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# Natal departure timing from spatially varying environments is dependent of individual ontogenetic status

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1 **Natal departure timing from spatially-varying environments is**  
2 **dependent of individual ontogenetic status**

3

4

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15

16

17 **Abstract** Natal departure timing represents one of the first crucial decisions for juveniles born  
18 in spatially-varying environments that ultimately disappear but our knowledge on its  
19 determinants is limited. The present study aimed at understanding the determinants of  
20 juvenile natal departure by releasing individually tagged juvenile pike (*Esox lucius* L.) with  
21 variable body size and trophic position in a temporary flooded grassland. Specifically, we  
22 whether natal departure depends on individual competitive status (*‘competition hypothesis’*),  
23 physiological tolerance to environmental conditions (*‘physiological hypothesis’*) or individual  
24 trophic position and the spatial heterogeneity of trophic resources (*‘trophic hypothesis’*). The  
25 results indicated that departure timing was negatively correlated with body size at release,  
26 showing that the dominance status among competing individuals was not the main trigger of  
27 juvenile departure. A positive correlation between departure timing and individual body size  
28 at departure was observed, suggesting that inter-individual variability in physiological  
29 tolerance did not explain departure patterns. While individual growth performances were  
30 similar irrespective of the timing of natal departure, stable isotope analyses revealed that  
31 juveniles with higher trophic position departed significantly earlier than individuals with  
32 lower trophic position. Therefore, the trade-off driving the use of spatially-varying  
33 environments was most likely dependent upon the benefits associated with energetic returns  
34 than the costs associated with inter-individual competition or physiological stress. This result  
35 highlighted how ontogeny, and particularly ontogenetic niche shift, can play a central role in  
36 juvenile’s decision to depart from natal habitats in a predatory species.

37 **Keywords** Temporary waters, dispersion, inter-individual variability, stable isotope analyses,  
38 ontogenetic niche shift.

39

## 40 **Introduction**

41 The departure of juveniles from their natal environment is a crucial ecological and  
42 evolutionary phenomenon for many organisms that directly influences individual survival and  
43 population functioning. It represents one of the first bottlenecks in many populations as high  
44 mortality rates usually occur at this life stage (Gaines and Bertness 1993; Clobert et al. 2001)  
45 and hazardous decisions may be fatal for juveniles born in spatially-varying environments  
46 (Chesson and Huntly 1997; Chesson 2000). In many aquatic ecosystems, drought and flood  
47 episodes dramatically influence both the availability and the suitability of habitats (Matthews  
48 1998; Humphries and Baldwin 2003). They also generate temporarily flooded habitats located  
49 at the interface between terrestrial and aquatic ecosystems that are exploited by a wide range  
50 of organisms (Williams 2006). These temporary waters serve, for instance, as critical seasonal  
51 habitats for reproduction and juvenile development of many animal species (Magoulick 2000;  
52 Schwartz and Jenkins 2000; Jopp et al. 2010).

53 For those species that cannot cope with the complete drying of temporary waters  
54 (Williams 2006), natal departure timing of juveniles from these environments is a crucial  
55 decision (Werner and Gilliam 1984; Kramer et al. 1997) since it is associated with important  
56 costs (e.g. mortality) and benefits (e.g. growth). Indeed, habitat use interpreted as a trade-off  
57 (Morris 2003) may be a useful approach to understanding the departure of juveniles from  
58 temporary environments. Such a trade-off occurs when an ecological, behavioural or  
59 physiological trait of an organism that confers advantage for performing one biological  
60 function simultaneously confers a disadvantage for another function (e.g., Chase and Leibold  
61 2003; Brönmark et al. 2008). The departure of juveniles from temporary environments  
62 provides a unique opportunity to help our understanding of habitat selection as a mechanism  
63 governed by a trade-off (e.g., Morris 2003; Bronmark et al. 2008). The use of harsh and  
64 spatially-varying environments by juvenile fish (i.e., temporary waters) represents one of such

65 trade-off (Fig. 1) because these habitats provide benefits that could balance associated costs  
66 compared to more stable environments (e.g., Schlosser 1987; Matthews and Marsh-Matthews  
67 2003; Brönmark et al. 2008). For instance, physiological stress associated with changes in  
68 physical/chemical water conditions such as hypoxia and/or hyperthermia can be balanced by  
69 foraging benefits and control immigration to and emigration from temporary waters (Fig. 1).  
70 Therefore, temporal and spatial fluctuations of the environment and interactions between  
71 individuals can dramatically change the trade-off outcomes, but little is known about the  
72 triggers of natal departure for juveniles facing such conflicting demands.

73         The present study aims at identifying the determinants of natal departure timing from  
74 temporary habitats using juvenile pike (*Esox lucius* L.) as a model. Pike is a freshwater top-  
75 predatory species and adults commonly use temporary waters such as flooded grassland to  
76 spawn (Craig 2008). Pike has a high fecundity and juvenile mortality represents a strong  
77 bottleneck in many populations (Casselman 1996; Bry et al. 1995; Craig 2008). After  
78 hatching, larvae and juveniles develop in temporary waters in spring, and individuals have to  
79 disperse to permanent waters as the water level decreases and the habitat availability and  
80 suitability decline in early summer (Craig 1996; Cucherousset et al. 2007a). In parallel with  
81 natal departure, juvenile pike also display a strong ontogenetic dietary shift from  
82 zooplanktivory toward piscivory (Bry et al. 1995; Craig 2008). Therefore, three mutually  
83 exclusive hypotheses were tested to identify the mechanisms triggering natal departure of  
84 juvenile pike. (1) The ‘*competition hypothesis*’ assumes that natal departure is driven by  
85 individual competitive status (e.g., Nilsson 2006). While facing a progressive decrease in  
86 habitat availability caused by a progressing drying out, it is expected that the smallest  
87 individuals leave before larger conspecifics, since they are poorer competitors (Fig. 2a). (2)  
88 The ‘*physiological hypothesis*’ assumes that natal departure is driven by physiological  
89 tolerance to environmental conditions (e.g., Chapman et al. 2002). Because of negative

90 allometric relationship for mass-specific gill surface area, small-bodied fish have more  
91 efficient oxygen exchange with water compared with large ones and, consequently, they are  
92 less sensitive to hypoxia (Hugues 1984; Robb and Abrahams 2003). Therefore, it is expected  
93 that body-size at departure decreases when environmental conditions deteriorate (Fig. 2b). (3)  
94 The '*trophic hypothesis*' assumes that natal departure is driven by individual trophic position  
95 and the spatial heterogeneity of trophic resources. Indeed, spawning areas generally do not  
96 provide a sufficient abundance of prey fish for individuals shifting their diet toward piscivory.  
97 Therefore, it is expected that those individuals that are most advanced in ontogenetic  
98 development depart first (Fig. 2c). To test these hypotheses and predictions, we stocked  
99 juveniles pike from the same cohort into a temporary habitat that dried out and subsequently  
100 monitored departure timing at the individual level. We also measured the consequences of  
101 departure timing on individual growth rates.

102

### 103 **Materials and methods**

#### 104 Study area

105 The study was carried out in May and June 2005 in a temporarily flooded grassland of the  
106 Brière marsh (France, 47°22'N, 02°11'W, Fig. 3: details about the study area available in  
107 Cucherousset et al. 2006). The study site covered 0.47 ha (at the start of the study) and was  
108 connected through a unique point to an adjacent 2.13 ha pond. It was selected because it is a  
109 typical spawning and nursery habitat and wild juvenile pike were previously captured there  
110 (Cucherousset et al. 2007a). Food resources strongly differed between the two habitats: the  
111 mean abundance of zooplankton was significantly higher in the flooded grassland than in the  
112 adjacent pond ( $185.5 \text{ mg.L}^{-1} \pm 94.6 \text{ SD}$  and  $104.0 \text{ mg.L}^{-1} \pm 77.9 \text{ SD}$ , respectively; Wilcoxon  
113 signed rank test,  $Z = -1.988$ ,  $P = 0.047$ ,  $n = 10$ ). Conversely, forage prey fish abundance was

114 twofold lower in the grassland compared to the pond ( $0.09 \text{ ind.m}^{-2}$  and  $0.20 \text{ ind.m}^{-2}$ ,  
115 respectively, Cucherousset 2006). Although mean daily temperature was similar between the  
116 two habitats (i.e.  $20.0^{\circ}\text{C} \pm 2.48 \text{ SD}$  and  $20.6^{\circ}\text{C} \pm 2.41 \text{ SD}$  in the flooded grassland and in the  
117 adjacent pond, respectively), daily variability was higher in the flooded grassland than in the  
118 adjacent pond (mean daily range =  $11.43^{\circ}\text{C} \pm 4.16 \text{ SD}$  and  $5.46^{\circ}\text{C} \pm 1.72 \text{ SD}$ , respectively;  
119 Wilcoxon test,  $Z = 5.303$ ,  $P < 0.001$ ,  $n = 37$ ). Mean daily maximal water temperature was  
120 significantly higher in the flooded grassland than in the adjacent pond ( $25.50^{\circ}\text{C} \pm 4.71 \text{ SD}$   
121 and  $22.9^{\circ}\text{C} \pm 3.55 \text{ SD}$ , respectively; Wilcoxon test,  $Z = 5.061$ ,  $P < 0.001$ ,  $n = 37$ ).

122

### 123 Monitoring

124 A total of 192 individually PIT-tagged pike were released into the study site on 20 May 2005  
125 (Cucherousset et al. 2007b). These individuals were young-of-year juveniles that came from  
126 manual fertilization of gametes of adults collected in the wild and were hatchery-reared and  
127 fed with zooplankton for 4-5 weeks. Individuals were selected to cover the range of body size  
128 and trophic level present in the entire cohort and, consequently, to include individuals with  
129 different ontogenetic and trophic position. Indeed, cannibalism often occurs when juvenile  
130 pike are reared in hatchery conditions (e.g., Bry et al. 1992), leading to the existence of  
131 zooplanktivorous and piscivorous individuals within the same cohort. Before releasing, each  
132 individual had been anaesthetized with eugenol ( $0.04 \text{ mL.L}^{-1}$ ), measured for fork length to the  
133 nearest mm (i.e. body-size at releasing,  $\text{BS}_R$ , average =  $51.1 \text{ mm} \pm 5.2 \text{ SD}$ ), fin-clipped for  
134 stable isotope analyses (SIA) to assess trophic level at release and tagged (Cucherousset et al.  
135 2007b; 2009). Pike departure from the grassland to the adjacent pond was monitored  
136 continuously with a fyke net (5 mm mesh) equipped with two wings and arranged in a V-  
137 shape directing the fish into the chamber. Another net was set in the opposite direction to  
138 monitor potential individuals returning to the grassland. However, no tagged individual was

139 captured in this fyke net. The nets were checked at least once a day throughout the study  
140 period. Recaptured individuals were anaesthetized, checked for tags, measured for fork length  
141 (i.e. body-size at departure,  $BS_D$ ) and fin-clipped again to evaluate their trophic position using  
142 SIA. This was performed only for individuals recaptured more than five days after release  
143 since the pelvic fin had redeveloped sufficiently to be clipped again and to reflect the food  
144 assimilated in the grassland. After recovery, fish were released in the adjacent pond. Trapping  
145 was conducted until the total drying out of the grassland (i.e. 16 June 2005, see details in  
146 Cucherousset et al. 2007b).

147

#### 148 Stable isotope analyses

149 Stable isotopes of carbon and nitrogen were used to estimate the origin of the carbon source  
150 ( $\delta^{13}C$ ) and the trophic level ( $\delta^{15}N$ ) of consumers and their prey (e.g., Fry 2006). Fin clipping  
151 of juvenile pike was selected because stable isotope values of fin and muscle tissues closely  
152 correlate, allowing non-lethal sampling and, consequently, repeated measurement on the same  
153 individuals (Cunjak et al. 2005; Jardine et al. 2005; Syvaranta et al. 2010). Young-of-the-year  
154 fish display fast somatic growth and rapid isotopic turnover rate (e.g., Bosley et al. 2002;  
155 Weidel et al 2010). Recently grown tissue was fin-clipped on recaptured juvenile pike, so it  
156 was assumed that significant ontogenic shifts over the experiment could be detected by means  
157 of SIA. SIA were performed for surviving fish that departed after five days post release ( $n =$   
158 29 among 37 individuals that emigrated, see Cucherousset et al. 2007b) using the samples  
159 collected at release ( $\delta^{13}C_R$  and  $\delta^{15}N_R$ ) and at departure ( $\delta^{13}C_D$  and  $\delta^{15}N_D$ ). To determine  
160 individual trophic position prior to release, samples of zooplankton ( $n = 3$ ), that represented  
161 the unique food item given to the juveniles pike, were collected at the hatchery. The main  
162 potential prey were also sampled in the flooded grassland on 13 May, just before the fish  
163 release: zooplankton (mainly *Cladocera* and *Copepoda*,  $n = 3$  pooled samples), macro



164 invertebrates (amphipoda: *Gammarus* sp. (pooled sample composed of 8 individuals) and  
165 juvenile red swamp crayfish (*Procambarus clarkii* Girard, pooled sample composed of 3  
166 individuals)) and forage fish (*Gambusia holbrooki* Girard, pooled sample composed of 3  
167 individuals). All samples were oven dried (60°C for 48h) and ground to a homogeneous  
168 powder using a mixer mill (Retsch MM 200), weighed (approximately 0.2 mg) and  
169 encapsulated in tin foil. SIA were performed at the Stable Isotopes in Nature Laboratory  
170 (SINLAB), University of New Brunswick, Canada.

171

## 172 Data analyses

173 After inspections of normality, Spearman's correlations were used to test the relationships  
174 between departure timing (in days from the release day,  $n = 29$ ) and  $BS_R$ ,  $BS_D$  and trophic  
175 level at release ( $\delta^{15}N_R$ ) and at departure ( $\delta^{15}N_D$ ). Significant p-values were corrected for  
176 multiple comparisons ( $n = 4$ ) using a Bonferroni procedure ( $\alpha = 0.05/4 = 0.0125$ ).

177 To further investigate the role of individual trophic position on natal departure, we  
178 analysed the stable isotope data using circular statistics (Schmidt et al. 2007). Here, this  
179 approach was applied at the individual level to compare *i*) the stable isotope shifts between  
180 the release and departure of individuals with different trophic levels at release and *ii*)  
181 determine whether these shifts differed from the stable isotope differences of zooplankton  
182 between the hatchery and the grassland. Specifically, we calculated the position of each  
183 individual pike (using tag number) in the isotopic niche space ( $\delta^{15}N$ - $\delta^{13}C$ , expressed in polar  
184 coordinates), and also the differences between values at release ( $\delta^{13}C_R$  and  $\delta^{15}N_R$ ) and at  
185 departure ( $\delta^{13}C_D$  and  $\delta^{15}N_D$ ). The difference between the positions of any given individual is  
186 characterized by an angle and a length. The same procedure was applied to zooplankton  
187 samples from the hatchery and from the grassland. To allow comparisons between individuals

188 with different trophic levels, individuals needed to be regrouped according to their trophic  
189 position at releasing. Therefore, we used hierarchical cluster analysis to group individuals into  
190 two clusters (hereafter referred to as '*low trophic level*' and '*high trophic level*') according to  
191  $\delta^{13}\text{C}_R$  and  $\delta^{15}\text{N}_R$  values. We then calculated the mean vector of change between releasing and  
192 departure, defined by its angle and length, for each trophic level group. Vectors were  
193 represented in arrows diagrams where decreasing  $\delta^{13}\text{C}$  values correspond to left-directed  
194 vectors and decreasing  $\delta^{15}\text{N}$  values correspond to bottom-orientated vectors (e.g., Wantzen et  
195 al. 2002; Schmidt et al. 2007). Rayleigh's tests were used to assess whether the distribution of  
196 the angles of change departed from uniformity, i.e. testing for a significant stable isotope  
197 shifts for each group and for zooplankton between the hatchery and the grassland. Afterwards,  
198 we used the Watson-William's two-sample test to determine whether those shifts differ  
199 between trophic level groups and from the stable isotope differences of zooplankton between  
200 the hatchery and the grassland.

201 Finally, we investigated the consequences of departure timing on individual growth  
202 rates. Growth rate ( $\text{mm}\cdot\text{day}^{-1}$ ) was calculated for each surviving individuals using the  
203 following formula:  $\text{growth rate} = (\text{BS}_D - \text{BS}_R) / \text{departure timing}$  (Cucherouset et al. 2007b).  
204 Then, we performed a cubic-split analysis (Schulter 1988) to determine the shape of the  
205 fitness function (with individual growth rate as a proxy) using a Generalized Additive Model  
206 with growth rate as a response variable and departure timing as a predictor. Except circular  
207 statistics, which were calculated using Oriana 3.11 (Kovach Computing Services, Anglesey,  
208 Wales), all statistical tests were performed using R (R Development Core Team 2007) with  $\alpha$   
209 = 0.05.

210

## 211 **Results**

212 Natal departure was relatively continuous throughout the monitoring period (Fig. 4) with, on  
213 average, 1.7 ( $\pm$  1.61 SD) individuals departing from the grassland each day. A negative  
214 correlation was found between the departure timing and  $BS_R$  (Spearman's correlation,  $r_s = -$   
215 0.77,  $p < 0.0001$ ,  $n = 29$ ) with the largest individuals at release departing first from the  
216 temporary water (Fig. 4a). Body-size of individuals departing from the flooded grassland  
217 significantly increased as they departed later (Fig. 4b), i.e. departure timing was positively  
218 correlated to  $BS_D$  (Spearman's correlation,  $r_s = 0.72$ ,  $p < 0.0001$ ,  $n = 29$ ). The departure  
219 timing was significantly and negatively correlated with  $\delta^{15}N_R$  and  $\delta^{15}N_D$  (Spearman's  
220 correlations,  $r_s = - 0.69$ ,  $p < 0.0001$ , and  $r_s = - 0.57$ ,  $p = 0.0011$ ,  $n = 29$ , respectively). Indeed,  
221 individuals with the highest trophic level at release and at departure, i.e. individuals the most  
222 advanced in their ontogenetic diet shift, departed earlier than individuals with the lowest  
223 trophic level at release and at departure (Fig. 4c-d).

224         Among the individuals analysed for stable isotope at departure and used for a  
225 hierarchical cluster analysis, nine individuals belonged to the low trophic level group and  
226 twenty individuals belonged to the high trophic level group. Both fish and zooplankton  
227 demonstrated significant differences in stable isotope values between the hatchery and the  
228 grassland (Table 1, Fig. 5). After release, individually tagged fish from hatchery diluted their  
229 stable isotope signatures toward grassland signatures, but dilution patterns differed between  
230 the two trophic level groups (Watson-Williams test,  $df = 1,27$ ,  $F = 20.546$ ,  $p < 0.001$ ).  
231 Specifically, individuals belonging to the low trophic level group displayed a change similar  
232 to the difference in zooplankton isotope values (Watson-Williams test,  $df = 1,10$ ,  $F = 0.007$ ,  $p$   
233  $= 0.933$ ), i.e. zooplanktivorous individuals continued to feed upon zooplankton in the  
234 grassland (Fig. 5). In contrast, the change for individuals belonging to the high trophic level  
235 group was significantly different from the difference in zooplankton isotope values (Watson-  
236 Williams test,  $df = 1,21$ ,  $F = 22.585$ ,  $p < 0.001$ ). Finally, no significant effect of departure

237 timing on individual growth rates was observed (Generalized Additive Model,  $df = 1$ ,  $F =$   
238  $0.501$ , Deviance explained = 1.82%,  $p = 0.485$ ,  $n = 29$ ).

239

## 240 **Discussion**

241 The timing of departure from natal habitats is crucial for juveniles of many organisms since it  
242 strongly affects population functioning. Some potential causes of inter-individual variations in  
243 departure timing have been previously reported, including the role of individual body size  
244 and/or growth. In amphibians for instance, departure rate of northern red-legged frogs (*Rana*  
245 *aurora*) from their natal pond and survival are positively correlated with individual body size  
246 and the date of metamorphosis (Chelgren et al. 2008). In nesting birds such as tree swallows  
247 (*Tachycineta bicolor*), space availability in the nest and food resources decline as nestlings  
248 grow, and inter-individual variability in wing length explains variations in the timing of  
249 fledging (Michaud and Leonard 2000). In other taxa such as fish, juveniles' decision to depart  
250 from natal habitat in brown trout (*Salmo trutta*) can be mostly driven by individual body size  
251 and growth rate (Acolas et al. 2012).

252 The present study, however, gives evidence that body size and individual growth alone  
253 may not adequately enlighten the dynamics of natal departure from spatially-varying  
254 environments. Individually tagged juvenile pike of different sizes were stocked in a temporary  
255 flooded grassland, and departure timing was monitored during the period of drying out.  
256 Although significant correlations were found between juvenile body size and departure timing,  
257 the patterns observed did not match with current hypotheses on the role of body size on the  
258 decision to emigrate. Firstly, the largest juvenile at release departed earlier, i.e. before food  
259 resources and habitat availability declined. Assuming that they are dominant over small  
260 juveniles (e.g., Nilsson 2006), competition between individuals could not explain juvenile's

261 decision to leave. Therefore, the competition hypothesis was rejected. Secondly, small-bodied  
262 fish are known to have more efficient oxygen exchange with water compared with large ones  
263 (Pauly 1981; Hugues 1984; Robb and Abrahams 2003), and should be more tolerant to  
264 hypoxia when water temperature gets higher and the temporary habitat dries out. However  
265 hypoxic and thermal stresses were likely not a major trigger in juveniles' decision to leave  
266 since juveniles that departed later were larger than early emigrants. Therefore, the  
267 physiological hypothesis was rejected. Conversely, juveniles that departed earlier were  
268 smaller at departure than late migrants and these individuals had already achieved their  
269 ontogenetic trophic niche shift toward piscivory. Stable isotope analyses revealed that about  
270 two third of the juveniles used in our experiment were piscivorous at release, meaning that  
271 they had developed cannibalistic behaviour as commonly reported for such species (e.g., Bry  
272 et al. 1992; Juanes 2003; Skov and Koed 2004).

273         Stable isotope analyses on recaptured individuals leaving the temporary habitat  
274 revealed that piscivorous individuals departed earlier than zooplanktivorous individuals, and  
275 it is likely that these individuals migrated to the adjacent pond in search of higher abundance  
276 of prey fish. Some piscivorous individuals, however, tended to shift back to a zooplankton  
277 diet soon after their release in the flooded grassland, as indicated by a slight decrease of  $\delta^{15}\text{N}$   
278 values in their tissues (Fig. 5). This shift back to zooplankton diet was likely to be suboptimal  
279 with lower benefits and/or higher costs (Fig. 1), and they finally emigrated shortly afterwards.  
280 This is in line with laboratory experiments by Galarowicz and Wahl (2005), who  
281 demonstrated that energy return ( $\text{J}\cdot\text{min}^{-1}$ ) of large young-of-the-year walleye (*Sander vitreus*  
282 Mitchill) was high when feeding on fish and low when feeding on zooplankton. Therefore, the  
283 trophic hypothesis is accepted, indicating that the trade-off driving the use of spatially-  
284 varying environments is likely to be more dependent upon the benefits associated with  
285 energetic returns than the costs associated with inter-individual conflicts or physiological

286 constraints. This highlights how ontogeny, and particularly ontogenetic niche shift toward  
287 higher trophic level, can play a central role in juvenile's decision to depart from natal habitats  
288 in a predator species.

289         As water level decreased, food availability and water quality (higher temperature and  
290 lower dissolved oxygen) concurrently declined and the risk of mortality from being trapped in  
291 desiccating pools became higher (Capone and Kushlan 1991; Magoulick and Kobza 2003). In  
292 our study, however, zooplankton abundance was higher in temporary flooded grassland than  
293 in the adjacent pond. Our results illustrated a trade-off between the costs linked to the risk of  
294 being stranded and suffering poor water conditions, and the benefits from higher energy  
295 returns resulting from higher food abundance and the advancement in the ontogenetic niche  
296 shift toward higher trophic level. Interestingly, we did not find any significant effect of natal  
297 departure timing on individual growth rate. Contrary to other studies (e.g., Post 2003;  
298 Galarowicz and Wahl 2005), an early shift toward piscivory and departure from the temporary  
299 grassland did not affect individual growth performance at early life stages in our experiment.  
300 Nevertheless, earlier natal departure might be indirectly beneficial to individual survival,  
301 since mortality risk was likely to sharply increase in the temporary flooded grassland as water  
302 level declined (Kushlan 1976; Capone and Kushlan 1991). As well, early transition to  
303 piscivory and departure from the natal temporary habitat might increase subsequent  
304 probabilities of surviving to predation during the summer and starvation over the winter (e.g.,  
305 Sogard 1997; Post 2003). Complementary investigations are now needed to further quantify  
306 potential delayed effects of early ontogenetic shift in diet and natal departure timing from  
307 spatially-varying environments on the life-history of individuals and their fitness.

308

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317

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433

434 **Table 1** Directional statistics quantifying the shift in stable isotope values of zooplankton and  
 435 the two trophic level groups of juvenile pike between the hatchery (values at release:  $\delta^{13}\text{C}_R$   
 436 and  $\delta^{15}\text{N}_R$ ) and the flooded grassland (values at departure:  $\delta^{13}\text{C}_D$  and  $\delta^{15}\text{N}_D$ ). Significant p-  
 437 values are in bold.

438

Group	n	Main vector		Raleigh's test	
		Direction (SD)	Length	Z	p-values
Zooplankton	3	258.4 (6.14)	0.994	2.97	<b>0.035</b>
Low trophic level	9	257.4 (17.4)	0.955	8.21	< <b>0.0001</b>
High trophic level	20	235.6 (7.5)	0.991	19.60	< <b>0.0001</b>

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442 **Figure legends**

443

444 **Fig. 1** A conceptual framework of the seasonal changes of (a) the costs (e.g. physiological  
445 stress), (b) the benefits (e.g. foraging return) and (c) the trade-off in spatially-varying  
446 environments (i.e. temporary waters, dotted line) and more stable environments (i.e.  
447 permanent waters, full line). Fish colonisation of and departure from spatially-varying  
448 environments are expected to occur when the cost are higher than the benefits, as indicated by  
449 the arrows. For instance, increased environmental harshness during drought is likely to induce  
450 a shift to more stable habitats (i.e. juvenile departure) when the instantaneous foraging return  
451 does not balance the associated physiological stress from hypoxia and hyperthermia in water.

452

453 **Fig. 2** The three hypotheses tested in this study to identify the mechanisms triggering juvenile  
454 pike departure from temporary waters: (a) *Competition hypothesis*: smallest individuals  
455 emigrate before larger conspecifics as they are less competitive, (b) *Physiological hypothesis*:  
456 largest individuals at releasing emigrate the first because there are less tolerant to hypoxia and  
457 hyperthermia, and (c) *Trophic hypothesis*: individuals with higher trophic level (i.e. the most  
458 advanced in their ontogenetic diet shift) emigrate first because the natal habitat does not  
459 provide enough food resources (see text for additional details).

460

461 **Fig. 3** Progressive drying out of a typical temporarily flooded grassland in the Briere marsh  
462 from spring to summer 2006 (a April 5<sup>th</sup>, b April 18<sup>th</sup>, c May 30<sup>th</sup>, d July 5<sup>th</sup>).

463

464 **Fig. 4** Correlations between departure timing (days) of juvenile pike (n = 29) from the  
465 flooded grassland and (a) body-size at releasing (BS<sub>R</sub>, mm), (b) body-size at departure (BS<sub>D</sub>,  
466 mm), (c) trophic level at releasing ( $\delta^{15}\text{N}_R$ , ‰), and (d) trophic level at departure ( $\delta^{15}\text{N}_D$ , ‰).  
467 The continuous lines represent the significant correlations and the dotted lines are the 95%  
468 confident intervals.

469

470 **Fig. 5** Arrow diagram for the isotopic shift of (a) zooplankton from the hatchery to the  
471 grassland, (b) individuals belong to the low trophic level group (n = 20) and (c) individuals  
472 belong to the high trophic level group (n = 9). For juvenile pike, each arrow represents a  
473 single individual and was calculated using the stable isotope values at the beginning (its  
474 release in the grassland) and at the end (its departure from the grassland) of the study. The  
475 straight dotted line is the mean vector of change among all individuals and the curved dotted  
476 line indicates the 95% confidence interval. Complementary statistics are provided in Table 1.

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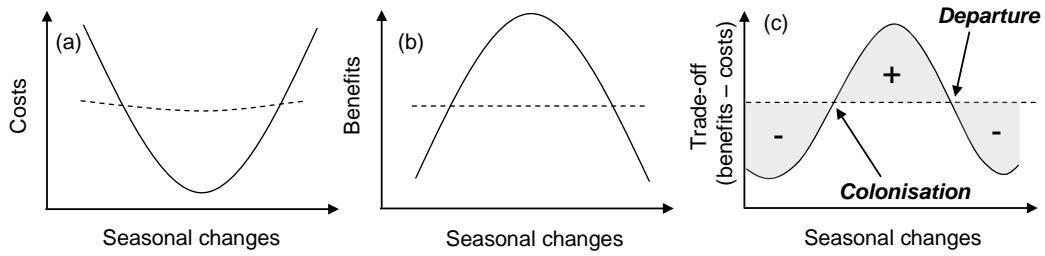
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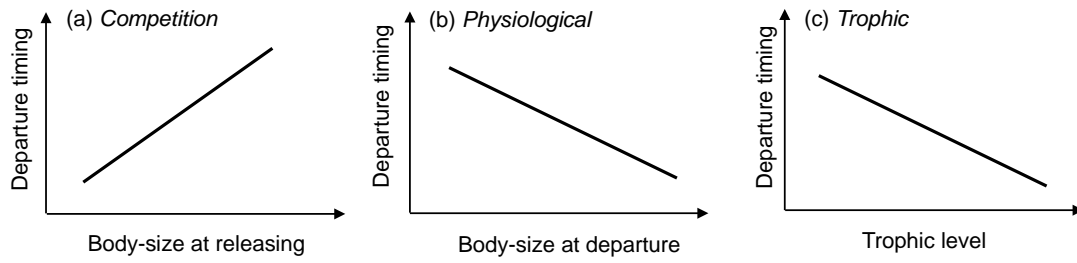
**Figure 1**



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**Figure 2**

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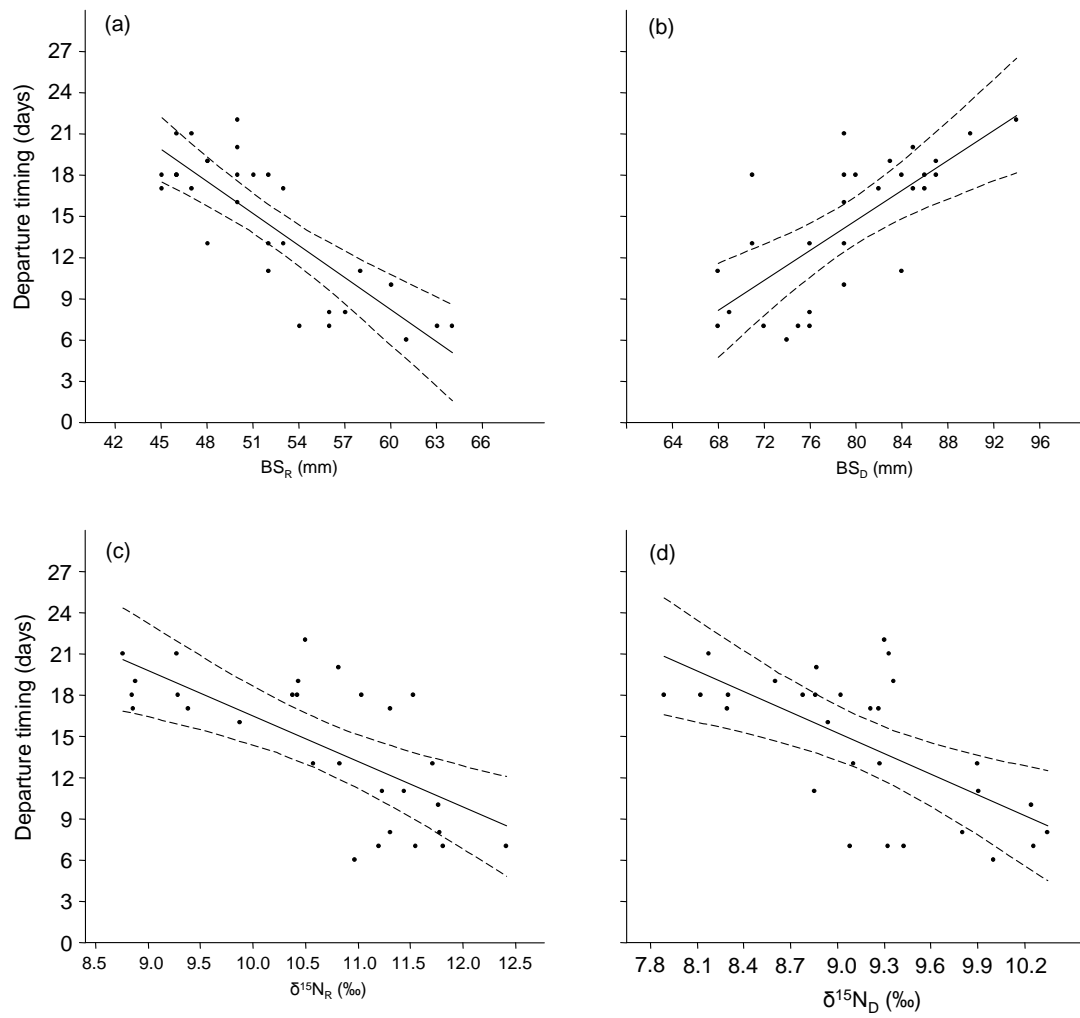
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**Figure 3**

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**Figure 4**

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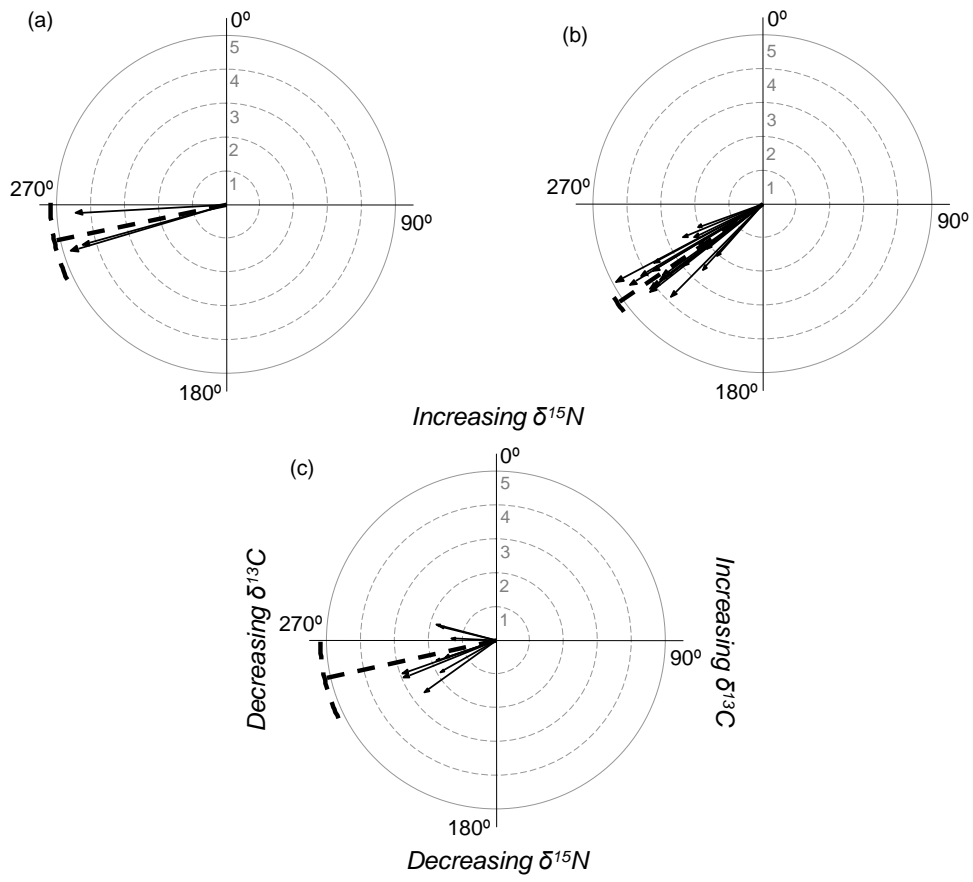
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**Figure 5**