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1 Investigating the phenology of seaward migration of juvenile  
2 brown trout (*Salmo trutta*) in two European populations

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## 13 **Abstract**

14 Recent evidence supports the existence of a downstream autumn migratory phenotype in juvenile  
15 anadromous brown trout (*Salmo trutta*), however the precise timing, extent and ecological  
16 significance of such behaviour remains ambiguous. We investigated the phenology of downstream  
17 migration of wild juvenile trout using passive integrated transponder (PIT) telemetry over an eight  
18 month period in two European rivers; the River Deerness, north-east England, and the River  
19 Villestrup, Denmark. The incidence of autumn-winter seaward migration was greater in the Deerness  
20 than the Villestrup, with at least 46 % of migrating juveniles detected prior to spring smoltification in  
21 the Deerness. Timing of migration was strongly regulated by factors associated with river discharge  
22 in both systems. While autumn and spring downstream migrants did not differ in size at the time of  
23 tagging in either system, evidence that spring migrants were of better condition, travelled faster  
24 (autumn: 11.0 km day<sup>-1</sup>; spring: 24.3 km day<sup>-1</sup>) and were more likely to leave the Deerness suggests  
25 autumn and spring migrant conspecifics respond to different behavioural motivations. Further  
26 investigation into the sex of autumn migrant juveniles, as well as the temporal and geographical  
27 variability in the incidence and fitness consequences of autumn emigration by juvenile trout would  
28 be beneficial.

29 **Keywords:** Autumn migration, smolt, life history, phenotype, phenology, telemetry

## 30 Introduction

31 Individuals of migratory species often exhibit wide variation in their spatial behaviour, varying  
32 from local residency to large-scale migration (Nathan et al. 2008; Chapman et al. 2011), including for  
33 fishes (Lucas & Baras, 2001). The literature concerning such variation within the Salmonidae is  
34 voluminous (reviewed in Dodson et al. 2013). The brown trout, *Salmo trutta* L., exemplifies such  
35 phenotypic plasticity with its spatial and temporal continuum of alternative migratory tactics, from  
36 locally-resident to potamodromous and anadromous forms (Jonsson & Jonsson, 2011; Boel et al.  
37 2014). Partial and differential migration, at the intrapopulation level, have been illustrated in  
38 numerous *S. trutta* populations, notably around Vangsvatnet Lake, Norway (Jonsson, 1985), in the  
39 Oir River, France (Cucherousset et al. 2005) and with regard to the extent of marine migration (del  
40 Villar-Guerra et al. 2013; Aarestrup et al. 2014).

41 Despite thorough accounts of behaviour, elements of juvenile salmonid space use and  
42 phenology of downstream migration remain poorly explained. It is traditionally considered that  
43 juvenile populations of anadromous brown trout and closely related Atlantic salmon, *S. salar*, remain  
44 in their native stream from one to several years before descending the river course as smolts in  
45 spring (Klemetsen et al. 2003). Therefore, when considering anadromous salmonid population  
46 dynamics, the freshwater output of a river typically refers to the production of spring migrants  
47 (Ibbotson et al. 2013). Estimates of juvenile salmonid population density are usually carried out in  
48 late spring when site fidelity is regarded as strong (Cunjak 1992) and one is typically unable to  
49 distinguish mortality from emigration when examining population losses over autumn and winter.  
50 Few published tracking or trapping studies have targeted juvenile trout outside spring (but see  
51 Jonsson & Jonsson, 2002, 2009; Marine Institute, 2014; Holmes et al. 2014; Taal et al. 2014). For  
52 example, in widely cited studies on trout migration, Elliott (1986, 1994) did not investigate evidence  
53 that small-scale emigration of Age 1+ trout parr from Black Brows Beck, NW England, appeared to  
54 occur year round and represented a high proportion, relative to spring smolt numbers.

55 Downstream movements of *S. salar* juveniles are well known in autumn (Youngson et al. 1983;  
56 Cunjak et al. 1989; Pinder et al. 2007; McGinnity et al. 2007; Jensen et al. 2012; Jonsson & Jonsson,  
57 2014; Taal et al. 2014), although the proportions of populations undertaking those movements, and  
58 their significance, are still not fully understood. By contrast, autumn descents of immature brown  
59 trout have been less widely recorded, but information is available in Irish (Marine Institute, 2014),  
60 Norwegian (Jonsson & Jonsson, 2002, 2009), Baltic (Taal et al. 2014) and New Zealand (Holmes et al.  
61 2014) populations. Based upon population-specific interpretations of phenotype, non-moribund,  
62 juvenile salmonid autumn migrants are regarded as pre-smolts, destined to enter the sea (McGinnity  
63 et al. 2007), or as comprising potamodromous population components that may be common in  
64 larger river systems (Cucherousset et al. 2005). Survival may also differ by population, for example  
65 the weakly brackish environment encountered by autumn migrants in the Baltic Sea does not  
66 require marine-level osmoregulatory competency for survival (Taal et al. 2014). Alternatively, ice,  
67 low river discharge and the absence of an estuary in which to reside are thought to cause poor  
68 survival of *S. salar* autumn migrants leaving the River Halselva, Norway and a lack of sympatric *S.*  
69 *trutta* conspecifics (Jensen et al. 2012). Autumn migrant *S. salar* do not appear suitably adapted to  
70 seawater (Riley et al. 2008), and sea survival rates of first-time, autumn-emigrant *S. trutta* in Norway  
71 are significantly lower than those in spring (Jonsson & Jonsson, 2009), however the viability of these  
72 phenotypes has been confirmed with returning *Salmo* adults (Jonsson & Jonsson, 2009; Riley et al.  
73 2009).

74 Despite enhanced awareness of an autumn downstream migratory phenotype in juvenile  
75 salmonids over recent years, our understanding of its ecological significance remains limited and  
76 somewhat contested. Recorded incidence of autumn migration has been associated with proximity  
77 to the marine environment (Ibbotson et al. 2013), elevated stream discharge (Youngson et al. 1983)  
78 and poor overwintering habitat (Riddell & Leggett, 1981), as well as the reproductive motivations of  
79 precociously mature male parr (Buck & Youngson, 1982; McGinnity et al. 2007; Jensen et al. 2012).  
80 Holmes et al. (2014) suggested that early emigration of larger trout parr from the Rainy River, New

81 Zealand reflected limited overwintering habitat availability and/or constrained feeding opportunities  
82 for individuals with high growth rates. Determining the value of alternative wintering habitats, in  
83 terms of trout survival, smolt output, performance in the sea and ultimately their fecundity , is  
84 important for river and fisheries managers in directing conservation, regulation and habitat  
85 management (Ibbotson et al. 2013), such as when considering the importance of year-round  
86 downstream fish passage.

87 In this study we examined and compared the phenology of downstream migration in two  
88 juvenile trout populations in north-east England and Denmark, using Passive Integrated Transponder  
89 (PIT) telemetry. We investigated the influence of environmental, subject-specific and tag-site specific  
90 variables on the probability of passage past fixed monitoring sites over an eight month period.

## 91 **Materials and Methods**

### 92 *Study areas*

93 The River Deerness (mean annual discharge  $\sim 0.5 \text{ m}^3 \text{ s}^{-1}$  in its lower reaches) is a small tributary  
94 (width in study reaches, 2-10 m) of the River Browney in NE England (54°44' N, 1°48' W) and flows  
95 into the North Sea via the River Wear (Fig. 1). The Wear has large stocks of Atlantic salmon and sea  
96 trout with annual resistivity (partial) counts of upstream adult migrants at Durham, 29 km from the  
97 sea, averaging 15,593 fish per year between 2007 and 2014 (Environment Agency, 2015). The  
98 Deerness drains a catchment of 52.4 km<sup>2</sup>, and is 16.3 km long, consisting largely of grassland to the  
99 west, and transitioning to woodland and lower-lying arable areas in the east. The brown trout  
100 population consists of multiple cohorts, with a mixture of resident and migratory adults, including  
101 anadromous trout (E. Winter, J. Tummers unpublished data).

102 The River Villestrup (56°46' N, 9°55' E) is the primary freshwater source for the strongly  
103 brackish Mariager Fjord, ultimately exchanging with the Kattegat Sea on the east coast of Jutland,  
104 Denmark (Fig. 1). The river has a mean annual discharge of  $1.1 \text{ m}^3 \text{ s}^{-1}$ . The Villestrup is approximately

105 20 km long, has a typical width in the studied reach of 4-10 m and drains a catchment of 126 km<sup>2</sup>.  
106 The average density of wild 0+trout is estimated at 125 per 100 m<sup>2</sup> (HELCOM, 2011). No stocking  
107 occurs. The inner fjord has salinities of 12-17 PSU in the upper 10 m of the water column used by  
108 trout, while deeper areas are more saline but often hypoxic. The shallow outer fjord has salinities of  
109 20-25 PSU. The Villestrup joins near the junction between the inner and outer fjord areas, on the  
110 north shore (Fig. 1).

### 111 *PIT tagging, recapture and telemetry*

112 Trout in the Deerness system were captured for PIT-tagging using electric-fishing equipment at  
113 six sites dispersed over *ca.* 15 km of stream length (Fig. 1). Tagging occurred between 9 July and 12  
114 September 2014 ( $n = 643$ ), with a small number ( $n = 23$ ) also tagged on 6 November 2014 (mean FL  $\pm$   
115 SD of all trout = 151 mm  $\pm$  23). In the Villestrup, trout were tagged on 26 September 2014 ( $n = 490$ ;  
116 mean FL  $\pm$  SD = 147 mm  $\pm$  27), using electric-fishing in a single reach *ca.* 8.5 km upstream of the river  
117 outlet (Fig. 1). Parr  $\geq 120$  mm (Larsen et al. 2013) and  $\leq 250$  mm from each study area were  
118 anaesthetised (Deerness: buffered MS-222, 100 mg L<sup>-1</sup>; Villestrup: Benzocaine, 25 mg L<sup>-1</sup>), weighed  
119 (to 0.1 g), measured (fork length, FL to 1 mm) and surgically implanted with a PIT-tag (Texas  
120 Instruments; model RI-TRP-RRHP, HDX, 134.2 kHz, length 23.1 mm, diameter 3.85 mm, weight 0.6 g  
121 in air). Tags and instruments were disinfected with 90% ethanol and air dried before use. Procedures  
122 were carried out by an experienced fish surgeon and following local animal welfare regulations.  
123 Following recovery, all individuals were returned to their site of capture. Recapture methodology  
124 used to investigate summer dispersal on the Deerness is presented in Online Resource 1.

125 Three pairs of stream-width swim-through half-duplex (HDX) PIT antennae were installed on a 5  
126 km stretch of the lower Deerness (Fig. 1; Bolland et al. 2009), operational from 24 September 2014  
127 at stations M2 and M3 and 13 October at station M1 (Fig. 1), until 31 May 2015. Due to occasional  
128 battery failure and a damaging high flow event in November causing severe loss of efficiency, the  
129 stations M1, M2 and M3 were operational 95.6, 98.1 and 98.1 % of the time, respectively. On the

130 Villestrup, a single pair of mains-powered antennae were placed 300 m upstream of the river outlet  
131 (Fig. 1), functional 88.7 % of the time from 26 September 2014 to 31 May 2015. Tags were detected  
132 by time-synchronised Master and Slave HDX readers (Texas Instruments SX2000; in-house build),  
133 interrogating the pairs of antennae eight times per second (Castro-Santos et al. 1996). Detection  
134 ranges between 20 and 80 cm were achieved and correct function on the Deerness was confirmed  
135 by passing a test tag through each antenna before and after each battery change (every  $4 \pm 2$  days),  
136 and by more detailed range testing periodically. Each Villestrup antenna had a timed auto-emitter  
137 check tag (Oregon RFID). Additionally on the Villestrup, a Wolf-type trap (Wolf, 1951) situated  
138 directly downstream of the PIT antennae captured migrating smolts from 18 March 2015 until the  
139 end of the study. For the purpose of this study, and by reference to standard terminology applied  
140 elsewhere (e.g. Ibbotson et al. 2013), all fish detected prior to 1 February were labelled autumn  
141 migrants, while those detected from 1 February to 31 May were labelled spring smolts.

142 Theoretical antenna efficiencies of 99, 100 and 100% were achieved for stations M1-3,  
143 respectively, by routinely passing a test tag through the system. In practice, several factors influence  
144 a tag's probability of detection, including environmental conditions, tag velocity, tag orientation and  
145 the presence of other tags (Zydlewski et al. 2006; Burnett et al. 2013). A practical estimate of  
146 efficiency is, hence, given by the ratio of fish detected at a site that are known to have passed  
147 through (Zydlewski et al. 2006), and was estimated at 98.4% for M2. The efficiencies of M1 and M3  
148 could not be estimated using this method, due to the absence of detection equipment downstream  
149 and the time lag between tagging events and the onset of monitoring, meaning the location of  
150 individuals prior to detection was uncertain. Using Zydlewski et al.'s (2006) method, the efficiency of  
151 the Villestrup station was estimated as 86.5% in spring, by identifying individuals caught in the  
152 downstream trap that were not detected by the PIT antennae.

153 *Population density estimations and environmental monitoring*



154 Quantitative estimates of trout densities ( $n \cdot 100 \text{ m}^{-2}$ ) were made at each of the Deerness  
155 tagging sites, using a multiple-pass depletion method (Carle & Strub, 1978) in July 2014 (average  
156 triple-pass catchability 97.2% for  $\geq$  Age 1) and subsequently in March 2015 (average triple-pass  
157 catchability 98.4% for  $\geq$  Age 1). Developmental state of recaptured individuals (parr, smolt [including  
158 part-smolt] or adult) was also recorded, based on phenotypic characteristics (e.g. parr marks, body  
159 colour, body shape; Tanguy et al. 1994), in order to predict the seaward movement of certain  
160 individuals.

161 One logger (HOBO®; model U20-001-01; Onset Computer Corporation), situated at M3 on the  
162 Deerness, recorded temperature (accuracy  $\pm 0.4 \text{ }^\circ\text{C}$ ) and water pressure (accuracy  $\pm 0.6 \text{ kPa}$ ,  
163 converted to river level) at 15-min intervals throughout the study. On the Villestrup, temperature  
164 was measured at the upper antenna (Tinytag plus 2; model TGP-4017, [www.geminidataloggers.com](http://www.geminidataloggers.com))  
165 and water level records were obtained from a fixed gauging station ca. 1 km upstream of the river  
166 outlet (Fig. 1).

### 167 *Statistical analyses*

168 The influence of environmental factors on the timing of downstream movement was analysed  
169 using generalised linear models (GLMs), comparing daily detection frequency with fluctuations in  
170 average daily water temperature ( $^\circ\text{C}$ ), photoperiod, average daily water level (m) and the change in  
171 average daily water level (m). Initial Poisson GLMs revealed non-linear residual patterns and  
172 overdispersion, which was corrected for using the negative binomial distribution with a log-link  
173 function (Richards, 2008). All combinations of explanatory variables were trialled, but never utilising  
174 collinear factors (e.g. temperature and photoperiod). Following this, we explored the effects of  
175 subject-specific variables on the probability of tagged trout being detected as autumn or spring  
176 migrants. Binomial GLMs with a cloglog link function, due to asymmetry in the numbers of migrants  
177 and non-migrants, were constructed using combinations of the independent factors fish length  
178 (mm), mass (g) and Fulton's condition factor, but never with collinear variables (e.g. length and

179 mass). The additional variables tag-site density ( $n \cdot 100m^{-2}$ , summer 2014), tag-site distance upstream  
180 (km), and date of tagging were also analysed for subjects on the Deerness. Twelve Deerness fish, one  
181 a spring migrant, one an upstream migrant and ten undetected, and two Villestrup fish, one a spring  
182 migrant and one undetected, were omitted from this analysis due to a lack of mass, and hence  
183 condition, records. All analyses were conducted in R 3.1.1 (R Core Team, 2014) with use of the MASS  
184 package (Venables & Ripley, 2002). Model selection followed the minimisation of Akaike's  
185 information criterion (AIC) values, which represents the best compromise between lack of precision  
186 (too many parameters) and bias (too few parameters). Models within  $\Delta 6$  AIC were retained,  
187 provided they were not increasingly complex versions of more efficient nested counterparts  
188 (outlined by Richards, 2008).

189 For further examination, we used independent-sample *t*-tests to compare the average length,  
190 mass, condition factor and net ground speed ( $km\ day^{-1}$ ) of autumn and spring migrating individuals.  
191 Chi-squared tests with Yates' continuity correction were used to determine if the proportion of  
192 Deerness fish caught, inspected and categorised as smolts in March and subsequently detected  
193 downstream differed by tag site, and if the proportion of Deerness downstream migrants reaching  
194 M1 differed between autumn and spring.

## 195 **Results**

196 Site fidelity was strong during summer 2014, with 83% of recaptured Deerness trout parr ( $n =$   
197 330) travelling no further than 60 m and  $< 0.01\%$  travelling over 200 m, from a previous known site  
198 of release (Online Resource 2). From autumn onwards, 140 (21.0%) of the 666 Deerness trout were  
199 PIT detected downstream of the site at which they were tagged and released, comprising 83 autumn  
200 migrants, 52 spring migrants and five individuals with activity spanning both periods (from here on  
201 labelled autumn migrants). Trout detected at M1 were assumed to have left the Deerness system,  
202 comprising 89 individuals in total (13.4%), 41 in autumn and 48 in spring. Migratory behaviour was  
203 observed throughout the period of study, with peaks of activity in October, November, March and

204 May (Fig. 2). Eleven upstream migrants from T1 to M3 were recorded, all occurring in autumn and  
205 none of which were detected leaving the stream. In March 2015, parr densities had decreased at all  
206 but one of the tagging sites (Table 1), by an overall average of 49%; a total of 50 tagged trout were  
207 recaptured in March across all release sites, of which 17 subsequently migrated downstream.

208 In the Villestrup, 195 of 490 tagged trout (39.8 %) were detected at the monitoring site and/or  
209 caught in the trap, comprising 49 autumn migrants, 136 spring migrants, and ten individuals with  
210 activity spanning both periods (from here on labelled autumn migrants). The Villestrup trout did not  
211 display a distinct autumnal peak of activity, however low levels of migratory behaviour were  
212 sustained throughout autumn and winter months. Activity of spring smolts peaked in late March,  
213 with continued high levels of movement throughout April and early May (Fig. 2).

#### 214 *Environmental regulators of downstream migratory behaviour*

215 Mean daily water temperature and water level were retained in the best model for predicting  
216 autumn migrant activity in the Deerness (Table 2), both sharing significant positive relationships with  
217 daily detection frequency. No other combinations of variables were retained under the selection  
218 criteria, reflecting their poor explanatory power. In contrast, the change in mean daily water level  
219 was the best predictor of spring migrant activity in the Deerness, with a significant positive  
220 relationship. Two further models were retained utilising the variables water level and photoperiod,  
221 however greater  $\Delta AIC$  values signified weaker explanatory power (Table 2). The best model  
222 predicting autumn migrant activity in the Villestrup retained both water level and temperature, but,  
223 in contrast to the Deerness, with a significant negative effect of temperature (Table 2). Under the  
224 selection criteria, five models were retained for predicting spring migrant activity in the Villestrup,  
225 with the best predictors being change in mean daily water level and water temperature in positive  
226 trends (Table 2). The removal of temperature produced a model with a  $\Delta AIC$  of 0.3, indicating the  
227 explanatory power of temperature is low and water level on its own is a powerful predictor of daily  
228 smolt counts.

229 *Phenotypic determinants of downstream migratory tendency*

230 The best model describing autumn migrant probability in the Deerness retained fish mass and  
231 tag site distance upstream as predictive parameters, both with significant negative trends (Table 3;  
232 Fig. 3). Three alternative models utilising combinations of length, condition, distance and date can  
233 be found in Table 3. The best model for predicting spring migration retained subject mass, condition  
234 factor and tag site distance upstream. Mass and tag site distance shared significant negative  
235 relationships with probability of spring detection, while condition factor shared a positive  
236 relationship (Table 3; Fig. 3). Notably, tag site distance was retained in all models for the Deerness,  
237 suggesting it is a strong predictor of migratory tendency for all downstream migrating juveniles, but  
238 particularly for spring smolts, given the higher coefficient estimates. This is supported by  
239 significantly more smolts (captured, inspected and classified in March 2015) than expected being  
240 detected originating from T1, the most downstream tag site, relative to sites further upstream (Chi-  
241 square:  $\chi^2_1 = 6.18$ ,  $p = 0.013$ ). Autumn and spring migratory tendency in the Villestrup were best  
242 predicted by fish mass and condition, both sharing negative relationships in each scenario (Table 3;  
243 Fig. 3). For the autumn migrants, mass was a particularly strong predictor on its own, given the  
244 removal of condition to produce a model with a  $\Delta AIC$  of only 0.7.

245 *Comparisons of migratory phenotypes*

246 There was no difference in length ( $t_{138} = 0.22$ ,  $p = 0.82$ ) or mass ( $t_{137} = 0.39$ ,  $p = 0.70$ ) at the time  
247 of tagging between autumn and spring migrants in the Deerness; however there was some evidence  
248 to suggest condition factor was greater in spring migrants ( $t_{137} = 2.00$ ,  $p = 0.048$ ; Fig. 3). Mean length  
249 and mass of upstream migrants was also significantly greater than that of all downstream migrants  
250 in the Deerness (Length:  $t_{149} = 3.55$ ,  $p < 0.001$ ; Mass:  $t_{147} = 4.62$ ,  $p < 0.001$ ; Fig. 3), although we found  
251 no difference in condition factor ( $t_{147} = 0.05$ ,  $p = 0.96$ ). There was no difference in length ( $t_{193} = 0.12$ ,  
252  $p = 0.90$ ), mass ( $t_{192} = 0.26$ ,  $p = 0.79$ ) or condition factor ( $t_{192} = 0.32$ ,  $p = 0.75$ ; Fig. 3) between autumn  
253 and spring migrants in the Villestrup. Individual net ground speed of downstream migrants in the

254 Deerness varied dramatically from less than 1 to 88 km day<sup>-1</sup> throughout the study period, but on  
255 average, spring migrants travelled significantly faster (24.3 km day<sup>-1</sup>) than autumn migrants (11.0 km  
256 day<sup>-1</sup>) ( $t_{127} = 3.82$ ,  $p < 0.001$ ; Fig. 4). Additionally, downstream migrants were classified as stream  
257 'emigrants' following a final detection at the most downstream monitoring site, *ca.* 700 m from the  
258 Deerness' confluence with the river Browney. A significantly greater proportion of spring migrants  
259 (84.6%) than autumn migrants (49.4%) became stream emigrants during the period in which they  
260 were first detected (Chi-square:  $\chi^2_1 = 15.5$ ,  $p < 0.001$ ). Five autumn non-emigrants were  
261 subsequently detected in the spring, four of which were then detected moving past M1.

## 262 Discussion

263 Extensive autumn downstream migrations were evident in juvenile brown trout (*Salmo trutta*)  
264 for both the Villestrup (Jutland, Denmark) and the Deerness (north-east England). Over 1.5 times the  
265 number of spring smolts were observed active between October and January in the Deerness.  
266 Moreover those leaving the system during autumn-winter represented 46% of all stream-emigrant  
267 juveniles in the study period. This contrasts the strong site fidelity observed during summer months  
268 and provides quantitative evidence of the protracted overwinter nature of the downstream  
269 migratory behaviour, broadly similar to that of the Marine Institute (2014), which states numbers of  
270 autumn migrating juveniles in the Burrishoole catchment, Ireland, have fluctuated between 18% and  
271 57% of the total annual juvenile downstream migrant count, since 1982. Both the Burrishoole and  
272 Deerness catchments are characterised by mild, oceanic climates and frequent flow elevations  
273 following rainfall, possibly accounting for the prolonged 'autumn' downstream migration.  
274 Nevertheless, Deerness migrants cannot fully account for the marked reduction in parr densities at  
275 sites T2-T5 by March 2015, which must also reflect either local movement outside tagging sites, low  
276 overwinter survival, or a combination of both.

277 Probability of migration was higher in the Villestrup, but incidence of autumn migration was  
278 lower (25% of the total juvenile stream-emigrant count), yet remains higher than that reported by

279 Jonsson and Jonsson (2009) in Norway. Migrants in the Villestrup are assumed to enter the brackish  
280 Mariager Fjord soon after passage through the PIT monitoring station, however autumn migrants  
281 may have low gill Na<sup>+</sup>K<sup>+</sup>-ATPase activity, as observed for autumn-emigrating *S. salar* juveniles (Riley  
282 et al. 2008). This could cause osmoregulatory stress, although salmonid parr have been known to  
283 reside in estuarine environments (Cunjak et al. 1989; Pinder et al. 2007). Conversely, individuals in  
284 the Deerness have much further to travel before reaching a saline environment, (meaning their  
285 migration strategy, i.e. anadromy or potamodromy, is unknown), and may explain why incidence of  
286 autumn migration is particularly high there. The recognition of an alternative juvenile downstream  
287 migratory phenotype is growing internationally and, hence, the potential contribution of these  
288 individuals to adult recruitment must be acknowledged.

289         The environmental factors regulating the phenology of downstream movement of salmonid  
290 smolts have been well studied, particularly the behavioural responses to water temperature, flow  
291 and light (e.g. Jonsson, 1991; Aarestrup et al. 2002; Aldvén et al. 2015). Stimuli for migration differ in  
292 their importance geographically between river systems and temporally between years (Hembre et  
293 al. 2001. This study suggests that water level (and hence river discharge) had the greatest influence  
294 on autumn migrant movement in both the Deerness and Villestrup, in accordance with Youngson et  
295 al. (1983), Jonsson and Jonsson (2002) and Holmes et al. (2014). This is not surprising, given the  
296 opportunity to minimise the energetic costs of migration, while high turbidity may offer greater  
297 protection from predators (Hvidsten & Hansen, 1989). The change in average daily water level was a  
298 better predictor of movement of spring migrants in both the Deerness and Villestrup. This suggests  
299 smolts in both systems are particularly receptive to dynamic fluctuations in the hydrograph, similar  
300 to Carlsen et al.'s (2004) conclusions that migrating juveniles can anticipate floods. Importantly, all  
301 models retained in Table 2 utilised an environmental variable associated with river discharge,  
302 suggesting it is a central migratory stimulus for both populations.

303 Autumn migrants in the Deerness and smolts in the Villestrup responded positively to higher  
304 temperature, analogous to results obtained by Jonsson and Ruud-Hansen (1985). Smolt activity in  
305 the Deerness was better predicted by photoperiod, which is known to regulate physiological changes  
306 associated with the parr-smolt transformation (Björnsson et al. 2011). The probability of autumn  
307 migration in the Villestrup shared a significant negative relationship with temperature (see also  
308 Jonsson & Jonsson, 2002), yet previous studies reporting increased migrant activity at cold  
309 temperatures are usually associated with ice melt (Hesthagen & Garnås, 1986; Carlsen et al. 2004).  
310 One possibility for the observed pattern is that peak flows may have coincided with low  
311 temperatures in winter, demonstrating a degree of behavioural independence with regard to  
312 seasonal variables. Also, the Villestrup is spring-fed, meaning temperatures are comparatively more  
313 stable to those of the Deerness. The relative importance of temperature, photoperiod and river  
314 discharge as migratory triggers may, however, fluctuate between years (Jensen et al. 2012; Aldvén et  
315 al. 2015), depending on precipitation and rate of temperature change. Longer-term and  
316 experimental studies in either system could reveal variability and mechanisms in the effect of  
317 environmental cues.

318 The probability of an individual conducting autumn or spring migration past fixed points on the  
319 Deerness decreased significantly in an upstream direction. Ibbotson et al. (2013) proposed a re-  
320 distribution of autumn migrating *S. salar* parr in a downstream direction was responsible for similar  
321 findings, rather than a targeted migration. One explanation for this may be to consider the potential  
322 disturbance caused by environmental events such as high autumn-winter flows. Territorial behaviour  
323 may be disrupted, initiating a re-establishment of dominance hierarchies and promoting the  
324 downstream displacement of subordinate individuals. While this may hold true for autumn-winter  
325 migrants, it is unlikely to be the case for spring smolts, but for which we found a reduced probability  
326 of detection from tag sites further upstream. Moreover, there appears no trend in the percentage of  
327 recaptured residents with distance upstream (Table 1), which would be expected if migration  
328 tendency decreased in an upstream direction. We, therefore, suggest a cumulative increase in

329 mortality probability with increasing distance upstream for both autumn and spring migrants, for  
330 example due to anthropogenic obstruction during migration, greater energetic costs or exposure to  
331 predators (Aarestrup & Koed, 2003; Gauld et al. 2013).

332 In early studies it was hypothesised that anadromous salmonid juveniles migrate at the first  
333 opportunity after reaching a threshold size (Elson, 1957; Fahy, 1985), yet for brown trout, smolt  
334 length can vary from <100 mm to >200 mm within the same river (Økland et al. 1993). Fast-growing  
335 individuals smolt at a younger age and smaller size than their slow-growing counterparts (Forseth et  
336 al. 1999). In the Deerness and Villestrup, autumn and spring migratory tendency were negatively  
337 affected by body mass, which was always a better predictor than body length. This may be  
338 counterintuitive, considering migration and post-migration survival is thought to be positively size-  
339 dependent (Bohlin et al. 1993), but could suggest migrating juveniles in these river systems were  
340 energetically constrained. Migration has been described as a biological response to adversity (Taylor  
341 & Taylor, 1977), and in the Deerness (autumn migrants) and Villestrup (all migrants) migratory  
342 tendency was negatively correlated with fish condition at tagging, which could result from adversity  
343 in the form of poor growth opportunities. Notably, the optimal size at migration in the Deerness and  
344 Villestrup systems could be lower than the size range of individuals sampled such that some of the  
345 tagged trout, especially males, may have been maturing.

346 The size of autumn and spring migrants did not differ at the time of tagging in either the  
347 Deerness or Villestrup, as found by Ibbotson et al. (2013) for *S. salar*. In contrast, some found  
348 autumn migrants to be significantly larger than spring migrants or residents of the same year-class,  
349 possibly indicating constrained habitat availability for faster-growing individuals or achievement of a  
350 high energy store status (Huntingford et al. 1992; Holmes et al. 2014). This hypothesis is not  
351 supported by our results. In the Deerness, spring migrants were of better condition than autumn  
352 migrants at the time of tagging and autumn and spring migratory tendencies shared opposed  
353 relationships with individual body condition. This may have been a result of competition, such that



354 subordinate individuals with lower body condition were displaced by their dominant counterparts,  
355 either preferentially leaving a low-growth potential environment or forced out of refugia with an  
356 overwinter reduction in stream carrying capacity (see Keeley, 2001). Migration in brown trout can be  
357 regulated by food availability (Wysujack et al. 2008), therefore autumn migrants could result from a  
358 competition-induced lack of resources for subordinates. On the contrary, we found no evidence to  
359 suggest the density of trout Age 1+ and older at each Deerness site could predict the proportion of  
360 autumn migrants. However, caution is needed, since local habitat has been shown to influence the  
361 autumnal movement of Atlantic salmon parr, perhaps due to differences in the proximity of  
362 overwintering habitat (Ibbotson et al. 2013).

363 Autumn upstream migrants in the Deerness, characteristic of precocious parr maturation  
364 (McCormick et al. 1998), were larger than downstream migrants. Precocious parr are predominantly  
365 males and the anadromous emigrants' sex ratio is typically heavily skewed towards females  
366 (Klemetsen et al. 2003) although autumn downstream migration has been linked to the reproductive  
367 motivations of precocious parr (Buck and Youngson, 1982). Fish sex was unknown in this study,  
368 although 22.5% of tagged and untagged parr morphotypes  $\geq 120$  mm, sampled on the Deerness in  
369 November 2014 were spermiating males (E. Winter, unpublished data). Cheap molecular methods  
370 for the sexing of juvenile salmonids from tissue samples are now available (Quéméré et al. 2014) and  
371 will aid sex-specific interpretation of movement patterns in parr morphotype salmonids.

372 Questions regarding the ecological significance of autumn migration of juvenile salmonids  
373 remain. Increased plasma thyroxine levels in autumn migrants are suggestive of a physiologically  
374 mediated migration (Riley et al. 2008; Zydlewski et al. 2005), however the behavioural motivations  
375 of autumn and spring migrants may differ, since autumn-migrating parr are not physiologically  
376 adapted for seawater entry (Riley et al. 2008). Deerness spring migrants travelled at a greater net  
377 ground speed, at rates similar to those obtained by Aarestrup et al. (2002) for radio tagged trout  
378 smolts, and were more likely to become stream emigrants than autumn migrants. While antennae

379 malfunction during a major spate in November 2014 may be partially responsible for a lack of  
380 autumn detections at M1, these results suggest the movements of Deerness autumn individuals are  
381 not exclusively marine-targeted. In the Villestrup it seems likely that downstream-migrating parr  
382 recorded at the PIT station at the bottom of the river subsequently enter the Mariager Fjord, though  
383 they could remain in the river outlet. It would, therefore, be valuable to determine the range of  
384 salinities and temperatures to which juvenile autumn emigrants are exposed and their survival in  
385 relation to their physiological readiness for seawater transition.

386 In conclusion, this study provides quantitative evidence for considerable autumn and winter  
387 downstream migration of juvenile brown trout in the rivers Deerness and Villestrup, along with  
388 correlative information on factors regulating behaviour, to parallel the wealth of knowledge  
389 concerning spring smolt migration. We propose different behavioural motivations for autumn and  
390 spring migrants, based on individual condition, the proportion of emigrants and rates of migration  
391 for each group in the Deerness. We emphasise the dynamic behavioural nature of the brown trout  
392 and suggest the autumn-migratory phenotype represents an important avenue within the migration  
393 continuum concept (Cucherousset et al. 2005; Dodson et al. 2013; Boel et al. 2014), dependent on  
394 environmental and physiological factors relating to individual fitness. An in-depth, experimental  
395 evaluation of the temporal, spatial and genetic variability of the extent of autumn migration of trout,  
396 and its influence on subsequent life history traits, would be beneficial to future conservation and  
397 management plans.

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565 **Figure legends**

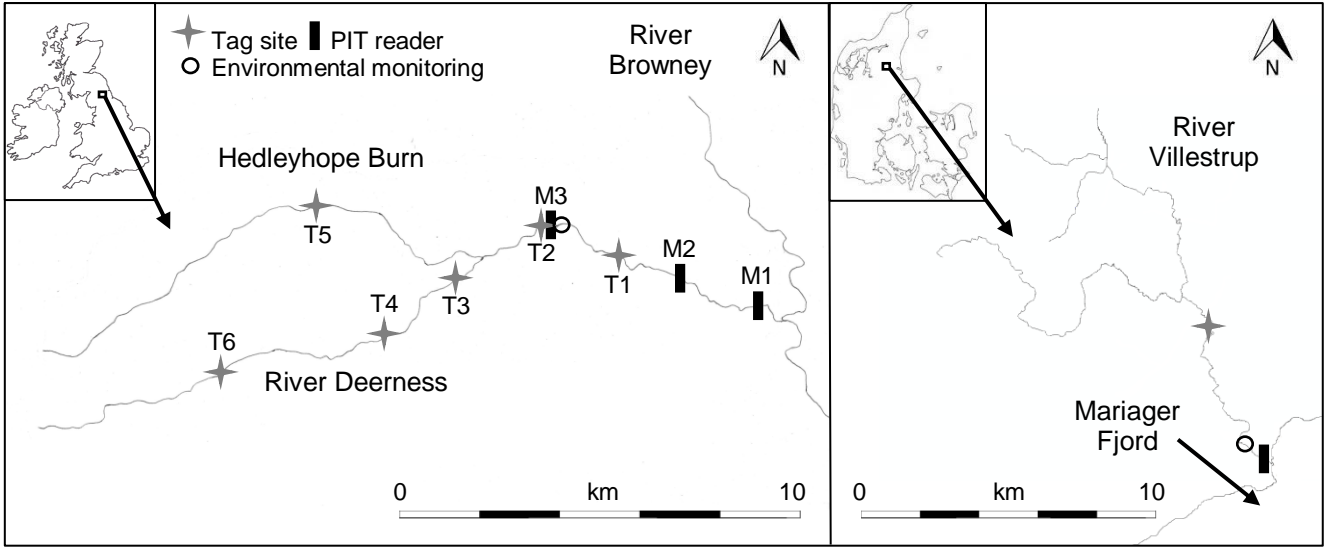
566 Fig. 1 Map of the Deerness and Villestrup study areas, showing the locations of tagging sites, fixed  
567 PIT readers and environmental monitoring stations with stars, thick lines and open circles,  
568 respectively. On the Deerness, an environmental monitoring station was also placed at M3. Inset  
569 maps show the location of the study areas nationally.

570 Fig. 2 Daily detection frequency of PIT tagged trout parr detected downstream of the site at which  
571 they were tagged and released on the Deerness (a) and Villestrup (c). Date of first detection only is  
572 displayed. Shaded regions represent periods of minimal or no detection efficiency due to PIT  
573 antennae malfunction. Individuals detected prior to 1 Feb were labelled autumn migrants and those  
574 detected from 1 Feb labelled spring smolts following published convention (Ibbotson et al. 2013). In  
575 addition, a downstream trap was operational from 18 March on the Villestrup, indicated by the  
576 arrow on panel (c). Average daily water temperature (solid lines) and average daily water level  
577 (dotted lines) are also displayed for the Deerness (b) and Villestrup (d)

578 Fig. 3 The mean length, mass and condition factor at tagging ( $\pm$  SEM) of undetected trout, autumn  
579 downstream migrants, spring downstream migrants and upstream migrants in the Deerness (top  
580 row) and the Villestrup (bottom row)

581 Fig. 4 The mean net ground speed ( $\pm$  SEM) of autumn and spring migrants in the Deerness.

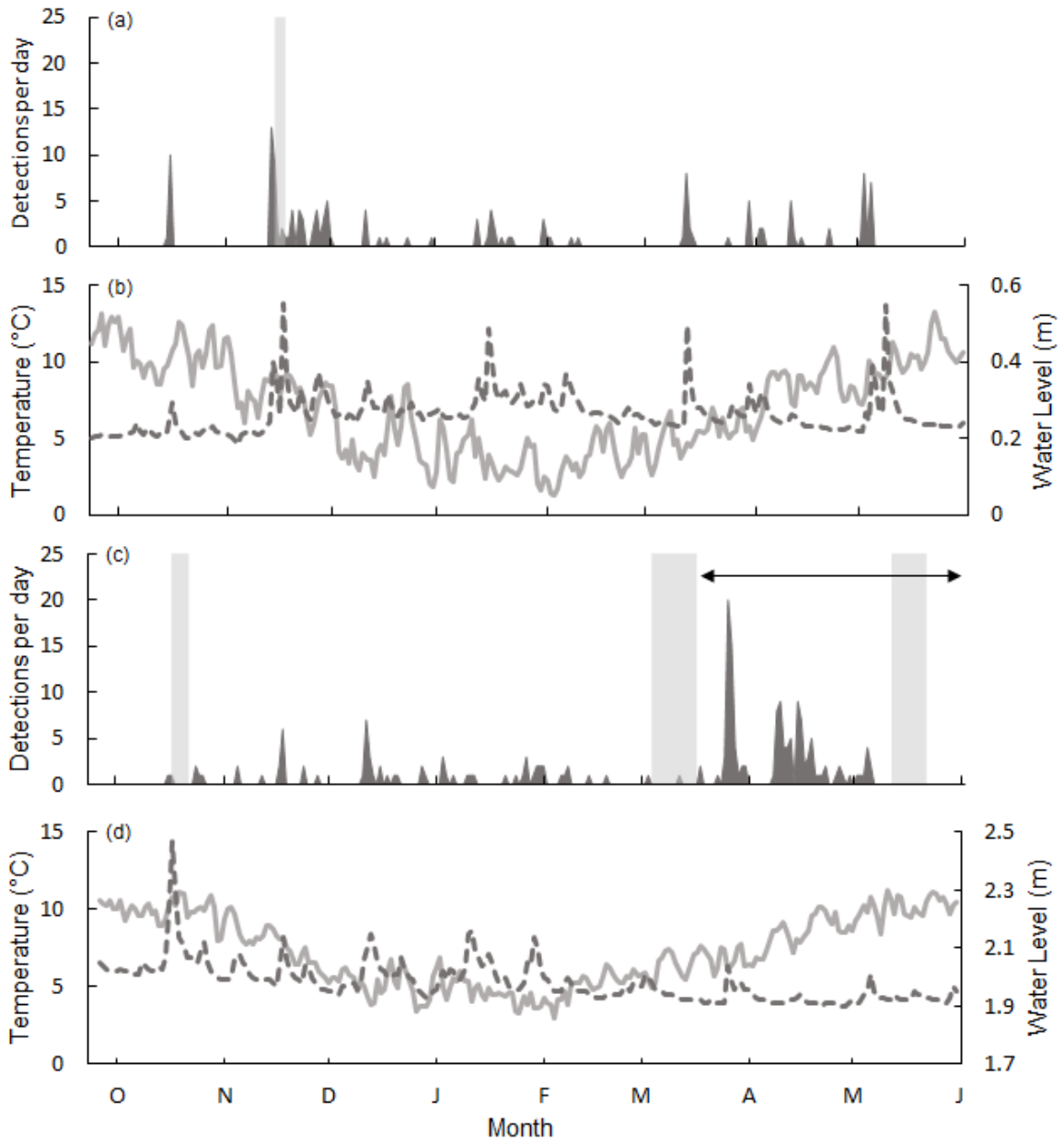
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584 Fig. 1

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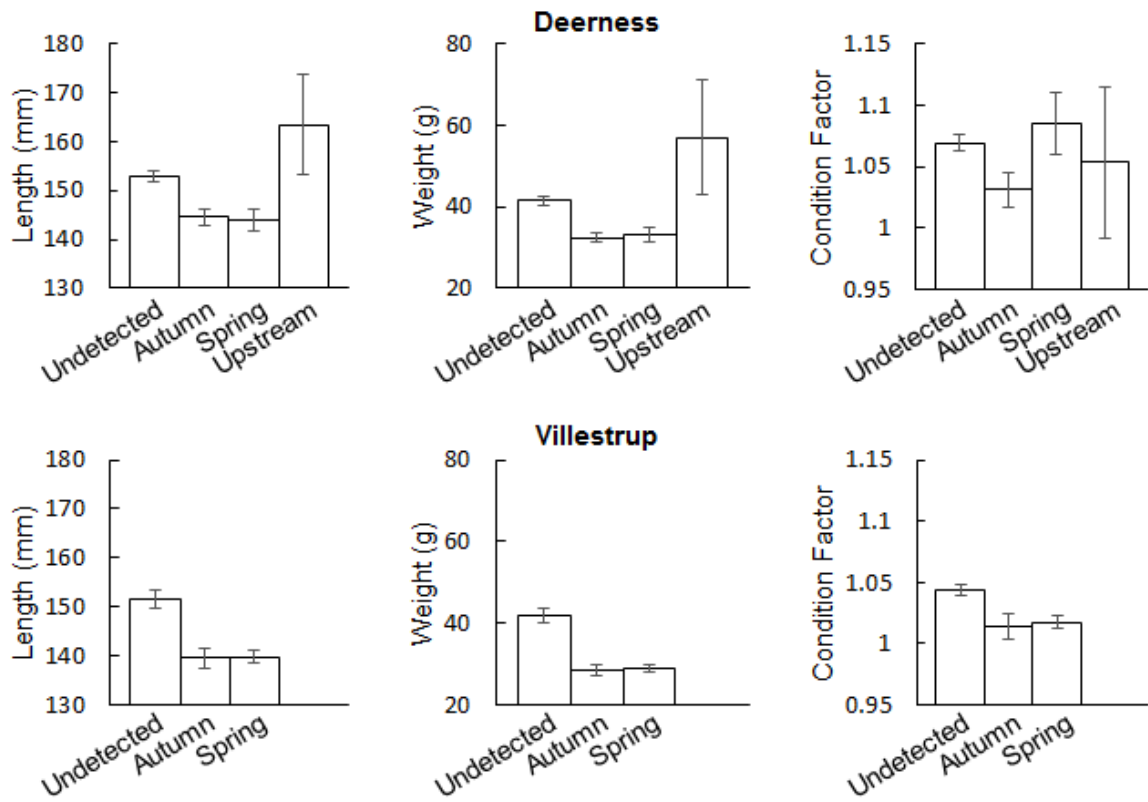
587 Fig. 2

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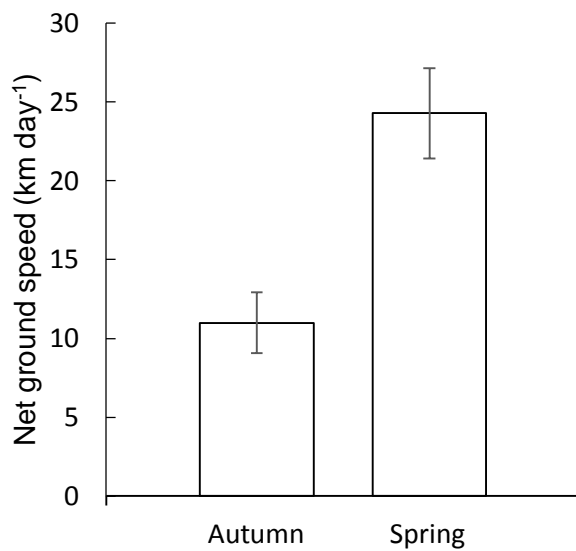
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593 Fig. 3

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596 Fig. 4

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598 Table 1: Details of tag site-specific variables on the Deerness, along with results of PIT telemetry and March recapture surveys by site.

Tag Site	Distance from river mouth (km)	Density '14 (n·100m <sup>-2</sup> )	Density '15 (n·100m <sup>-2</sup> )	%Δ Density	No. fish tagged	% Migrated Downstream	% Recaptured residents	% Loss from mortality or local dispersal
T1	4.2	12.0	14.3	+19.2	214	33.6	4.2	62.2
T2	6.2	9.2	3.7	-59.8	99	10.1	6.1	83.8
T3	8.6	12.2	1.9	-84.4	91	28.6	3.3	68.1
T4	10.8	9.5	1.5	-84.2	55	18.2	7.3	74.5
T5	11.8	12.2	2.3	-81.1	140	12.1	2.1	85.8
T6	14.5	7.7	7.5	-2.6	67	7.5	10.4	82.1

599

600

601 Table 2: Generalised linear model outputs of migration phenology analyses. All retained models within 6  $\Delta$ AIC are displayed. Significant variables are in  
 602 bold, with values for predictor variables representing coefficient estimates.

Model	AICc	$\Delta$ AICc	df	Intercept	Water Level	$\Delta$ Water Level	Water Temperature	Photoperiod
Deerness Autumn								
1	202.3	0.0	4	<b>-12.00</b>	<b>33.30</b>		<b>0.24</b>	
Deerness Spring								
1	166.8	0.0	3	<b>-1.76</b>		<b>22.83</b>		
2	168.3	1.5	4	<b>-9.51</b>	<b>20.24</b>			<b>0.004</b>
3	169.1	2.3	3	<b>-5.84</b>	<b>17.35</b>			
Villemstrup Autumn								
1	207.7	0.0	4	<b>-20.80</b>	<b>10.83</b>		<b>-0.34</b>	
2	208.6	0.9	4	<b>-18.23</b>	<b>11.02</b>			<b>-0.011</b>
Villemstrup Spring								
1	311.7	0.0	4	<b>-1.87</b>		<b>27.04</b>	<b>0.20</b>	
2	312.0	0.3	3	-0.26		21.68		
3	316.1	4.4	4	-29.64	13.77			<b>0.004</b>
4	316.4	4.7	4	<b>-34.35</b>	<b>16.62</b>		<b>0.28</b>	
5	317.3	5.6	3	-17.57	9.10			

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605 Table 3: Generalised linear model outputs of migration tendency analyses. All retained models within 6  $\Delta$ AIC are displayed. Significant variables are in bold,  
 606 with values for predictor variables representing coefficient estimates.

Model	AICc	$\Delta$ AICc	df	Intercept	Length	Weight	Condition	Density	Distance	Days
Deerness Autumn										
1	487.4	0.0	3	0.26		<b>-0.032</b>			<b>-0.136</b>	
2	489.7	2.3	5	<b>4.29</b>	<b>-0.023</b>		<b>-1.86</b>		<b>-0.146</b>	0.006
3	489.7	2.3	4	<b>3.93</b>	<b>-0.022</b>		-1.42		<b>-0.137</b>	
4	491.3	3.9	3	<b>2.48</b>	<b>-0.022</b>				<b>-0.143</b>	
Deerness Spring										
1	340.7	0.0	4	-1.35		<b>-0.041</b>	<b>1.79</b>		<b>-0.178</b>	
2	341.0	0.3	3	<b>3.42</b>	<b>-0.029</b>				<b>-0.178</b>	
3	343.0	2.3	3	0.24		<b>-0.035</b>			<b>-0.164</b>	
Villemstrup Autumn										
1	353.9	0.0	3	2.15		<b>-0.023</b>	-3.33			
2	354.6	0.7	2	<b>-1.21</b>		<b>-0.024</b>				
3	356.0	2.1	3	4.34	<b>-0.014</b>		<b>-4.19</b>			
4	358.4	4.5	2	-0.002	<b>-0.014</b>					
5	359.3	5.4	2	2.34			<b>-4.22</b>			
Villemstrup Spring										
1	527.0	0.0	3	<b>4.70</b>		<b>-0.026</b>	<b>-4.42</b>			
2	532.6	5.6	3	<b>7.40</b>	<b>-0.017</b>		<b>-5.47</b>			

607 **Online Resource 1: Investigating the phenology of downstream migration in juvenile trout.**

608 **Methodology of Deerness recapture surveys in summer 2014, used to investigate summer-time**  
609 **dispersal of trout parr.**

610 Following the initial PIT-tagging of trout parr at sites along the Deerness, recapture sessions  
611 during the summer of 2014 enabled the re-sampling of individuals to determine their level of  
612 movement. Three single-pass electrofishing surveys were conducted at each site in contiguous stop-  
613 netted 20 m stream sections over a period of *ca.* two months (early July to mid September 2014).  
614 The distance surveyed was increased in each session from initially 100 m to finally 200 m upstream  
615 and downstream of each starting point. During the first recapture session at sites T2, T3 and T4, and  
616 during the first two recapture sessions at sites T1, T5 and T6, any untagged individuals captured  
617 were tagged and subsequently released back into the population. The frequencies of maximum  
618 longitudinal distances covered by each recaptured fish from a previous site of release showed a  
619 typical inverse-power distribution. Following the methods of Bubb et al. (2004), linear  
620 transformation using a double-ln plot enabled regression analysis. Upstream and downstream  
621 dispersal were analysed separately and the regression lines compared. To maximise sample size, the  
622 recorded dispersal ranges were combined from all study sites.

### 623 **References**

624 Bubb, D. H., T. J. Thom & M. C. Lucas, 2004. Movement and dispersal of the invasive signal crayfish  
625 *Pacifastacus leniusculus* in upland rivers. *Freshwater Biology*, 49: 357-368.

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629 **Online Resource 2: Investigating the phenology of downstream migration in juvenile trout.**

630 **Results and analysis of the Deerness recapture surveys of trout parr dispersal in summer 2014.**

631 A total number of 330 fish were recaptured during single pass recapture surveys on the  
 632 Deerness between late July and mid-September 2014. The maximum distance covered by any one  
 633 trout tagged and recaptured within the same Deerness study site, July to September 2014, was 260  
 634 m, however many recaptured individuals (50.2%) remained within the 20m zone in which they were  
 635 first released, and the majority (83.0%) travelled no further than 60m from previous known locations  
 636 (Fig. S1). The probability,  $M$ , of moving a dispersal distance of  $D$  m was described by an inverse-  
 637 power function using the inverse cumulative proportion of dispersers in each 20 m sample zone  
 638 from the site of release (Bubb et al. 2004):

639 
$$M = CD^{-n}$$

640  $C$  and  $n$  are scaling constants. A highly significant negative relationship between  $\ln M$ , both upstream  
 641 and downstream, and  $\ln D$  was found (Upstream:  $F_{1,7} = 82.7, p < 0.001, R^2 = 0.92$ ; Downstream:  $F_{1,10}$   
 642  $= 121.7, p < 0.001, R^2 = 0.92$ ; Fig. S2) under the equations:

643 
$$\ln M \text{ (upstream)} = 7.25 - 2.26(\ln D)$$

644 
$$\ln M \text{ (downstream)} = 7.22 - 2.21(\ln D)$$

645 No significant difference between the gradients of the two regression lines was found ( $t_{20} = -0.18, p$   
 646  $= 0.86$ ), meaning trout were equally likely to disperse upstream and downstream (Fig. S2).

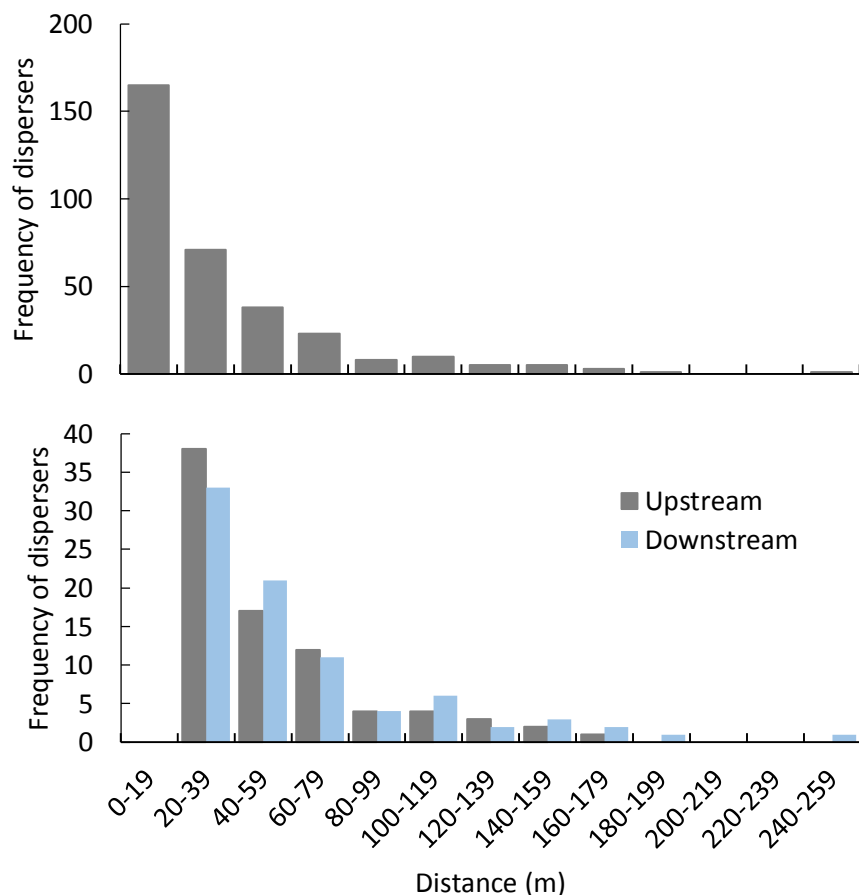


Fig. S1: Frequency distribution of the maximum longitudinal movements made by trout from a previous release site (top), with upstream and downstream movements separated (bottom), all study sites combined.

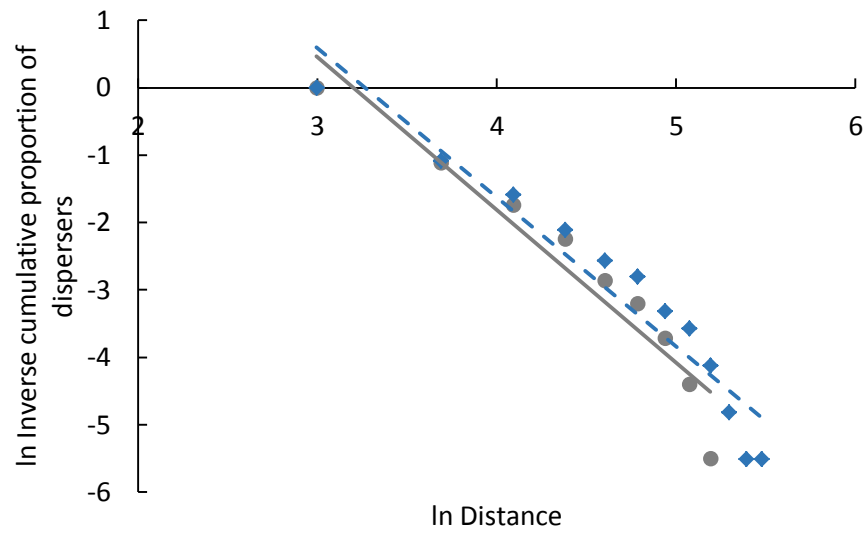


Fig. S2: Double-In plot of the inverse cumulative proportion of dispersers in upstream (grey) and downstream (blue) directions.

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648 **References**

649 Bubb, D. H., T. J. Thom & M. C. Lucas, 2004. Movement and dispersal of the invasive signal crayfish  
 650 *Pacifastacus leniusculus* in upland rivers. *Freshwater Biology*, 49: 357-368.

