

# Dispersal strategies of juvenile pike (*Esox lucius* L.): Influences and consequences for body size, somatic growth and trophic position

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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, the mechanisms and individual consequences of dispersal remain poorly understood. Here, riverine Northern pike (*Esox lucius*) juveniles (age 0+ (young-of-the-year) and 1+ years) 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 than those remaining on nursery grounds (“stayers”). For trophic position, 0+ dispersers were of significantly lower trophic position than stayers, but with this not apparent in the 1+ fish. Following dispersal into the river, the dispersers grew significantly faster than stayers and, on recapture, were significantly larger, but with no significant differences in their final trophic positions. Early dispersal into the river was, therefore, not associated with early dietary shifts to piscivory and the attainment of larger body sizes of individuals whilst in their natal habitats, contrary to prediction. These results suggest that despite an increasing risk of mortality for individuals dispersing early from natal areas, there are long-term benefits via elevated growth rates and, potentially, higher fitness. Such early dispersal behaviour could be driven by early competitive displacement.

## KEYWORDS

natal dispersal, Northern pike, piscivory, stable isotope analysis

## 1 | 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 (Alcalay, Tsurim, & Ovadia, 2018; Halpin, 2000). Dispersal involves the movement of individuals away from others, such as siblings, who are left behind in the original area; unlike migration, dispersers do not necessarily return to that area (Schwarz & Bairlein, 2004; Semlitsch, 2008).

Trade-offs between dispersal and mortality mean that although dispersal can deliver substantial individual benefits (e.g. access to higher food resources leading to faster growth rates), the risks can also be high (Bonte et al., 2012). The trade-off between the costs and benefits of dispersal often results in considerable variability in the dispersal behaviour of individuals (Cucherousset, Paillisson, & Roussel, 2013; Rosten, Gozlan, & Lucas, 2016). Providing that their new environment is sufficiently productive, dispersed individuals often gain fitness advantages via their subsequent exploitation of new resources in a less competitive environment (Bonte, De Roissart, Wybouw, & Van Leeuwen, 2014; Lima & Dill, 1990; Skov et al., 2011). However, this can be at the cost of an elevated mortality risk due to increased exposure to predators (Waser, Nichols, & Hadfield, 2013). Nevertheless, the growth rates of dispersers are likely to increase if the new environment enables the utilisation of underexploited food resources in a low competitive environment, especially if those resources are of high quality (Smith & Skulason, 1996; Waser et al., 2013).

The costs of dispersal will, however, vary between individuals with, for example, those of larger body size potentially being less vulnerable to predation during the dispersal period (Bonte et al., 2012). Explanations of why only some individuals disperse to new habitats thus require comparisons of the ecological attributes of individuals that disperse ("dispersers") versus those that stay ("stayers") (Chapman et al., 2011; Cucherousset et al., 2013). For example, metrics such as trophic position potentially provide a useful indicator of the competitive ability of the dispersers and stayers to access high-quality resources in their different environments (Bolnick et al., 2003). Whilst the costs of dispersing are correspondingly relatively well understood, 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.). During their juvenile life stage, *E. lucius* undergo an ontogenetic dietary switch from insectivory to piscivory, but the size and age at which this switch occurs varies within and between populations (Mittelbach & Persson, 1998; Wolska-Neja & Neja, 2006), with this then influencing their movements and behaviours (Cucherousset et al., 2013). The study system was the lower River Frome in Southern England (Figure 1). The *E. lucius* population of this river 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 (Knight, Gozlan, & Lucas, 2008; Mann & Beaumont, 1990). Individuals remaining in natal habitats grow significantly slower than those that disperse (Mann & Beaumont, 1990), which is suggested to be due to dietary differences resulting from individual variations in the ontogenetic diet shift, coupled with lower prey availability (Mann, 1982). Thus, two hypotheses on individual variability in dispersal were tested here: (1) dispersers are of higher trophic position

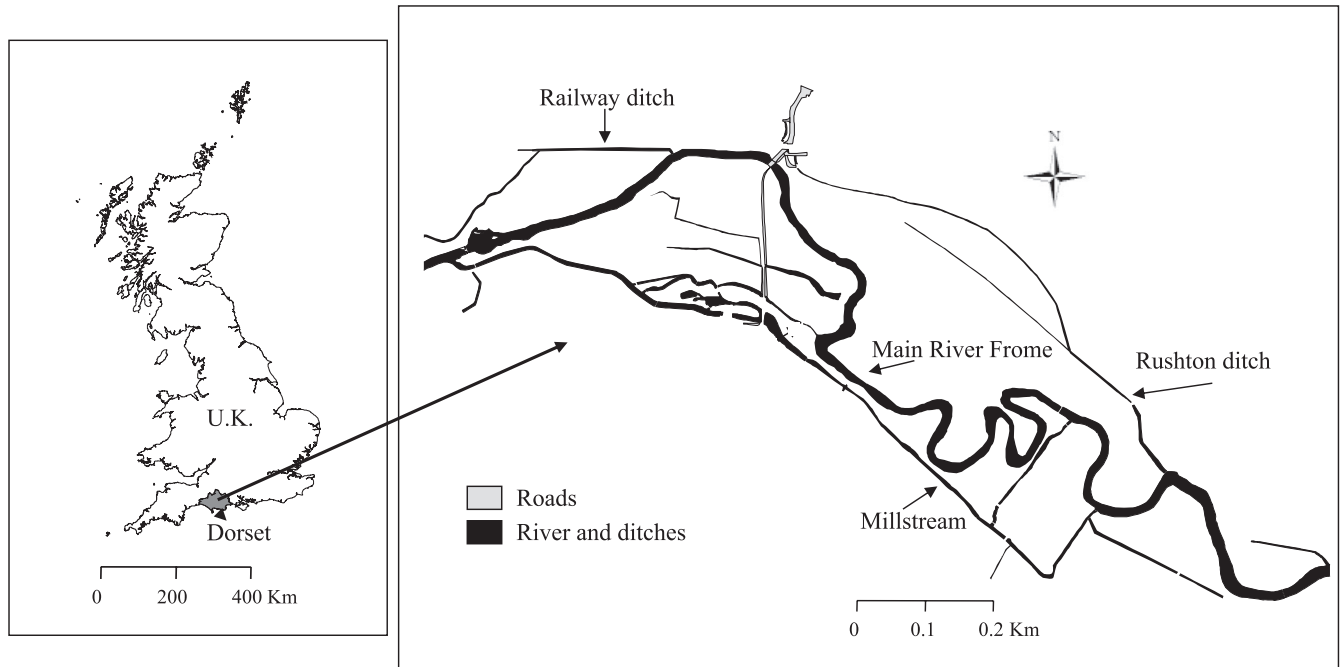
and larger body size than stayers at the time of their dispersal from natal habitats; and (2) dispersal-driven habitat partitioning results in dispersers subsequently experiencing faster growth rates in the main river than stayers in the natal habitat.

## 2 | METHODS

### 2.1 | Sampling and data collection

Juvenile *E. lucius* were sampled in two side channels (hereafter referred to as "ditches") of the River Frome in Southern England (50.6798°N, -2.1817°W) (Figure 1; Masters et al., 2002; Nyqvist, Cucherousset, Gozlan, & Britton, 2017). The ditches were generally  $\leq 5$  m in width and  $\leq 1$  m in depth, and adult *E. lucius* were observed spawning there in spring. To enable fish to be categorised as either dispersers or stayers, sampling was completed between 18th June and 12th October 2010. To identify stayers, electric fishing was completed monthly in each ditch, using back-mounted electric fishing equipment (Smith-Root LR-24, USA). 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-hr sampling) throughout the study period, with nets checked daily and all fish being processed. Fish were then released in the main riverside of the fyke nets, as the fish were moving in this direction when captured. Irrespective of sampling method, captured individuals were checked for the presence of a PIT tag (i.e. whether they were a new capture or a recapture); if they were a new capture, they 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 removed for age determination. Individuals of FL over 85 mm were then tagged with a 23.1 mm passive integrated transponder (PIT) tag 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 (range 0.3% to 3.5%).

Following this period of identifying stayers and dispersers, the consequences of these strategies for individuals were assessed by recapturing tagged individuals by electric fishing on a regular basis in the following two years. 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, handheld 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:



**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 (taken from Nyqvist et al., 2017)

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

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 their nitrogen stable isotope ratio (as  $\delta^{15}N$ ), as their values in fin tissues correlate strongly with those of dorsal muscle tissue (Busst, Bašić, & Britton, 2015; Winter, Nyqvist, & Britton, 2019). The collection of fin tissue does not adversely affect fish survival or growth (Gjerde & Refstie, 1988) and enables temporal monitoring of changes in the trophic position of individual fish (Cucherousset et al., 2013). Specimens of water louse *Asellus aquaticus* dominated the macro-invertebrate samples that were collected from the ditches using a sweep net at the same time as the pike were captured. Consequently, they were used to provide the isotopic values of a putative macro-invertebrate prey species of the juvenile *E. lucius*. The *A. aquaticus* samples were pooled ( $n = 2$  to 4 per SIA sample). All samples were then oven dried at 60°C to constant weight, before processing and analysis at the Cornell Isotope Laboratory. Trophic position (TP) for individual pike was then calculated using the formula:

$$TP = \left[ \left( \delta^{15}N_{Pike} - \delta^{15}N_{MeanPrey} \right) / 3.4 \right] + 2$$

where  $\delta^{15}N_{Pike}$  is the  $\delta^{15}N$  data for the individual *E. lucius*,  $\delta^{15}N_{MeanPrey}$  is the mean  $\delta^{15}N$  of the putative prey resource of *E. lucius* (*A. aquaticus*), 3.4 represents a widely used single trophic level fractionation in  $\delta^{15}N$ , and 2 corresponds to the general trophic level of *A. aquaticus* (Vander Zanden, Shuter, Lester, & Rasmussen, 2000).

## 2.2 | 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. Generalised 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.

### 3 | 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, that is 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; Figure 2). 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). However, when analysed by age-group, the 0+ dispersers had a significantly lower TP than 0+ stayers (ANOVA:  $F_{1,28} = 41.63$ ,  $p < .01$ ), but with this not apparent in the 1+ fish (ANOVA:  $F_{1,24} = 1.95$ ,  $p = .18$ ) (Figure 2).

Of the 56 tagged *E. lucius*, 50 were subsequently recaptured, with the length of time being capture and recapture being between 51 and 579 days (mean  $220 \pm 32$  days). There were significantly more pike recaptured in their ditches ( $n = 44$ ) than in the river ( $n = 6$ ) ( $\chi^2 = 28.88$ ;  $p < .01$ ). On recapture, the body sizes of dispersers were significantly larger than stayers ( $p < .01$ ; Table 2), where the effects of age and the number of days at large were significant covariates in the model ( $p < .05$ ; Table 2). Similarly, the SGR of dispersers was significantly higher than stayers ( $p = .05$ , Table 3),

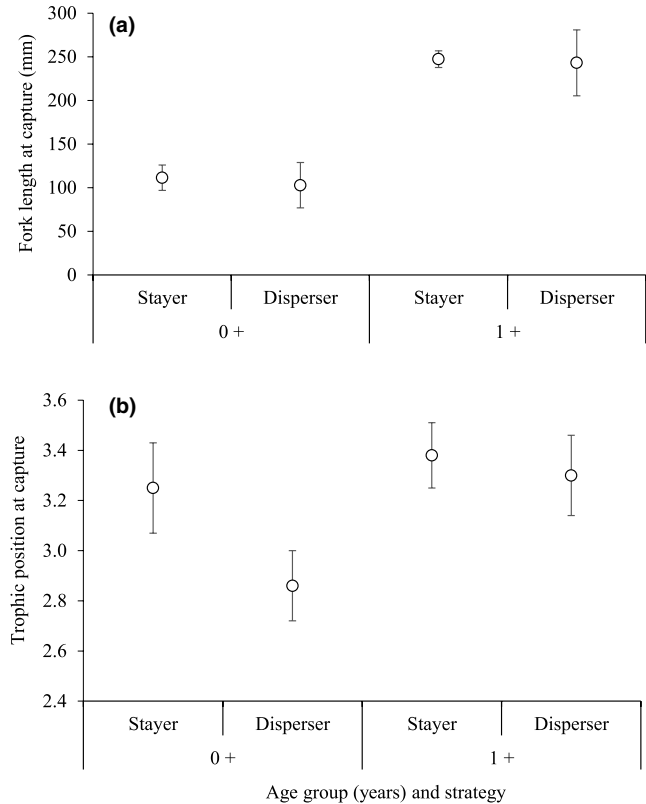
**TABLE 1** Results of GLMs testing the effects of dispersal status (i.e. stayer/disperser; “Dispersal”), capture date and age on the fork length (FL) and trophic position (TP) of all *Esox lucius* captured in the ditches

(a) FL at capture: Wald $\chi^2 = 1.35$ , $p = .25$	
	$p$
Capture date	.82
Age	<.01
Dispersal	.25
Mean length at capture (mm):	
Stayer	$197 \pm 10$
Disperser	$215 \pm 28$
(b) TP at capture: Wald $\chi^2 = 0.03$ , $p = .86$	
	$p$
Capture date	.85
Age	.46
Dispersal	.86
Mean length at capture (mm):	
Stayer	$3.13 \pm 0.16$
Disperser	$3.18 \pm 0.42$

with the date and length of capture being significant covariates in the model ( $p < .01$ ; Table 3). However, the trophic positions of recaptured stayers and dispersers were not significantly different ( $p = .46$ ; Table 2).

### 4 | DISCUSSION

This study tested two hypotheses relating to juvenile dispersal from natal areas: dispersers would be larger and of higher trophic position than stayers and, provided the dispersers avoided mortality, would then benefit from faster growth rates. The hypothesis on dispersers being larger and of higher trophic position was developed as these fish were considered to have greater energy reserves to move and the body sizes that lower their predation risk (Cucherousset et al., 2013). However, the results revealed that dispersers were not significantly different in body size than stayers and, when controlled for age, were not significantly different in trophic position. When the two age groups were analysed separately, 0+ dispersers were of significantly lower trophic position than stayers, a counter-intuitive outcome contrary to the hypothesis, but with this not apparent in the 1+ fish. Following dispersal into the main river, the dispersers grew significantly faster than stayers, as per the hypothesis, but did not gain additional benefit by having a higher trophic position than stayers.



**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

These results suggest that dispersers existed in a trade-off between the costs of movement, including potentially higher risks of predation, versus their potential for achieving faster growth rates in the main river. Indeed, the recaptured dispersers in the river did have significantly faster growth rates than the stayers, although the low sample size of the dispersers ( $n = 6$ ) means some caution is needed in this interpretation. Nevertheless, this faster growth potentially leads to fitness benefits, such as males achieving larger body sizes for age that could confer reproductive advantages through being more attractive to females during reproduction. In the 0+ pike, it was the fish of significantly lower trophic position that were the dispersers from the ditches. This result was contrary to both the hypothesis and Cucherousset et al. (2013), who demonstrated that juvenile pike of higher trophic position departed significantly earlier from drying natal grounds than individuals of lower trophic position, suggesting their early dispersal was assisted by these fish having higher energetic returns to facilitate their movement. That this was not the case in our study suggests that the dispersal of juvenile pike from the natal ditches in our study was being influenced by other factors, potentially including the permanence of their habitats. The ability to compete for scarce resources is a primary aspect of population dynamics that influences individual fitness (Vøllestad & Quinn, 2003). An increase in pike density has been revealed to depress energetic status and lower growth rates among pike (Edeline et al., 2010). The dispersal of the 0+ individuals of lower trophic positions might,

therefore, have been a consequence of direct interference, intimidation and/ or competitive exclusion from other individuals. This could not, however, be explicitly tested here and was not apparent in the 1+ fish. Indeed, Wey, Spiegel, Montiglio, and 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.

Dispersal can have indirect fitness advantages by reducing competition in populations via increasing the overall access to resources (Waser et al., 2013). The fitness advantage of dispersing depends on the environment reached after dispersal, with those of high productivity and low predation risk 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 might have been driven by higher competitive intensity near redds (Einum et al., 2012). This study thus provides some additional support for the dispersal of our 0+ pike also being driven by competitive exclusion. This is further emphasised by natal habitats, such as the riverside channels of the present study, naturally having a high density of juvenile pike that compete for food resources of low diversity, primarily macro-invertebrates (e.g. *A. aquaticus*) and some small-bodied fishes (mainly *P. phoxinus*). Dispersing to a less populated area would, therefore, be advantageous in terms of potentially increasing their access to food and refuge habitat, especially as the main River Frome provides a greater diversity of prey fishes (including dace *Leuciscus leuciscus* and grayling *Thymallus thymallus*) in the main channel that are rarely present in the ditches (Pinder, Harrison, & Britton, 2019), as well as *P. phoxinus* being in much higher abundances (M. Nyqvist, unpublished data).

An increasing number of studies are demonstrating that differences in personality traits between individuals underlie other observed ecological patterns that vary among individuals (Cote,

**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 large 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 $\chi^2 = 7.32, p < .01$	
	<i>p</i>
Dispersal	<.01
Age	.04
Days at large	<.01
Month x year	.24
Mean length at capture (mm):	
Stayer	244 ± 14
Disperser	301 ± 38
(b) TP at recapture: Wald $\chi^2 = 0.54, p = .46$	
	<i>p</i>
Dispersal	.46
Age	.97
Days at large	<.01
Month x year	.75
Trophic position at capture	.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 $\chi^2 = 3.85, p = .05$	
	<i>p</i>
Dispersal	.05
Age	.30
Length at capture	<.01
Days at large	.43
Month x year	<.01
Mean specific growth rate:	
Stayer	0.11 ± 0.02
Disperser	0.16 ± 0.05



Fogarty, Weinersmith, Brodin, & Sih, 2010; Laskowski & Bell, 2014). In particular, boldness in fish has been directly linked to differences in dispersal (Cote et al., 2010; Fraser, Gilliam, Daley, Le, & Skalski, 2001) 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, 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. 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.

#### AUTHOR CONTRIBUTIONS

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.

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#### DATA AVAILABILITY STATEMENT

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

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