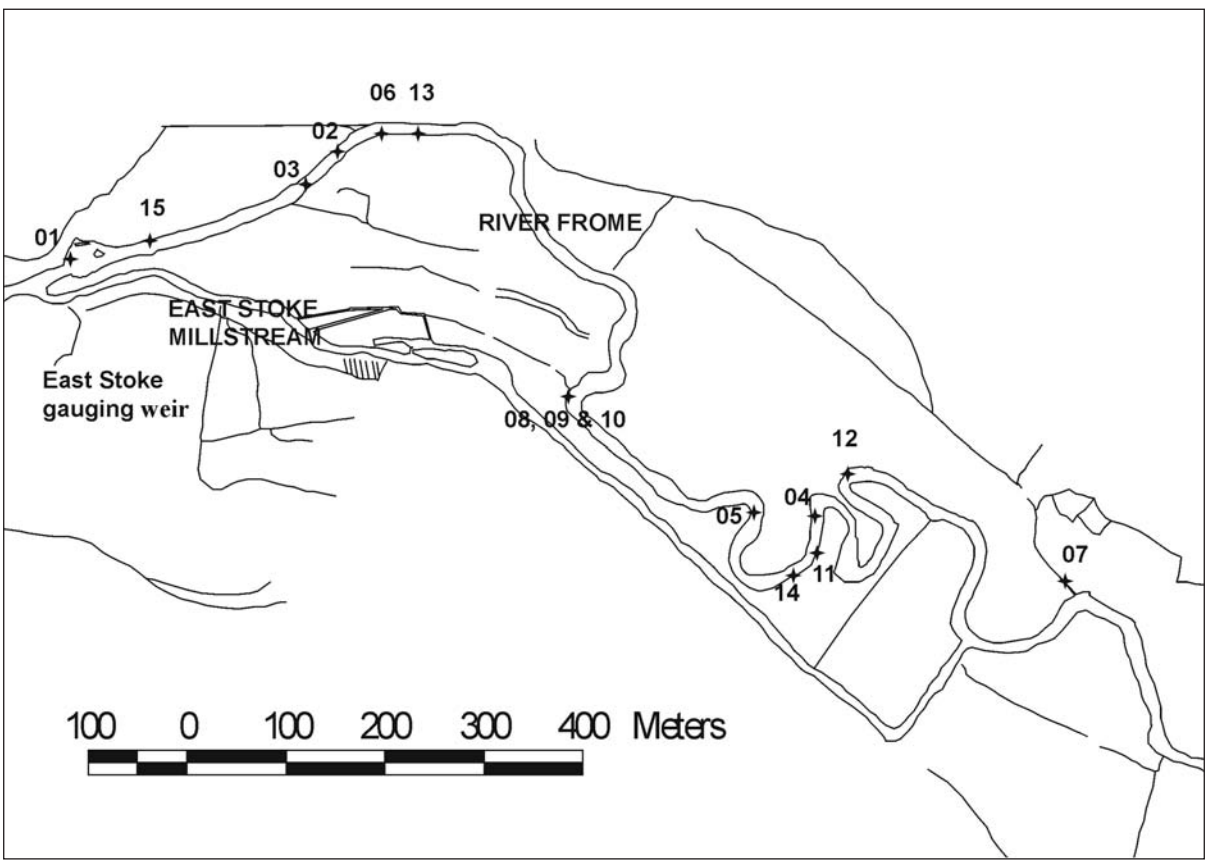

Fig. 1 – Capture locations for each pike (01, 02, 03 etc.) within the main study area.

Radio tagging

Fifteen pike, captured by angling or electric fishing within the main study area, were anaesthetised in a 1 mll^{-1} dilution of 2-phenoxyethanol in river water and implanted with TW-5 radio tags (Biotrack Ltd, Wareham, UK) under aseptic conditions, using sterilised instruments and tags, as described in full by Beaumont *et al*. (2002) (Table 1). Tagging was carried out in accordance with the UK Animals (Scientific Procedures) Act 1986. Tag dimensions were: length=8.0 cm, diameter=1.6 cm, weight=22 g in air, 7 g in water, and the antenna type was an internal coil. The ratio of fish weight to tag weight in water was <0.5% in all cases. Pike were sexed through external examination of the urogenital region (Casselman, 1974).

Each pike was released at its capture location after recovery from anaesthesia (Fig. 1), this being considered less stressful than a prolonged period of post-operative captivity (Crossman, 1977). To avoid potential distortion of results following tag implantation, data were not recorded until at least ten days after tagging (Jepsen *et al*., 2001; Beaumont *et al*., 2002). Growth rates and condition factors have been shown to be unaffected amongst pike tagged using a similar procedure (Jepsen and Aarestrup, 1999). Pike 04 and Pike 08 died during the study, ca. 10 months and ca. 15 months after tagging. The deaths were assumed to be due to natural causes, although the remains of Pike 08 were too decomposed to allow for post-mortem investigation, and the body of Pike 04 could not be recovered (Masters, 2003).

Table 1 – Data collected for each pike, arranged in order of ascending TMLD. 'No. fixes' gives the number of fixes recorded for each pike whilst 'No. days' gives the number of days between the date of tagging and the date that the last fix was recorded. L_F and W are the fork length and weight at time of capture. The dates for home range tracks were: 1) July 2000, 2) September 2000, 3) December 2000, 4) March 2000, 5) July 2000, 6) September 2000, 7) December 2001 and 8) March 2002. TMLD and MCD are also given. Pike 08 was only present in the study area during home range track 4), therefore MCD could not be calculated. For Pike 01 and Pike 06, MCDs are based upon data from home range tracks 1) to 4) and 3), 4) and 8), respectively, during which the fish were within the main study area.

Pike	Date of tagging	Sex	L_F cm	W kg	No. fixes	No. days	Present in home range tracks	TMLD m	MCD m
15	8 Nov 2001	♂	64	2.3	130	240	7 and 8	162	20
13	31 Jul 2001	♀	52	1.7	232	346	6 to 8	231	167
10	17 Jan 2001	♂	64	2.8	310	542	4 to 8	546	264
12	22 May 2001	♂	69	3.2	218	416	5 to 8	653	447
05	23 Aug 2000	♀	60	1.7	401	689	2 to 8	762	541
03	08 Jun 2000	♀	66	3.0	500	748	1 to 8	781	325
11	22 May 2001	♂	58	1.7	225	416	5 to 8	1142	371
02	24 May 2000	♂	71	3.6	471	773	1 to 8	1385	333
14	4 Sep 2001	♀	54	1.4	166	316	6 to 8	1498	1377
07	30 Nov 2000	♀	93	8.2	296	581	4 to 8	1524	638
09	17 Jan 2001	♀	81	4.0	324	544	4 to 8	1899	1230
04	31 July 2000	♀	66	3.0	172	243	2 to 4	2694	1415
08	17 Jan 2001	♀	95	8.2	111	417	4	2857	n/a
06	16 Oct 2000	♂	87	>5.0	239	633	3, 4 and 8	5643	27
01	24 May 2000	♀	86	5.2	295	1276	1 to 4	5916	336

Tracking

The positions of radio tagged pike were determined from the riverbank, or from an inflatable boat, using hand-held radio receivers and three-element Yagi antennae. Tracks to establish short-term home ranges of pike were conducted on a seasonal basis. During these home range tracks pike were located three times a day (morning, midday and evening), for a period of 13 days, giving a maximum of 39 location records (fixes) per fish. Eight home range tracks took place during 2000-2002, occurring in 1) July 2000, 2) September 2000, 3) December 2000, 4) March 2001, 5) July 2001, 6) September 2001, 7) December 2001 and 8) March 2002. Time was usually insufficient to allow pike that had moved out of the main study area to be included in home range tracks.

Additional fixes were collected throughout the study, to provide longer term movement data. Due to the pike being tagged and released on different dates, the number of fixes recorded and the number of days upon which pike were tracked varies between individuals (Table 1). Time constraints did not allow pike that left the main study area to be located as often as those remained, resulting in relatively fewer fixes for these fish. Tracking concluded in July 2002.

Analysis

To compare long-term spatial behaviours between individuals, for each pike, the distance between the capture point and every fix was determined; distances being measured along the midline of the river using a modified version of RANGES V (Kenward and Hodder, 1996). Distance from the capture point was plotted against time, separately for each pike.

Spatial behaviour was further described using two indices, the Total Maximum Linear Displacement (TMLD) and the Maximum Core Displacement (MCD).

Total Maximum Linear Displacement (TMLD)

TMLD was the total longitudinal distance used by each pike during the entire period it was tracked, measured along the midline of the river i.e. the distance between the furthermost upstream downstream locations. Spearman's rank correlations were used to look for relationships between TMLD and a) pike length b) the number of fixes obtained for each pike and c) the number of days between the first and last fixes for each pike. Differences between the sexes were examined using a two-sample t-test (assuming unequal variation).

Maximum Core Displacement (MCD)

Convex cluster polygon home ranges were calculated for every individual in each home range track (using RANGES V) after removal of outlying fixes (Hodder *et al*., 1998; Kenward, 2001; Kenward *et al*., 2001). The cluster analysis technique used was the C_{tx} type, as defined by Kenward *et al*. (2001), clusters henceforth being referred to as 'core ranges.' The mean distance from the capture location of all the fixes within each separate core range was then calculated, this mean distance being termed the core "centre". Core ranges were 36±4 m long (mean ± s.e.), as measured along the midline of the river, making the core centre a suitable measure of location to describe long term spatial behaviour, over the scale of the river. MCD then, for each individual, was the distance between the furthermost upstream and downstream cluster centres, from all home range tracks combined. Whilst TMLD is a measure of the total length of river used by pike, MCD provides a measure of the longitudinal distance along which core areas of activity were distributed.

Use of side channels

This study focussed upon the spatial behaviour of pike within the main river channel, the behaviour of pike within side channels connected to the River Frome having been previously examined by Masters *et al*. (2002). In order to describe the linear movement of pike along the river channel, fixes occurring in side channels were recorded as the distance between the capture location and the point where the side channel connected to the river. By this method, a fix, for example, 10 m downstream of the capture location and 10 m along a drainage

ditch, could not be confused with a separate fix, 20 m downstream of the capture location. To give an indication of the extent of side channel use in every home range track, the proportion of fixes occurring within the side channels was determined for each fish and a median value then calculated from all pike during that track.

Results

The results showed that considerable variation in spatial behaviour occurred between individuals, with TMLDs ranging from 162 m to 5916 m (Fig. 2, Table 1). There were no correlations between TMLD and either the length of time for which a pike was tracked (R_s=0.37, n=15, *P*=0.18), or the number of fixes recorded for each fish (R_s=-0.05, n=15, *P*=0.85), therefore the observed variation in TMLD was not simply a reflection of the different datasets. There was no significant difference in TMLD between the sexes (Two-sample t-test: DF=9, t=0.43, *P*=0.68). There was a significant positive correlation between TMLD and the fork length of pike (R_s=0.69, n=15, *P*<0.01), although TMLD could vary widely between similarly sized fish (e.g. Pike 03 and 04, Table 1, Figs. 2.a and 2.c).

Many of the pike, displayed a high degree of site fidelity, being found in the same few hundred metres of river throughout the time they were tracked (Pike 15, 13, 10, 12, 05, 03, 02; Figs. 2.a and 2.b), with MCDs being correspondingly low (20 m to 541 m, Table 1). In contrast, Pike 06 and 08 used widely separated areas of river at different times of the year (Fig. 2.c). Rather than a split into simple "static" and "mobile" groups then, a continuum of spatial behaviours existed, with pike displaying behaviours intermediate to the two "extremes" described above, for example, the behaviour of Pike 11 was similar to that of Pike 06 and 08 but on a smaller longitudinal scale, whilst Pike 07 showed periodic returns to its capture location whilst more commonly residing some 500 m upstream (Figs. 2.b and 2.c).

Short-term excursions were performed by several pike (Pike 05, 03, 02, 14 and 09) increasing the length of their TMLDs (Figs. 2.a and 2.b, Table 1), whilst MCD could also be increased if an excursion coincided with a home range track (Pike 05, 14 and 09, Figs. 2.a and 2.b, Table 1). Following excursions, Pike 05, 03, 02 and 14 all returned to their usual areas of residency. A permanent relocation was performed by Pike 01, which stayed within ca. 300 m of its capture site for ca. 11 months before ranging over several kilometres and settling 2000 m to 3000 m upstream (Fig. 2.c, Table 1).

Wide ranging movements similar to those of Pike 01 prior to relocation were also performed by Pike 04, which had shifted its area of residency downstream by some 500 m during November 2001, resulting in a high MCD for this fish (Fig. 2.c, Table 1).

The effect of season and/or discharge upon spatial behaviour

The timing of the movements of the two pike that used widely separated areas of river at different times of year (Pike 06 and 08) were broadly seasonal in nature, but discharge also appeared to be a factor; both pike moving upstream during a flood in December 2002 when more minor flood events earlier in the year had not resulted in upstream movements (Fig. 2.c). For several pike, excursive behaviour, or a more prolonged relocation, coincided with periods of flooding (Pike 05, 03, 14 and 04; Figs. 2.a and 2.c).

Increased movements during the spring were seen amongst some, but not all, of the pike (e.g. Pike 02, 14, 09, 04 and 01) and such movements were not necessarily repeated the following year (Pike 09 and 01, Fig. 2.b).

Utilisation of side channel habitats

Only two of the fifteen pike tracked were never found in side channels either during or between home range tracks (Pike 14 and 15). No pike were found in side channels during home range tracks 1) and 2) but pike were often found in side channels during home range tracks 3) and 4) (Fig. 3). Generally, lower percentage utilisation occurred in subsequent tracks, although one individual (Pike 12) made extensive use of a side channel during home range track 7) (Fig. 3).

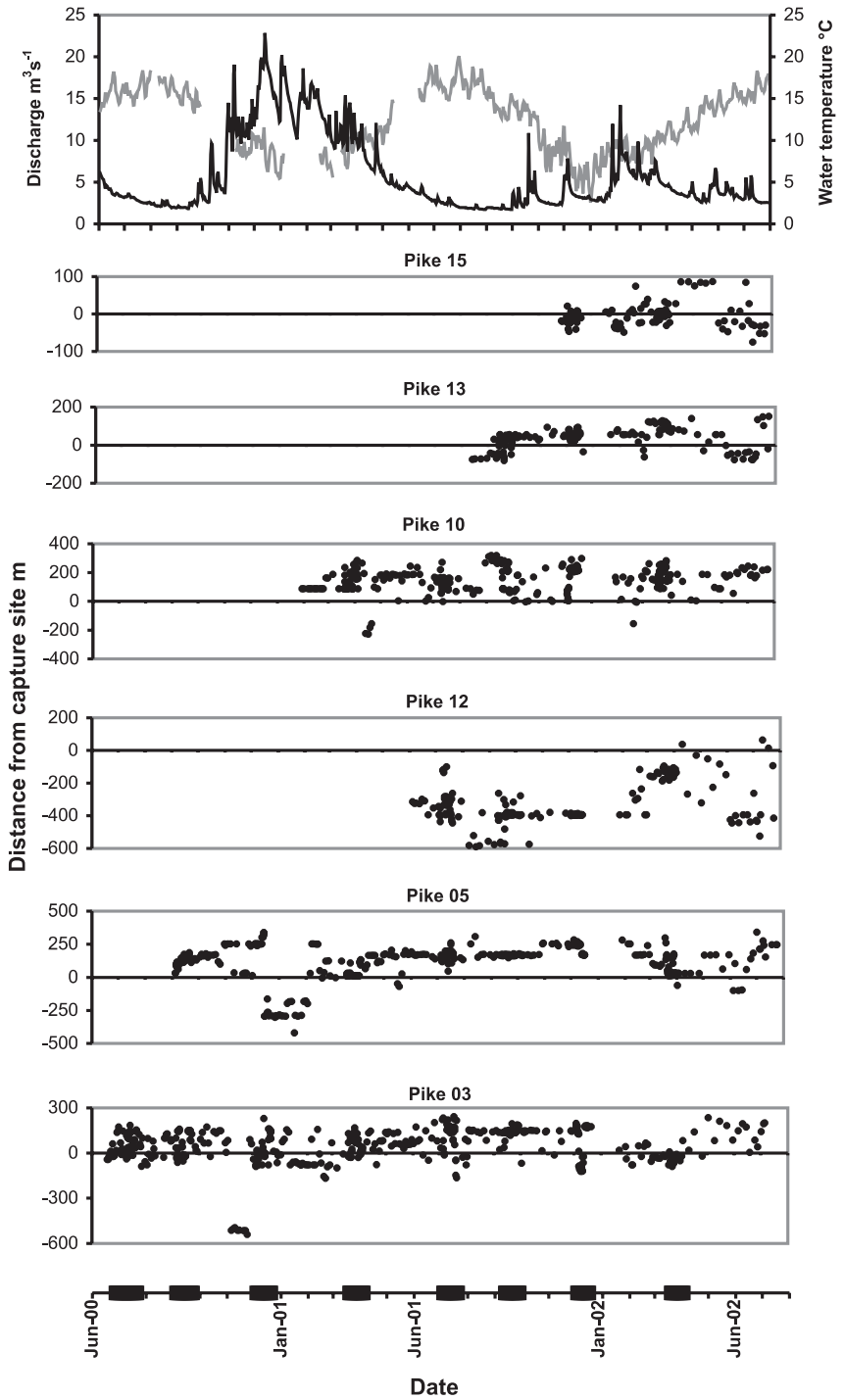

Fig. 2a – The distance from the capture location for every fix recorded from each pike over the entire time they were tracked, arranged in order of ascending Total Maximum Linear Displacement (Pike 15, 13, 10, 12, 05, 03). Mean daily discharge and water temperature data are also shown. Periods when home range tracking took place are indicated (■).

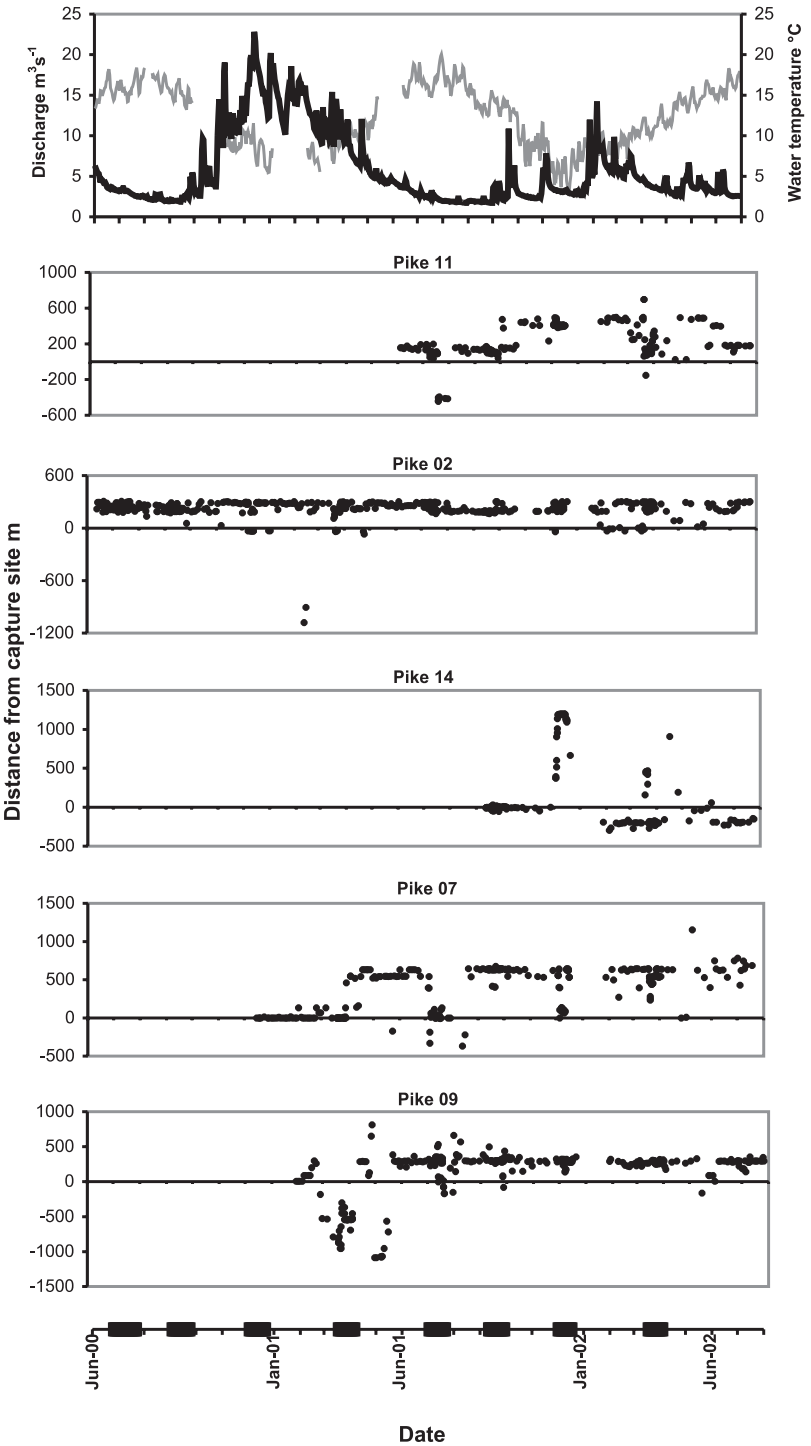

Fig. 2b – The distance from the capture location for every fix recorded from each pike over the entire time they were tracked, arranged in order of ascending Total Maximum Linear Displacement (Pike 11, 02, 14, 07, 09). Mean daily discharge and water temperature data are also shown. Periods when home range tracking took place are indicated (■).

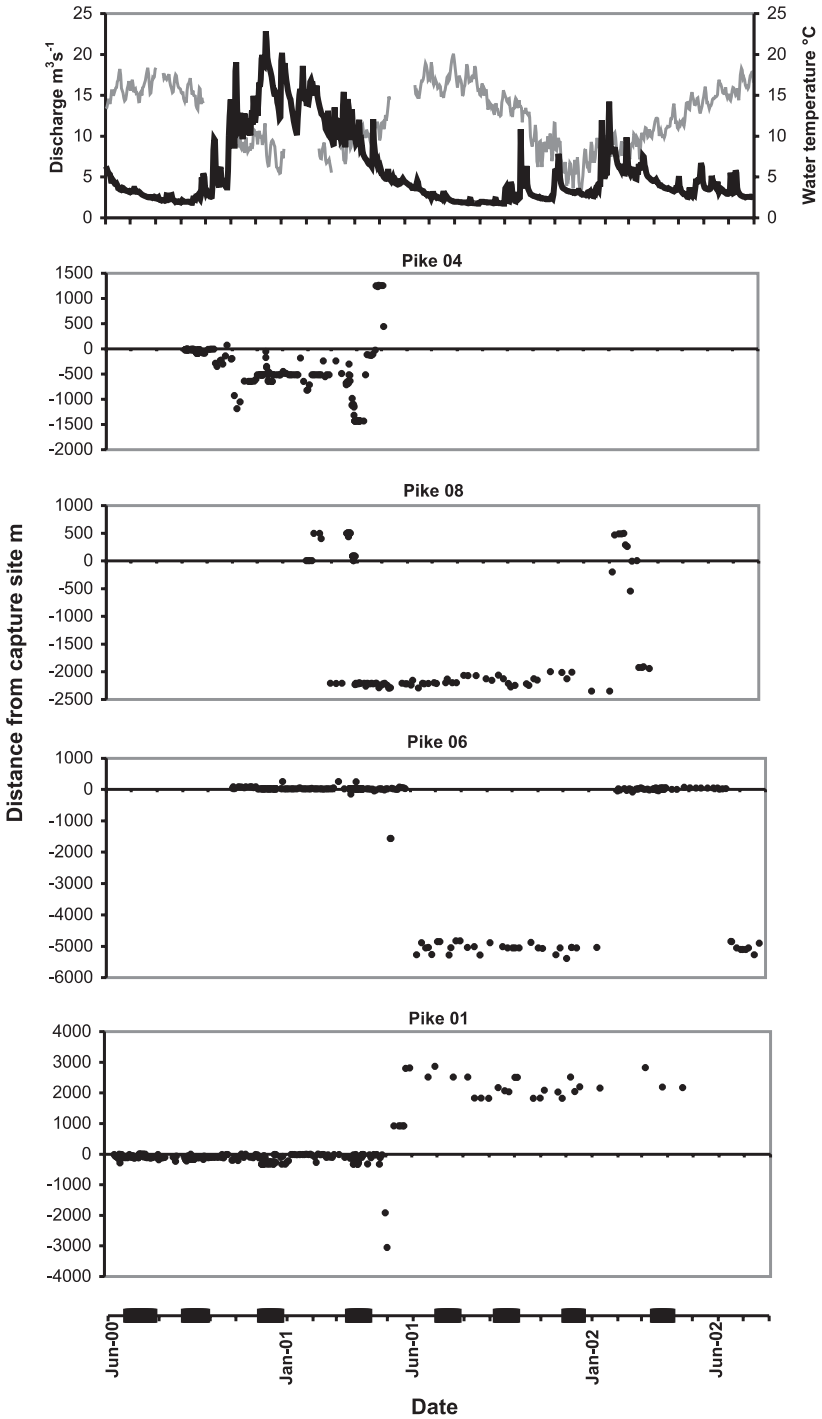

Fig. 2c – The distance from the capture location for every fix recorded from each pike over the entire time they were tracked, arranged in order of ascending Total Maximum Linear Displacement (Pike 04, 08, 06, 01). Mean daily discharge and water temperature data are also shown. Periods when home range tracking took place are indicated (■).

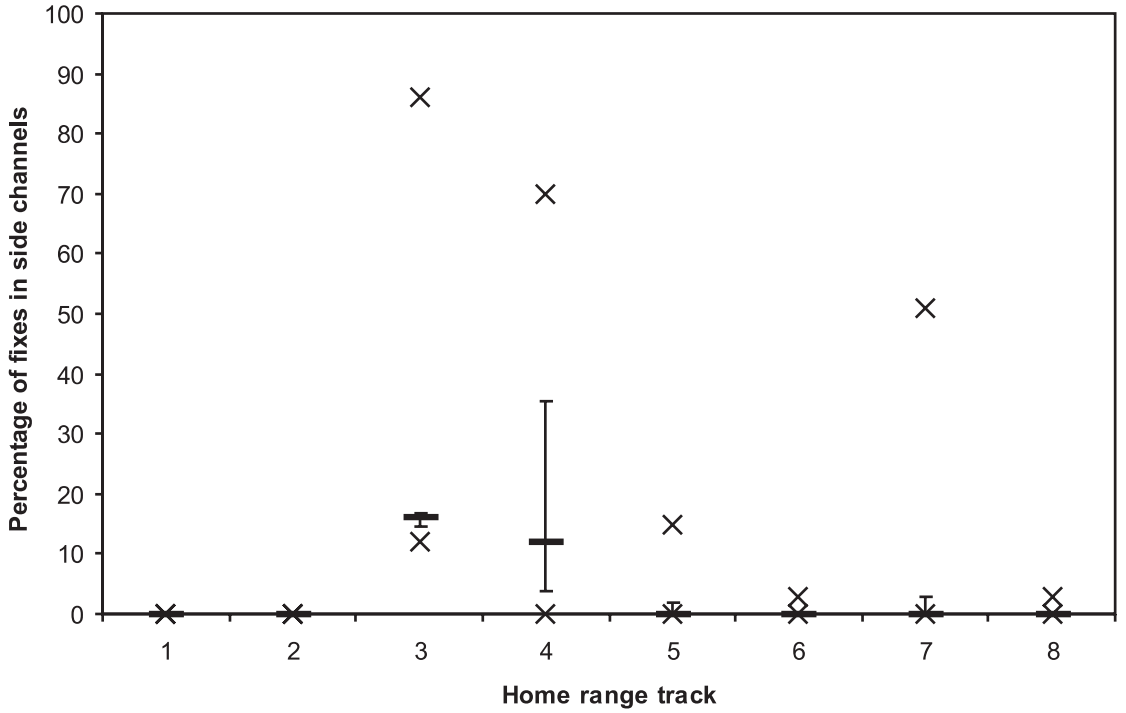

Fig. 3 – The median (—), maximum (×) and minimum (×) percentage of fixes occurring in side channels in each home range track, together interquartile range, recorded from individual pike.

Discussion

Pike in the River Frome showed a highly variable repertoire of spatial behaviour that did not fit the previous model of static and mobile individuals (Mann, 1980). This result supports the view of pike as versatile predators (Chapman and Mackay, 1984) and reflects the variety of spatial behaviours reported for lacustrine pike. There was a continuum of spatial behaviours, from individuals that always remained within a few hundred metres of river (e.g. Pike 13, 15) to individuals that made repeated journeys of several kilometres (e.g. Pike 06, 08). Relocations could also occur, with Pike 01 moving to a distant stretch of river and not returning for the remainder of the study period.

The two indices used to describe spatial behaviour (TMLD and MCD) allowed for distinctions to be made between the total length of river used and the length of river in which activity was concentrated. However, MCD does require careful interpretation; larger values being obtained when home range tracks coincided with excursive behaviour by pike. Long-term radio tracking, between home range tracks, allowed such excursive behaviour to be placed in context with activity throughout the year.

Whilst pike that were always found within a few hundred metres of their capture site could be viewed as being "static", we feel the term is inappropriate, as it would ignore both the movements within the length of river occupied, and also the occurrence of excursive movements. Pike 06 and 08 could easily have been described as 'static' fish, had they been involved in a mark-recapture or shorter-term radio tracking study. Despite both displaying repeated long distance movements between widely separated areas of river, within the upstream and downstream home ranges the patterns of fixes are similar to those of pike with the shortest TMLDs.

Explanations for the different spatial behaviours exhibited by the pike must of necessity be speculative at this stage. The positive correlation between pike length and TMLD suggests that larger pike may move more freely within the river than smaller pike; consistent with the hypothesis of Grimm and Klinge (1996) that smaller pike, being at greater risk of predation, show more restricted distributions.

The large upstream movements of Pike 06 and 08 were indicative of spawning migrations, although until such time as this behaviour can be shown to be of adaptive significance to the population (Lucas and Baras, 2001) the term 'migration' must be treated with appropriate caution. Both fish frequented known spawning grounds whilst residing in the main study area and Pike 08 was seen spawning in March 2001.

Upstream movement by Pike 06 and 08 appeared to be related to increased discharge in 2001. In November 2002, after the conclusion of the present study, Pike 06 again returned to the same upstream location, at the onset of a period of flooding (CEH, unpublished data), implying that a similar movement may have occurred prior to the fish being tagged in October 2000, when the period of major flooding had just begun. Downstream movements appeared to coincide with the end of the spawning period in both 2001 and 2002 and on the day after Pike 08 was seen spawning, the fish was detected in the main study area, and then subsequently >2000 m downstream, just 1.5 hours later.

Differences occurred between Pike 06 (♀) and 08 (♀), both in spatial behaviour within the main study area and in the timing of downstream movements. Whilst upstream, Pike 08 ranged more widely than Pike 06, and visited several different side channels, whereas Pike 06 was almost always found near the same channel where it had originally been caught and released. Pike 06 remained in the main study area longer than Pike 08 in both years. Without a larger sample size it was not possible to state whether these particular differences represented individual variation, or more widespread differences in behaviour between the sexes (Frost and Kipling, 1967; Lucas, 1992).

The spawning period is a time of increased activity for lacustrine pike (Lucas, 1992) and this appeared also to be the case for some riverine individuals, although others remained in one area throughout the spring. Miller *et al*. (2001) demonstrated the existence of natal homing amongst pike and it can be hypothesised that those individuals that showed the most restricted longitudinal distribution along the river remained within the vicinity of their natal spawning site for their entire life whereas wider ranging individuals may have dispersed away from the natal spawning site, possibly returning on a seasonal basis. However, during the spring pike were not necessarily restricted to one particular area (e.g. Pike 08 and 11) and different areas could be occupied in successive years (e.g. Pike 01 and 09). Natal homing alone cannot account for the variety of movement patterns displayed.

Langford (1979) noted that flood flows could lead to the displacement of pike, and this could account for some of the excursions recorded during the present study (e.g. Pike 03 and 05). Excursive movements perhaps lead to relocation, if a better quality habitat is found (in terms of increased prey availability or reduced competition) and this may have occurred for Pike 01.

Side channels are clearly of great importance to pike under certain conditions. These areas were known to be used for spawning (Mann, 1980), but were also found to be utilised extensively well in advance of the spawning period, particularly during elevated discharges in autumn/winter 2000/2001 (Masters *et al*., 2002). Similar exploitation of side channels was noted by Gerlier and Luquet (1999). During summer months side channels were rarely occupied. Although some of the side channels in the study area became inaccessible to pike during the summer, due to shallow water at the mouth, others remained accessible, but were still rarely occupied. When pike left the main river channel, the side channels entered were usually those closest to the areas where they normally resided but it is notable that during the upstream movements of Pike 06 and 08, numerous side channels were passed during their return to the main study area.

In order to further study the variation in the spatial behaviours observed, ideally pike need to be followed throughout their lives and the importance of

intraspecific and interspecific interactions also need to be considered. Studying pike throughout their lives is an aim for future studies, and can be achieved by techniques such as individually marking young-of-the-year pike prior to their dispersal from the spawning grounds, using Passive Integrated Transponders (Lucas, 1999), together with radio telemetry techniques adapted for use with small (Beaumont and Masters, 2003) and large pike.

Acknowledgements

We would like to thank Alison Aldous, Jon Bass, Caroline Boffey, Ian Farr, Chris Flower, Carolyn Knight, Bethan Lewis, Neasa McDonnell, Luke Scott and Sarah Venis for their invaluable assistance in the field. Carolyn Knight is further thanked for her help producing Figure 1. The advice and practical assistance provided by Mike Ladle was greatly appreciated. We would like to thank local landowners for granting us access to the river, and the Environment Agency for supplying discharge data and aerial photographs used to produce a digitised map of the river. Jerome Masters was registered as a Ph.D. student at the University of St Andrews and was in receipt of a Freshwater Biological Association Frost Scholarship. Further funding was received from NERC.

References

Beaumont, W.R.C., Cresswell, B., Hodder, K.H., Masters, J.E.G. & Welton, J.S. 2002. A simple activity monitoring radio tag for fish. *Hydrobiologia*, 483: 219-224.

Beaumont, W.R.C. & Masters, J.E.G. 2003. A method for the external attachment of miniature radio tags to pike *Esox lucius*. *Fish. Manag. Ecol*., 10: 407-409.

Burkholder, A. & Bernard, D.R. 1994. *Movements and distribution of radio-tagged northern pike in Minto Flats*. Alaska Department of Fish and Game, Fishery Manuscript No. 94-1, Anchorage, USA.

Casselman, J.M. 1974. External sex determination of northern pike, *Esox lucius* Linnaeus. *Trans. Am. Fish. Soc*., 103: 343-347.

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

Cook, M.F. & Bergersen, E.P. 1988. Movements, habitat selection and activity periods of northern pike in Eleven Mile Reservoir, Colorado. *Trans. Am. Fish. Soc*., 117: 495-502.

Crossman, E.J. 1977. Displacement, and home range movements of muskellunge determined by ultrasonic tracking. *Env. Biol. Fishes*, 1: 145-158

Diana, J.S. 1980. Diel activity pattern 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.

Frost, W.E. & Kipling, C. 1967. A study of the reproduction, early life, weight-length relationship and growth of pike, *Esox lucius* L., in Windermere. *J. Anim. Ecol*., 36: 651-693.

Gerlier, M. & Luquet, J-F. 1999. Preliminary study on the spawning migration of pike (*Esox lucius*) in the River Ill, a tributary of the Rhine. *In* Moore, A. & Russell, I. eds. *Third conference on fish telemetry in Europe*, pp. 129-136. Lowestoft, Suffolk, UK. Centre for Environment, Fisheries and Aquaculture Science. 246 pp.

Grimm, M.P. & Klinge, M. 1996. Pike and some aspects of its dependence on vegetation. *In* Craig, J.F. ed. *Pike: biology and exploitation*, 125-156 pp. London, Chapman and Hall. 298 pp.

Helfman, G.S., Collette, B.B. & Facey, D.E. 1997. Fishes as predators. *In*: *The diversity of fishes*, pp. 321-333. Massachusetts, Blackwell Science. 544 pp.

Hodder, K.H., Kenward, R.E., Walls, S.S. & Clarke, R.T. 1998. Estimating core ranges: A comparison of techniques using the common buzzard (*Buteo buteo*). *J. Raptor Res*., 32: 82-89.

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. Behaviour of pike (*Esox lucius* L.) >50 cm in a turbid reservoir and in a clearwater lake. *Ecol. Freshwat. Fish*, 10: 26-34.

Kenward, R.E. 2001. *A manual for wildlife radio tagging*. London, Academic Press. 311 pp

Kenward, R.E. & Hodder, K.H. 1996. *RANGES V: An analysis system for biological location data*. Centre for Ecology and Hydrology, UK.

Kenward, R.E., Clarke, R.T., Hodder, K.H. & Walls, S.S. 2001. Density and linkage estimators of home range: Nearest-neighbour clustering defines multinuclear cores. *Ecology*, 82: 1905-1920.

Lamouroux, N., Capra, H., Pouilly, M. & Souchon, Y. 1999. Fish habitat preferences in large streams of southern France. *Freshwat. Biol.,* 42: 673-687.

Langford, T.E., 1979. Observations on sonic tagged coarse fish in rivers. *In Proceedings of the 1st British Freshwater Fisheries Conference* 106-114 pp. Liverpool UK, University of Liverpool.

Lucas, M.C. 1992. Spawning activity of male and female pike, *Esox lucius* L. determined by acoustic tracking. *Can. J. Zool.*, 70: 191-196.

Lucas, M.C. 1999. Recent advances in the use of telemetry and tracking applied to freshwater fishes. *In*: Le Mayo, Y. ed. *Proceedings of the fifth European wildlife telemetry conference* 254-264 pp. Strasbourg, France.

Lucas, M.C. & Baras, E. 2001. *Migration of freshwater fishes*. Oxford, UK, Blackwell Science Ltd., 420 pp.

Lucas, M.C., Priede, I.G., Armstrong, J.D., Gindy, A.N.Z. & De Vera, L. 1991. Direct measurement of metabolism, activity and feeding behaviour of pike, *Esox lucius* L., in the wild, by the use of heart rate telemetry. *J. Fish Biol.*, 39: 325-345.

Mackay, W.C. & Craig, J.F. 1983. A comparison of four systems for studying the activity of pike, *Esox lucius* L. and perch *Perca fluviatilis* L. and *P. flavescens* (Mitchell). *In* Pincock, D.G. ed. *Proceedings of the fourth international conference on wildlife biotelemetry*, 22-30 pp. Halifax, Canada, University of Nova Scotia.

Mann, R.H.K. 1980. The numbers and production of pike (*Esox lucius*) in two Dorset rivers. *J. Anim. Ecol.*, 49: 889-915

Masters, J.E.G. 2003. Temporal variation in the behaviour of pike *Esox lucius* L. University of St Andrews, Fife. (PhD Thesis)

Masters, J.E.G., Welton, J.S., Beaumont, W.R.C., Hodder, K.H., Pinder, A.C., Gozlan, R.E. & Ladle, M. 2002. Habitat utilisation by pike *Esox lucius* L. during winter floods in a southern English chalk river. *Hydrobiologia*, 483: 185-191.

Miller, L.M., Kallemeyn, L., Senanan, W. 2001. Spawning-site and natal site fidelity by northern pike in a large lake: mark recapture and genetic evidence. *Trans. Am. Fish. Soc.*, 130: 307-316.

Ovidio, M. & Philippart, J.C. 2002. The impact of small physical obstacles on upstream movements of six species of fish. *Hydrobiologia*, 483: 55-69.

Raat, A.J.P. 1988. Synopsis of biological data on the northern pike *Esox lucius* Linnaeus 1758. *FAO Fish. Syn.*, No. 30 Rev 2: 178 pp.