Accepted: 20 February 2017

DOI: 10.1111/eff.12355

ORIGINAL ARTICLE

WILEY Ecology of FRESHWATER FISH

Relationships between individual movement, trophic position and growth of juvenile pike (*Esox lucius*)

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Abstract

Variation in movement between individuals can have important ecological effects on populations and ecosystems, yet the factors driving differences in movement and their consequences remain poorly understood. Here, individual variability in the movements of juvenile (age 0 + and 1 + year) pike *Esox lucius* was assessed using passive integrated transponder (PIT) telemetry in off-channel nursery areas over a 26- month period. Differences in the movement patterns of individuals were tested against their body sizes, ages, growth rates and trophic positions using data collected through a combination of catch-and-release sampling and stable isotope analyses. Results revealed that variation in movement between individuals was affected by age, with 1 + individuals moving more than individuals of age 0 + , but not length. Individuals whose TP was low on their initial capture event moved significantly less than those with a higher initial TP. Individuals that moved more grew faster and achieved a higher final TP. These results suggest that higher activity (i.e., increased movement) increases resource acquisition that enhances growth rates, which could ultimately maximise individual performances.

KEYWORDS

Inter-individual variation, movement, PIT telemetry, stable isotope analyses

1 | INTRODUCTION

The majority of animals rely on a certain level of displacement to forage, avoid predators and compete for resources, making movement an important attribute for growth and survival (Bergman, Schaefer, & Luttich, 2000; Turchin, 1998). Although movements that are associated with increased fitness are predicted to be favoured (Stearns, 1992), considerable intraspecific variability in movement exists, as observed in mammals (e.g., Pinter-Wollman, 2009), birds (e.g., Catry et al., 2011) and fish (e.g., Kobler, Klefoth, Mehner, & Arlinghaus, 2009). This variability in movement is therefore suggested to reflect the underlying behavioural strategies of individuals (Austin, Bowen, & McMillan, 2004; Salomon, 2009). For instance, activity that involves risk taking is often considered to be indicative of boldness (Bell, 2005; Harcourt, Sweetman, Johnstone, & Manica, 2009), with bolder individuals tending to be superior competitors, and thus grow faster and have increased fitness (Höjesjö, Johnsson, & Bohlin, 2002; Sundström, Petersson, Höjesjö, Johnsson, & Järvi, 2004). Studies of the causes and consequences of individual movement are, however, rare due to the difficulty of repeated sampling of the same individuals and observing them in their natural habitat (Archard & Braithwaite, 2010; Bell, Hankison, & Laskowski, 2009). Although ontogeny might affect variability, with individuals becoming more variable and/or specialised with age (Polis, 1984), age is not often accounted for in field studies of animal behaviour.

Individual variation in somatic growth rates that result in variation in body sizes, such as size dimorphism, is a widespread feature of many animals, especially for species that have indeterminate growth and continue to grow after maturity (Blanckenhorn, 2005; Stamps, 2007). The maintenance of individual variation in growth rates is theorised as being associated with trade-offs between the foraging behaviours of the individual and the expression of their life history traits. For example, the growth-mortality trade-off theory predicts that individuals with higher levels of activity acquire resources that facilitate faster growth rates, but in doing so, they take more risks, exposing them to predation risk (Stamps, 2007; Werner & Anholt, 1993). Alternatively, trade-offs between activity levels and growth rates might occur where individuals with increased activity have reduced growth rates due to their increased energy expenditure not being balanced with the acquisition of additional trophic resources (Killen, Brown, & Gamperl, 2007; Rennie, Collins, Shuter, Rajotte, & Couture, 2005; Závorka, Aldvén, Näslund, Höjesjö, & Johnsson, 2015). The composition of the diet of individuals can also affect the expression of their life history traits, such as juvenile growth rates and age at sexual maturity (Caswell, 2001). In this respect, measures of the trophic niche can have high utility in revealing the contrasting abilities of individuals to acquire variable resources in competitive situations (Bolnick et al., 2003). Despite the potential importance in revealing the mechanisms underpinning individual variability in movement and its ecological consequences, studies attempting to relate the trophic position of individuals with their somatic growth rates, body sizes and movement patterns are rare.

Consequently, the aim of this study was to determine how trophic position (TP), body size, age and somatic growth rates influenced the movement patterns of individuals in a model fish population. The model species was the piscivorous pike *Esox lucius* using the population in the River Frome, southern England, as the study system. We specifically concentrated on their juvenile life stages (age 0 + and 1 + years), as previous work on this population has highlighted considerable variability in their body lengths at these ages (e.g., Mann & Beaumont, 1990). We tested the following predictions: (i) individual movement varies between age classes, with age 1 + individuals moving more than those at 0 + ; (ii) within age classes, larger individuals with higher TPs move more than smaller individuals at lower TPs; and (iii) irrespective of age class, individuals that move more achieve higher growth rates and attain a higher TP compared to individuals that move less.

2 | MATERIALS AND METHODS

2.1 | Model species and study population

As a long-lived and large apex predator fish species with a circumpolar distribution, the biology and ecology of pike has been extensively studied (Craig, 1996; Forsman et al., 2015; Raat, 1988). Considerable variation in early life growth rates has been found in both wild populations (Cucherousset, Paillisson, & Roussel, 2007; Mann & Beaumont, 1990) and captive situations (Bry, Bonamy, Manelphe, & Duranthon, 1995; Ziliukiene & Ziliukas, 2006). Several studies have revealed a high level of interindividual variability in their spatial behaviour (Jepsen, Beck, Skov, & Koed, 2001; Masters et al., 2005; Vehanen, Hyvarinen, Johansson, & Laaksonen, 2006) and trophic ecology (Beaudoin, Tonn, Prepas, & Wassenaar, 1999; Chapman, Mackay, & Wilkinson, 1989; Skov, Lousdal, Johansen, & Berg, 2003). Pike is therefore a strong model organism for studying individual spatial behaviours related to growth and foraging. In the focal population, adult pike tend to spawn in narrow side channels and agricultural drainage ditches connected to the main river (Mann & Beaumont, 1990). While some young-of-the-year fish (0 + cohort) move from these nursery grounds into the main river during their first summer, others are known to remain in these ditches until at least their second year of life (Mann & Beaumont, 1990).

In this study, the age 0 + and 1 + pike inhabiting three side channels (hereafter referred to as "ditches") of the River Frome (namely Rushton Ditch, Railway Ditch and Flood relief channel) connected to the main river (50°41′9″ N; 2°11′9″ W) were studied between January 2009 and March 2011 (Figure 1). Rushton ditch is a 400-m-long channel of up to 1 m deep and from 2.4 to 4 m in width; Railway ditch is approximately 250 m long, up to 0.75 m deep and 2.3 to 3.6 m wide;

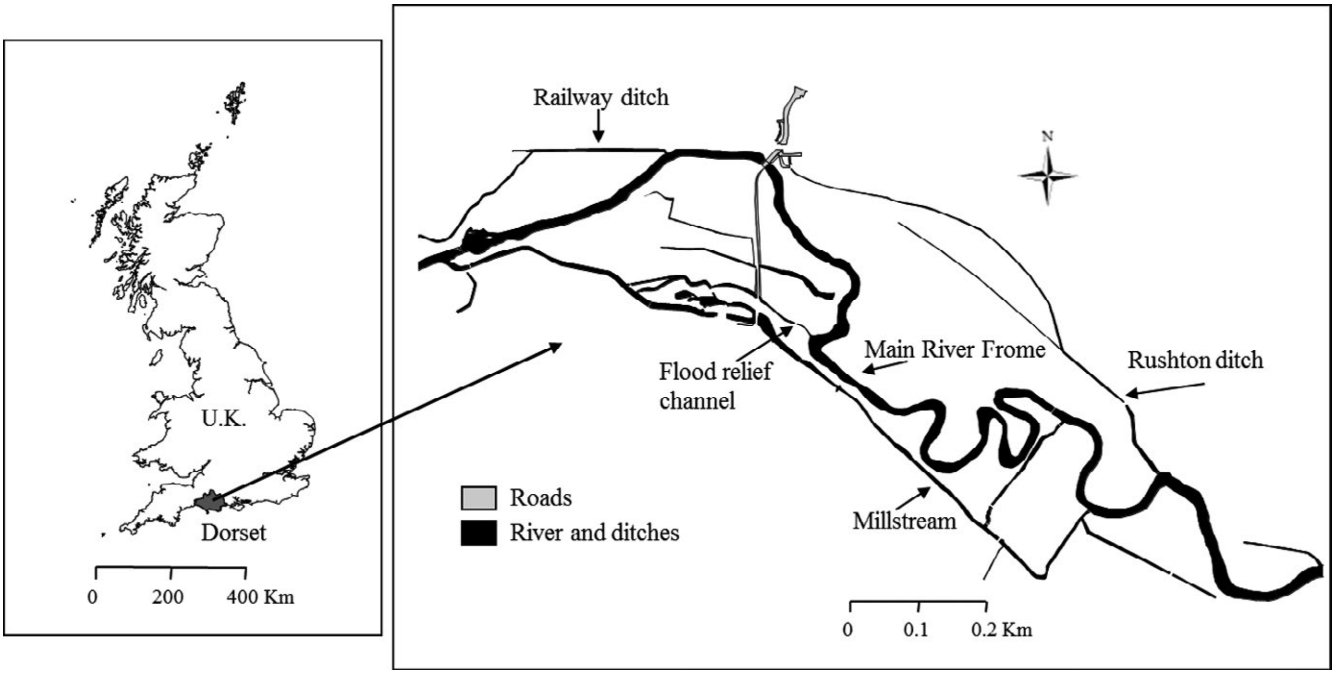

FIGURE 1 Map of the study site of the River Frome in Dorset, UK

and the Flood relief channel is 160 m long with depths to 1.5 m and widths from 2.3 to 3.6 m. A variety of fish species (e.g., eels *Anguilla anguilla*, minnows *Phoxinus phoxinus*) also inhabit and/or utilise the ditches as part of their life cycle, with pike using them as spawning and nursery habitats (Mann & Beaumont, 1990). All ditches are heavily vegetated (majority: *Glyceria fluitans*, *Phalariss arundinacea*, *Callitriche stagnalis*, *Potamogeton natans*, *Carex riparia*, *Juncus effusus*) with some tree cover, and the majority of the substrate was silt. The ditches are very slow flowing and support a rich diversity of aquatic invertebrates (Armitage, Szoszkiewicz, Blackburn, & Nesbitt, 2003). Each ditch was divided into 10 m patches, with these marked out using semi-permanent, numbered wooden posts. The widths of the ditch patches were measured at their boundaries and in the middle (i.e., every 5 m).

2.2 | Sample collection

The pike used in the study were sampled using a Smith-Root LR-24 back-mounted electric fisher (50 MHz pulsed DC at approximately 2 Amps). Captured fish were anaesthetised (tricaine methanesulphonate (MS-222), 3.5 ml/L of river water) before being measured (fork length [FL], nearest mm). Scales were then sampled for subsequent age determination, and pelvic fin clips were taken for stable isotope analyses. The stable isotope ratios of fin tissue correlate strongly with those of dorsal muscle tissue (Jardine, Gray, McWilliam, & Cunjak, 2005), but with the advantage of fin clips being less destructive and not adversely affecting fish survival and growth (Gjerde & Refstie, 1988). Pike were tagged by surgically implanting a 23.1 mm passive integrated transponder (PIT) tag (Texas Instruments, half-duplex, 3.85 mm diameter, 0.6 g). The smallest fish tagged that was included in the analyses was 138 mm and 17.0 g, with the tag to body mass ratio for fish of age 0 + and 1 + ranging from 0.6% to 3.5%, and 0.3% to 0.8% respectively. PIT tags were inserted into the coelomic cavity of the fish through a small incision made on the left side below the sideline slightly posterior to the pelvic fin. Prior to their tagging, pike were scanned for the presence of an existing PIT tag to enable recaptured individuals to be recognised. After recovery from anaesthesia in oxygenated fresh river water, individuals were released close to their individual capture point. Electric fishing surveys were completed prior to and after each tracking period had been completed (see next subsection).

The study was approved by an independent ethical review committee of Bournemouth University, with all tagging and tissue biopsy procedures completed under licence according to the UK Animals (Scientific Procedures) Act 1986 by the UK Home Office.

2.3 | Tracking surveys

Tracking of the PIT-tagged fish was undertaken over three independent time periods during the study (hereafter referred to as “tracking periods” that comprise of individual “tracking surveys”): spring 2009 (24/03/2009 to 31/05/2009; $n = 17$ tracking surveys), spring 2010 (11/03/2010 to 27/05/2010; $n = 13$) and winter 2011 (05/01/2011 to 22/02/2011; $n = 12$). The rationale of these tracking periods was that studies suggest that more intense movement occurs in pike during early winter when temperatures increase slightly and during spring from mid-March to mid-May, with this coinciding with spawning in adults (Koed, Balleby, Mejlhede, & Aarestrup, 2006). During the three tracking periods, tracking was conducted on a regular basis every 4 to 6 days in order that consistent patterns in individual movements could be detected. Note that the Railway ditch was not monitored in winter 2011 due to few individual pike ($n = 2$) being captured prior to the tracking period.

Each tracking survey comprised of tracking of tagged fish using a portable PIT antenna system, as per Roussel, Haro, and Cunjak (2000) and Cucherousset et al. (2010). The detection range of the antenna, measured as the distance between the plane of the antenna loop and the tag, varied with tag orientation, ranging from 55 cm when the tag was horizontal to 85 cm when the tag was vertical. The antenna was generally swept just above the water surface to detect the fish, but when the water was deeper than the detection distance of 55 cm, the antenna was submerged vertically to increase detection efficiency. The pike were tracked in a downstream direction from each side of the bank (Cucherousset et al., 2010), with the exception being Railway ditch where it was only possible from one bank. The antenna had an extendable pole with a maximum length of 4 m, which allowed scanning across the whole width of each ditch.

Each tracking survey covered all the ditches on the same day and took approximately 4.5 hr (Railway Ditch 1.5 hr, Flood relief 1 hr and Rushton ditch 2 hr). To test for the effect of time of day on tracking efficiency and movement, surveys in spring 2009 were conducted at different times of day: from dawn (06:00 to 08:00 hr, $n = 5$), during daylight (10:00 to 14:00 hr, $n = 6$) and towards dusk (16:00 to 18:00 hr, $n = 6$). As this revealed no significant effect of time of day on the number of fish detected (Table S1), as also detected by Cucherousset et al. (2010), all subsequent tracking surveys were conducted during daylight hours (09:00 to 17:00 hr). During each survey, the patch number, and the distances along the length of the patch and to the closest bank (nearest 0.1 m), were recorded for each detected individual. The detection efficiency of the tracking was calculated using the formula: $100N_dN_p^{-1}$, where N_d was the number of tagged individuals detected during a tracking survey, which were later recaptured, and N_p was the number of tagged individuals present (recaptured) in the ditches (Cucherousset et al., 2010). The tracking efficiency was determined using the last tracking surveys of each tracking period in each ditch. By only including recaptured pike in the calculations, we ensured that the detection efficiency was based on living fish. Detection efficiency depends on the species studied (Cucherousset et al., 2010), but also on the water depth. In similar tracking studies, although conducted in streams with lower water depths, detections efficiencies of 19.6% to 81.9% have been reported (Cucherousset et al., 2007; Enders, Clarke, Pennell, Ollerhead, & Scruton, 2007; Roussel et al., 2000). At the conclusion of each tracking period, another electric fishing survey was also completed during which detected fish attempted to be recaptured, with the data collected as previously outlined. Only recaptured, tagged individuals were included in subsequent analyses to avoid the inclusion of data from tags that had been expelled from fish or where the fish had died, and thus removed these aspects as potential confounding factors.

2.4 | Stable isotope analysis (SIA)

Trophic position of individuals was quantified using the stable isotope of nitrogen (δ^{15}N) that shows enrichment of 2% to 4‰ from resource to consumer (Post, 2002). To provide the baseline isotopic signals of the putative food resources of the fish, specimens of water louse *Asellus aquaticus* were collected at the completion of each electric fishing survey. This macroinvertebrate was the most abundant species in the ditches and has constituted an important part of the diet of juvenile pike in the River Frome (Mann, 1982). One SIA sample of *A. aquaticus* comprised of two to four individuals. The samples were oven dried (60°C for 48 hr), ground into a homogenous powder, weighed (all samples were 0.5–1 mg), and analysed at Cornell Isotope Laboratory, USA. Initial data outputs were in the format of delta (δ^{15}N) isotope ratios, expressed in ‰. TP for each individual pike was then calculated using the formula: TP = ([fish δ^{15}N – mean prey δ^{15}N]/3.4) + 2, where 3.4 represents a widely used single trophic level fractionation in δ^{15}N, and 2 corresponds to the trophic level of primary consumers (Vander Zanden, Shuter, Lester, & Rasmussen, 2000).

2.5 | Data analyses

Ages of the individual, recaptured pike were determined by analysing their scales on a projecting microscope (×48 magnification), with counting the number of annual growth marks. A quality control procedure was used whereby a second operator aged 25% of the scales independently. The growth rates of individual pike were measured using the specific growth rate (SGR), expressed as the change in fork length (mm) for each tracking period, where SGR = $(\ln[L_f]-\ln[L_i])*100/t$, with L_i and L_f being the initial and final lengths (mm) of the individual, and t is the number of days between the length measurements.

To enable movement metrics of individual pike to be calculated, the initial step was to plot each fish location that was collected on each tracking occasion into two-dimensional coordinate values *y* (metre transects along the ditch length) and *x* (metre equidistant strata across the ditch width), following Roussel, Cunjak, Newbury, Caissie, and Haro (2004) and Cucherousset, Paillisson, Cuzol, and Roussel (2009). The equidistant strata were calculated based on the average width obtained from three measurements of each 10-m-long patch of the ditch. First, the mean position for each individual fish was calculated by averaging the *x*-coordinate values obtained for all detections (x_1, x_2, x_3,...) to calculate $\bar{x}$ and the *y*-coordinate values obtained for all detections (y_1, y_2, y_3,...) to calculate $\bar{y}$ This mean arithmetic position ($\bar{x}$,$\bar{y}$) was defined as the centroid of the positions from where the distance to all other points (i.e., individual positions obtained at each tracking) is the smallest (Lair, 1987). Secondly, we calculated the radial distances (m) for each detection (d_1, d_2, d_3,...). The radial distances for each detection were calculated as the measured distances from the mean position ($\bar{x}$,$\bar{y}$) and every location (x_1- y_1, x_2-y_2, x_3-y_3,...) to provide an estimation of fish position dispersal around its arithmetic mean position ($\bar{x}$,$\bar{y}$). The arithmetic mean radial distance ($\bar{d}$) was then calculated by averaging the radial distances (d_1, d_2, d_3,...). Distances (v_1, v_2, v_3,...) between two successive positions (from x_1- y_1 to x_2-y_2, from x_2-y_2 to x_3-y_3,...) were calculated and subsequently divided by time between two consecutive detections (in days) to provide a measurement of the mean arithmetic distance (m) travelled per day ($\bar{v}$) (Roussel et al., 2004). While daily distance moved is a measure of distances between subsequent detection positions per day, radial distances provide an estimation of fish dispersal around its arithmetic mean position. Radial distances are therefore more indicative of the home range of individuals.

2.6 | Statistical analyses

To obtain normal and homogenous variances prior to parametric analyses, mean radial distance moved ($\bar{d}$), mean distance travelled per day ($\bar{v}$) and SGR were log transformed. The mean radial distance ($\bar{d}$) and mean distance travelled per day ($\bar{v}$) were used in the preliminary analyses testing for differences between ditches, while the individual radial distances (d_1, d_2, d_3,...) and distances between successive position (v_1, v_2, v_3,...) were used in the linear mixed effect models. All analyses were conducted using R 3.2.5 (R development core team 2012).

The effects of age or tracking period on the number of detections were tested using one-way ANOVAs with either age or tracking period as fixed factors. As there were no age-1 fish sampled in 2009, analyses using sampling periods in 2010 and 2011 were conducted to assess whether there would be an interaction between age (0 + , 1 +) and season (spring 2010, winter 2011) on movement. As no interaction was found (Table S2), all three sampling periods were used in the subsequent analyses without the interaction age x sampling period.

To determine the causes for interindividual variability in movement, linear mixed effect models (LMMs) were conducted using the lme function in the nlme package (Pinheiro, Bates, DebRoy, Sarkar, & Core Team, 2015). Radial distances (d_1, d_2, d_3,...) or daily distances (v_1, v_2, v_3,...) moved were fitted as the response variable and age, period, initial TP and initial FL as predictors. Possible serial autocorrelation within individual movement measures was accounted for by a corAR1 argument for radial distance and daily distances moved. Individual ID was nested within ditch as a random effect and age, period, initial FL and initial TP were fitted as fixed factors.

Individuals were sampled for length to calculate growth rate, and fin clips were taken to attain a value for TP at the end of each tracking session. Consequences of individual movement on SGR or final TPs were tested by running LMMs with each movement metric as a predictor and SGR or final TP as the response variable. Thus, either daily distance moved or radial distances were fitted as predictors together with initial TP, age and period, and individual ID was nested within ditch as a random effect. All models were first run with full two-way interactions and then simplified until no further model simplification could be made without removing a significant interaction ($p < .05$) (Zuur, Ieno, Walker, Savaliev, & Smith, 2009). Marginal R^2 and conditional R^2 values for each model were calculated using the "piecewiseSEM" package (Lefcheck, 2015). The marginal R^2 describes the proportion of variance explained by the fixed factors alone, whereas the conditional R^2 describes the variance explained by fixed and random factors (Nakagawa & Schielzeth, 2013). The standardised regression coefficients that were scaled by mean and variance, and 95%

TABLE 1 Number of fish per age group tagged during the study, the number subsequently detected during tracking and the number of detected fish that were recaptured

Age	Number of fish tagged	Number of detected tagged fish	Number of detected fish recaptured	Mean time (± SE) (days) between tagging and recapture
0+	101	96	35	206 ± 3.8
1+	30	27	15	186 ± 2.1

confidence intervals (CI) were calculated for each predictor in the nlme models with the "piecewiseSEM" package. Traits were considered as significantly contributing to the model if their confidence intervals did not overlap zero.

Unless stated otherwise, where error is expressed around the mean, it represents standard error.

3 | RESULTS

3.1 | Numbers of tagged and tracked fish

A total of 101 0 + and 30 1 + pike were tagged in the ditches during the study (Table 1). Of the tagged fish, there were 35 0 + and 15 1 + pike that were detected during tracking periods and recaptured subsequently (Table 1). Therefore, 38% of the tagged pike were included in subsequent analyses, with all individuals were only detected in the ditches where they were tagged. A mean detection deficiency of 70.7% ± 1.7% of the pike tagged and recaptured in the ditches was obtained during the three tracking periods. There were no significant differences in body lengths at capture between recaptured and nonrecaptured individuals (Table S3). There was also no relationship between body size at tagging and the number of subsequent detections (Spearman's correlation, r = −0.11, *p* > .05). The overall mean number of detections per fish across the three tracking periods was 8.6 ± 0.6 (range 2 to 17), but did not differ significantly between ages (ANOVA, $F_{1,48} = 0.51$, *p* > .05), or between tracking period for either 0 + (ANOVA, $F_{1,27} = 1.10$, *p* > .05) or 1 + pike (ANOVA, $F_{1,13} = 0.45$, *p* > .05). The mean time between two successive detections (including all three tracking periods) was 7.0 days (± 0.2) and ranged between 4 and 28 days. No significant relationship between time between successive detections and the calculated distance between fish locations was found (Pearson's correlation, r = − 0.10, *p* > .05).

3.2 | Causes for variability in individual movement

There was considerable variation in the movement of individuals between age classes and tracking periods. The radial distance ($\bar{d}$) for 0 + fish in spring 2009 ranged from 2.6 to 42.1 m (mean 13.4 ± 6.9), in spring 2010 from 5.8 to 25.0 m (mean 12.0 ± 2.5) and in winter 2011 from 1.2 to 3.1 m (mean 2.0 ± 4.8). In 1 + pike, it was 10.4 to 25.0 m (mean 16.7 ± 1.8) in spring 2010 and 1.3 to 64.9 m (mean 17.0 ± 0.2) in winter 2011. The conditional and marginal R^2 for the model with radial distance as a response variable were 0.47 and 0.11 respectively, and for the model with daily distance moved as response variable 0.11 and 0.06 respectively. Both radial distance and daily distances moved differed between ages and tracking periods; individuals of age 1 + moved more than 0 + , and there was significantly less movement in winter than spring (Table 2). The effects of initial fish length were, however, not significant. The daily distances of individuals with higher initial TP were significantly less than those with lower initial TP (Table 2).

TABLE 2 Results of linear mixed models used to test for the effects of age, period, initial TP and FL on individual radial distance and daily distance moved and the coefficients and 95% confidence intervals for all traits

Response variable	Source of Variation	*df*	Estimate (S.E.)	*t*	*p*	Coefficient	Lower 95% CI	Upper 95%
Radial distance	**Age (0 + vs. 1 +)**	366	1.39 (0.49)	2.84	**0.005**	**1.18**	**0.43**	**2.35**
	Period (Spring 2010)	366	−0.59 (0.37)	−1.61	0.109	−0.5	−1.31	0.13
	Period (Winter 2011)	366	−1.35 (0.48)	−2.82	**0.005**	**−1.15**	**−2.29**	**−0.41**
	Initial TP	366	−0.13 (0.30)	−0.44	0.659	−0.06	−0.73	0.46
	Initial FL	366	0.00 (0.00)	−0.34	0.730	−0.05	−0.01	0.01
	Intercept	366	2.98 (1.31)	2.27	**0.024**			
Daily distance	**Age (0 + vs. 1 +)**	320	0.45 (0.21)	2.14	**0.033**	**0.58**	**0.04**	**0.87**
	Period (Spring 2010)	320	−0.09 (0.16)	−0.53	0.594	−0.11	−0.41	0.24
	Period (Winter 2011)	320	−0.47 (0.19)	−2.49	**0.013**	**−0.60**	**−0.83**	**−0.10**
	Initial TP	320	−0.24 (0.12)	−2.01	**0.045**	**−0.16**	**−0.48**	**−0.005**
	Initial FL	320	0.00 (0.00)	0.50	0.620	0.05	−0.003	0.005
	Intercept	320	1.51 (0.49)	3.05	**0.003**			

Variables in bold have *p* values >.05 and 95% confidence intervals that do not overlap zero, and therefore considered to contribute significantly to the model.

3.3 | Consequences of variability in individual on growth and TP

The conditional and marginal R^2 were 0.99 and 0.19 respectively for both models testing the effects of radial distance or daily distance on SGR (Table 3), indicating high descriptive power of the models. SGR was age-dependent with age 0+ fish growing faster than 1+, whereas tracking period had no significant effects on SGR (Table 3). Both radial distance and daily distances moved correlated positively to individual SGR, however, this correlation was dependent on initial TP and age (Table 3). Individuals with a higher initial TP had a higher SGR and the significant interaction term between initial TP and each movement metric revealed that individuals with a higher initial TP tended to move less (Table 3; Figure 2). The interaction between age and radial distances affecting SGR was due to fish of age 0+ growing faster but moving less than age 1+ fish (Figure 2).

The conditional and marginal R^2 were 0.91 and 0.04 respectively for the model testing the effects of radial distance on final TP, and 0.93 and 0.04 respectively for the model testing the effects of daily distance on final TP (Table 4). The model showed that final TP was dependent on age in the model that included radial distances as a fixed factor, while period had no significant effects on either model (Table 4). Radial distance and daily distances moved had significant positive effects on final TP, although this was affected by initial TP as described above for the effect on SGR (Table 4).

4 | DISCUSSION

The individual movements of the juvenile pike were significantly influenced by age, with fish of 1+ year showing greater movements than 0+ fish, with this consistent with the first prediction. Although initial TP was significantly and negatively associated with daily movements, body size had no significant influence on individual movement, contrary to the second prediction. In line with the third prediction, individuals that moved more achieved a higher somatic growth rate and an elevated final TP. These results suggest that individuals with higher levels of activity (i.e., more movement) acquire higher quality resources (as revealed by higher TP) and achieve higher growth rates (as SGR). It should be noted that the fate of the tagged fish that were never detected or recaptured in the study were unable to be determined. Given that mortality or tag loss within the ditch would result in the tag still being detected, then it was assumed these individuals either emigrated into the main channel or were depredated by a bird or mammal (Cucherousset et al., 2007) and thus removed from the study areas. Irrespective, this remains speculative and thus the fate of these fish is not considered further.

That the development of older fish having larger home ranges (as radial distances) and moving greater distances (as daily distances) was independent of fish length is ecologically important, as previous work on this pike population has revealed that size dimorphism is a feature of their juvenile life stages. This dimorphism has been associated with movements from the ditches into the main river channel, whereby fish that remained in the ditches were smaller than migrants moving into the main river channel (Mann & Beaumont, 1990). However, the timing of this migration into the river, or the drivers responsible for this, was not determined (Mann & Beaumont, 1990). While some fish in our study were also likely to have made this movement, we could not track them within the river, and thus, our focus was on the fish remaining in the ditch. As the significant differences in individual movements of these fish were a function of age, not length, then the influence of size dimorphism on these movements appeared minimal. This nonsignificant influence of length on juvenile movements contrasts to adult pike, where movement rates are often a function of

TABLE 3 Results of linear mixed models on the effects of individual radial distance (LLM 1) and daily distance (LLM2) on the specific growth rate of individuals and the coefficients and 95% confidence intervals for all traits

LMM	Source of Variation	*df*	Estimate (S.E.)	*t*	*p*	Coefficient	Lower 95% CI	Upper 95%
1	**Age (0+ vs. 1+)**	365	−0.06 (0.02)	−2.94	**.004**	**−0.63**	**−0.10**	**−2.18**
	Period (Spring 2010)	365	0.02 (0.02)	1.09	.277	0.13	−0.02	6.45
	Period (Winter 2011)	365	−0.03 (0.04)	−0.62	.538	−0.65	−0.11	5.59
	Radial distance	365	0.00 (0.00)	4.14	**< .0001**	−0.001	**0.0001**	**4.45**
	Initial TP	365	0.04 (0.00)	109.85	**< .0001**	**0.23**	**0.04**	**3.63**
	Initial TP x Radial distance	365	0.00 (0.00)	−4.60	**< .0001**	−0.001	**−0.0002**	**−6.20**
	Intercept	365	0.01 (0.02)	0.30	.768			
2	**Age (0+ vs. 1+)**	319	−0.06 (0.02)	−2.94	**.004**	**−0.64**	**−0.11**	**−2.30**
	Period (Spring 2010)	319	0.02 (0.02)	1.09	.277	0.13	−0.02	6.55
	Period (Winter 2011)	319	−0.03 (0.04)	−0.62	.537	−0.67	−0.11	5.69
	Daily distance	319	0.00 (0.00)	2.65	**.008**	−0.0002	**0.0002**	**5.35**
	Initial TP	319	0.04 (0.00)	103.56	**< .0001**	**0.23**	**0.04**	**3.70**
	Initial TP x Daily distance	319	0.00 (0.00)	−2.99	**.003**	−0.0003	**−0.0002**	**−8.07**
	Intercept	319	0.01 (0.02)	0.35	.727			

Variables in bold have *p* values >.05 and 95% confidence intervals that do not overlap zero, and therefore considered to contribute significantly to the model.

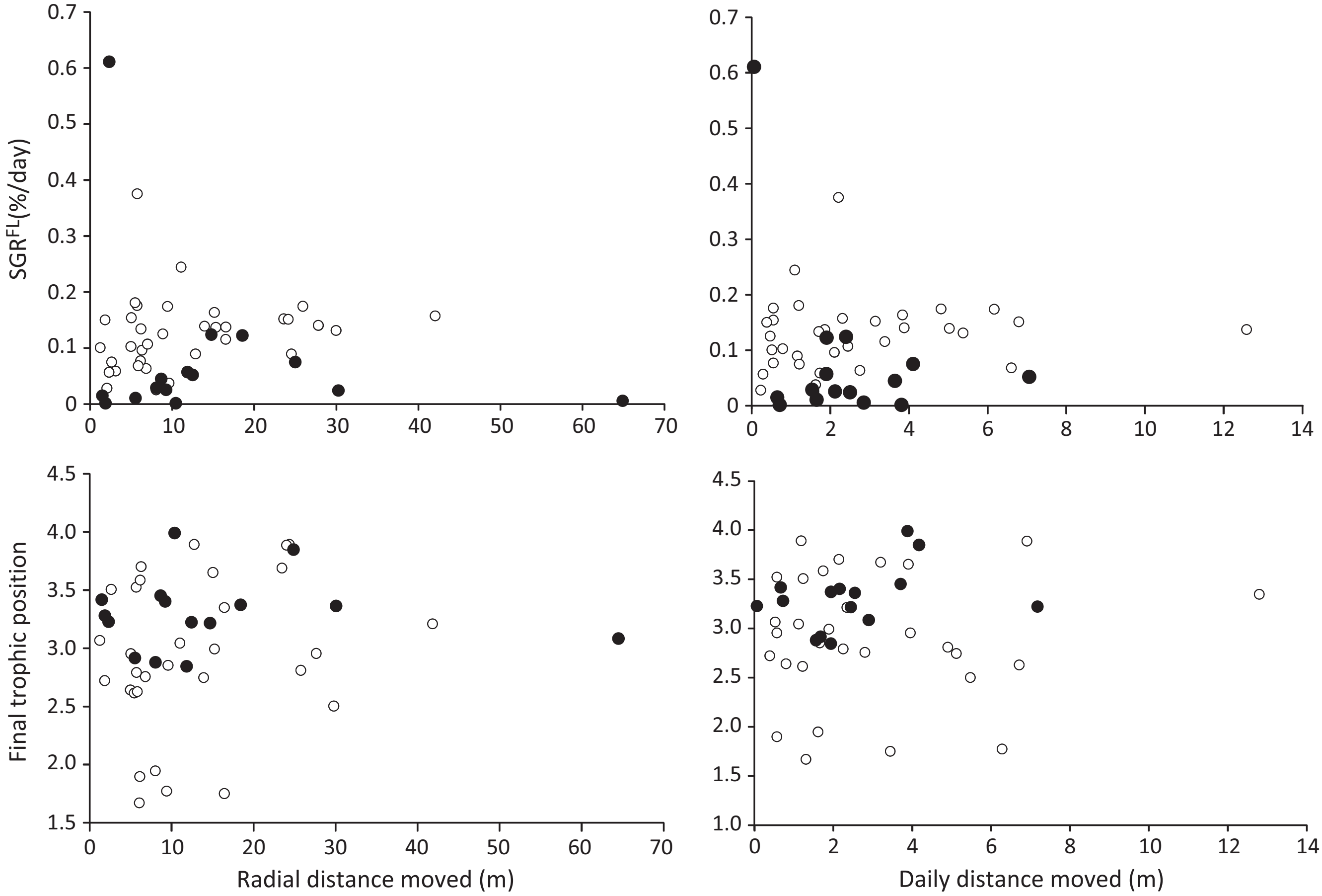

FIGURE 2 Specific growth rate (%/day) (upper panels) and final trophic position (lower panels) in relation to radial distance (left) and individual daily distance moved (right) for individuals of *Esox lucius* of age 0 + (white) and age 1 + (black)

TABLE 4 Results of linear mixed models on the effects of individual radial distance (LMM 1) and daily distance (LMM 2) on the final trophic position of individuals and the coefficients and 95% confidence intervals for all traits

LMM	Source of Variation	*df*	Estimate (S.E.)	*t*	*p*	Coefficient	Lower 95% CI	Upper 95%
1	**Age (0 + vs. 1 +)**	328	−0.41 (0.21)	−2.00	**.046**	**−0.62**	**−0.82**	**−0.01**
	Period (Spring 2010)	328	0.27 (0.20)	1.32	.186	0.40	−0.13	0.66
	Period (Winter 2011)	328	0.37 (0.39)	0.94	.346	0.55	−0.40	1.13
	Radial distance	328	0.07 (0.02)	4.00	**.0001**	**−0.01**	**0.03**	**0.11**
	Initial TP	328	0.04 (0.07)	0.49	.624	−0.01	−0.11	0.18
	Initial TP x Radial distance	328	-0.03 (0.01)	−4.45	**< .0001**	**−0.02**	**−0.04**	**−0.01**
	Intercept	328	2.85 (0.30)	9.59	**< .0001**			
2	Age (0 + vs. 1 +)	286	−0.41 (0.21)	−1.95	.052	−0.61	−0.82	0.004
	Period (Spring 2010)	286	0.26 (0.20)	1.26	.210	0.38	−0.15	0.66
	Period (Winter 2011)	286	0.36 (0.39)	0.93	.354	0.54	−0.41	1.14
	Daily distance	286	0.04 (0.02)	2.47	**.014**	**−0.01**	**0.01**	**0.07**
	Initial TP	286	−0.04 (0.08)	−0.55	.585	−0.04	−0.19	0.11
	Initial TP x Daily distance	286	−0.01 (0.01)	−2.79	**.006**	**−0.01**	**−0.02**	**−0.004**
	Intercept	286	3.07 (0.31)	10.07	**< .0001**			

Variables in bold have *p* values >.05 and 95% confidence intervals that do not overlap zero, and therefore considered to contribute significantly to the model.

body size (e.g., Kobler, Klefoth, Wolter, Fredrich, & Arlinghaus, 2008). In the study river, Masters et al. (2005) revealed adult pike exhibit a continuum of spatial behaviours, with some individuals always using the same few hundred metres of river, while others use stretches over several kilometres. While influenced by pike length, the length range of these tracked fish was considerable (520 to 950 mm), with considerable variation in movement patterns between individuals of relatively similar size (Masters et al., 2005). While it is difficult to extrapolate adult behaviour to juveniles, the length range of juvenile pike used here was relatively narrow (138 to 301 mm) and thus might have been insufficient to result in strong size-structured movement patterns. That age was a significant determinant of movement might then have been through it being a function of time, with older fish in the ditches having longer to establish larger home ranges in which they were able to make higher daily movements. This could align to "prior residence advantage," where individuals that are present first in a new habitat obtain, and subsequently defend, the most profitable sites, with this often apparent in the behavioural ecology of salmonid fishes (e.g., Harwood, Griffiths, Metcalfe, & Armstrong, 2003).

The development of the differences in movement patterns between individuals might also have been influenced by their underlying behaviours that relates to their propensity for risk taking. We have previously documented individual consistency in foraging activity across risky situations consisting of the presence/absence of a competitor or predator laboratory experiments using 0 + pike collected from this particular population (Nyqvist, Gozlan, Cucherousset, & Britton, 2012, 2013). Bolder individuals maintained a high foraging activity through time, while shyer individuals maintained a low foraging activity, but without consequences on growth (Nyqvist et al., 2012, 2013). The individual variation in movement detected in the present study might thus relate to the degree of risk-taking behaviour but with consequences on growth. Under the experimental settings of Nyqvist et al. (2012), pike were kept in isolation, meaning that the intraspecific interactions, including effects of competition or dominance hierarchies on individual growth, were removed, which was not the case for the pike in the ditches. Apart from the important effect of intraspecific interactions, a heterogeneous environment may also play a significant role in providing the potential for habitat and resource segregation to occur and so, subsequently, enables divergent growth within a population. Laskowski et al. (2016) tested individual behaviour of wild adult pike captured from a lake in standardised open-field behavioural assays. The measured standardised behaviour did not relate to growth rate (Laskowski et al., 2016). In contrast, our results show that individual movement had positive consequences on growth and trophic positions in juvenile pike in the wild. This difference may be explained by the differences in habitat complexity. While size dimorphism has been reported in our study population (Mann & Beaumont, 1990), no size differences were reported for the pike in the particular lake studied by Laskowski et al. (2016).

That individuals that moved achieved higher growth rates and an elevated final trophic position in our study may be related to the mortality-growth trade-off mediated by foraging activity (Werner & Anholt, 1993). Foraging activities increase the probability of predator detection and thus increased movements should lead to increased mortality risk (Werner & Anholt, 1993). Reduced activity in the presence of predators is also an important antipredator behaviour (Lima & Dill, 1990). In many animals, vulnerability to predation decreases with increasing body size, and especially in juvenile fish due to the issue of gape-size limitation in piscivorous animals (Nilsson & Bronmark, 2000). Growth rate is therefore an important determinant of the probability of individual survival and is often used as a fitness proxy (Brown, Jones, & Braithwaite, 2007). Experimental studies on several fish species have revealed growth differences relating to foraging activity (Imsland, Jenssen, Jonassen, & Stefansson, 2009; Jobling & Baardvik, 1994; Martin-Smith & Armstrong, 2002). Studies on rainbow trout *Oncorhynchus mykiss* have demonstrated that individuals taking greater risks while foraging grew faster, but survived at a lower rate in the presence of predators than individuals taking fewer risks (Biro, Abrahams, Post, & Parkinson, 2004, 2006).

An increasing number of studies demonstrate that individual specialisation in resource use in a population often develops where there is low interspecific competition but high intraspecific competition (Araújo, Bolnick, & Layman, 2011; Bolnick et al., 2011; Svanbäck & Bolnick, 2007). Individual resource specialisation appears to be particularly common among apex predator fishes (Araújo et al., 2011), which may be explained by that they usually have few interspecific competitors in the community. In our study site, juvenile pike density, a proxy for intraspecific competition (Araújo et al., 2011), was high with few (if any) other predatory species present. While individual specialisation in resource use often results in the development of related morphological traits (Bolnick et al., 2003; Cucherousset et al., 2011; Smith & Skulason, 1996), cannibalism has been suggested to be the proximate cause of bimodal size distributions in some fish species (Claessen, de Roos, & Persson, 2000). Thus, a factor potentially contributing to the observed consequences for growth rates and trophic ecology in our studied pike may be the combined effect of intraspecific competition with cannibalism.

In conclusion, individual variation in movement was negatively associated with TP, and increased movement had positive influences on individual growth rates and subsequent TP in these juvenile pike. We suggest that individual variability in movement and TPs reflects variation in foraging activity, which may be underpinned by personality traits, but with causal drivers also involving pressures from intraspecific competition and trade-off with mortality risk, especially the risk from cannibalism.

ACKNOWLEDGEMENTS

We are grateful to the numerous persons participating in the fieldwork. We thank anonymous reviewers for helpful comments on this manuscript. This work was funded by a PhD studentship from Bournemouth University and support from The Swedish Cultural Foundation in Finland.

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How to cite this article: Nyqvist MJ, Cucherousset J, Gozlan RE, Britton JR. Relationships between individual movement, trophic position and growth of juvenile pike (*Esox lucius*). *Ecol Freshw Fish*. 2018;27:398–407. https://doi.org/10.1111/eff.12355