Ecology of FRESHWATER FISH

Individual variability in dispersal strategies provides benefits for body size and somatic growth, but not trophic position in juvenile pike (Esox lucius L.)

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1   **Individual variability in dispersal strategies provides benefits for body size and somatic**

2   **growth, but not trophic position in juvenile pike (*Esox lucius* L.)**

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16   Running head: Natal dispersal of pike

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1

19   **Abstract**

20

21   Individual variability in dispersal strategies, where some individuals disperse and others remain

22   resident, is a common phenomenon across many species. Despite its important ecological

23   consequences, however, the mechanisms and individual advantages of dispersal remain poorly

24   understood. Here, riverine Northern pike (*Esox lucius*) juveniles (young-of-the-year and age

25   1+ year) were used to investigate the influence of body size and trophic position (at capture)

26   on the dispersal from off-channel natal habitats, and the subsequent consequences for body

27   sizes, specific growth rate and trophic position (at recapture). Individuals that dispersed into

28   the river ('dispersers') were not significantly different in body size or trophic position than

29   those remaining on nursery grounds ('stayers'). Once in the river, however, the dispersers grew

30   significantly faster than stayers and, on recapture, were significantly larger, but with no

31   significant differences in their trophic positions. Early dispersal into the river was therefore not

32   facilitated by dietary shifts to piscivory and the attainment of larger body sizes of individuals

33   whilst in their natal habitats. These results suggest that there are long-term benefits for

34   individuals dispersing early from natal areas via elevated growth rates and, potentially, higher

35   fitness, with the underlying mechanisms potentially relating to competitive displacement.

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37   **Key words**: Natal dispersal, Northern pike, piscivory, stable isotope analysis.

2

Introduction

Most animals have the capacity to disperse from one place to another to some degree or during important life stages. The dispersal of an individual can have important consequences for individual fitness, population dynamics and spatial distributions (Clobert, Danchin, Dhondt & Nichols, 2001). Movements from natal areas into habitats that provide enhanced foraging opportunities are common in many species, and this can have considerable social, ecological and evolutionary consequences (Weiß, Kulik, Ruiz-Lambides & Widdig, 2016). However, this natal dispersal can have considerable costs and tends to exist in trade-offs with increased predation risk (Halpin, 2000; Alcalay, Tsurim & Ovadia, 2018). Dispersal is generally considered as a discrete mechanism from migration (Schwarz & Bairlein, 2004) and involves the movement of individuals away from others, such as siblings, who are left behind in the original area, and without necessarily returning to that area (Semlitsch, 2008).

Trade-offs between dispersal and mortality mean that although dispersal can deliver substantial individual benefits, the risks can also be high (Bonte et al., 2012). Consequently, there is often substantial variability in the dispersal behaviours between individuals (Cucherousset, Paillisson & Roussel, 2013). Whilst dispersing individuals incur increasing costs and have elevated mortality risk, dispersed individuals often gain fitness advantages via their subsequent exploitation of new resources in a less competitive environment (Waser, Nichols & Hadfield, 2013), providing that environment is sufficiently productive (Bonte, De Roissart, Wybouw & Van Leeuwen, 2014). Indeed, in freshwater fishes, dispersal can be a mechanism for individuals to decrease intraspecific competitive interactions and/ or predation risk (Lima & Dill, 1990; Skov et al., 2011). For example, small-bodied roach *Rutilus rutilus* are more likely

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63   to disperse from areas of higher predation risk to areas of lower predation risk than large-bodied

64   individuals (Chapman *et al.,* 2011). However, the high activity rates of these dispersing small

65   individuals might then elevate their predation risk, especially as their sizes makes them more

66   vulnerable to predators that are otherwise gape-limited (Nilsson & Brönmark, 2000).

67

68   In dispersal strategies that relate to predation risk and growth (Chapman *et al.,* 2013), there is

69   thus high potential for the individual growth rates of the dispersing individuals to increase via

70   reducing density dependent competition and/ or enabling the utilization of underexploited

71   trophic resources in the new environment and/ or niche partitioning (Smith & Skulason, 1996,

72   Waser *et al.,* 2013). To explain why only some individuals disperse to new habitats requires

73   understanding the ecological attributes of these dispersers and comparison to those that do not

74   disperse (Chapman *et al.,* 2011, Cucherousset *et al.,* 2013). Metrics such as trophic position

75   potentially provides a useful indicator of the competitive ability of individuals to access high

76   quality resources (Bolnick *et al.,* 2003). Whilst the costs of dispersing are ubiquitous,

77   knowledge on the individual advantages that dispersal provides remains relatively limited

78   (Bonte *et al.,* 2012).

79

80   The aim of this study was, therefore, to test hypotheses relating to the drivers and benefits of

81   individual differences in dispersal during the juvenile life-stages of the piscivorous Northern

82   pike (*Esox lucius* L.). The study system was the lower River Frome in Southern England (Fig.

83   1). This *E. lucius* population has been previously associated with individual variability in

84   dispersal from their off-channel natal habitats (Mann 1980), where some young-of-the-year

85   fish (0+ cohort) move from off-channel natal habitats into the main river during their initial

86   summer of life, whilst others remain in natal habitats until at least their second year of life

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87   (Mann & Beaumont, 1990, Knight, Gozlan & Lucas, 2008). Individuals remaining on natal

88   habitats then grow significantly slower than those that disperse (Mann & Beaumont, 1990),

89   which has been linked to dietary differences and prey availability (Mann, 1982). The timing of

90   the ontogenetic shift from zooplanktivory toward piscivory varies between individuals

91   (Wolska-Neja and Neja 2006; Cucherousset et al., 2013). Thus, two hypotheses on individual

92   variability in dispersal were tested: (1) dietary ontogeny is a driver of juvenile dispersal, with

93   dispersers having higher trophic positions and larger body sizes than stayers when they disperse

94   from natal habitats (as per Cucherousset et al., (2013)); and (2) dispersal-driven habitat

95   partitioning is a driver of individual growth life histories, with dispersers subsequently

96   experiencing faster growth rates in the new habitat.

97

98   **Methods**

99

100   ***Sampling and data collection***

101   Juvenile *E. lucius* were sampled in two side-channels (hereafter referred to as 'ditches') of the

102   River Frome Southern England (50°419 N; 2°119 W) (Fig. 1; Masters *et al.,* 2002; Nyqvist,

103   Gozlan, Cucherousset & Britton, 2017). The ditches were generally ≤ 5 m in width and ≤ 1 m

104   in depth, and adult *E. lucius* were observed spawning there in spring. Juvenile *E. lucius* were

105   regularly captured from the ditches using an electric fishing backpack (Smith-Root LR-24,

106   USA) from January 2009 to October 2011 (Nyqvist *et al.,* 2017). Individuals were

107   anaesthetised (MS-222), measured for body size (as fork length, FL, nearest mm), had a fin

108   biopsy taken (for subsequent stable isotope analyses, SIA), and scales were removed for age

109   determination. Individuals of FL over 85 mm were tagged with 23.1 mm passive integrated

110   transponder (PIT) tags to enable their individual identification on recapture (Zydlewski, Haro,

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111 Whalen & McCormick, 2001). At these fish lengths, tag weights were generally below 2 % of

112 body weight.

113

114 To enable fish to be categorized as either dispersing from the ditches ('dispersers') or

115 remaining in the ditches ('stayers'), more intensive sampling was completed between 18th June

116 and 12th October 2010. To identify differences in the body size and trophic position (TP)

117 between stayers and dispersers, sampling utilized two methods. To identify stayers, electric

118 fishing was completed monthly in each ditch, using the LR-24 backpack as described above.

119 To identify dispersers, fyke nets of 8 mm mesh were placed in the ditches within 5 m of their

120 connections to the main river to enable capture of individuals moving from the ditches into the

121 river. The fyke nets were continuously in use (24 hour sampling) throughout the study period,

122 with nets checked daily and all fish being processed. Fish were then released in the main river

123 side of the fyke nets, as the fish were moving in this direction when captured. All captured *E.*

124 *lucius*, irrespective of sampling method, were checked for the presence of a PIT tag (i.e.

125 whether they were a new capture or a recapture), measured for FL and fin samples taken for

126 subsequent stable isotope analysis and calculation of TP.

127

128 Following this period of identifying stayers and dispersers, the consequences of these strategies

129 for individuals were assessed by recapturing individuals by electric fishing. For stayers, electric

130 fishing using the LR-24 backpack in the ditches was used, with all captured fish checked for a

131 PIT tag, measured and a fin clip taken. For dispersers, the main river channel was also sampled

132 by electric fishing. At low water levels, hand-held electric fishing from a small boat was used.

133 At sufficiently high river levels, a boat specifically adapted for electric fishing in rivers was

134 used that had a series of cathodes trailing from the back and two circular anodes with droppers

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135   hanging at the front. Again, all captured fish were checked for a PIT tag, measured and a fin

136   clip taken, and then returned. For all recaptured tagged fish (ditches and main river), their

137   length increment was determined and converted to specific growth rate (SGR) that expressed

138   the length change over time:

139   SGR = $[\ln(L_f)-\ln(L_i)]*100/t$

140   where L_i and L_f were the initial and final fork lengths (mm) of the individual, and t was the

141   number of days between capture and recapture (Nyqvist *et al.,* 2017).

142

143   The fin samples were analysed for the nitrogen stable isotope ($\delta^{15}N$), as these values in fin

144   tissues correlate strongly with those of dorsal muscle tissue (Jardine, Gray, McWilliam &

145   Cunjak*,* 2005; Busst, Bašić & Britton, 2015). Fin clipping has been found not adversely affect

146   fish survival or growth (Gjerde & Refstie, 1988), and enables temporal monitoring of

147   individual trophic niche shift (Cucherousset *et al.,* 2013). Specimens of water louse *Asellus*

148   *aquaticus* were obtained at the same time and location as the pike were captured to provide the

149   baseline isotopic values of their putative prey. These were the main macroinvertebrate species

150   in the ditches, with no other species sampled in sufficient quantity to enable their SIA. The *A.*

151   *aquaticus* samples were pooled (n = 2 to 4 per SIA sample). All samples were then oven dried

152   at 60ºC to constant weight, before processing and analysis at the Cornell Isotope Laboratory,

153   New York, USA. Trophic position (TP) for individual pike was then calculated using the

154   formula: TP = $[(\delta^{15}N_{Fish} - \delta^{15}N_{MeanPrey}) / 3.4] + 2$, where 3.4 represents a widely used single

155   trophic level fractionation in $\delta^{15}N$, and 2 corresponds to the trophic level of primary consumers

156   (Vander Zanden, Shuter, Lester & Rasmussen, 2000).

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159   ***Statistical analyses***

160   To investigate trophic and size-dependent dispersal, the individuals captured in the fyke nets

161   (dispersers) were compared to those in the ditches (stayers) in summer 2010. Generalized linear

162   models (GLMs) were performed with TP or FL as the dependent variable, dispersal status

163   (stayer/disperser) as the independent variable, and age (0+ and 1+), and capture date as

164   covariates. Outputs were the mean FL and TP of stayers and dispersers (adjusted for the effects

165   of covariates) and the significance of the differences.

166

167   To analyse differences in FL and TP between stayers and dispersers prior to dispersal (at first

168   capture in the ditches) and at their recapture (either in the ditches or river), GLMs were used.

169   FL and TP were the dependent variables, dispersal status (disperser/stayer) was the independent

170   variable, and age (0+ and 1+), days between capture and recapture ('days at large'), recapture

171   date (as the interaction of month and year) were covariates. Outputs were the mean FL and TP

172   of recaptured stayers and dispersers (adjusted for the effects of covariates), and the significance

173   of their differences. Differences in SGR between recaptured stayers and dispersers were also

174   analysed in a GLM, where SGR was the dependent variable, dispersal status was the

175   independent variable, and with initial length at capture, age, number of days between capture

176   and recapture, and date of recapture (as the interaction of month and year) being covariates.

177   All analyses were conducted in STATISTICA (v. 12) and SPSS (v. 22). Errors around means

178   are 95 % confidence limits unless stated otherwise. The study was conducted under the UK

179   Home Office project licence number PPL 30/2626 and following ethical review.

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Results

There were 56 juvenile E. lucius sampled during summer 2010 for the study, of which 30 were age 0+ and 26 were age 1+ year. Of these fish, 33 were captured in the ditches (so were designated as 'stayers'; 0+: n = 17; 1+: n = 16) and 23 in the fyke nets (so were designated as 'dispersers'; 0+: n = 13; 1+: n = 10). No fish that had been identified as a stayer on its initial capture was subsequently recaptured either in the fyke nets or the main river, i.e. it did not disperse during the study period.

There were no significant differences in FL at capture detected between fish sampled in the ditches by electric fishing (stayers) versus those in the fyke nets (dispersers), with only age at capture having a significant, positive effect on individual FL (Table 1; Fig. 2). Although dispersers had a significantly lower TP than stayers in the 0+ fish (ANOVA: $F_{1,28} = 41.63$, P < 0.01), this was not apparent in the 1+ fish (ANOVA: $F_{1,24} = 1.95$, P = 0.18; Fig. 2). However, when the TP data were combined for the age groups and the effects of covariates accounted for, the differences between the TP of stayers and dispersers were not significant (Table 1).

Of the 56 tagged *E. lucius*, 50 were subsequently recaptured. There were significantly more pike recaptured in their ditches (n = 44) than in the river (n = 6) ($\chi^2 = 28.88$; *P* < 0.01). The number of days between captures and recaptures ranged from 51 to 579 days. On recapture, the body sizes of dispersers were significantly larger than stayers (P < 0.01; Table 2), where the effects of age and the number of days at large were significant covariates in the model (P < 0.05; Table 2). Similarly, the SGR of dispersers was significantly higher than stayers (P = 0.05, Table 3), with the date and length of capture being significant covariates in the model (P <

9

206   0.01; Table 3). However, the trophic positions of recaptured stayers and dispersers were not

207   significantly different (P = 0.46; Table 2).

208

209   **Discussion**

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211   Natal dispersal is a ubiquitous phenomenon, with this study revealing that dispersal from natal

212   ditches was not related to the body size or trophic position of the individual 0+ and 1+ pike,

213   although 0+ dispersers were of significantly lower trophic position than 0+ stayers. This finding

214   was contrary to the first hypothesis that predicted dispersers would be those individuals of

215   higher trophic position and larger body sizes through their ontogenetic shift to piscivory

216   occurring on the natal habitats. The results were, however, consistent with the second

217   hypothesis, as following their dispersal into the main river; dispersers experienced significantly

218   higher growth rates than stayers and had achieved larger body sizes on their recapture, although

219   the number of recaptured individuals in the river was relatively low. Despite pike moving out

220   from the ditches at age 0+ not having higher trophic positions than those staying in ditches,

221   their piscivory would enable their foraging on the more abundant and diverse prey populations

222   of the main river channel compared to the small ditches, thus facilitating their ability to grow

223   faster and attain larger body sizes.

224

225   Our results suggest that dispersers exist in a trade-off between their increased predation risk in

226   the river with the higher potential for achieving faster growth rates. The finding that an

227   ontogenetic dietary shift towards piscivory by individual pike was not the driver of juvenile

228   dispersal from the natal habitats here was in contrast to Cucherousset *et al.* (2013), who

229   demonstrated that the natal departure timing of juvenile pike from a temporally flooded

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230   grassland nursery was dependent on this. In the latter case, the risk of the complete drying of

231   temporary waters meant that the natal departure timing of juvenile fish was directly associated

232   with direct costs and benefits (i.e. survival vs. mortality). It was also occurring relatively early

233   in their life when trophic differences between individuals might have been more apparent

234   (Kramer, Rangeley & Chapman, 1997). In the ditches of this study, the water was permanent

235   and, therefore, the drivers of dispersal would not have included the avoidance of shallow waters

236   in, and drying of, the natal habitat. Improved knowledge linking ecosystem stability and natal

237   dispersal is therefore needed.

238

239   Dispersal can have indirect fitness advantages by reducing competition in populations via

240   increasing the overall access to resources (Waser *et al.,* 2013). This fitness advantage of

241   dispersing does, however, depend on the environment reached after dispersal, with those of

242   high productivity providing greater advantages (Bonte *et al.,* 2014). In juvenile Atlantic salmon

243   *Salmo salar* in natural streams, it was the smaller bodied individuals that moved away from

244   areas in the vicinity of their redd and, as the summer progressed, they experienced higher

245   growth rates (Einum *et al.,* 2012). This dispersal by smaller individuals may be driven by the

246   competitive intensity near redds (Einum *et al.,* 2012). Natal habitats, such as the river side

247   channels of the present study, naturally have a high density of juvenile pike that compete for

248   food resources of low diversity (primarily macroinvertebrates (e.g. *Asellus aquaticus*) and

249   some small bodied fishes (mainly minnow *Phoxinus phoxinus*). Dispersing to a less populated

250   area would, therefore, be advantageous in terms of increased access to food and refuge habitat,

251   as the main River Frome provides a greater diversity of prey fishes (including dace *Leuciscus*

252   *leuciscus* and grayling *Thymallus thymallus* that are present in the main channel and not the

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253   ditches; Pinder, Harrison & Britton, 2019), as well as *P. phoxinus* in much higher abundances

254   (unpublished data, the authors).

255

256   Relatively high individual variation in the competitive ability for resources may explain the

257   non-significant relationships between trophic position and dispersal strategy detected in our

258   study. The ability to compete for scarce resources is a primary aspect of population dynamics

259   that influences individual fitness (Vøllestad & Quinn, 2003). Edeline *et al.* (2010) revealed that

260   an increase in pike density depressed their energetic status and lowered growth rates. The 0+

261   individuals of lower trophic positions that dispersed from the ditches in our study may,

262   therefore, be a consequence of social stress or due to direct interference intimidation or

263   competitive exclusion from other individuals, although this could not be explicitly tested here

264   and was not apparent in the 1+ fish. Indeed, Wey, Spiegel, Montiglio & Mabry (2015)

265   suggested that the influence on dispersal of interactions of behavioural phenotypes and the

266   social environment experienced by individuals remains poorly understood, and requires further

267   work.

268

269   An increasing number of studies are demonstrating that differences in personality traits

270   between individuals underlie other observed ecological patterns that vary among individuals

271   (e.g. Cote, Fogarty, Weinersmith, Brodin & Sih, 2010, Laskowski and Bell 2014). In particular,

272   boldness in fish has been directly linked to differences in dispersal (Fraser, Gilliam, Daley, Le

273   & Skalski, 2001, Cote *et al.,* 2010) and settlement in new habitats (Armstrong, Braithwaite &

274   Huntingford, 1997). Indeed, juveniles from the pike population studied here have previously

275   been found to exhibit bold and shy personality types during experimental settings, with bolder

276   individuals expressing a higher level of foraging activity (Nyqvist, Gozlan, Cucherousset &

277 Britton*, 2012*; Nyqvist, Gozlan, Cucherousset & Britton, 2013). As trophic position is an

278 indication of the trophic niche and foraging ecology at the individual and population level

279 (Bolnick *et al.,* 2003), the 0+ stayers which had higher trophic position in the current study

280 might have been the bolder individuals, whereas the 0+ dispersers of lower trophic position

281 would have been the shy behavioural phenotype, which would be a counter-intuitive outcome.

282

283 In conclusion, it was demonstrated that dispersing juveniles had similar body sizes to stayers,

284 with 0+ dispersers having a lower trophic position than 0+ stayers. Thus, their dispersal might

285 have been driven by social stress, competitive displacement or intimidation in the highly

286 populated, permanently-flooded, ditches. Individuals that successfully dispersed into the river

287 and survived benefited by increased growth rates and so the attainment of larger body sizes

288 when compared with stayers. Therefore, these outputs highlight the importance of habitat

289 exclusion of less competitive individuals in driving variation in dispersal and indicate their

290 potential for causing long-term consequences on individual fitness and population dynamics.

291

292 **Data availability**

293 The data that support the findings of this study are available from the corresponding author

294 upon reasonable request.

295

296 **References**

297

298 Armstrong, J. D., Braithwaite, V. A. & Huntingford, F. A. (1997). Spatial strategies of wild

299   Atlantic salmon parr: exploration and settlement in unfamiliar areas. *Journal of Animal*

300   *Ecology*, *66*, 203-211.

13

301   Alcalay, Y., Tsurim, I. & Ovadia, O. (2018). Female mosquitoes disperse further when they

302   develop under predation risk. *Behavioral Ecology*, *29*, 1402-1408.

303   Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister,

304   M.L. (2003). The ecology of individuals: Incidence and implications of individual

305   specialization. *American Naturalist*, *161*, 1-28.

306   Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V.,

307   Matthysen, E., Mustin, K., Saastamoinen, M. & Schtickzelle, N. (2012). Costs of

308   dispersal. *Biological Reviews*, 87, 290-312.

309   Bonte, D., De Roissart, A., Wybouw, N. & Van Leeuwen, T. (2014). Fitness maximization

310   by dispersal: evidence from an invasion experiment. *Ecology*, *95*, 3104-3111.

311   Busst, G.M., Bašić, T. & Britton, J.R. (2015). Stable isotope signatures and trophic-step

312   fractionation factors of fish tissues collected as non-lethal surrogates of dorsal muscle.

313   *Rapid Communications in Mass Spectrometry*, *29*, 1535-1544.

314   Chapman, B.B., Hulthén, K., Blomqvist, D.R., Hansson, L.A., Nilsson, J.Å., Brodersen, J.,

315   Anders Nilsson, P., Skov, C. & Brönmark, C. (2011). To boldly go: individual differences

316   in boldness influence migratory tendency. *Ecology Letters*, *14*, 871-876.

317   Chapman, B.B., Eriksen, A., Baktoft, H., Brodersen, J., Nilsson, P.A., Hulthen, K.,

318   Brönmark, C., Hansson, L.A., Grønkjær, P. & Skov, C. (2013). A foraging cost of

319   migration for a partially migratory cyprinid fish. *PLoS ONE*, 8, e61223.

320   Clobert, J., Danchin, E., Dhondt, A. & Nichols, J.D. (2001). Dispersal. Oxford University

321   Press, New York. 2001. pp. 452.

322   Cote, J., Fogarty, S., Weinersmith, K., Brodin, T. & Sih, A. (2010). Personality traits and

323   dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proceedings of the*

324   *Royal Society of London: Biological Sciences*, *277*, 1571-1579.

14

325 Cucherousset, J., Paillisson, J.M. & Roussel, J.M. (2013). Natal departure timing from

326   spatially varying environments is dependent of individual ontogenetic status.

327   *Naturwissenschaften*, 100, 761-768.

328 Edeline, E., Haugen, T.O., Weltzien, F.A., Claessen, D., Winfield, I.J., Stenseth, N.C. &

329   Vøllestad, L.A. (2010). Body downsizing caused by non-consumptive social stress

330   severely depresses population growth rate. *Proceedings of the Royal Society of London:*

331   *Biological Sciences*, 277, 843-851.

332 Einum, S., Finstad, A.G., Robertsen, G., Nislow, K.H., McKelvey, S. & Armstrong, J.D.

333   (2012). Natal movement in juvenile Atlantic salmon: a body size-dependent strategy.

334   *Population Ecology*, 54, 285-294.

335 Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N. & Skalski, G.T. (2001). Explaining

336   leptokurtic movement distributions: Intrapopulation variation in boldness and exploration.

337   *American Naturalist*, 158, 124-135.

338 Gjerde, B. & Refstie, T. (1988). The effect of fin-clipping on growth-rate, survival and sexual

339   maturity of rainbow-trout. *Aquaculture*, 73, 383-389.

340 Halpin, P.M. (2000). Habitat use by an intertidal salt-marsh fish: trade-offs between predation

341   and growth. *Marine Ecology Progress Series*, 198, 203-214.

342 Jardine, T.D., Gray, M.A., McWilliam, S.M. & Cunjak, R.A. (2005). Stable isotope

343   variability in tissues of temperate stream fishes. *Transactions of the American Fisheries*

344   *Society*, 134, 1103-1110.

345 Knight, C.M., Gozlan, R.E. & Lucas, M.C. (2008). Can seasonal home range size in pike

346   *Esox lucius* predict excursion distance? *Journal of Fish Biology*, 73, 1058–1064.

15

347 Kramer, D.L., Rangeley, R.W. & Chapman, L.J. (1997). Habitat selection: patterns of spatial

348   distribution from behavioural decisions. - In: Godin J.G. and Fitzgerald G.J. (eds.),

349   Behavioural Ecology of Fishes. Oxford University Press, pp. 37–80.

350 Laskowski, K.L. & Bell, A.M. (2014). Strong personalities, not social niches, drive

351   individual differences in social behaviours in sticklebacks. *Animal Behaviour*, *90*, 287-

352   295.

353 Lima, S. L. & Dill, L. M. (1990). Behavioral decisions made under the risk of predation - a

354   review and prospectus. *Canadian Journal of Zoology*, *68*, 619-640.

355 Mann, R. H. K. (1980). The numbers and production of pike (Esox lucius) in 2 Dorset rivers.

356   *Journal of Animal Ecology*, *49*, 899-915.

357 Mann, R. H. K. (1982). The annual food-consumption and prey preferences of pike (Esox

358   lucius) in the river Frome, Dorset. *Journal of Animal Ecology*, *51*, 81-95.

359 Mann, R.H.K. & Beaumont, W. (1990). Fast- and slow-growing pike, *Esox lucius* L., and

360   problems of age-determinations from scales. *Aquaculture and Fisheries Management*, *21*,

361   471-478.

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

363   & Ladle, M. (2002). Habitat utilisation by pike Esox lucius L. during winter floods in a

364   southern English chalk river. *Hydrobiologia*, 483, 185-191.

365 Nilsson, P.A. & Brönmark, C. (2000). Prey vulnerability to a gape-size limited predator:

366   behavioural and morphological impacts on northern pike piscivory. *Oikos*, *88*, 539-546.

367 Nyqvist, M.J., Gozlan, R.E., Cucherousset, J. & Britton, J.R. (2012). Boldness syndrome in a

368   solitary predator is independent of body size and growth rate. *PLoS One*, *7*, e31619.

369 Nyqvist, M.J., Gozlan, R.E., Cucherousset, J. & Britton, J.R. (2013). Absence of a context-

370   general behavioural syndrome in a solitary predator. *Ethology*, *119*, 156–166.

16

371   Nyqvist M.J., Cucherousset, J., Gozlan, R.E. & Britton, J.R. (2017). Relationships between

372   individual movement, trophic position and growth of juvenile pike (*Esox lucius*). *Ecology*

373   *of Freshwater Fish*, *27*, 398-407.

374   Pinder, A.C., Harrison, A.J. & Britton, J.R. (2019). Temperature effects on the physiological

375   status and reflex impairment in European grayling *Thymallus thymallus* from catch-and

376   release angling. *Fisheries Research*, *211*, 169-175.

377   Schwarz, C. & Bairlein, F. (2004). Dispersal and migration. *Animal Biodiversity and*

378   *Conservation*, *27*, 297–298.

379   Semlitsch, R.D. (2008). Differentiating migration and dispersal processes for pond-breeding

380   amphibians. *The Journal of Wildlife Management*, *72*, 260-267.

381   Skov, C., Baktoft, H., Brodersen, J., Brönmark, C., Chapman, B.B., Hansson, L.A. &

382   Nilsson, P.A. (2011). Sizing up your enemy: individual predation vulnerability predicts

383   migratory probability. *Proceedings of the Royal Society of London: Biological Sciences*,

384   *278*, 1414 -1418.

385   Smith, T. B. & Skulason, S. (1996). Evolutionary significance of resource polymorphisms in

386   fishes, amphibians, and birds. *Annual Reviews in Ecology and Systematics*, *27*, 111-133.

387   Vander Zanden, M., Shuter, B., Lester, N. & Rasmussen, J. (2000). Within- and among-

388   population variation in the trophic position of a pelagic predator, lake trout (*Salvelinus*

389   *namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences*, *57*, 725-731.

390   Vøllestad, L. A. & Quinn, T. P. (2003). Trade-off between growth rate and aggression in

391   juvenile coho salmon, *Oncorhynchus kisutch*. *Animal Behaviour*, *66*, 561-568.

392   Waser, P.M., Nichols, K.M. & Hadfield, J.D. (2013). Fitness consequences of dispersal: Is

393   leaving home the best of a bad lot? *Ecology*, *94*, 1287-1295.

17

394   Weiß, B.M., Kulik, L., Ruiz-Lambides, A.V. & Widdig, A. (2016). Individual dispersal

395   decisions affect fitness via maternal rank effects in male rhesus macaques. *Scientific*

396   *Reports*, *6*, p.32212.

397   Wey, T.W., Spiegel, O., Montiglio, P.O. & Mabry, K.E. (2015). Natal dispersal in a social

398   landscape: considering individual behavioral phenotypes and social environment in

399   dispersal ecology. *Current Zoology*, *61*, 543-556.

400   Wolska-Neja, B. & Neja, Z. (2006). Grow-out of nothern pike (*Esox lucius* L.) larvae under

401   uncontrolled conditions. *Acta Ichthyologica et Piscatoria*, *2*, 105-112.

402   Zydlewski, G. B., Haro, A., Whalen, K. G. & McCormick, S. D. (2001). Performance of stationary

403   and portable passive transponder detection systems for monitoring of fish movements. *Journal*

404   *of Fish Biology*, 58, 1471-1475.

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406   **Author contributions statement**

407   All authors conceived and designed the study. MN, JRB, JC and RG performed field and

408   laboratory work. MN and JRB analysed the data, and all authors contributed materials and

409   analysis tools. MN led the writing of the paper and all authors contributed to editing, and

410   approved the final version for submission.

18

Table 1. Results of GLMs testing the effects of dispersal status (i.e. stayer/disperser; 'Dispersal'), capture date and age on the fork length (FL) and trophic position (TP) of all *Esox lucius* captured in the ditches.

(a) FL at capture: Wald χ^2 = 1.35, P = 0.25

	P
Capture date	0.82
Age	< 0.01
Dispersal	0.25

Mean length at capture (mm):

Stayer	197 ± 10
Disperser	215 ± 28

(b) TP at capture: Wald χ^2 = 0.03, P = 0.86

	P
Capture date	0.85
Age	0.46
Dispersal	0.86

Mean length at capture (mm):

Stayer	3.13 ± 0.16
Disperser	3.18 ± 0.42

19

Table 2. Results of GLMs testing the effects of dispersal status (i.e. stayer/disperser; 'Dispersal'), recapture date and year, age, number of days at larger and on the fork length (FL) and trophic position (TP) of all recaptured *Esox lucius* (n = 50): 0+: n = 33 (28 stayers and 5 dispersers); 1+: n = 17 (16 stayers and 1 disperser).

(a) FL at recapture: Wald $\chi^2 = 7.32$, P < 0.01

	P
Dispersal	<0.01
Age	0.04
Days at large	<0.01
Month x year	0.24

Mean length at capture (mm):

Stayer	244 ± 14
Disperser	301 ± 38

(b) TP at recapture: Wald $\chi^2 = 0.54$, P = 0.46

	P
Dispersal	0.46
Age	0.97
Days at large	<0.01
Month x year	0.75
Trophic position at capture	0.52

Mean length at capture (mm):

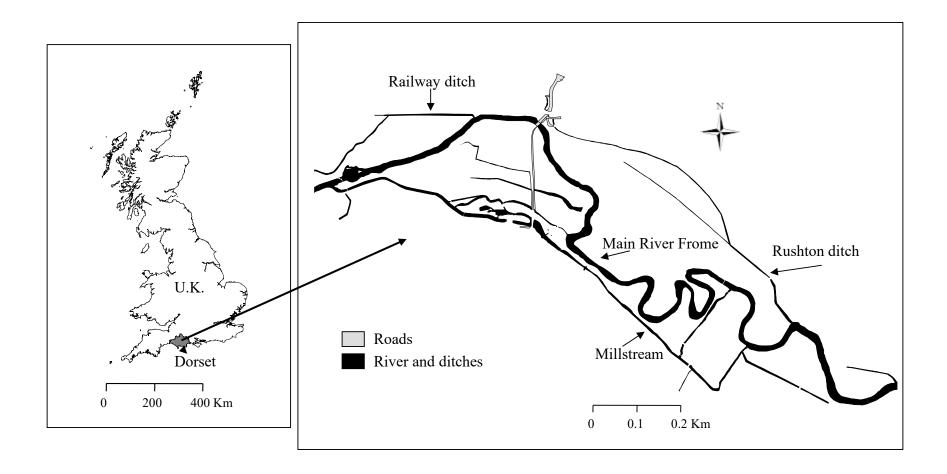| Stayer	3.16 ± 0.16
Disperser	2.98 ± 0.44

20

Table 3. Results of a GLM on the effects of dispersal status (i.e. stayer/ disperser; 'dispersal'), fork

length (FL), date of capture, age, and length at initial capture dispersal status (recaptured in ditch or

river) on the specific growth rate (SGR) of all recaptured *Esox lucius* (N = 50; 0+: n = 33; 28 stayers,

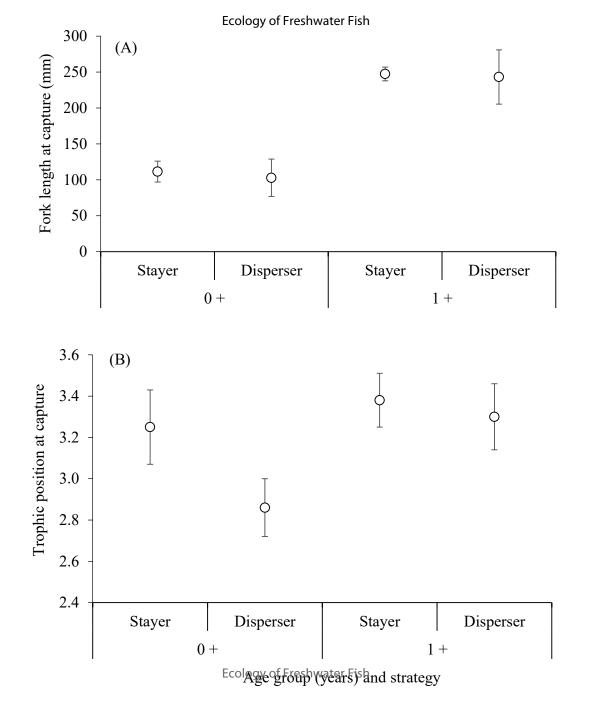5 dispersers; 1+: n = 17; 16 stayers and 1 disperser).

Specific growth rate: Wald χ^2 = 3.85, P = 0.05	
	P
Dispersal	0.05
Age	0.30
Length at capture	< 0.01
Days at large	0.43
Month x year	< 0.01
Mean specific growth rate:	
Stayer	0.11 ± 0.02
Disperser	0.16 ± 0.05

21

Figure captions

Figure 1. Left: location of the study area in the United Kingdom. Right: overview of the study sites showing the Rushton and Railway Ditches, the ditches where the pike were sampled, plus other side channels and the main river channel.

Figure 2. Length at capture (A) and trophic position at capture (B) of 0+ and 1+ pike according to their movement strategy (stayer/ disperser). Error bars are 95 % confidence limits.

22