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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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Running head: Natal dispersal of pike

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Abstract

Individual variability in dispersal strategies, where some individuals disperse and others remain resident, is a common phenomenon across many species. Despite its important ecological consequences, however, the mechanisms and individual advantages of dispersal remain poorly understood. Here, riverine Northern pike (*Esox lucius*) juveniles (young-of-the-year and age 1+ year) were used to investigate the influence of body size and trophic position (at capture) on the dispersal from off-channel natal habitats, and the subsequent consequences for body sizes, specific growth rate and trophic position (at recapture). Individuals that dispersed into the river ('dispersers') were not significantly different in body size or trophic position than those remaining on nursery grounds ('stayers'). Once in the river, however, the dispersers grew significantly faster than stayers and, on recapture, were significantly larger, but with no significant differences in their trophic positions. Early dispersal into the river was therefore not facilitated by dietary shifts to piscivory and the attainment of larger body sizes of individuals whilst in their natal habitats. These results suggest that there are long-term benefits for individuals dispersing early from natal areas via elevated growth rates and, potentially, higher fitness, with the underlying mechanisms potentially relating to competitive displacement.

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

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 to disperse from areas of higher predation risk to areas of lower predation risk than large-bodied individuals (Chapman *et al.,* 2011). However, the high activity rates of these dispersing small individuals might then elevate their predation risk, especially as their sizes makes them more vulnerable to predators that are otherwise gape-limited (Nilsson & Brönmark, 2000).

In dispersal strategies that relate to predation risk and growth (Chapman *et al.,* 2013), there is thus high potential for the individual growth rates of the dispersing individuals to increase via reducing density dependent competition and/ or enabling the utilization of underexploited trophic resources in the new environment and/ or niche partitioning (Smith & Skulason, 1996, Waser *et al.,* 2013). To explain why only some individuals disperse to new habitats requires understanding the ecological attributes of these dispersers and comparison to those that do not disperse (Chapman *et al.,* 2011, Cucherousset *et al.,* 2013). Metrics such as trophic position potentially provides a useful indicator of the competitive ability of individuals to access high quality resources (Bolnick *et al.,* 2003). Whilst the costs of dispersing are ubiquitous, knowledge on the individual advantages that dispersal provides remains relatively limited (Bonte *et al.,* 2012).

The aim of this study was, therefore, to test hypotheses relating to the drivers and benefits of individual differences in dispersal during the juvenile life-stages of the piscivorous Northern pike (*Esox lucius* L.). The study system was the lower River Frome in Southern England (Fig. 1). This *E. lucius* population has been previously associated with individual variability in dispersal from their off-channel natal habitats (Mann 1980), where some young-of-the-year fish (0+ cohort) move from off-channel natal habitats into the main river during their initial summer of life, whilst others remain in natal habitats until at least their second year of life

(Mann & Beaumont, 1990, Knight, Gozlan & Lucas, 2008). Individuals remaining on natal habitats then grow significantly slower than those that disperse (Mann & Beaumont, 1990), which has been linked to dietary differences and prey availability (Mann, 1982). The timing of the ontogenetic shift from zooplanktivory toward piscivory varies between individuals (Wolska-Neja and Neja 2006; Cucherousset *et al.,* 2013). Thus, two hypotheses on individual variability in dispersal were tested: (1) dietary ontogeny is a driver of juvenile dispersal, with dispersers having higher trophic positions and larger body sizes than stayers when they disperse from natal habitats (*as per* Cucherousset *et al.,* (2013)); and (2) dispersal-driven habitat partitioning is a driver of individual growth life histories, with dispersers subsequently experiencing faster growth rates in the new habitat.

Methods

Sampling and data collection

Juvenile *E. lucius* were sampled in two side-channels (hereafter referred to as ‘ditches’) of the River Frome Southern England (50°419 N; 2°119 W) (Fig. 1; Masters *et al.,* 2002; Nyqvist, Gozlan, Cucherousset & Britton, 2017). The ditches were generally ≤ 5 m in width and ≤ 1 m in depth, and adult *E. lucius* were observed spawning there in spring. Juvenile *E. lucius* were regularly captured from the ditches using an electric fishing backpack (Smith-Root LR-24, USA) from January 2009 to October 2011 (Nyqvist *et al.,* 2017). Individuals were anaesthetised (MS-222), measured for body size (as fork length, FL, nearest mm), had a fin biopsy taken (for subsequent stable isotope analyses, SIA), and scales were removed for age determination. Individuals of FL over 85 mm were tagged with 23.1 mm passive integrated transponder (PIT) tags to enable their individual identification on recapture (Zydlewski, Haro, Whalen & McCormick, 2001). At these fish lengths, tag weights were generally below 2 % of body weight.

To enable fish to be categorized as either dispersing from the ditches ('dispersers') or remaining in the ditches ('stayers'), more intensive sampling was completed between 18th June and 12th October 2010. To identify differences in the body size and trophic position (TP) between stayers and dispersers, sampling utilized two methods. To identify stayers, electric fishing was completed monthly in each ditch, using the LR-24 backpack as described above. To identify dispersers, fyke nets of 8 mm mesh were placed in the ditches within 5 m of their connections to the main river to enable capture of individuals moving from the ditches into the river. The fyke nets were continuously in use (24 hour sampling) throughout the study period, with nets checked daily and all fish being processed. Fish were then released in the main river side of the fyke nets, as the fish were moving in this direction when captured. All captured *E. lucius*, irrespective of sampling method, were checked for the presence of a PIT tag (i.e. whether they were a new capture or a recapture), measured for FL and fin samples taken for subsequent stable isotope analysis and calculation of TP.

Following this period of identifying stayers and dispersers, the consequences of these strategies for individuals were assessed by recapturing individuals by electric fishing. For stayers, electric fishing using the LR-24 backpack in the ditches was used, with all captured fish checked for a PIT tag, measured and a fin clip taken. For dispersers, the main river channel was also sampled by electric fishing. At low water levels, hand-held electric fishing from a small boat was used. At sufficiently high river levels, a boat specifically adapted for electric fishing in rivers was used that had a series of cathodes trailing from the back and two circular anodes with droppers hanging at the front. Again, all captured fish were checked for a PIT tag, measured and a fin clip taken, and then returned. For all recaptured tagged fish (ditches and main river), their length increment was determined and converted to specific growth rate (SGR) that expressed the length change over time:

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

where L_i and L_f were the initial and final fork lengths (mm) of the individual, and t was the number of days between capture and recapture (Nyqvist *et al.,* 2017).

The fin samples were analysed for the nitrogen stable isotope ($\delta^{15}N$), as these values in fin tissues correlate strongly with those of dorsal muscle tissue (Jardine, Gray, McWilliam & Cunjak, 2005; Busst, Bašić & Britton, 2015). Fin clipping has been found not adversely affect fish survival or growth (Gjerde & Refstie, 1988), and enables temporal monitoring of individual trophic niche shift (Cucherousset *et al.,* 2013). Specimens of water louse *Asellus aquaticus* were obtained at the same time and location as the pike were captured to provide the baseline isotopic values of their putative prey. These were the main macroinvertebrate species in the ditches, with no other species sampled in sufficient quantity to enable their SIA. The *A. aquaticus* samples were pooled (n = 2 to 4 per SIA sample). All samples were then oven dried at 60ºC to constant weight, before processing and analysis at the Cornell Isotope Laboratory, New York, USA. Trophic position (TP) for individual pike was then calculated using the formula: $TP = [(\delta^{15}N_{Fish} - \delta^{15}N_{MeanPrey}) / 3.4] + 2$, where 3.4 represents a widely used single trophic level fractionation in $\delta^{15}N$, and 2 corresponds to the trophic level of primary consumers (Vander Zanden, Shuter, Lester & Rasmussen, 2000).

Statistical analyses

To investigate trophic and size-dependent dispersal, the individuals captured in the fyke nets (dispersers) were compared to those in the ditches (stayers) in summer 2010. Generalized linear models (GLMs) were performed with TP or FL as the dependent variable, dispersal status (stayer/disperser) as the independent variable, and age (0+ and 1+), and capture date as covariates. Outputs were the mean FL and TP of stayers and dispersers (adjusted for the effects of covariates) and the significance of the differences.

To analyse differences in FL and TP between stayers and dispersers prior to dispersal (at first capture in the ditches) and at their recapture (either in the ditches or river), GLMs were used. FL and TP were the dependent variables, dispersal status (disperser/stayer) was the independent variable, and age (0+ and 1+), days between capture and recapture (‘days at large’), recapture date (as the interaction of month and year) were covariates. Outputs were the mean FL and TP of recaptured stayers and dispersers (adjusted for the effects of covariates), and the significance of their differences. Differences in SGR between recaptured stayers and dispersers were also analysed in a GLM, where SGR was the dependent variable, dispersal status was the independent variable, and with initial length at capture, age, number of days between capture and recapture, and date of recapture (as the interaction of month and year) being covariates. All analyses were conducted in STATISTICA (v. 12) and SPSS (v. 22). Errors around means are 95 % confidence limits unless stated otherwise. The study was conducted under the UK Home Office project licence number PPL 30/2626 and following ethical review.

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 <

0.01; Table 3). However, the trophic positions of recaptured stayers and dispersers were not significantly different (P = 0.46; Table 2).

Discussion

Natal dispersal is a ubiquitous phenomenon, with this study revealing that dispersal from natal ditches was not related to the body size or trophic position of the individual 0+ and 1+ pike, although 0+ dispersers were of significantly lower trophic position than 0+ stayers. This finding was contrary to the first hypothesis that predicted dispersers would be those individuals of higher trophic position and larger body sizes through their ontogenetic shift to piscivory occurring on the natal habitats. The results were, however, consistent with the second hypothesis, as following their dispersal into the main river; dispersers experienced significantly higher growth rates than stayers and had achieved larger body sizes on their recapture, although the number of recaptured individuals in the river was relatively low. Despite pike moving out from the ditches at age 0+ not having higher trophic positions than those staying in ditches, their piscivory would enable their foraging on the more abundant and diverse prey populations of the main river channel compared to the small ditches, thus facilitating their ability to grow faster and attain larger body sizes.

Our results suggest that dispersers exist in a trade-off between their increased predation risk in the river with the higher potential for achieving faster growth rates. The finding that an ontogenetic dietary shift towards piscivory by individual pike was not the driver of juvenile dispersal from the natal habitats here was in contrast to Cucherousset *et al.* (2013), who demonstrated that the natal departure timing of juvenile pike from a temporally flooded grassland nursery was dependent on this. In the latter case, the risk of the complete drying of temporary waters meant that the natal departure timing of juvenile fish was directly associated with direct costs and benefits (i.e. survival vs. mortality). It was also occurring relatively early in their life when trophic differences between individuals might have been more apparent (Kramer, Rangeley & Chapman, 1997). In the ditches of this study, the water was permanent and, therefore, the drivers of dispersal would not have included the avoidance of shallow waters in, and drying of, the natal habitat. Improved knowledge linking ecosystem stability and natal dispersal is therefore needed.

Dispersal can have indirect fitness advantages by reducing competition in populations via increasing the overall access to resources (Waser *et al.,* 2013). This fitness advantage of dispersing does, however, depend on the environment reached after dispersal, with those of high productivity providing greater advantages (Bonte *et al.,* 2014). In juvenile Atlantic salmon *Salmo salar* in natural streams, it was the smaller bodied individuals that moved away from areas in the vicinity of their redd and, as the summer progressed, they experienced higher growth rates (Einum *et al.,* 2012). This dispersal by smaller individuals may be driven by the competitive intensity near redds (Einum *et al.,* 2012). Natal habitats, such as the river side channels of the present study, naturally have a high density of juvenile pike that compete for food resources of low diversity (primarily macroinvertebrates (e.g. *Asellus aquaticus*) and some small bodied fishes (mainly minnow *Phoxinus phoxinus*). Dispersing to a less populated area would, therefore, be advantageous in terms of increased access to food and refuge habitat, as the main River Frome provides a greater diversity of prey fishes (including dace *Leuciscus leuciscus* and grayling *Thymallus thymallus* that are present in the main channel and not the ditches; Pinder, Harrison & Britton, 2019), as well as *P. phoxinus* in much higher abundances (unpublished data, the authors).

Relatively high individual variation in the competitive ability for resources may explain the non-significant relationships between trophic position and dispersal strategy detected in our study. The ability to compete for scarce resources is a primary aspect of population dynamics that influences individual fitness (Vøllestad & Quinn, 2003). Edeline *et al.* (2010) revealed that an increase in pike density depressed their energetic status and lowered growth rates. The 0+ individuals of lower trophic positions that dispersed from the ditches in our study may, therefore, be a consequence of social stress or due to direct interference intimidation or competitive exclusion from other individuals, although this could not be explicitly tested here and was not apparent in the 1+ fish. Indeed, Wey, Spiegel, Montiglio & Mabry (2015) suggested that the influence on dispersal of interactions of behavioural phenotypes and the social environment experienced by individuals remains poorly understood, and requires further work.

An increasing number of studies are demonstrating that differences in personality traits between individuals underlie other observed ecological patterns that vary among individuals (e.g. Cote, Fogarty, Weinersmith, Brodin & Sih, 2010, Laskowski and Bell 2014). In particular, boldness in fish has been directly linked to differences in dispersal (Fraser, Gilliam, Daley, Le & Skalski, 2001, Cote *et al.*, 2010) and settlement in new habitats (Armstrong, Braithwaite & Huntingford, 1997). Indeed, juveniles from the pike population studied here have previously been found to exhibit bold and shy personality types during experimental settings, with bolder individuals expressing a higher level of foraging activity (Nyqvist, Gozlan, Cucherousset &

Britton, 2012; Nyqvist, Gozlan, Cucherousset & Britton, 2013). As trophic position is an indication of the trophic niche and foraging ecology at the individual and population level (Bolnick *et al.,* 2003), the 0+ stayers which had higher trophic position in the current study might have been the bolder individuals, whereas the 0+ dispersers of lower trophic position would have been the shy behavioural phenotype, which would be a counter-intuitive outcome.

In conclusion, it was demonstrated that dispersing juveniles had similar body sizes to stayers, with 0+ dispersers having a lower trophic position than 0+ stayers. Thus, their dispersal might have been driven by social stress, competitive displacement or intimidation in the highly populated, permanently-flooded, ditches. Individuals that successfully dispersed into the river and survived benefited by increased growth rates and so the attainment of larger body sizes when compared with stayers. Therefore, these outputs highlight the importance of habitat exclusion of less competitive individuals in driving variation in dispersal and indicate their potential for causing long-term consequences on individual fitness and population dynamics.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Author contributions statement

All authors conceived and designed the study. MN, JRB, JC and RG performed field and laboratory work. MN and JRB analysed the data, and all authors contributed materials and analysis tools. MN led the writing of the paper and all authors contributed to editing, and approved the final version for submission.

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 $\chi^2 = 1.35$, $P = 0.25$	
	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 $\chi^2 = 0.03$, $P = 0.86$	
	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

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

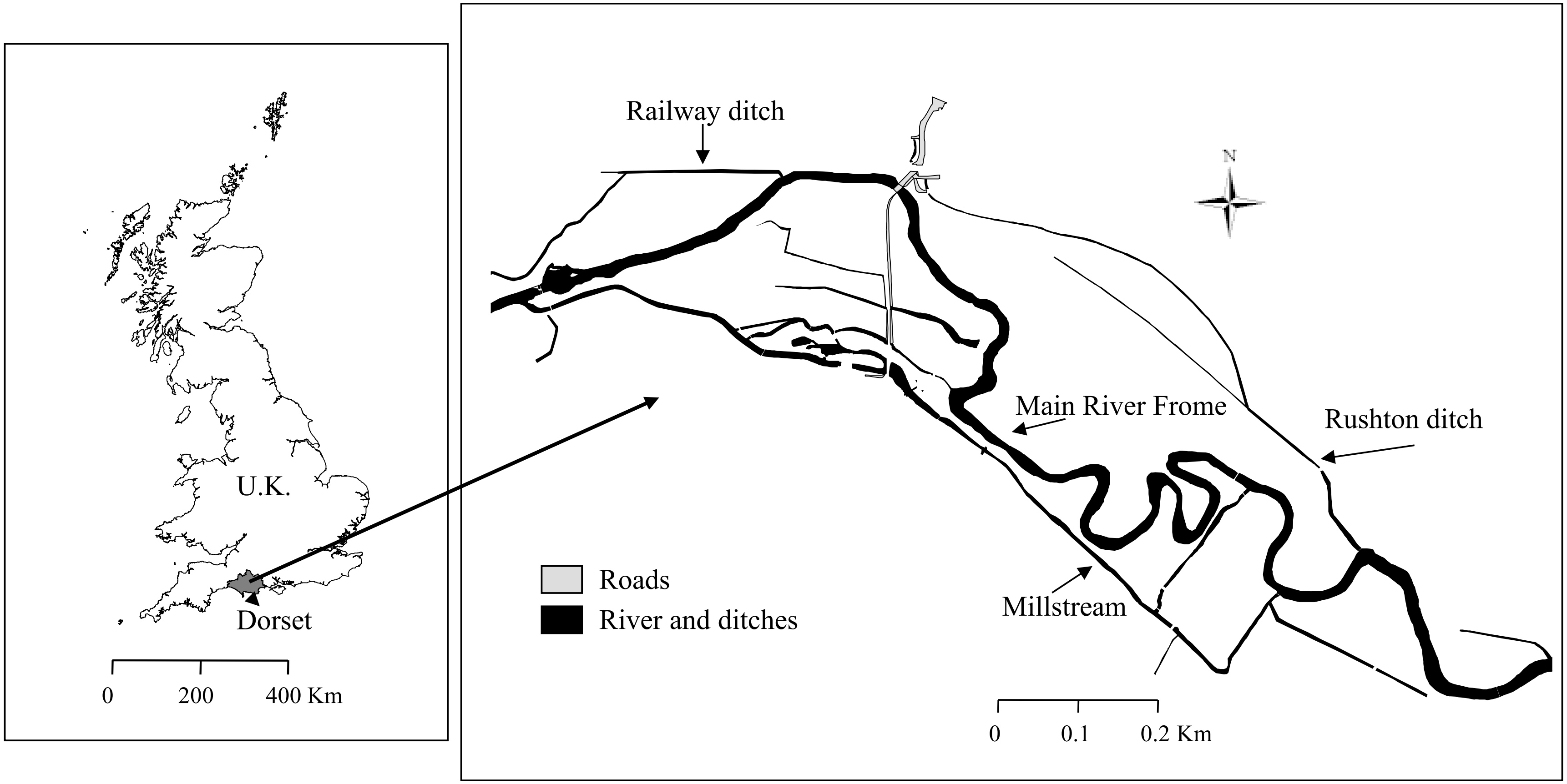
Table 3. Results of a GLM on the effects of dispersal status (i.e. stayer/ disperser; ‘dispersal’), fork length (FL), date of capture, age, and length at initial capture dispersal status (recaptured in ditch or river) on the specific growth rate (SGR) of all recaptured *Esox lucius* (N = 50; 0+: n = 33; 28 stayers, 5 dispersers; 1+: n = 17; 16 stayers and 1 disperser).

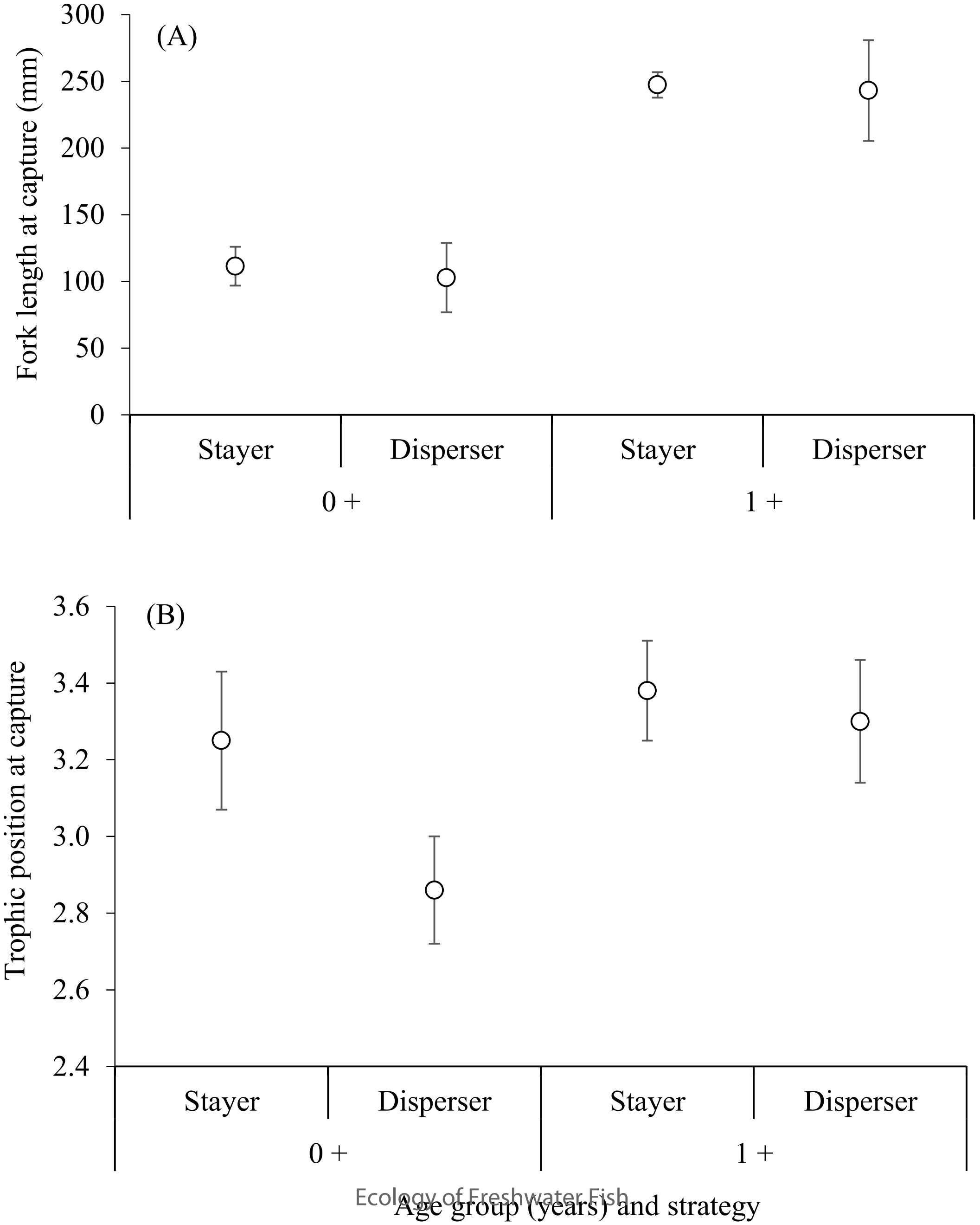
Specific growth rate: Wald $\chi^2 = 3.85$, $P = 0.05$	
	P
Dispersal	0.05
Age	0.30
Length at capture	< 0.01
Days at large	0.43
Month x year	< 0.01
Mean specific growth rate:	
Stayer	0.11 ± 0.02
Disperser	0.16 ± 0.05

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.


U.K.
Dorset
0
200
400 Km
Railway ditch
N
Main River Frome
Rushton ditch
Millstream
Roads
River and ditches
0
0.1
0.2 Km


(A)
Fork length at capture (mm)
300
250
200
150
100
50
0
Stayer
Disperser
Stayer
Disperser
0 +
1 +
(B)
Trophic position at capture
3.6
3.4
3.2
3.0
2.8
2.6
2.4
Stayer
Disperser
Stayer
Disperser
0 +
1 +
Age group (years) and strategy