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

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Abstract

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

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

Introduction

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

Despite thorough accounts of behaviour, elements of juvenile salmonid space use and phenology of downstream migration remain poorly explained. It is traditionally considered that juvenile populations of anadromous brown trout and closely related Atlantic salmon, *S. salar*, remain in their native stream from one to several years before descending the river course as smolts in spring (Klemetsen et al. 2003). Therefore, when considering anadromous salmonid population dynamics, the freshwater output of a river typically refers to the production of spring migrants (Ibbotson et al. 2013). Estimates of juvenile salmonid population density are usually carried out in late spring when site fidelity is regarded as strong (Cunjak 1992) and one is typically unable to distinguish mortality from emigration when examining population losses over autumn and winter. Few published tracking or trapping studies have targeted juvenile trout outside spring (but see Jonsson & Jonsson, 2002, 2009; Marine Institute, 2014; Holmes et al. 2014; Taal et al. 2014). For example, in widely cited studies on trout migration, Elliott (1986, 1994) did not investigate evidence that small-scale emigration of Age 1+ trout parr from Black Brows Beck, NW England, appeared to 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 ~0.5 m^3s^{-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^2, 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 m^3s^{-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^2.

106   The average density of wild 0+trout is estimated at 125 per 100 m^2 (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 ±

115   SD of all trout = 151 mm ± 23). In the Villestrup, trout were tagged on 26 September 2014 (*n* = 490;

116   mean FL ± SD = 147 mm ± 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^{-1}; Villestrup: Benzocaine, 25 mg L^{-1}), 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 ± 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 ($n \cdot 100$ 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 ≥ Age 1) and subsequently in March 2015 (average triple-pass

157   catchability 98.4% for ≥ 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 ±0.4 °C) and water pressure (accuracy ±0.6 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)

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 (°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·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 Δ6 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.

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 ΔAIC 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 ΔAIC 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.

Phenotypic determinants of downstream migratory tendency

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The best model describing autumn migrant probability in the Deerness retained fish mass and

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tag site distance upstream as predictive parameters, both with significant negative trends (Table 3;

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Fig. 3). Three alternative models utilising combinations of length, condition, distance and date can

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be found in Table 3. The best model for predicting spring migration retained subject mass, condition

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factor and tag site distance upstream. Mass and tag site distance shared significant negative

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relationships with probability of spring detection, while condition factor shared a positive

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relationship (Table 3; Fig. 3). Notably, tag site distance was retained in all models for the Deerness,

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suggesting it is a strong predictor of migratory tendency for all downstream migrating juveniles, but

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particularly for spring smolts, given the higher coefficient estimates. This is supported by

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significantly more smolts (captured, inspected and classified in March 2015) than expected being

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detected originating from T1, the most downstream tag site, relative to sites further upstream (Chi-

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square: χ^2_1 = 6.18, p = 0.013). Autumn and spring migratory tendency in the Villestrup were best

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predicted by fish mass and condition, both sharing negative relationships in each scenario (Table 3;

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Fig. 3). For the autumn migrants, mass was a particularly strong predictor on its own, given the

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removal of condition to produce a model with a ΔAIC of only 0.7.

244

Comparisons of migratory phenotypes

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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

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of tagging between autumn and spring migrants in the Deerness; however there was some evidence

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to suggest condition factor was greater in spring migrants (t_{137} = 2.00, p = 0.048; Fig. 3). Mean length

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and mass of upstream migrants was also significantly greater than that of all downstream migrants

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in the Deerness (Length: t_{149} = 3.55, p < 0.001; Mass: t_{147} = 4.62, p < 0.001; Fig. 3), although we found

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no difference in condition factor (t_{147} = 0.05, p = 0.96). There was no difference in length (t_{193} = 0.12,

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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

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and spring migrants in the Villestrup. Individual net ground speed of downstream migrants in the

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254   Deerness varied dramatically from less than 1 to 88 km day^{-1} throughout the study period, but on

255   average, spring migrants travelled significantly faster (24.3 km day^{-1}) than autumn migrants (11.0 km

256   day^{-1}) (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: χ^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.

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   Moreoverthose 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^+K^+-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

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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 ≥ 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.

398 Acknowledgements

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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 (± 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)

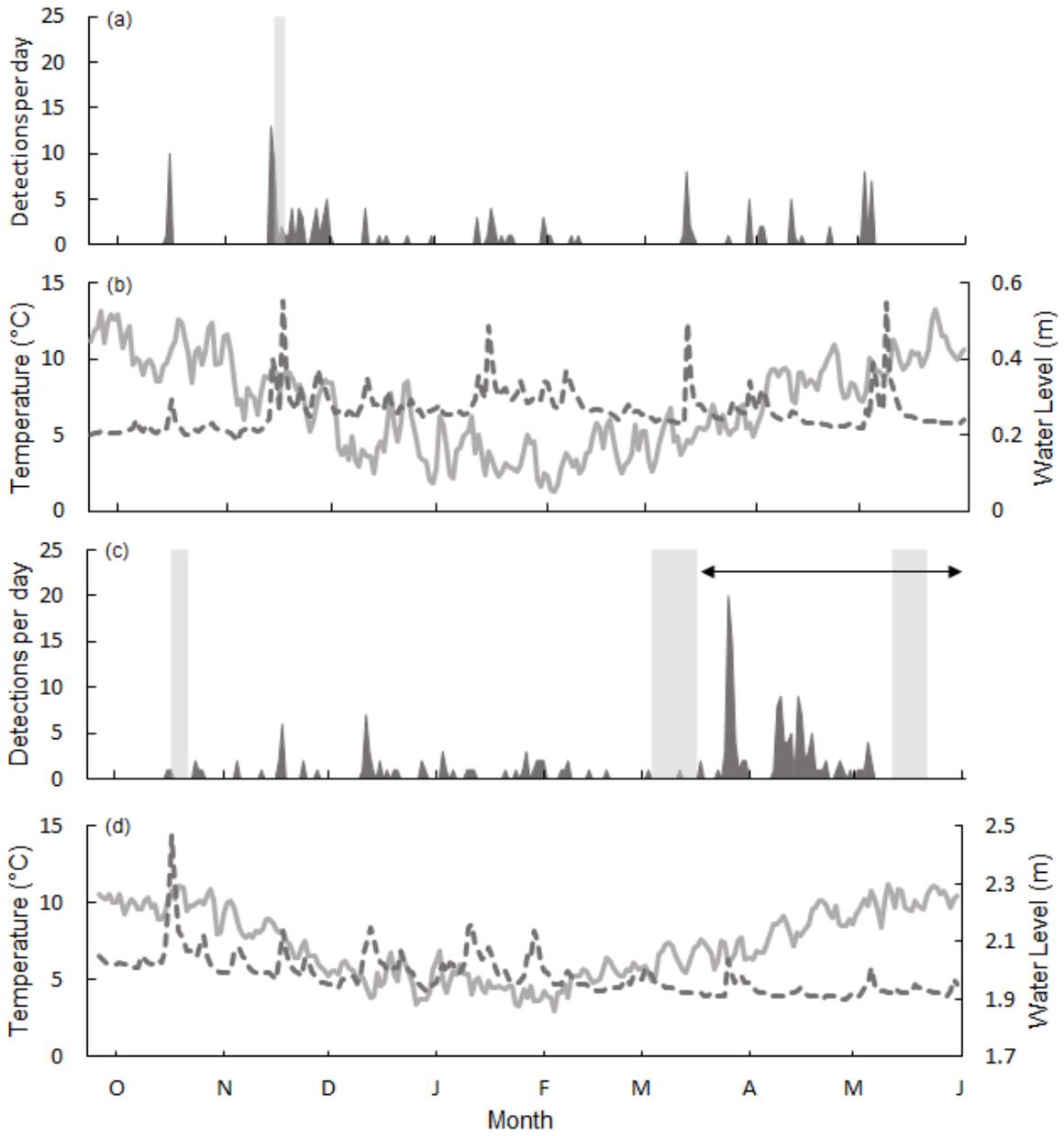581   Fig. 4 The mean net ground speed (± SEM) of autumn and spring migrants in the Deerness.

582

583

584   Fig. 1
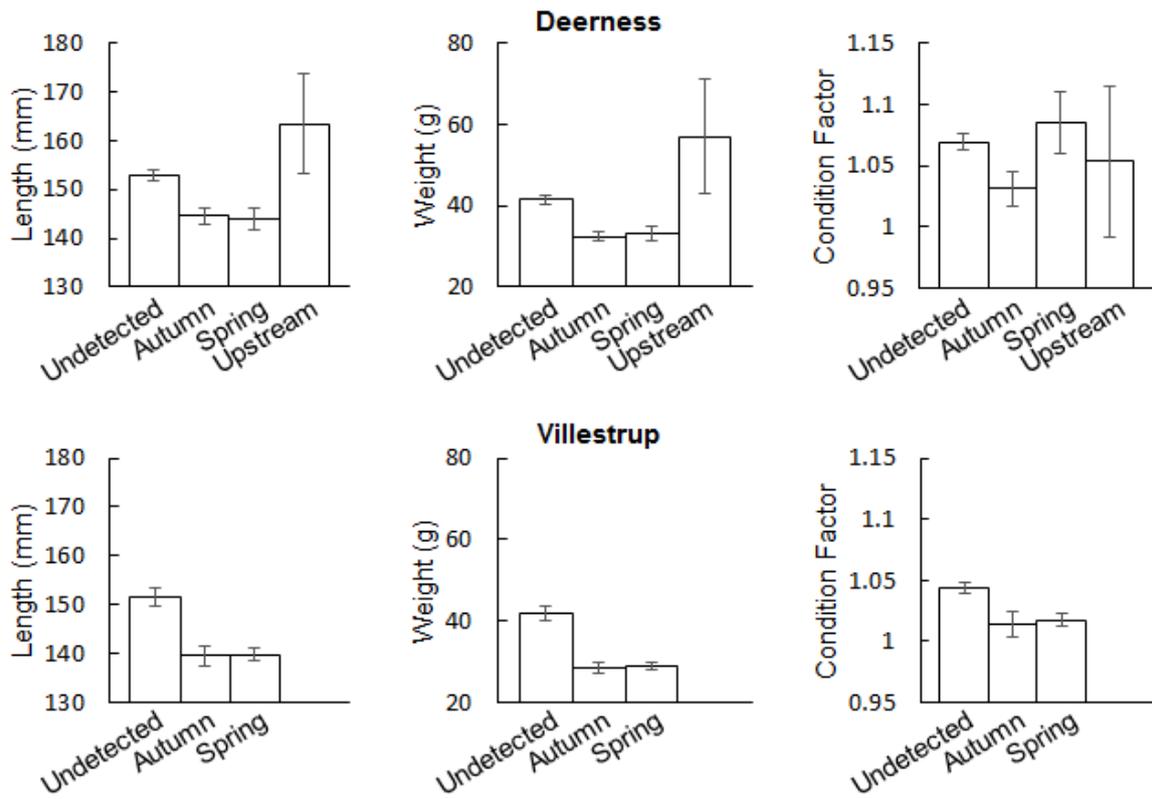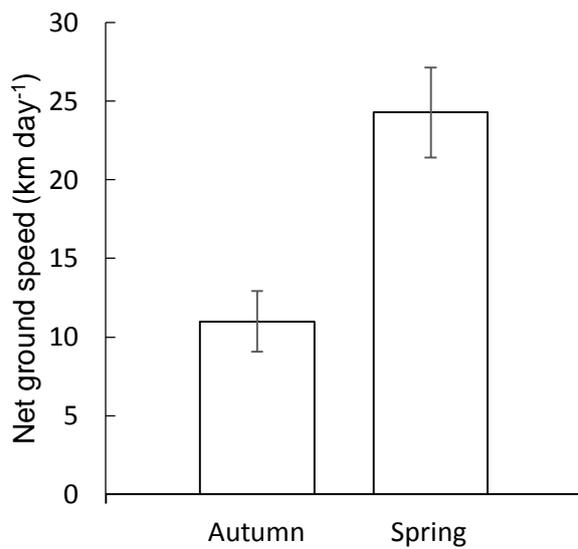
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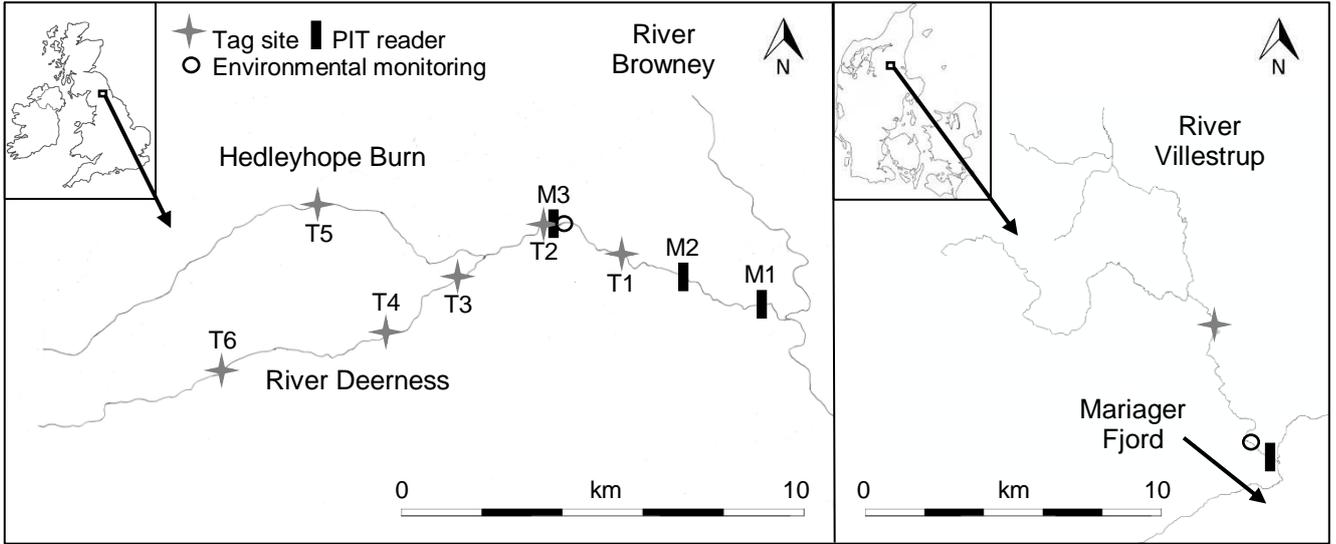
587   Fig. 2

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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^{-2})	Density '15 (n·100m^{-2})	%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

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

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

603
604

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

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

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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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$M$ (upstream) $= 7.25 - 2.26$(ln$D$)

644   ln$M$ (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).
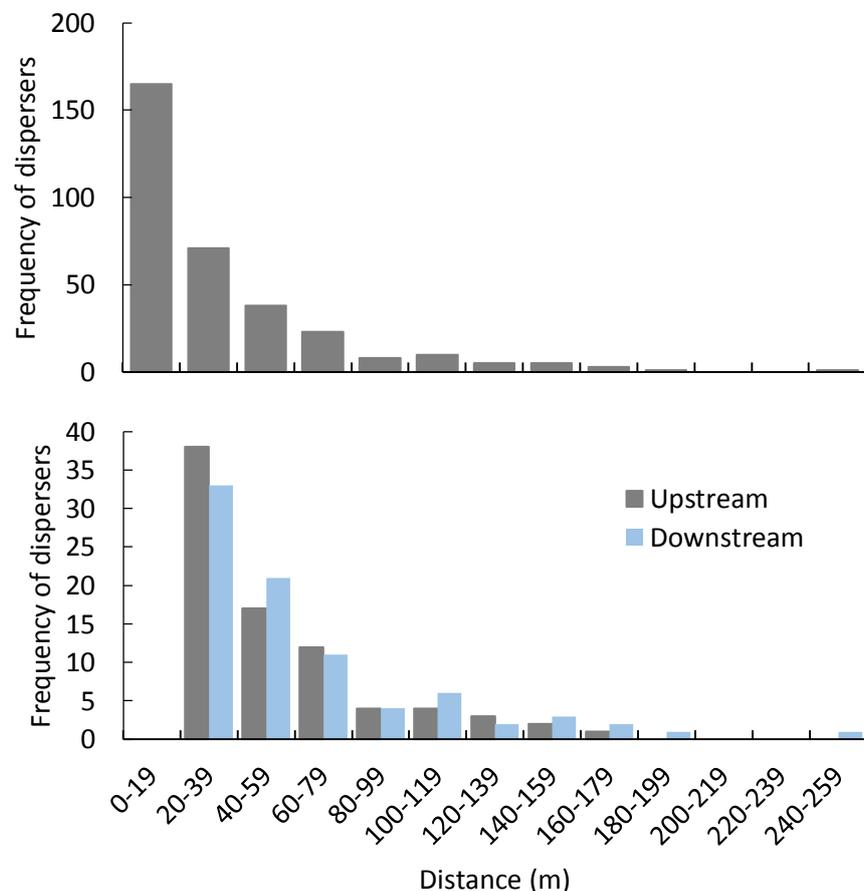

Fig. S1: Frequency distribution of the maximum longitudinal movements made
by trout from a previous release site (top), with upstream and downstream
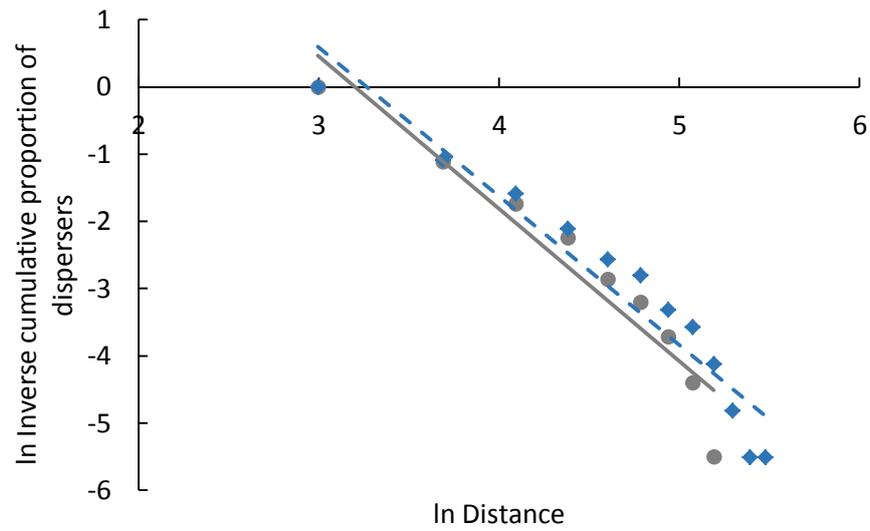movements separated (bottom), all study sites combined.

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

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References

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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.

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