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3 Relationships between individual movement, trophic position and growth of

4 juvenile pike (*Esox lucius*)

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18 Running headline: Individual movement, trophic position and growth in pike

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23

24 **Abstract**

25

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

41

42 **Key words:** Inter-individual variation, movement, PIT telemetry, stable isotope
43 analyses.

44

45 **Introduction**

46

47 The majority of animals rely on a certain level of displacement to forage, avoid
48 predators and compete for resources, making movement an important attribute for
49 growth and survival (Turchin 1998; Bergman *et al.* 2000). Although movements that are
50 associated with increased fitness are predicted to be favoured (Stearns 1992),
51 considerable intraspecific variability in movement exists, as observed in mammals (e.g.
52 Pinter-Wollman 2009), birds (e.g. Catry *et al.* 2011) and fish (e.g. Kobler *et al.* 2009).
53 This variability in movement is therefore suggested to reflect the underlying
54 behavioural strategies of individuals (Austin *et al.* 2004; Salomon 2009). For instance,
55 activity that involves risk taking is often considered to be indicative of boldness (Bell
56 2005; Harcourt *et al.* 2009), with bolder individuals tending to be superior competitors,
57 and thus grow faster and have increased fitness (Höjesjö *et al.* 2002; Sundström *et al.*
58 2004). Studies of the causes and consequences of individual movement are, however,
59 rare due to the difficulty of repeated sampling of the same individuals and observing
60 them in their natural habitat (Bell *et al.* 2009; Archard & Braithwaite 2010). Although
61 ontogeny might affect variability, with individuals becoming more variable and/or
62 specialised with age (Polis 1984), age is not often accounted for in field studies of
63 animal behaviour.

64

65 Individual variation in somatic growth rates that result in variation in body sizes, such
66 as size dimorphism, is a widespread feature of many animals, especially for species that
67 have indeterminate growth and continue to grow after maturity (Blanckenhorn 2005;
68 Stamps 2007). The maintenance of individual variation in growth rates is theorised as
69 being associated with trade-offs between the foraging behaviours of the individual and

70 the expression of their life history traits. For example, the growth-mortality trade-off
71 theory predicts that individuals with higher levels of activity acquire resources that
72 facilitate faster growth rates, but in doing so, they take more risks, exposing them to
73 predation risk (Werner & Anholt 1993; Stamps 2007). Alternatively, trade-offs between
74 activity levels and growth rates might occur where individuals with increased activity
75 have reduced growth rates due to their increased energy expenditure not being balanced
76 with the acquisition of additional trophic resources (Rennie *et al.* 2005; Killen *et al.*
77 2007; Závorka *et al.* 2015). The composition of the diet of individuals can also affect
78 the expression of their life history traits, such as juvenile growth rates and age at sexual
79 maturity (Caswell 2001). In this respect, measures of the trophic niche can have high
80 utility in revealing the contrasting abilities of individuals to acquire variable resources
81 in competitive situations (Bolnick *et al.* 2003). Despite the potential importance in
82 revealing the mechanisms underpinning individual variability in movement and its
83 ecological consequences, studies attempting to relate the trophic position of individuals
84 with their somatic growth rates, body sizes and movement patterns are rare.

85

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

95 than smaller individuals at lower TPs; and (iii) irrespective of age class, individuals that
96 move more achieve higher growth rates and attain a higher TP compared to individuals
97 that move less.

98

99 **Materials and Methods**

100

101 **Model species and study population**

102 As a long-lived and large apex predator fish species with a circumpolar distribution, the
103 biology and ecology of pike has been extensively studied (Raatt 1988; Craig 1996,
104 Forsman *et al.* 2015). Considerable variation in early-life growth rates has been found in
105 both wild populations (Mann & Beaumont 1990; Cucherousset *et al.* 2007) and captive
106 situations (Bry *et al.* 1995; Ziliukiene & Ziliukas 2006). Several studies have revealed a
107 high level of inter-individual variability in their spatial behaviour (Jepsen *et al.* 2001;
108 Masters *et al.* 2005; Vehanen *et al.* 2006) and trophic ecology (Chapman *et al.* 1989;
109 Beaudoin *et al.* 1999; Skov *et al.* 2003). Pike is therefore a strong model organism for
110 studying individual spatial behaviours related to growth and foraging. In the focal
111 population, adult pike tend to spawn in narrow side-channels and agricultural drainage
112 ditches connected to the main river (Mann & Beaumont 1990). While some young-of-
113 the-year fish (0+ cohort) move from these nursery grounds into the main river during
114 their first summer, others are known to remain in these ditches until at least their second
115 year of life (Mann & Beaumont 1990).

116

117 In this study, the age 0+ and 1+ pike inhabiting three side-channels (hereafter referred to
118 as ‘ditches’) of the River Frome (namely Rushton Ditch, Railway Ditch and Flood relief
119 channel) connected to the main river (50°41'9" N; 2°11'9" W) were studied between

120 January 2009 and March 2011 (Fig. 1). Rushton ditch is a 400 m long channel of up to 1
121 m deep and from 2.4 to 4 m in width; Railway ditch is approximately 250 m long, up to
122 0.75 m deep and 2.3 to 3.6 m wide; and the Flood relief channel is 160 m long with
123 depths to 1.5 m and widths from 2.3 to 3.6 m. A variety of fish species (e.g. eels
124 *Anguilla anguilla*, minnows *Phoxinus phoxinus*) also inhabit and/or utilise the ditches as
125 part of their lifecycle, with pike using them as spawning and nursery habitats (Mann &
126 Beaumont 1990). All ditches are heavily vegetated (majority: *Glyceria fluitans*,
127 *Phalaris arundinacea*, *Callitriche stagnalis*, *Potamogeton natans*, *Carex riparia*,
128 *Juncus effusus*) with some tree cover and the majority of the substrate was silt. The
129 ditches were very slow flowing and supported a rich diversity of aquatic invertebrates
130 (Armitage *et al.* 2003). Each ditch was divided into 10 m patches, with these marked
131 out using semi-permanent, numbered wooden posts. The widths of the ditch patches
132 were measured at their boundaries and in the middle (i.e. every 5 m).

133

134 **Sample collection**

135 The pike used in the study were sampled using a Smith-Root LR-24 back-mounted
136 electric fisher (50 MHz pulsed DC at approximately 2 Amps). Captured fish were
137 anaesthetised (tricaine methanesulphonate (MS-222), 3.5 mL/L of river water) before
138 being measured (fork length (FL), nearest mm). Scales were then sampled for
139 subsequent age determination and pelvic fin clips were taken for stable isotope analyses.
140 The stable isotope ratios of fins tissue correlate strongly with those of dorsal muscle
141 tissue (Jardine *et al.* 2005), but with the advantage of fin clips being less destructive and
142 not adversely affecting fish survival and growth (Gjerde & Refstie 1988). Pike were
143 tagged by surgically implanting a 23.1 mm passive integrated transponder (PIT) tag
144 (Texas Instruments, half-duplex, 3.85 mm diameter, 0.6 g). The smallest fish tagged

145 that was included in the analyses was 138 mm and 17.0 g, with the tag to body mass
146 ratio for fish of age 0+ and 1+ ranging from 0.6 to 3.5 %, and 0.3 to 0.8 %, respectively.
147 PIT tags were inserted into the coelomic cavity of the fish through a small incision
148 made on the left side below the sideline slightly posterior to the pelvic fin. Prior to their
149 tagging, pike were scanned for the presence of an existing PIT tag to enable recaptured
150 individuals to be recognised. After recovery from anaesthesia in oxygenated fresh river
151 water, individuals were released close to their individual capture point. Electric fishing
152 surveys were completed prior to and after each tracking period had been completed (see
153 next sub-section).

154

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

158

159 **Tracking surveys**

160 Tracking of the PIT tagged fish was undertaken over three independent time periods
161 during the study (hereafter referred to as ‘tracking periods’ that comprise of individual
162 ‘tracking surveys’): spring 2009 (24/03/2009 to 31/05/2009; n = 17 tracking surveys),
163 spring 2010 (11/03/2010 to 27/05/2010; n = 13) and winter 2011 (05/01/2011 to
164 22/02/2011; n = 12). The rationale of these tracking periods was that studies suggest
165 that more intense movement occurs in pike during early winter when temperatures
166 increase slightly and during spring from mid-March to mid-May, with this coinciding
167 with spawning in adults (Koed *et al.* 2006). During the three tracking periods, tracking
168 was conducted on a regular basis every 4 to 6 days in order that consistent patterns in
169 individual movements could be detected. Note that the Railway ditch was not monitored

170 in winter 2011 due to few individual pike ($n = 2$) being captured prior to the tracking
171 period.

172

173 Each tracking survey comprised of tracking of tagged fish using a portable PIT antenna
174 system, as per Roussel *et al.* (2000) and Cucherousset *et al.* (2010). The detection range
175 of the antenna, measured as the distance between the plane of the antenna loop and the
176 tag, varied with tag orientation, ranging from 55 cm when the tag was horizontal to 85
177 cm when the tag was vertical. The antenna was generally swept just above the water
178 surface to detect the fish, but when the water was deeper than the detection distance of
179 55 cm, the antenna was submerged vertically to increase detection efficiency. The pike
180 were tracked in a downstream direction from each side of the bank (Cucherousset *et al.*
181 2010), with the exception being Railway ditch where it was only possible from one
182 bank. The antenna had an extendable pole with a maximum length of 4 m, which
183 allowed scanning across the whole width of each ditch.

184

185 Each tracking survey covered all the ditches on the same day and took approximately
186 4.5 hours (Railway Ditch 1.5 h, Flood relief 1h and Rushton ditch 2 h). To test for the
187 effect of time of day on tracking efficiency and movement, surveys in spring 2009 were
188 conducted at different times of day: from dawn (06:00 to 08:00 hours, $n = 5$), during
189 daylight (10:00 to 14:00 hours, $n = 6$) and towards dusk (16:00 to 18:00 hours, $n = 6$).
190 As this revealed no significant effect of time of day on the number of fish detected
191 (Table S1), as also detected by Cucherousset *et al.* (2010), all subsequent tracking
192 surveys were conducted during daylight hours (09:00 to 17:00 hours). During each
193 survey, the patch number, and the distances along the length of the patch and to the
194 closest bank (nearest 0.1 m), were recorded for each detected individual. The detection

195 efficiency of the tracking was calculated using the formula: $100N_dN_p^{-1}$, where N_d was
196 the number of tagged individuals detected during a tracking survey, which were later
197 recaptured, and N_p was the number of tagged individuals present (recaptured) in the
198 ditches (Cucherousset *et al.* 2010). The tracking efficiency was determined using the
199 last tracking surveys of each tracking period in each ditch. By only including recaptured
200 pike in the calculations, we ensured that the detection efficiency was based on living
201 fish. Detection efficiency depends on the species studied (Cucherousset *et al.* 2010), but
202 also on the water depth. In similar tracking studies, although conducted in streams with
203 lower water depths, detection efficiencies of 19.6 to 81.9 % have been reported
204 (Roussel *et al.* 2000; Cucherousset *et al.* 2007; Enders *et al.* 2007). At the conclusion of
205 each tracking period, another electric fishing survey was also completed during which
206 detected fish attempted to be recaptured, with the data collected as previously outlined.
207 Only recaptured, tagged individuals were included in subsequent analyses to avoid the
208 inclusion of data from tags that had been expelled from fish or where the fish had died,
209 and thus removed these aspects as potential confounding factors.

210

211 **Stable isotope analysis (SIA)**

212 Trophic position of individuals was quantified using the stable isotope of nitrogen
213 ($\delta^{15}\text{N}$) that shows enrichment of 2 to 4‰ from resource to consumer (Post 2002). To
214 provide the baseline isotopic signals of the putative food resources of the fish,
215 specimens of water louse *Asellus aquaticus* were collected at the completion of each
216 electric fishing survey. This macroinvertebrate was the most abundant species in the
217 ditches and has constituted an important part of the diet of juvenile pike in the River
218 Frome (Mann 1982). One SIA sample of *A. aquaticus* comprised of 2 to 4 individuals.
219 The samples were oven dried (60°C for 48 h), ground into a homogenous powder,

220 weighed (all samples were 0.5 - 1 mg), and analysed at Cornell Isotope Laboratory,
221 USA. Initial data outputs were in the format of delta ($\delta^{15}\text{N}$) isotope ratios, expressed in
222 ‰. TP for each individual pike were then calculated using the formula: $\text{TP} = [(\text{fish } \delta^{15}\text{N}$
223 $- \text{mean prey } \delta^{15}\text{N})/3.4] + 2$, where 3.4 represents a widely used single trophic level
224 fractionation in $\delta^{15}\text{N}$, and 2 corresponds to the trophic level of primary consumers
225 (Vander Zanden *et al.* 2000).

226

227 **Data analyses**

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

236

237 To enable movement metrics of individual pike to be calculated, the initial step was to
238 plot each fish location that was collected on each tracking occasion into two-
239 dimensional coordinate values y (metre transects along the ditch length) and x (metre
240 equidistant strata across the ditch width), following Roussel *et al.* (2004) and
241 Cucherousset *et al.* (2009). The equidistant strata were calculated based on the average
242 width obtained from three measurements of each 10 m long patch of the ditch. First, the
243 mean position for each individual fish was calculated by averaging the x coordinate
244 values obtained for all detections (x_1, x_2, x_3, \dots) to calculate \bar{x} , and the y coordinate values

245 obtained for all detections (y_1, y_2, y_3, \dots) to calculate \bar{y} . This mean arithmetic position (\bar{x} ,
246 \bar{y}) was defined as the centroid of the positions from where the distance to all other
247 points (i.e. individual positions obtained at each tracking) is the smallest (Lair 1987).
248 Secondly, we calculated the radial distances (m) for each detection (d_1, d_2, d_3, \dots). The
249 radial distances for each detection was calculated as the measured distances from the
250 mean position (\bar{x}, \bar{y}) and every location ($x_1-y_1, x_2-y_2, x_3-y_3, \dots$) to provide an estimation
251 of fish position dispersal around its arithmetic mean position (\bar{x}, \bar{y}). The arithmetic
252 mean radial distance (\bar{d}) was then calculated by averaging the radial distances ($d_1, d_2,$
253 d_3, \dots). Distances (v_1, v_2, v_3, \dots) between two successive positions (from x_1-y_1 to $x_2-y_2,$
254 from x_2-y_2 to x_3-y_3, \dots) were calculated and subsequently divided by time between two
255 consecutive detections (in days) to provide a measurement of the mean arithmetic
256 distance (m) travelled per day (\bar{v}) (Roussel *et al.* 2004). While daily distance moved is a
257 measure of distances between subsequent detection positions per day, radial distances
258 provide an estimation of fish dispersal around its arithmetic mean position. Radial
259 distances are therefore more indicative of the home range of individuals.

260

261 **Statistical analyses**

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

269

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

277

278 To determine the causes for inter-individual variability in movement, linear mixed
279 effect models (LMMs) were conducted using the lme function in the nlme package
280 (Pinheiro *et al.* 2015). Radial distances (d_1, d_2, d_3, \dots) or daily distances (v_1, v_2, v_3, \dots)
281 moved were fitted as the response variable and age, period, initial TP and initial FL as
282 predictors. Possible serial autocorrelation within individual movement measures was
283 accounted for by a `cor=corAR1` argument for radial distance and daily distances moved.
284 Individual ID was nested within ditch as a random effect and age, period, initial FL and
285 initial TP were fitted as fixed factors.

286

287 Individuals were sampled for length to calculate growth rate and fin clips were taken to
288 attain a value for TP at the end of each tracking session. Consequences of individual
289 movement on SGR or final TPs were tested by running LMMs with each movement
290 metric as a predictor and SGR or final TP as the response variable. Thus, either daily
291 distance moved or radial distances were fitted as predictors together with initial TP, age
292 and period, and individual ID was nested within ditch as a random effect. All models
293 were first run with full two-way interactions and then simplified until no further model
294 simplification could be made without removing a significant interaction ($P < 0.05$)

295 (Zuur *et al.* 2009). Marginal R^2 and conditional R^2 values for each model were
296 calculated using the ‘piecewiseSEM’ package (Lefcheck 2015). The marginal R^2
297 describes the proportion of variance explained by the fixed factors alone, whereas the
298 conditional R^2 describes the variance explained by fixed and random factors (Nakagawa
299 & Schielzeth 2013). The standardized regression coefficients that were scaled by mean
300 and variance and 95 % confidence intervals (CI) were calculated for each predictor in
301 the nlme models with the “piecewiseSEM” package. Traits were considered as
302 significantly contributing to the model if their confidence intervals did not overlap zero.

303

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

306

307 **Results**

308

309 **Numbers of tagged and tracked fish**

310 A total of 101 0+ and 30 1+ pike were tagged in the ditches during the study (Table 1).
311 Of the tagged fish, there were 35 0+ and 15 1+ pike that were detected during tracking
312 periods and recaptured subsequently (Table 1). Therefore, 38 % of the tagged pike were
313 included in subsequent analyses, with all individuals were only detected in the ditches
314 where they were tagged. A mean detection deficiency of 70.7 ± 1.7 % of the pike tagged
315 and recaptured in the ditches was obtained during the three tracking periods. There were
316 no significant differences in body lengths at capture between recaptured and non-
317 recaptured individuals (Table S3). There was also no relationship between body size at
318 tagging and the number of subsequent detections (Spearman’s correlation, $r = -0.11$, $p >$
319 0.05). The overall mean number of detections per fish across the 3 tracking periods was

320 8.6 ± 0.6 (range 2 to 17), but did not differ significantly between ages (ANOVA, $F_{1,48} =$
321 0.51, $P > 0.05$), or between tracking period for either 0+ (ANOVA, $F_{1,27} = 1.10$, $P >$
322 0.05) or 1+ pike (ANOVA, $F_{1,13} = 0.45$, $P > 0.05$). The mean time between two
323 successive detections (including all three tracking periods) was 7.0 days (± 0.2 SE) and
324 ranged between 4 and 28 days. No significant relationship between time between
325 successive detections and the calculated distance between detections was found
326 (Pearson's correlation, $r = -0.10$, $p > 0.05$).

327

328 **Causes for variability in individual movement**

329 There was considerable variation in the movement of individuals between age-classes
330 and tracking periods. The radial distance (\bar{d}) for 0+ fish in spring 2009 ranged from 2.6
331 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
332 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
333 16.7 ± 1.8) in spring 2010 and 1.3 to 64.9 m (mean 17.0 ± 0.2) in winter 2011. The
334 conditional and marginal R^2 for the model with radial distance as a response variable
335 were 0.47 and 0.11, respectively, and for the model with daily distance moved as
336 response variable 0.11 and 0.06, respectively. Both radial distance and daily distances
337 moved differed between ages and tracking periods; individuals of age 1+ moved more
338 than 0+ and there was significantly less movement in winter than spring (Table 2). The
339 effects of initial fish length were, however, not significant. The daily distances of
340 individuals with higher initial TP were significantly less than those with lower initial TP
341 (Table 2).

342

343 **Consequences of variability in individual on growth and TP**

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

355

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

363

364 **Discussion**

365

366 The individual movements of the juvenile pike were significantly influenced by age,
367 with fish of 1+ years showing greater movements than 0+ fish, with this consistent with
368 the first prediction. Although initial TP was significantly and negatively associated with

369 daily movements, body size had no significant influence on individual movement,
370 contrary to the second prediction. In line with the third prediction, individuals that
371 moved more achieved a higher somatic growth rate and an elevated final TP. These
372 results suggest that individuals with higher levels of activity (i.e. more movement)
373 acquire higher quality resources (as revealed by higher TP) and achieve higher growth
374 rates (as SGR). It should be noted that the fate of the tagged fish that were never
375 detected or recaptured in the study were unable to be determined. Given that mortality
376 or tag loss within the ditch would result in the tag still being detected then it was
377 assumed these individuals either emigrated into the main channel or were depredated by
378 a bird or mammal (Cucherousset *et al.* 2007) and thus removed from the study areas.
379 Irrespective, this remains speculative and thus the fate of these fish is not considered
380 further.

381

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

394 minimal. This non-significant influence of length on juvenile movements contrasts to
395 adult pike, where movement rates are often a function of body size (e.g. Kobler *et al.*
396 2008). In the study river, Masters *et al.* (2005) revealed adult pike exhibit a continuum
397 of spatial behaviours, with some individuals always using the same few hundred metres
398 of river, whilst others use stretches over several kilometres. Whilst influenced by pike
399 length, the length range of these tracked fish was considerable (520 to 950 mm), with
400 considerable variation in movement patterns between individuals of relatively similar
401 size (Masters *et al.* 2005). Whilst it is difficult to extrapolate adult behaviour to
402 juveniles, the length range of juvenile pike used here was relatively narrow (138 to 301
403 mm) and thus might have been insufficient to result in strong size-structured movement
404 patterns. That age was a significant determinant of movement might then have been
405 through it being a function of time, with older fish in the ditches having longer to
406 establish larger home ranges in which they were able to make higher daily movements.
407 This could align to ‘prior residence advantage’, where individuals that are present first
408 in a new habitat obtain, and subsequently defend, the most profitable sites, with this
409 often apparent in the behavioural ecology of salmonid fishes (e.g. Harwood *et al.* 2003).
410
411 The development of the differences in movement patterns between individuals might
412 also have been influenced by their underlying behaviours that relates to their propensity
413 for risk-taking. We have previously documented individual consistency in foraging
414 activity across risky situations consisting of the presence/absence of a competitor or
415 predator laboratory experiments using 0+ pike collected from this particular population
416 (Nyqvist *et al.* 2012, 2013). Bolder individuals maintained a high foraging activity
417 through time, while shyer individuals maintained a low foraging activity, but without
418 consequences on growth (Nyqvist *et al.* 2012, 2013). The individual variation in

419 movement detected in the present study might thus relate to the degree of risk-taking
420 behaviour but with consequences on growth. Under the experimental settings of Nyqvist
421 *et al.* (2012), pike were kept in isolation, meaning that the intraspecific interactions,
422 including effects of competition or dominance hierarchies on individual growth, were
423 removed, which was not the case for the pike in the ditches. Apart from the important
424 effect of intraspecific interactions, a heterogeneous environment may also play a
425 significant role in providing the potential for habitat and resource segregation to occur
426 and so, subsequently, enables divergent growth within a population. Laskowski *et al.*
427 (2016) tested individual behaviour of wild adult pike captured from a lake in
428 standardized open-field behavioural assays. The measured standardized behavior did not
429 relate to growth rate (Laskowski *et al.* 2016). In contrast, our results show that
430 individual movement had positive consequences on growth and trophic positions in
431 juvenile pike in the wild. This difference may be explained by the differences in habitat
432 complexity. While size dimorphism has been reported in our study population (Mann &
433 Beaumont 1990), no size differences were reported for the pike in the particular lake
434 studied by Laskowski *et al.* (2016).

435

436 That individuals that moved achieved higher growth rates and an elevated final trophic
437 position in our study may be related to the mortality-growth trade-off mediated by
438 foraging activity (Werner & Anholt 1993). Foraging activities increase the probability
439 of predator detection and thus increased movements should lead to increased mortality
440 risk (Werner & Anholt 1993). Reduced activity in the presence of predators is also an
441 important antipredator behavior (Lima & Dill 1990). In many animals, vulnerability to
442 predation decreases with increasing body size, and especially in juvenile fish due to the
443 issue of gape-size limitation in piscivorous animals (Nilsson & Bronmark 2000).

444 Growth rate is therefore an important determinant of the probability of individual
445 survival and is often used as a fitness proxy (Brown *et al.* 2007). Experimental studies
446 on several fish species have revealed growth differences relating to foraging activity
447 (Jobling & Baardvik 1994; Martin-Smith & Armstrong 2002; Imsland *et al.* 2009).
448 Studies on rainbow trout *Oncorhynchus mykiss* have demonstrated that individuals
449 taking greater risks while foraging grew faster, but survived at a lower rate in the
450 presence of predators than individuals taking fewer risks (Biro *et al.* 2004, 2006).

451

452 An increasing number of studies demonstrate that individual specialisation in resource
453 use in a population often develops where there is low interspecific competition but high
454 intraspecific competition (Svanbäck & Bolnick 2007; Araújo *et al.* 2011; Bolnick *et al.*
455 2011). Individual resource specialisation appears to be particularly common among
456 apex predator fishes (Araújo *et al.* 2011), which may be explained by that they usually
457 have few interspecific competitors in the community. In our study site, juvenile pike
458 density, a proxy for intraspecific competition (Araújo *et al.* 2011), was high with few (if
459 any) other predatory species present. While individual specialisation in resource use
460 often results in the development of related morphological traits (Smith & Skulason
461 1996; Bolnick *et al.* 2003; Cucherousset *et al.* 2011), cannibalism has been suggested to
462 be the proximate cause of bimodal size distributions in some fish species (Claessen *et*
463 *al.* 2000). Thus, a factor potentially contributing to the observed consequences for
464 growth rates and trophic ecology in our studied pike may be the combined effect of
465 intraspecific competition with cannibalism.

466

467 In conclusion, individual variation in movement was negatively associated with TP and
468 increased movement had positive influences on individual growth rates and subsequent

469 TP in these juvenile pike. We suggest that individual variability in movement and TPs
470 reflects variation in foraging activity, which may be underpinned by personality traits,
471 but with causal drivers also involving pressures from intra-specific competition and
472 trade-off with mortality risk, especially the risk from cannibalism.

473

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478

479 **References**

480

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686

687 **Supporting Information**

688 Table S1. Results table of summary of one-Way ANOVAs for number of detections,
689 radial distance moved and daily distance moved as a function of time of day (06:00-
690 08:00, 10:00-14:00, 16:00-18:00).

691 Table S2. Results table of linear mixed models used to test for the effects of age, period,
692 initial TP and FL and their interactions on individual radial distance and daily distance
693 moved.

694 Table S3. Results table of linear mixed models used to test for the effects of capture
695 after tagging, age, date of tagging and their interactions on fork lengths at tagging and
696 tag/body mass ratio of individuals.

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 (\pm SE) (days) between tagging and recapture
0+	101	96	35	206 \pm 3.8
1+	30	27	15	186 \pm 2.1

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. Variables in bold have P values > 0.05 and 95 % confidence intervals that do not overlap zero, and therefore considered to contribute significantly to the model.

Response variable	Source of Variation	d.f.	Estimate (S.E.)	t	P	Coefficient	Lower	Upper
							95 % CI	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			

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. Variables in bold have P values > 0.05 and 95 % confidence intervals that do not overlap zero, and therefore considered to contribute significantly to the model.

LMM	Source of Variation	d.f.	Estimate (S.E.)	t	P	Coefficient	Lower 95 % CI	Upper 95 %
1	Age (0+ vs. 1+)	365	-0.06 (0.02)	-2.94	0.004	-0.63	-0.10	-2.18
	Period (Spring 2010)	365	0.02 (0.02)	1.09	0.277	0.13	-0.02	6.45
	Period (Winter 2011)	365	-0.03 (0.04)	-0.62	0.538	-0.65	-0.11	5.59
	Radial distance	365	0.00 (0.00)	4.14	< 0.0001	-0.001	0.0001	4.45
	Initial TP	365	0.04 (0.00)	109.85	< 0.0001	0.23	0.04	3.63
	Initial TP x Radial distance	365	0.00 (0.00)	-4.60	< 0.0001	-0.001	-0.0002	-6.20
	Intercept	365	0.01 (0.02)	0.30	0.768			
2	Age (0+ vs. 1+)	319	-0.06 (0.02)	-2.94	0.004	-0.64	-0.11	-2.30
	Period (Spring 2010)	319	0.02 (0.02)	1.09	0.277	0.13	-0.02	6.55
	Period (Winter 2011)	319	-0.03 (0.04)	-0.62	0.537	-0.67	-0.11	5.69
	Daily distance	319	0.00 (0.00)	2.65	0.008	-0.0002	0.0002	5.35
	Initial TP	319	0.04 (0.00)	103.56	< 0.0001	0.23	0.04	3.70
	Initial TP x Daily distance	319	0.00 (0.00)	-2.99	0.003	-0.0003	-0.0002	-8.07
	Intercept	319	0.01 (0.02)	0.35	0.727			

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. Variables in bold have P values > 0.05 and 95 % confidence intervals that do not overlap zero, and therefore considered to contribute significantly to the model.

LMM	Source of Variation	d.f.	Estimate (S.E.)	t	P	Coefficient	Lower	Upper
							95 % CI	95 %
1	Age (0+ vs. 1+)	328	-0.41 (0.21)	-2.00	0.046	-0.62	-0.82	-0.01
	Period (Spring 2010)	328	0.27 (0.20)	1.32	0.186	0.40	-0.13	0.66
	Period (Winter 2011)	328	0.37 (0.39)	0.94	0.346	0.55	-0.40	1.13
	Radial distance	328	0.07 (0.02)	4.00	0.0001	-0.01	0.03	0.11
	Initial TP	328	0.04 (0.07)	0.49	0.624	-0.01	-0.11	0.18
	Initial TP x Radial distance	328	-0.03 (0.01)	-4.45	< 0.0001	-0.02	-0.04	-0.01
	Intercept	328	2.85 (0.30)	9.59	< 0.0001			
2	Age (0+ vs. 1+)	286	-0.41 (0.21)	-1.95	0.052	-0.61	-0.82	0.004
	Period (Spring 2010)	286	0.26 (0.20)	1.26	0.210	0.38	-0.15	0.66
	Period (Winter 2011)	286	0.36 (0.39)	0.93	0.354	0.54	-0.41	1.14
	Daily distance	286	0.04 (0.02)	2.47	0.014	-0.01	0.01	0.07
	Initial TP	286	-0.04 (0.08)	-0.55	0.585	-0.04	-0.19	0.11
	Initial TP x Daily distance	286	-0.01 (0.01)	-2.79	0.006	-0.01	-0.02	-0.004
	Intercept	286	3.07 (0.31)	10.07	< 0.0001			

Figure captions

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

Fig. 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).

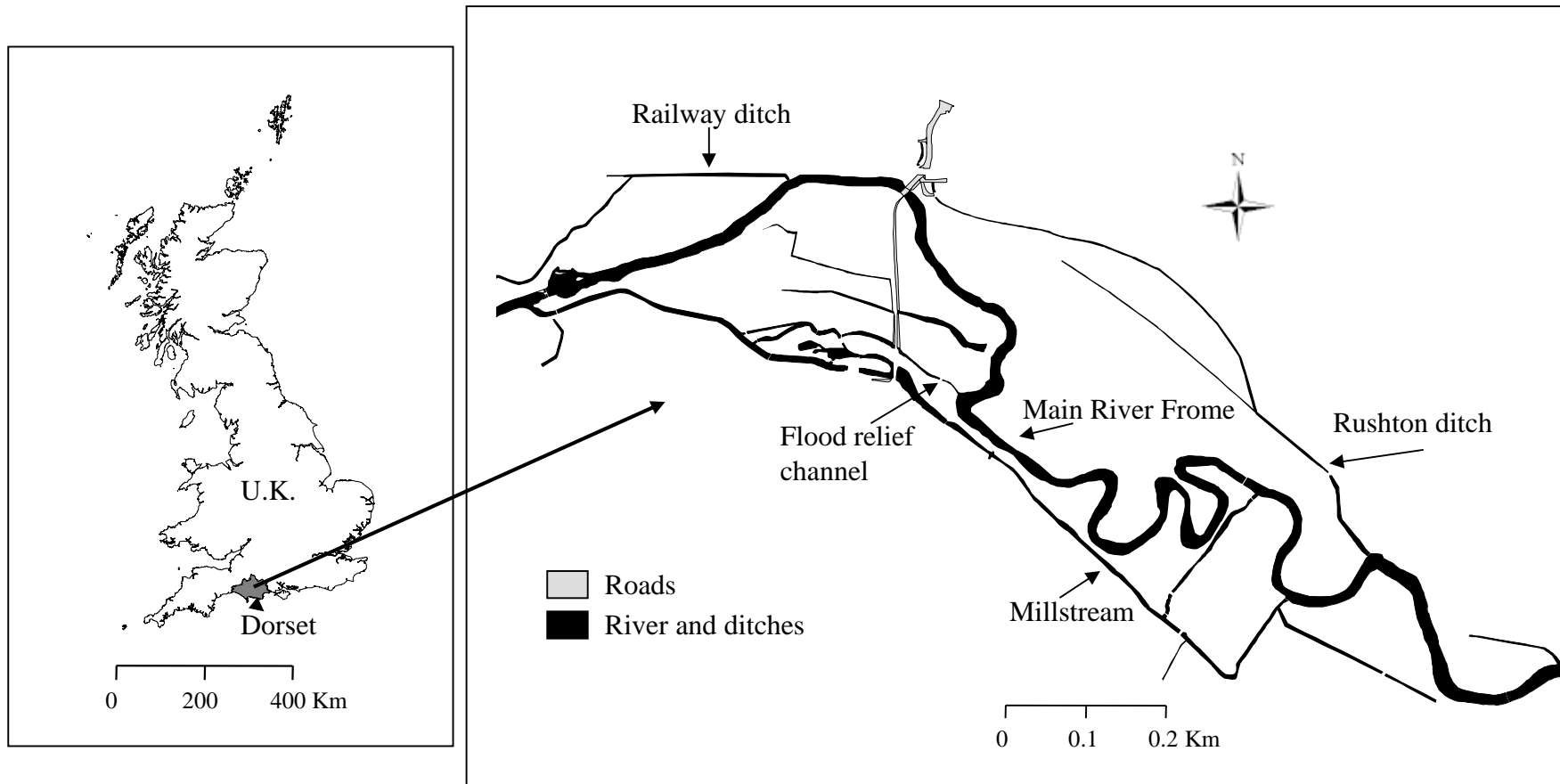


Figure 1.

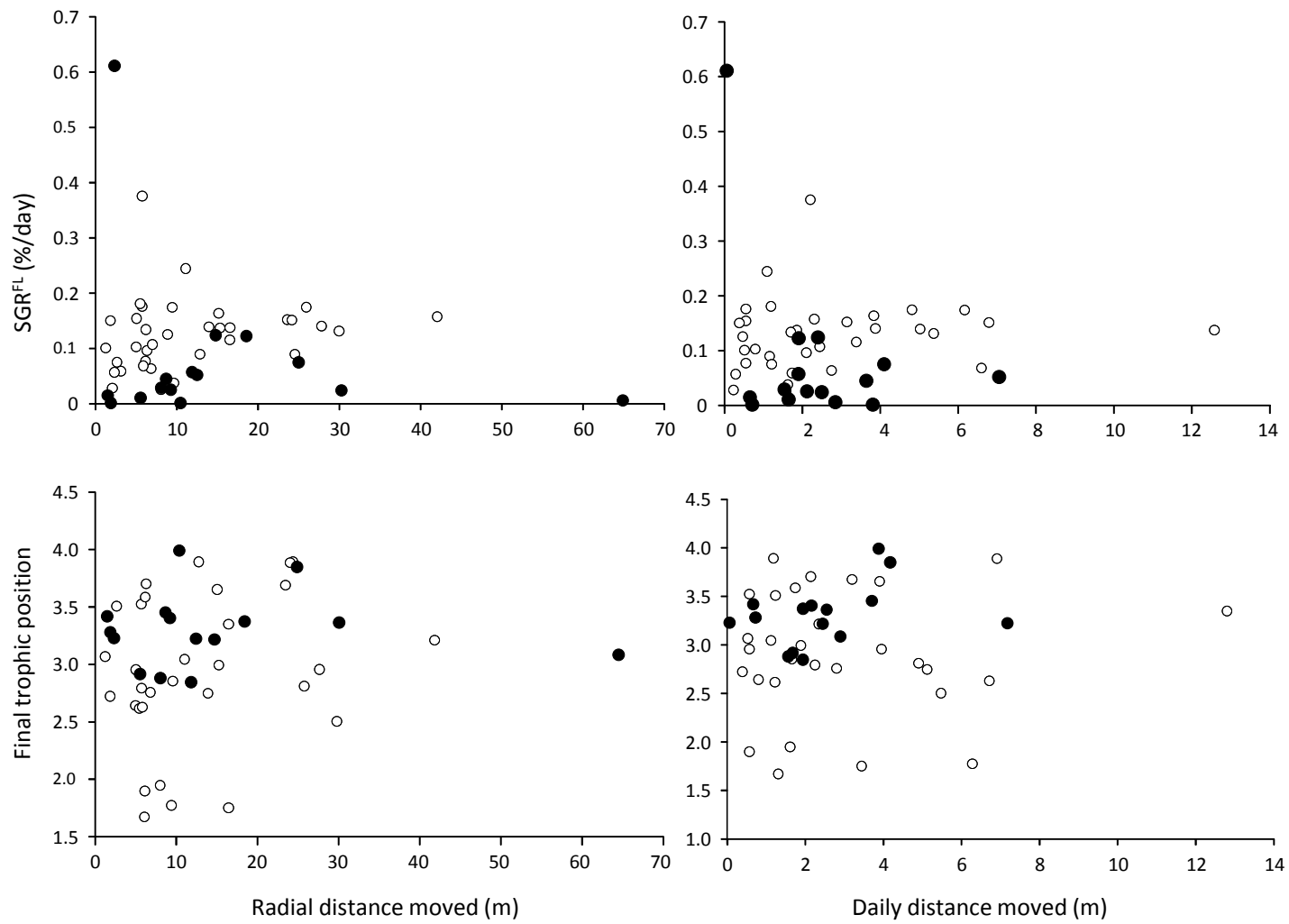


Figure 2.