Movements and dispersal of brown trout (*Salmo trutta* Linnaeus, 1758) in Mediterranean streams: influence of habitat and biotic factors

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Abstract Dispersal is a critical determinant of animal distribution and population dynamics, and is essential information for management planning. We studied the movement patterns and the influence of habitat and biotic factors on Mediterranean brown trout (*Salmo trutta*) by mark-recapture methods in three headwater streams of the Ebro Basin (NE Iberian Peninsula). Fish were sampled by electrofishing on five occasions over 18-24 months and movements of over 3,000 individually tagged trout (age 1+ onwards) were recorded. Most of the tagged fish exhibited limited movement and were recaptured within 100 m from the initial capture section. Small seasonal differences in the movement pattern were observed, but in two of the streams, displacement distances increased prior the spawning period in autumn. The frequency distributions of dispersal distances were highly leptokurtic and skewed to the right and fitted well to a two-group exponential model, thus trout populations were composed of mobile and stationary individuals, the latter being the predominant component in the populations (71.1 - 87.5 % of individuals). The mean dispersal distances, for fish captured at least in three sampling events, ranged 20.7 - 45.4 m for the stationary group and 229.4 - 540.5 m for the mobile group. Moving brown trout were larger than non-moving individuals and exhibited higher growth rates in two of the streams. Habitat features were not consistently linked to movement rates, but there were some interaction effects between stream and habitat characteristics such as depth, cover and water velocity.

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2   **Mediterranean streams: influence of habitat and biotic factors**

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13 **Abstract**

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15   essential information for management planning. We studied the movement patterns and the

16   influence of habitat and biotic factors on Mediterranean brown trout (*Salmo trutta*) by mark-

17   recapture methods in three headwater streams of the Ebro Basin (NE Iberian Peninsula). Fish

18   were sampled by electrofishing on five occasions over 18-24 months and movements of over

19   3,000 individually tagged trout (age 1+ onwards) were recorded. Most of the tagged fish

20   exhibited limited movement and were recaptured within 100 m from the initial capture section.

21   Small seasonal differences in the movement pattern were observed, but in two of the streams,

22   displacement distances increased prior the spawning period in autumn. The frequency

23   distributions of dispersal distances were highly leptokurtic and skewed to the right and fitted well

24   to a two-group exponential model, thus trout populations were composed of mobile and

25   stationary individuals, the latter being the predominant component in the populations (71.1 - 87.5

26   % of individuals). The mean dispersal distances, for fish captured at least in three sampling

27   events, ranged 20.7 - 45.4 m for the stationary group and 229.4 - 540.5 m for the mobile group.

28   Moving brown trout were larger than non-moving individuals and exhibited higher growth rates

29   in two of the streams. Habitat features were not consistently linked to movement rates, but there

30   were some interaction effects between stream and habitat characteristics such as depth, cover and

31   water velocity.

32   **Introduction**

33   Dispersal, defined as the movement of individuals between locations, is a key process that

34   allows fish to occupy the most suitable habitat for survival, growth and breeding by adapting to

35   both temporal and spatial changes in environmental or biotic conditions (Railsback et al., 1999;

36   Lucas & Baras, 2001). Fish movement can be highly variable between individuals, species and

37   streams (Rodríguez, 2002). Most research on fish dispersal in streams shows heterogeneous

38   populations comprising both sedentary and mobile individuals (Rodríguez, 2002; Rasmussen &

39   Belk, 2017). The movement distribution (*i.e.* distance moved *vs*. probability of occurrence) is

40   then best predicted by leptokurtic dispersal models which are characterized by high peaks

41   associated with the sedentary fish, and longer tails associated with a lower proportion of mobile

42   fish (Skalski & Gilliam, 2000; Rodríguez, 2002). This modelling framework has been applied to

43   describe the general movement patterns of fish and a predictive tool was recently developed

44   based on the positive correlation of movement distances with four variables: fish length, aspect

45   ratio of the caudal fin, stream size, and duration of the study (Radinger & Wolter, 2014). At a

46   local scale, both abiotic and biotic factors affect the degree of movement, variability and

47   dispersal rates. For instance, some studies have reported an increase in exploratory behaviour

48   (*i.e.* higher proportions of mobile fish) with decreasing habitat heterogeneity (Albanese,

49   Angermeier & Dorai-Raj, 2004; Heggenes et al., 2007); the presence of fish cover (*e.g.* woody

50   debris and boulders) has been related to a reduction in fish movement (Aparicio & Sostoa, 1999;

51   Harvey, Nakamoto & White, 1999); and population density has been positively linked to fish

52   movement rates (Hesthagen, 1988).

53   The mobility and dispersal patterns of brown trout *Salmo trutta* Linnaeus, 1758, have been

54   reported to be largely variable. Some populations are mainly sedentary (Northcote, 1992; Burrell

55   et al., 2000; Knouft & Spotila, 2002), while others are dominated by individuals that move

56   extensively (Clapp, Clark Jr & Diana, 1990; Meyers, Thuemler & Kornely, 1992; Ovidio et al.,

57   1998). The movement patterns of brown trout have been widely studied within its native range in

58   central and northern Europe, as well as in its introduced range in North America (see Rodríguez,

59   2002, and references therein), but the information on brown trout movements in rivers flowing to

60   the Mediterranean Sea, in its southern native range, is scarce. There is only a study in the Rhône

61   River focussed on the movements of age 0+ individuals (Vatland & Caudron, 2015). Brown trout

62   populations in the Mediterranean Basin are highly genetically differentiated from central and

63   northern Europe populations and are considered as distinct lineages (Bernatchez, 2001; Cortey,

64   Pla & García-Marín, 2004). These populations have experienced a marked decline in the last

65   decades due to stream habitat degradation (Benejam et al., 2016), overfishing (Almodóvar &

66   Nicola, 2004), and introgressive hybridization with hatchery stocks (Aparicio et al., 2005).

67   Climate change scenarios for the Mediterranean predict additional reductions in brown trout

68   distributional range, due to rising water temperatures (Almodóvar et al., 2012). Consequently,

69   there is an urgent need to develop sound conservation and management strategies for preserving

70   these populations. With increasing river fragmentation, quantifying the scale and magnitude of

71   Mediterranean brown trout dispersal patterns and determining the factors that drive these, are

72   necessary to optimize management planning.

73   The overall purpose of this study was to examine the movement patterns of brown trout

74   populations from three separate streams of a Mediterranean catchment of the Iberian Peninsula

75   and the influence of biotic and abiotic factors. The three study streams are small, have a high

76   gradient, and considerable habitat heterogeneity. When all habitats required to complete the

77   cycle of a fish's life-history are in spatial proximity, lower movement distances are expected

78   (Albanese, Angermeier & Dorai-Raj, 2004). Also, structural habitat complexity increases

79   protection from predators, refuge from disturbances (*e.g.* flooding) and prey availability,

80   reducing territory size and fish mobility (Heggenes et al., 2007; Závorka et al., 2015). The

81   objectives of this study were to employ mark-recapture approaches over a period of 18 – 24

82   months to determine (1) the degree of mobility (*i.e.* proportion of stationary and mobile

83   individuals) and extent of displacement distances, (2) seasonal variations in the pattern of

84   movements, and (3) the effect of habitat characteristics and biotic factors on trout movement.

85

86   **Materials and methods**

87

88   Study area

89   The marking and recapturing of individuals were conducted in three streams (Noguera

90   Pallaresa, Flamisell and Noguera Vallferrera) of the Segre River basin (Catalonia, NE Iberian

91   Peninsula) (Fig. 1). The Segre is the largest catchment in the Southern Pyrenees (265 km long,

92   22580 km^2 of basin area and about 100 $m^3 s^{-1}$ of average water flow), and is the main tributary of

93   the Ebro River, the river with the highest water flow in the Iberian Peninsula (annual mean is

94   about 426 $m^3 s^{-1}$) discharging into the Mediterranean Sea (for more details see Rovira, Alcaraz &

95   Ibáñez, 2012). A tributary of the Segre River is the Noguera Pallaresa River (154 km of length

96   and 37.1 $m^3 s^{-1}$ of average flow), where three different reaches were selected (Fig. 1): the main

97   stem (42° 44'N, 0° 58'E, hereafter NP) and two tributaries, the Flamisell (42° 27'N, 0° 59'E,

98   FLM) and the Noguera Vallferrera (42° 34'N, 1° 19'E, NV). The three reaches had a mean

99   stream width less than 10 m, showed a high gradient, and channel morphology consisted

100   primarily of pool-run-riffle sequences under a forest canopy. Physical characteristics of study

101   reaches are shown in Table 1. The hydrological regime is snow-fed, thus, the highest flows

102   generally occur in spring after snowmelt (Ebro Water Authority; http://www.chebro.es/). Brown

103   trout was the only fish species present and populations belong to the Mediterranean lineage

104   (Aparicio et al., 2005). During the study, sport fishing was closed in the study area.

105

106   Sampling design

107   Study reaches were continuous and ranged from 2400 m long in the NP, 1500 in the FLM to

108   1200 m long in the NV. The reaches were selected on the basis of being wadeable and the

109   absence of barriers to fish movement or significant tributaries within the study boundaries. Each

110   reach was divided into 25-40 m-long sections (mean length: 30.6 m ± 4.3 SD), the boundaries of

111   which usually coincided with habitat discontinuities in the channel morphology (pool-run-riffle

112   sequence). Brown trout were marked in October 1992 in NP and in March 1993 in NV and FLM.

113   Four subsequent mark-recapture sampling events were conducted in each reach: NP was sampled

114   in 1993 (May and October) and 1994 (July and October), and both NV and FLM reaches were

115   sampled in 1993 (July and October) and 1994 (July and October). Autumn surveys (October)

116   were performed just prior or at the beginning of the spawning season, which in the study area

117   occurs from the end of October to early December. Therefore, movement data from October

118   sampling included the possible fish displacements related to spawning. Sampling sections were

119   isolated with block nets (mesh size 5 mm) and three-pass electrofishing removal was conducted

120   in an upstream direction (500 V, 1.0 A pulsed DC). Captured fish were anaesthetised (MS-222

121   solution), measured for fork length (FL, mm), and weighed (g). Sex was determined externally

122   for mature individuals in autumn (*i.e.* October) surveys by the production of milt or visible

123 evidence of eggs beneath the body wall. The adipose fin was clipped on all captured fish, which

124 constituted a permanent batch mark to distinguish recaptured individuals.

125   All fish larger than 120 mm FL (corresponding at least to age 1+ individuals, see

126 Supplementary Figure 1-3) were tagged with uniquely coded Visible Implant Tags (VI-tags;

127 Northwest Marine Technology, Shaw Island, Washington, USA) in the adipose tissue posterior

128 to eye. Fish smaller than 120 mm were not tagged, because the tissue available for placing the

129 tag was too thin, thus leading to extremely low retention rates (Niva, 1995). After handling, fish

130 were allowed to recover from anaesthesia and released into the mid-point of the capture section.

131 In recapture surveys, each fish's VI-tag code was read, and those untagged fish larger than 120

132 mm FL (*i.e.* captured for the first time or having lost the VI-tag) were tagged following the

133 above procedure.

134   Habitat variables were measured along transects perpendicular to the flow at 10-m intervals.

135 Water depth and mean water velocity (at 0.6 times total water depth) were measured every 1m

136 along transects, and averaged for each section. For each transect, the percent cover of each

137 substrate category (Table 1) was visually estimated, averaged per section and an index of

138 substrate coarseness was derived for each section following Bain, Finn & Booke (1985). Fish

139 cover was estimated as the percentage area of a section covered by woody debris, rocks or

140 undercut banks.

141   Permission for electrofishing and capture of *S. trutta* individuals was approved by the

142 competent authorities: Departament de Medi Ambient i Habitatge de la Generalitat de Catalunya

143 (current Departament d'Agricultura, Ramaderia, Pesca, Alimentació i Medi Natural) (SF/602) of

144 the regional authorities of Catalonia.

145

146

147   Data analyses

148   Fish movement (*i.e.* distance covered) was measured from the midpoint of the recapture

149   section to the midpoint of its previous capture section. A movement distance of 0 m was

150   assigned to individuals captured and recaptured in the same section. Thus, the minimum

151   detectable movement was the distance between two or more sections (*i.e.* larger than 25-40 m).

152   Movement patterns were quantified using frequency distributions (two-tailed) of distances

153   moved. Positive values were assigned to upstream movements and negative values to

154   downstream movements. Mark-recapture studies are generally biased since long movements are

155   less frequently measured than short distances (Albanese, Angermeier & Gowan, 2003). To assess

156   this source of bias, all movement observations were weighted by determining the total possible

157   movements sampled for each distance and weighting the under-sampled distances (Porter &

158   Dooley, 1993; Albanese, Angermeier & Gowan, 2003). The movement distributions were not

159   significantly different after adjustment (Kolmogorov-Smirnov test, $P > 0.40$ for all comparisons),

160   suggesting a good study design (Porter & Dooley, 1993). Therefore, unweighted distributions

161   were used for all analyses.

162   Trout were classified as moving (individuals leaving the home section between sampling

163   events) and non-moving (sedentary individuals not leaving the home section) individuals.

164   Differences in distance covered by moving fish among streams and sampling events were

165   analysed with analysis of variance (two-way ANOVA). The kurtosis and skewness of the

166   frequency distribution of distances moved by brown trout were obtained with the package

167   *moments* (version 0.14) for program R, and were used as an indicator of individual level

168   variation in movement behaviour (Skalski & Gilliam, 2000). Dispersal range was estimated as

169   the distance between the two most distant sections in which an individual was recorded, and only

170   fish captured at least in three sampling events (elapsed time between first and last capture was 7

171   to 24 months) were included in the analyses. The frequency distribution of dispersal range was

172   fitted to a two-group exponential function (Rodriguez 2002):

$$f(x) = p\frac{\lambda_s}{2}e^{-\lambda_s x} + (1-p)\frac{\lambda_m}{2}e^{-\lambda_m x}$$

174   where x is the distance covered, λ_s correspond to the inverse of mean dispersal distance for the

175   stationary component, λ_m correspond to the inverse of mean dispersal distance for the mobile

176   component, p is the proportion of stationary individuals, and thus, 1- p is the proportion of

177   mobile individuals. Parameters p, λ_s and λ_m are estimated from movement data (see Rodriguez,

178   2002). Estimated movement parameters were then compared to the expected movement

179   parameters for stream-resident brown trout obtained with the package *fishmove* (version 0.3-3)

180   for program R, which models dispersal in relation to species, fish length, aspect ratio of the

181   caudal fin, stream size and duration of the study (Radinger & Wolter, 2014).

182   In order to examine the relationship between fish growth rate and movement, the specific

183   growth rate (SGR, in % day^{-1}) for a given fish in the summer period was calculated as SGR =

184   (ln(final fork length) – ln(initial fork length)) × 100 / (days between captures). Differences in the

185   growth rate–fork length relationship between moving and non-moving individuals were tested

186   with analysis of covariance (ANCOVA), for each stream. Software Pop/Pro 1.0 (Kwak, 1992)

187   was used to estimate population size per section and capture probability per size class (*i.e.* trout

188   smaller and larger than 120 mm) from the three-pass electrofishing data. Fish density

189   (individuals ha^{-1}) and biomass (kg ha^{-1}) per section were estimated by dividing number and

190   weight by the area sampled. Variations in fish density and biomass among streams were analysed

191   with multiple analysis of variance (MANOVA). MANOVA is used when several dependent

192   variables are measured on each sampling unit. MANOVA compares the mean vectors of k

193   groups; whereas equality of the mean vector implies that the k means are equal for each variable,

194   if two means differ for just one variable then we conclude that the mean vectors of the k groups

195   are different (Sokal & Rohlf, 1995). We used η^2 (eta squared) as a measure of effect size (i.e.

196   importance of factors). Similarly to r^2, η^2 is the proportion of variation explained for a certain

197   effect.

198   The effects of biotic and abiotic stream features of sampling sections on trout departure ratio

199   (defined as the proportion of individuals leaving section i from the total number of recaptures of

200   trout initially marked in section i) were analysed with Generalized Linear Models (GLMs). We

201   performed a global analysis including the three different streams, and then streams were analysed

202   separately. In each case, an information-theoretic approach was used to find the best

203   approximating models (Burnham & Anderson, 2002). GLMs were built including all possible

204   combinations of environmental and biotic variables, excluding interactions, due to the large

205   number of variables included. Two additional criteria were used to define the set of candidate

206   models: those performing significantly better than the null model and with a variance inflation

207   factor ≤ 5, in order to avoid multicollinearity effects. The second order Akaike Information

208   Criterion (AICc) was used to assess the degree of support for each candidate model. AICc was

209   rescaled to obtain ΔAICc values (ΔAICc = AICc$_i$ − minimum AICc), since models with ΔAICc $\leq$

210   2 have the most substantial support. The relative plausibility of each candidate model was

211   assessed by calculating Akaike's weights (w_i), which range from 0 to 1, and can be interpreted as

212   the probability that a given model is the best model in the candidate set. Because no model was

213   clearly the best one (*i.e.* $w_i \geq 0.9$) model-average regression coefficients were calculated using

214   the relative importance of each independent variable (Burnham & Anderson, 2002). Model-

215   averaged coefficients were compared with those from the full model to assess the impact of

216   model selection bias on parameter estimates. All data analyses were performed with R software

217   version 3.3.2.

218

219   **Results**

220   Recapture rates and VI-tag retention

221   A total of 13,340 individuals were captured and fin-clipped during the study period, and

222   7050 of them were larger than 120 mm FL and tagged (NP: 2201; FLM: 1181; NV: 3668). Mean

223   FL of tagged fish was 165.1 mm ± 34.7 SD in the NP, 162.8 mm ± 38.1 SD in the FLM and

224   183.0 mm ± 42.1 SD in the NV. Capture probabilities estimated from electrofishing depletion

225   surveys ranged from 0.40 to 0.88 ($\mu = 0.65$) for trout larger than 120 mm, and from 0.14 to 0.49

226   ($\mu = 0.38$) for individuals smaller than 120 mm. The proportion of the new trout individuals (*i.e.*

227   fish not fin-clipped) larger than 120 mm FL captured for the first time was similar among

228   streams and decreased sharply until the end of the study, with a maximum reduction of about 60

229   % between the first and the second sampling (Figure 2). The decline in the proportion of new

230   individuals smaller than 120 mm FL captured in the second survey was less pronounced (Figure

231   2), probably because of recruitment and reduced capturability. Despite the high recapture rates,

232   the recovery percentage of VI-tag (*i.e.* fish larger than 120 mm) was relatively low due to tag

233   loss. Overall, mean VI-tag retention rate was 45.0 % but varied in relation to fish size. Trout

234   smaller than 180 mm FL at tagging showed mean retention rates of 32.4 % whereas the rate was

235   74.9 % for trout larger than 240 mm FL.

236

237   Movements and dispersal patterns

238   Overall, movements of brown trout between consecutive sampling events were relatively

239   short since the 53.4 % (ranging between 48.1 and 54.4 %) of the total recaptures ($N = 3073$) were

240   in the same stream section of previous capture. When fish moving out from home section were

241   analysed separately, most of the displacements were between contiguous sections, and long-

242   range movements were infrequent; for instance, only the 2.18 % of the movements were over

243   400 m in NV, being 2.37 % in NP and 3.35 % in FLM. Distance covered by fish moving out

244   from home section was not significantly related to fork length (ANCOVA, $P > 0.29$ in all rivers)

245   or length × season interaction ($P > 0.15$), so an ANOVA was used. Distance covered by fish

246   showed significant temporal variations in both the NP (ANOVA, $F_{3,\ 426} = 4.49$, $P = 0.004$, $\eta^2 =$

247   0.24) and NV ($F_{3,\ 795} = 9.45$, $P < 0.0001$, $\eta^2 = 0.26$) streams, with trout covering larger distances

248   in autumn (Figure 3), but seasonal differences were not significant in the FLM stream ($F_{3,\ 198} =$

249   1.08, $P = 0.36$).

250   In the three streams the distance-frequency distributions were highly leptokurtic and skewed

251   to the right, the Kurtosis values were 28.9 for FLM, 19.6 for NV and 144.6 for NP. The two-

252   group exponential model provided a good fit to the frequency distributions of dispersal range

253   (Figure 4). Based on the estimates of p, the proportion of stationary individuals in the three

254   streams ranged from 71.1 to 87.5 % and, thus, the percentage of mobile individuals varied from

255   12.5 to 28.9 % (Table 2). The mean dispersal range, calculated as $1/\lambda$ (see methods), ranged

256   from 20.7 to 45.4 m for the stationary group and from 229.4 to 540.5 m for the mobile group

257   (Table 2). These dispersal ranges were similar to that expected by the general model for stream

258   resident brown trout estimated with *fishmove* package, which calculates a mean movement

259   distance of 25.1 m for the stationary group and 428.3 m for the mobile group.

260

261   Influence of biotic and abiotic factors on movements

262   Several biotic and abiotic factors were associated with brown trout movement patterns.

263   Overall, the information theoretic analysis of the candidate set of GLMs selected eight plausible

264   models (*i.e.* ΔAICc < 2) to explain variability in departure ratio (*i.e.* proportion of individuals

265   leaving section *i* from the total number of recaptures of trout initially marked in section *i*) in

266   relation to stream features. The best explanatory variables (SP values in Table 3), were water

267   depth, fish cover and fish biomass. Interestingly, fish biomass was preferentially selected over

268   density, despite the high correlation between them (Pearson's $r = 0.94$, $N = 246$, $P < 0.0001$). All

269   three variables (water depth, cover and biomass) were negatively related to departure ratio; in

270   contrast, organic substrate, water velocity, substrate coarseness and fish density had a positive

271   relationship with departure ratio. Season had the weakest relationship with trout departure ratio.

272   However, the lower correlation between observed and predicted values and larger parameters

273   bias indicated some differences among streams (Table 3, Supplementary Table 1). When

274   analysed separately by streams, similar patterns were observed, with some variations linked to

275   specific stream habitat characteristics (Table 1, Table 3). For instance, in the FLM stream where

276   higher departure ratios (ANOVA, $F_{2, 243} = 11.67$, $P < 0.0001$) and lower biomass and density

277   values (MANOVA, Wilks's $\lambda = 0.513$; $F_{4, 484} = 47.92$; $P < 0.0001$) were reported, physical

278   features (*i.e.* fish cover, substrate coarseness and water depth) and fish biomass were the best

279   explanatory variables. Seasonal variation in departure ratio confirmed previous observed results

280   (Figure 3); thus, while no seasonal differences were observed in the FLM stream, autumn

281   departure ratio (*i.e.* pre-spawn movements) was higher in the NV stream, and lower in the NP

282   stream. In the NV stream, along with fish biomass and season, the most important variable was

283   water velocity, all negatively related to departure ratio. In the NP stream, fish density and

284   biomass showed a contrasting pattern (Table 3), which might be explained by differences in fish

285   length, since NP fish were the smallest (ANOVA, $F_{2, 3070} = 184.60$, $P < 0.0001$).

286   Moving brown trout were significantly larger than non-moving individuals in the three

287   study streams ($P < 0.029$ and $\eta^2 > 0.16$, in all cases), but distances moved were not significantly

288   correlated with trout fork length ($P > 0.15$, in all cases). In both FLM and NV streams, specific

289   growth rate of moving trout ($\mu \pm$ standard error: 0.132 ± 0.006 % day^{-1} in the FLM and $0.057 \pm$

290   0.002 % day^{-1} in the NV) was significantly higher than non-moving trout (0.103 ± 0.005 and

291   0.050 ± 0.001 % day^{-1}) (ANCOVA, $F_{1, 242} = 5.73$, $P < 0.05$, $\eta^2 = 0.19$, in FLM, and $F_{1, 1262} =$

292   6.07, $P < 0.05$, $\eta^2 = 0.28$ in NV), but no significant differences were observed in the NP stream

293   (0.048 ± 0.002 % day^{-1} for moving fish and 0.052 ± 0.002 % day^{-1} for non-moving fish) ($F_{1, 327} =$

294   1.06, $P = 0.31$).

295

296   **Discussion**

297   Movements and dispersal patterns

298

299   Brown trout exhibited limited mobility and few fish performed long-range movements.

300   Between successive sampling events, a significant proportion of fish moved from their home

301   section, but most of them moved less than 100 m and settled in contiguous sections (*i.e.* adjacent

302   channel units). Individuals move in response to changing resource abundance and quality, thus

303   movement extent should depend on the distance to a suitable habitat (Fausch et al., 2002), with

304   longer movement distances presumably occurring when suitable habitats are widely spaced

305   (Wiens, 2001). Therefore, the low mobility exhibited by brown trout from this study could

306   indicate that the different habitats required to complete its life cycle are in spatial proximity

307 (Northcote, 1992; Gowan et al., 1994; Albanese, Angermeier & Dorai-Raj, 2004). Spatial habitat

308 heterogeneity is usually higher in small streams than in larger rivers, where habitat units are

309 more widely spaced (Gorman & Karr, 1978), and habitat heterogeneity reduces territory size and

310 mobility (Heggenes et al., 2007). Consequently, limited movements of no more than a few

311 hundred meters are frequently reported for trout populations in small streams (Heggenes, 1988;

312 Knouft & Spotila, 2002) when compared to those from large and long rivers, where longer

313 movements, up to several kilometres, have been observed (Clapp, Clark Jr & Diana, 1990;

314 Young, 1994; Zimmer, Schreer & Power, 2010). Therefore, the size of the study streams could

315 have influenced the limited range of movements observed (Woolnough, Downing & Newton,

316 2009).

317   Although there was substantial intra-population variation in movement behaviour, the

318 studied populations were dominated by stationary individuals, in concordance with most of the

319 studies on movement in stream salmonids (Rodriguez, 2002, and references therein). Our results

320 also match the estimated movement parameters (*i.e.* proportion of stationary and mobile

321 individuals, and mean dispersal distances) provided by predictive models for stream-resident

322 brown trout (Radinger & Wolter, 2014), for both the stationary and the mobile component. The

323 displacement range of the stationary component was less than 50 meters, and thus, is considered

324 as a restricted movement (Rodríguez, 2002). Despite being in low proportion, mobile individuals

325 are important since they are responsible for exchange between populations and successful

326 colonization of new habitats (Vera et al., 2010; Kennedy, Rosell & Hayes, 2012).

327   Many studies dealing with brown trout movements showed a seasonal increase in mobility

328 due to upstream spawning migration and downstream movement for overwintering (Clapp, Clark

329 Jr & Diana, 1990; Meyers, Thuemler & Kornely, 1992; Ovidio et al., 1998). Our results showed

330   temporal differences in the distance covered by moving fish, thus suggesting that seasonal

331   changes in environmental conditions or the reproductive cycle of fish affected trout movements.

332   There was an increase in distances moved in autumn surveys in both the NP and the NV stream,

333   just before the spawning period, although this cannot be considered a true spawning migration

334   because movement did not involve most of the population nor were distances moved long-range.

335   In streams where spawning sites are located in or near the rearing habitats, as occurred in the

336   studied reaches where gravel beds were widely distributed, spawning-related movements may be

337   minimal or involve short distances (Northcote, 1992; Nakamura, Maruyama & Watanabe,

338   2002).

339   Movement data were based on recaptured (*i.e.* surviving) tagged fish, thus several potential

340   sources of bias could have affected our results. For instance, VI-tag insertion and adipose fin

341   clipping may result in different behaviour or mortality rate compared to the non-tagged fish.

342   However, studies on salmonid species suggest that adipose fin clipping and VI tag insertion do

343   not affect condition, growth or survival (*e.g.* Bryan & Ney, 1994; Shepard et al., 1996), thus the

344   behaviour of tagged fish is representative of the population. Another potential source of bias

345   could be related to the relatively low percentage of VI-tags recovered, not only due to tag loss

346   but also to natural mortality, which is expected in a nearly two years study. Although it was not

347   measured, annual mortality for adult brown trout is estimated to be 43-72 % in similar Pyrenean

348   rivers (Gouraud et al., 2000). Tag loss may bias abundance estimates from mark-recapture

349   methods (Frenette & Bryant, 1996), but movement estimates are not biased since differences in

350   behaviour between tagged and tag-loss fish are not expected. Therefore, both mortality and tag

351   loss only affect movement estimates by reducing total data gathered, but this was avoided by

352   maximizing sample size increasing the number of fish tagged. Trout leaving the sampling area

353 probably also accounted for a percentage of missed recaptures, thus leading to an

354 underestimation of long-range movements (Gowan et al., 1994). However, the high proportion of

355 recaptures of fin-clipped fish suggests that the emigration from the study area was proportionally

356 low compared to the trout population monitored (Gowan et al., 1994).

357

358 Relationship of habitat and biotic factors with brown trout movements

359

360   Fish movements are mediated by biotic and abiotic factors affecting individual fitness

361 (Gowan et al., 1994; Railsback et al., 1999; Bélanger & Rodríguez, 2002). Our results showed

362 that departure ratio was not consistently linked to particular habitat features, suggesting that

363 movement behaviour probably does not depend on a single parameter but on a complex

364 combination and availability of several factors. For instance, fish inhabiting shallower sections in

365 the FLM stream showed higher departure ratios than those from deeper waters. Among the study

366 streams, the FLM had the lowest mean water depth, therefore deeper waters, which confer

367 greater protection against predators (Lonzarich & Quinn, 1995), were a valuable resource

368 motivating trout movement. In the same sense, sections with higher fish cover in the FLM and

369 NP stream showed lower departure ratios, probably because of the refugia provided from

370 predators and fast currents (Harvey, Nakamoto & White, 1999; Ayllón et al., 2014). Finally, the

371 negative effect of water velocity on departure ratio in the NV stream could be mediated by an

372 increase in prey delivery rate in high velocity areas (Leung, Rosenfeld & Bernhardt, 2009), thus

373 promoting residency.

374   Movements of stream fishes have been associated with fish size and growth rates. There is

375 evidence from previous studies that movement distances increase with fish length, particularly

376   for trout larger than 300-400 mm FL (Meyers, Thuemler & Kornely, 1992; Young, 1994; Quinn

377   & Kwak, 2011). In the three study streams moving fish were larger than non-moving trout, but

378   there was no relationship between distance moved and fish size. Results are probably skewed by

379   the scarcity of large fish, since only few individuals (< 0.5 %) exceeded 300 mm FL, or the fact

380   that large dominant fish could displace subordinate individuals, thus leading a movement

381   cascade of fish of all sizes and obscuring length-related patterns (Gowan & Fausch, 2002;

382   Railsback & Harvey, 2002). Mobility is energetically expensive and increases risk of predation

383   since fish have to move through unfamiliar space (Pépino, Rodríguez & Magnan, 2015).

384   Nevertheless, mobility appeared to confer an advantage on trout growth rate. Several authors

385   have reported that, when resources are scattered, mobile fish maximize food supply and

386   compensate energetic costs of movement, thus increasing growth rate (e.g. Hilderbrand &

387   Kershner, 2004; Závorka et al., 2015).

388

389   Management implications

390

391   Most of the remnant brown trout populations of the Mediterranean lineage are confined to

392   streams where many artificial in-stream barriers have been built for hydropower generation. For

393   example, more than 400 weirs and dams are distributed in the Spanish Pyrenean rivers (Espejo &

394   García, 2010), mainly for small-scale hydropower production. Barriers can restrict movement

395   pathways among critical habitats for spawning, feeding or refuge (Dunham, Vinyard & Rieman,

396   2011), thus stream longitudinal connectivity is a key consideration in the management and

397   conservation of the brown trout. The low rate of average movement at population level reported

398   here suggests that management of brown trout populations in headwater streams, similar to those

399   studied here, should focus on the conserving high quality habitats, whereas stream connectivity

400   may not be as critical since relatively small stream length may provide sufficient habitat to meet

401   all life-history needs. However, connectivity could become important when other anthropogenic

402   impacts are present or the population verges the threshold of the minimum viable size

403   (Hilderbrand & Kershner, 2011). Then, the importance of medium and long distance movements

404   may be higher for population persistence, by allowing fish to withstand locally unfavourable

405   conditions or favouring the recolonization after the disturbance (Fausch et al., 2009).

406   Finally, since brown trout is an important game species, in populations with limited

407   dispersal fishing regulations could exert a high influence on trout abundance. Overfishing and

408   depletion of fishery stocks seem more probable in stream reaches inhabited by trout populations

409   with low mobility because substantial immigration of new individuals or eventual displacement

410   of fish to safer areas (*i.e.* closed fishing reaches) are infrequent. To improve native trout

411   abundance in streams with significant fishing pressure, no-kill regulations are advised or, at least,

412   hardening existing regulations to avoid overexploitation.

413

414   **Acknowledgements**

418

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592

Table 1(on next page)

Stream features during the sampling period.

FLM: Flamisell, NP: Noguera Pallaresa, and NV: Noguera Vallferrera. Mean ± standard deviation, when necessary, is shown.

1

Variable	Stream		
	FLM	**NP**	**NV**
Length (m)	1500	2400	1200
Mean elevation (m)	1250	1780	1175
Mean slope (m km^{-1})	53.3	20.8	62.5
Mean base flow (m^3 s^{-1})	1.52	0.95	1.29
Temperature range (ºC)	4.2 – 15.3	0.1 – 15.1	2.5 – 15.4
pH range	7.3 – 8.9	7.4 – 8.8	6.7 – 8.1
Conductivity range (µS cm^{-1})	77 – 171	46 – 187	20 – 95
Mean stream width (m)	4.97 ± 1.39	4.34 ± 2.36	6.80 ± 1.09
Mean water depth (cm)	9.94 ± 4.66	20.02 ± 6.46	17.14 ± 2.77
Mean current velocity (m s^{-1})	0.66 ± 0.26	0.59 ± 0.27	0.70 ± 0.14
Mean bottom substrate (%)			
Boulders (> 256 mm)	31.47 ± 13.82	30.84 ± 18.74	48.87 ± 12.67
Cobble (65 – 256 mm)	34.14 ± 11.89	34.68 ± 15.17	32.45 ± 10.95
Gravel (2 – 65 mm)	15.01 ± 6.17	14.89 ± 10.37	7.69 ± 3.04
Sand (0.1 – 2 mm)	10.60 ± 4.23	10.77 ± 10.16	3.74 ± 3.04
Silt (< 0.1 mm)	3.45 ± 2.55	4.41 ± 4.54	2.04 ± 1.13
Organic	4.33 ± 3.04	4.13 ± 3.17	5.17 ± 3.01
Mean fish density (Ind. ha^{-1})	1345.9 ± 1322.2	1901.4 ± 989.3	3862.5 ± 1559.0
Mean fish biomass (Kg ha^{-1})	67.5 ± 59.8	107.8 ± 82.8	344.7 ± 182.7
Mean fish cover (%)	15.46 ± 8.81	10.18 ± 7.57	22.47 ± 6.52

2

Table 2(on next page)

Parameter estimates from the two-group exponential model to calculate the proportion of stationary (p) and mobile ($1 - p$) individuals, and mean dispersal range ($1/\lambda$) of brown trout population.

FLM: Flamisell, NP: Noguera Pallaresa, and NV: Noguera Vallferrera. λ (m^{-1}) is the inverse of the mean displacement range, lower values of λ correspond to more mobile individuals.

1

Stream	Population component	Proportion (%)	Parameter estimate	Mean dispersal range (m)
FLM	Stationary	87.5	$\lambda_s = 0.02201$	45.4
	Mobile	12.5	$\lambda_m = 0.00185$	540.5
NP	Stationary	85.6	$\lambda_s = 0.04184$	23.9
	Mobile	14.4	$\lambda_m = 0.00269$	371.7
NV	Stationary	71.1	$\lambda_s = 0.04822$	20.7
	Mobile	28.9	$\lambda_m = 0.00436$	229.4

2

Table 3 (on next page)

Model averaged parameter estimates, by means of an information theoretic approach, from GLMs analysis of the influence of stream features of sampling sections on brown trout departure ratio (see text for definition).

FLM: Flamisell, NP: Noguera Pallaresa, and NV: Noguera Vallferrera. Model-averaged regression coefficients (β) are parameter coefficients averaged by model weight (w_i) across all candidate models (ΔAICc < 2) in which the given parameter occurs; selection probability (SP) indicates the importance of an independent variable, and parameter bias is the difference between the averaged estimates (β) and the full model coefficients. The number (N) of candidate models (ΔAICc < 2) and Pearson's correlation coefficient (r) between observed and model predicted values are also shown.

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1

Model parameter	All Rivers Model N = 8; r = 0.47			FLM Model N = 3; r = 0.79			NP Model N = 12; r = 0.62			NV Model N = 5; r = 0.72		
	β	SP	Bias	β	SP	Bias	β	SP	Bias	β	SP	Bias
Intercept	74.999		0.237	-73.138		-0.227	4.288		4.772	91.815		0.030
Mean Depth (cm)	-1.442	1.000	-0.021	-2.745	1.000	-0.239	-0.123	0.208	-2.289	2.352	0.224	0.019
Fish Cover (%)	-1.109	1.000	-3.069	-1.772	1.000	0.242	-1.339	1.000	-0.396	-0.264	0.366	-0.239
Fish Biomass (kg ha^{-1})	-0.017	0.623	-0.782	-0.097	1.000	-0.515	-0.025	0.148	-3.881	-0.038	1.000	-1.123
Organic Substrate (%)	0.118	0.182	-5.555	1.246	0.126	-2.124	0.390	0.292	-2.289	0.761	0.464	0.104
Water Velocity (m s^{-1})	0.991	0.153	-10.204	-5.704	0.323	0.867	5.981	0.318	-0.923	-55.562	1.000	-0.214
Fish Density (Ind ha^{-1})	0.012	0.147	-29.545	*Not selected*			0.014	0.891	-1.178	*Not selected*		
Substrate Coarseness	0.305	0.104	6.702	46.146	1.000	0.021	2.951	0.339	-1.425	4.977	0.212	0.004
Pre Spawn Season	-0.125	0.077	2.550	*Not selected*			-9.752	1.000	0.112	14.314	1.000	-0.131

2

Figure 1

Map of the study area.

(A) Location of the study streams: Noguera Pallaresa (NP), Flamisell (FLM) and Noguera Vallferrera (NV). Location of the sampled stream reaches is highlighted with a rectangle. The photos show representative habitats in the streams sampled. (B) NP. (C) NV. (D) FLM.
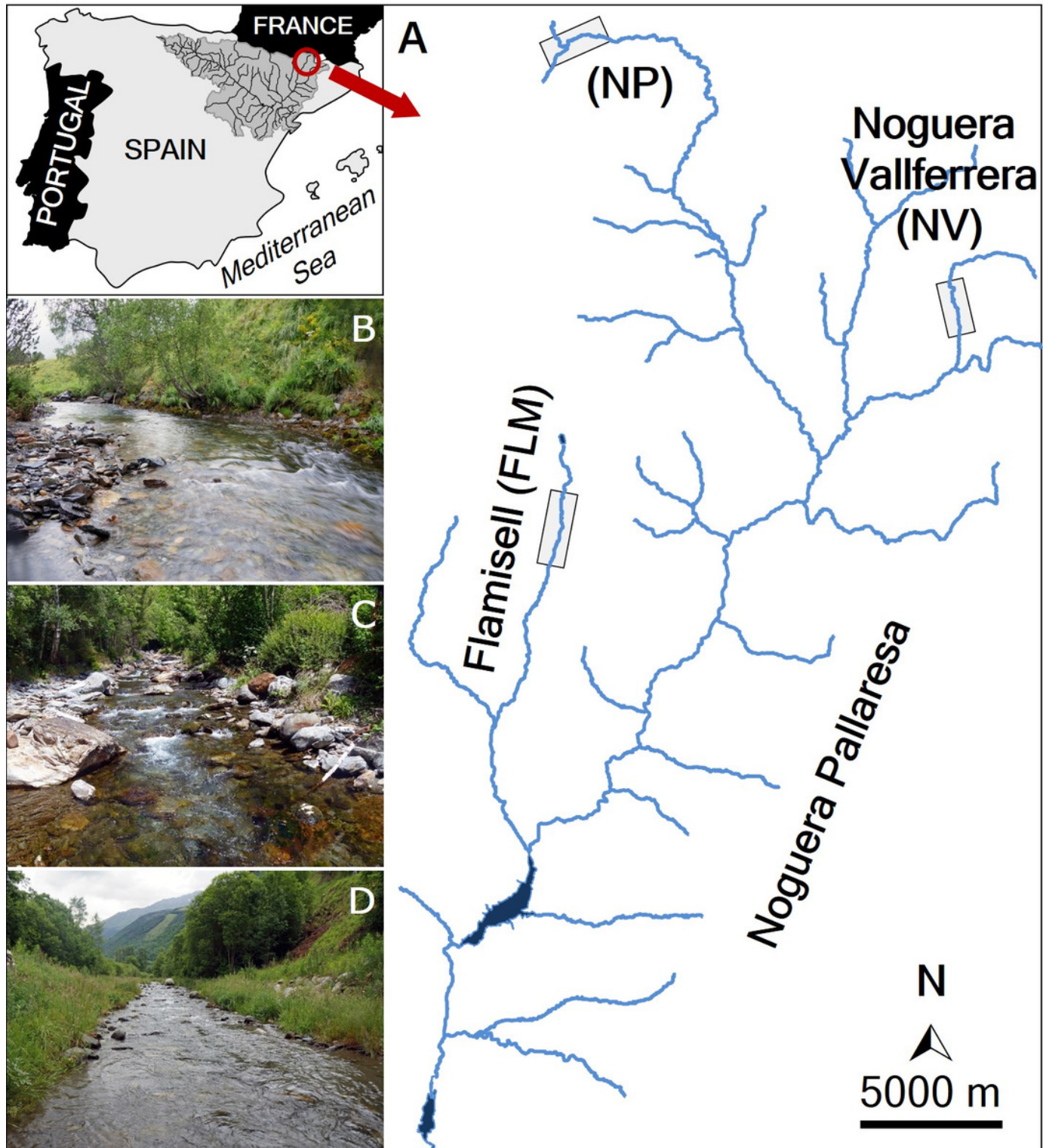
Figure 2

Evolution of the percentage of brown trout ≤120 mm fork length and >120 mm fork length captured for the first time (*i.e.* adipose fin not clipped), on each sampling event in the study streams.

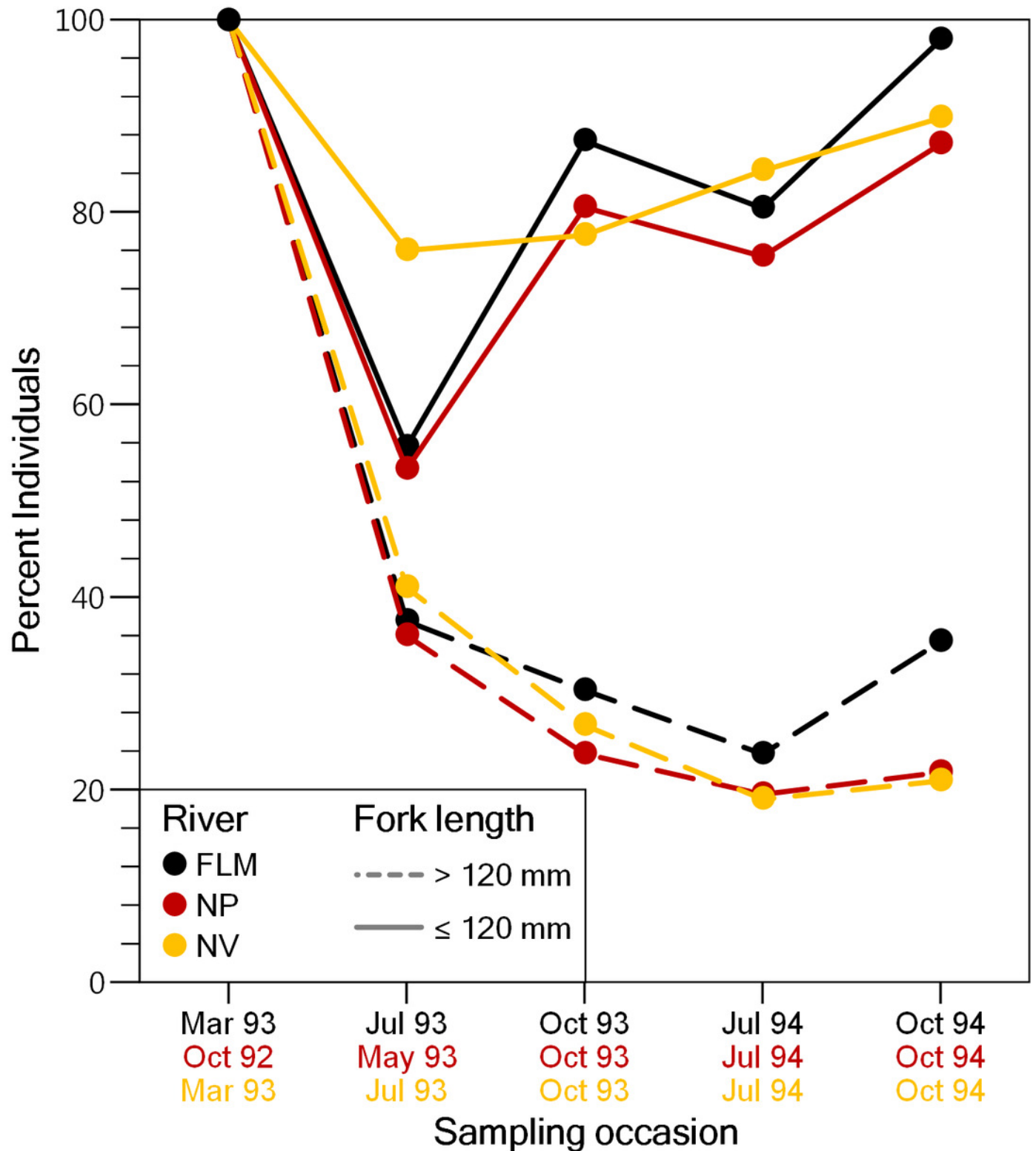FLM: Flamisell. NP: Noguera Pallaresa. NV: Noguera Vallferrera.

Figure 3

Box-plot of absolute distance moved, by brown trout individuals recaptured out from home section, per sampling occasion in the study streams.

The box corresponds to the 25th and 75th percentiles, the dark line inside the box represents the median, the error bars are the confidence intervals at the 95 % confidence level, and the filled circle is the mean. (A) Flamisell. (B) Noguera Pallaresa. (C) Noguera Vallferrera.
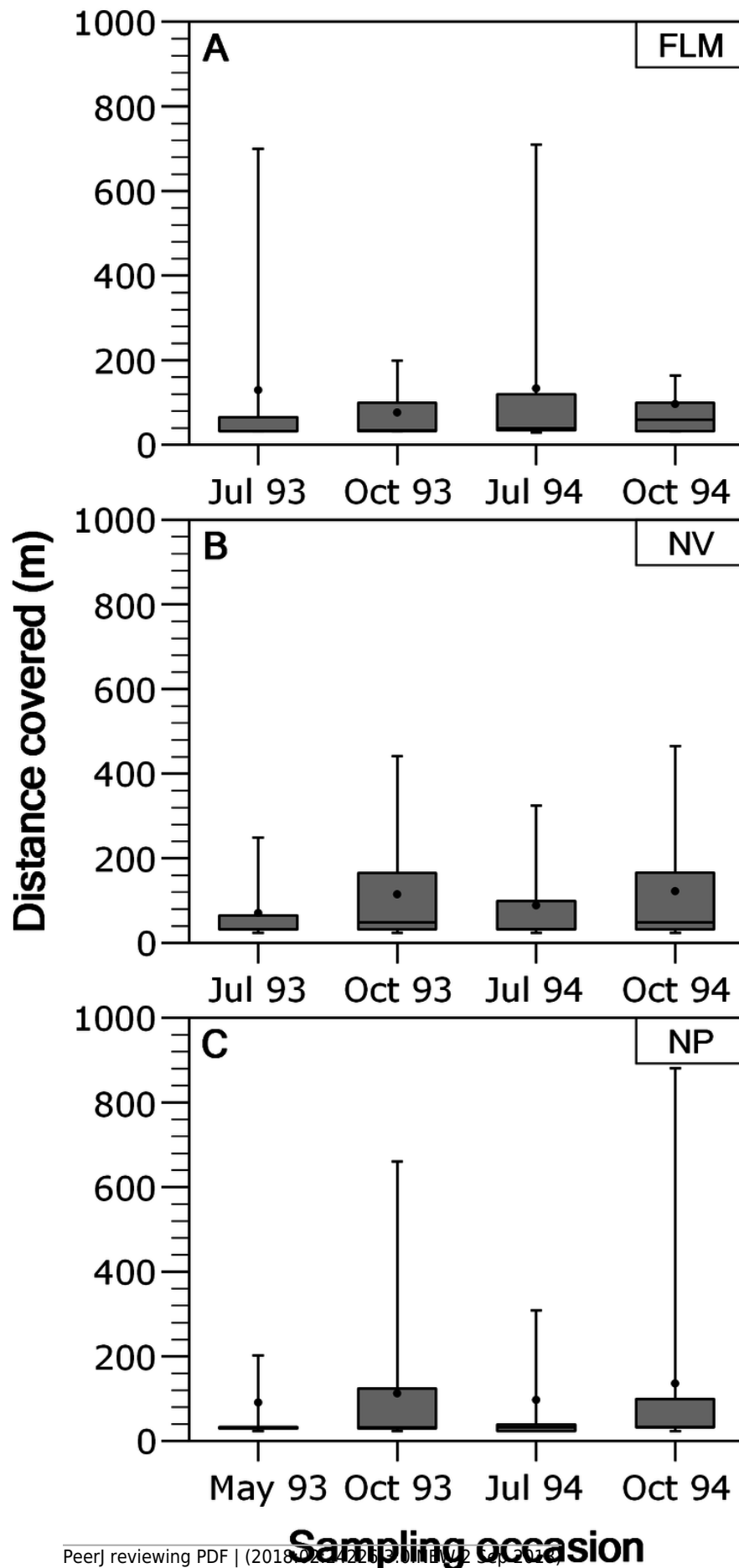
Figure 4

Brown trout frequency distributions of the dispersal range fitted with a two-group exponential model in the study streams.

The solid lines are the linear regression fits for the estimated stationary (open circles) and mobile (filled circles) components of the fish populations. Distance classes are calculated from absolute values of distance moved, y-axis is in logarithmic scale. (A) Flamisell. (B) Noguera Pallaresa. (C) Noguera Vallferrera.