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

Enric Aparicio[1] · Rafel Rocaspana[2] · Adolfo de Sostoa[3] · Antoni Palau-Ibars[4] · Carles Alcaraz[5]

[1] (✉) GRECO, Institute of Aquatic Ecology, University of Girona, E-17071 Girona, Catalonia, Spain. e-mail: enric.aparicio@gmail.com ORCID: 0000-0001-8810-0783

[2] Gesna Estudis Ambientals, S.L., Linyola, Catalonia, Spain

[3] Department of Animal Biology and Biodiversity Research Institute (IRBIO), University of Barcelona, Barcelona, Catalonia, Spain

[4] Department of Environment and Soil Sciences, University of Lleida, Lleida, Catalonia, Spain

[5] IRTA Marine and Continental Waters, Carretera Poble Nou Km 5.5, E-43540 Sant Carles de la Ràpita, Catalonia, Spain

14   **Abstract**

15   Dispersal is a critical determinant of animal distribution and population dynamics,

16   and is essential information for management planning. We studied the movement

17   patterns and the influence of habitat and biotic factors on Mediterranean brown trout

18   (*Salmo trutta*) by mark-recapture methods in three headwater streams of the Ebro Basin

19   (NE Iberian Peninsula). Fish were sampled by electrofishing on five occasions over 18-

20   24 months and movements of over 3,000 individually tagged trout (age 1+ onwards)

21   were recorded. Most of the tagged fish exhibited limited movement and were recaptured

22   within 100 m from the initial capture section. Small seasonal differences in the

23   movement pattern were observed, but in two of the streams, displacement distances

24   increased prior the spawning period in autumn. The frequency distributions of dispersal

25   distances were highly leptokurtic and skewed to the right and fitted well to a two-group

26   exponential model, thus trout populations were composed of mobile and

27   stationaryedentary individuals, the latter being the predominant component in the

28   populations (71.1 - 87.5 % of individuals). The mean dispersal distance, for fish

29   captured at least in three sampling events, ranged 20.7 - 45.4 m for the

30   stationaryedentary group and 229.4 - 540.5 m for the mobile group. Movingbile brown

31   trout were larger than non-movingmobile individuals and exhibited higher growth rates

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

33   but there were some interaction effects between stream and habitat characteristics such

34   as depth, cover and water velocity. The low mobility exhibited by Mediterranean brown

35   trout has important implications for developing conservation plans and fisheries

36   management.[A1]

Introduction

Dispersal, defined as the movement of individuals between locations, is a key process that allows fish to occupy the most suitable habitat for survival, growth and breeding by adapting to both temporal and spatial changes in environmental or biotic conditions (Railsback et al. 1999; Lucas and Baras 2001). Fish movement can be highly variable~~may exhibit considerable variation~~ between individuals, species and streams (Rodríguez 2002). Most research on fish dispersal in streams shows heterogeneous populations comprising both sedentary and mobile individuals (Rodriguez 2002; Rasmussen & Belk 2017). The movement distribution (*i.e.* distance moved *vs.* probability of occurrence) is then best predicted by leptokurtic dispersal models which are characterized by high peaks associated with the sedentary fish, and longer tails associated with a lower proportion of mobile fish (Skalski & Gilliam 2000; Rodríguez 2002). This modelling framework has been applied to describe the general movement patterns of fish and a predictive tool was recently developed based on the positive correlation of movement distances with four variables: fish length, aspect ratio of the caudal fin, stream size, and duration of the study (Radinger & Wolter 2014). At a local scale, both abiotic and biotic factors affect the degree of movement, variability and dispersal rates. For instance, some studies have reported an increase in exploratory behaviour (*i.e.* higher proportions of mobile fish) with decreasing habitat heterogeneity (Albanese et al. 2004; Heggenes et al. 2007); the presence of fish cover (*e.g.* woody debris and boulders) has been related to a reduction in fish movement (Aparicio & Sostoa 1999; Harvey et al. 1999); and population density has been positively linked to fish movement rates (Hesthagen 1988).

The mobility and dispersal patterns of brown trout *Salmo trutta* Linnaeus, 1758, have been reported to be largely variable~~, thus, while s~~. Some populations are mainly

62   sedentary (Northcote 1992; Burrell et al. 2000; Knouft and Spotila 2002), while others

63   ~~population~~ are dominated by individuals that move extensively (Clapp et al. 1990;

64   Meyers et al. 1992; Ovidio et al. 1998). The movement patterns of brown trout have

65   been widely studied within its native range in central and northern Europe, as well as in

66   its introduced range in North America (see Rodríguez 2002 and references therein), but

67   the information on brown trout movements in rivers flowing to the Mediterranean Sea,

68   in its southern native range, is scarce. There is only a study in the Rhône River focussed

69   on the movements of age 0+ individuals (Vatland & Caudron 2015). Brown trout

70   populations in the Mediterranean Basin are highly genetically differentiated from

71   central and northern Europe populations and are considered as distinct lineages

72   (Bernatchez, 2001; Cortey et al. 2004). These populations have experienced a marked

73   decline in the last decades due to stream habitat~~s~~ degradation (Benejam et al. 2016),

74   overfishing (Almodóvar & Nicola 2004), and introgressive hybridization with hatchery

75   stocks (Aparicio et al. 2005). Climate change scenarios for the Mediterranean

76   ~~additionally~~ predict a__dditional__ reduction__s__ in brown trout distribution__al__ range, due to

77   rising water temperatures (Almodóvar et al. 2012). Consequently, there is an urgent

78   need to develop sound conservation and management strategies for preserving these

79   populations. With increasing river fragmentation, quantifying the scale and magnitude

80   of Mediterranean brown trout dispersal patterns and determining the factors that drive

81   these, are necessary to optimize management planning.

82   The overall purpose of this study was to examine the movement patterns of ~~stream~~

83   ~~resident~~ brown trout populations from three separate streams of a Mediterranean

84   catchment of the Iberian Peninsula and the influence of biotic and abiotic factors. The

85   three study streams are small, have a high gradient__,__ and ~~the channel-unit habitats are~~

86   ~~close together, therefore displaying high~~ considerable habitat heterogeneity. When all

87   habitats required to complete the cycle of a fish's life-history are in spatial proximity,

88   lower movement distances are expected (Albanese et al. 2004). Also, structural habitat

89   complexity increases protection from predators, refuge from disturbances (*e.g.* flooding)

90   and prey availability, reducing territory size and fish mobility (Heggenes et al. 2007;

91   Závorka et al. 2015). The objectives of this study were to employ mark-recapture

92   approaches over a period of 18 – 24 months to determine (1) the degree of mobility (*i.e.*

93   proportion of stationary~~edentary~~ and mobile individuals) and extent of displacement

94   distances, (2) seasonal variations in the pattern of movements, and (3) the effect of

95   habitat characteristics and biotic factors on trout movement.

96

97   **Materials and methods**

98

99   Study area

100   The marking and recapturing of individuals were conducted in three streams

101   (Noguera Pallaresa, Flamisell and Noguera Vallferrera) of the Segre River basin

102   (Catalonia, NE Iberian Peninsula) (Fig. 1). The Segre is the largest catchment in the

103   Southern Pyrenees (265 km long, 22580 km^2 of basin area and about 100 $m^3 s^{-1}$ of

104   average water flow), and is the main tributary of the Ebro River, the river with the

105   highest water flow in the Iberian Peninsula (annual mean is about 426 $m^3 s^{-1}$)

106   discharging into the Mediterranean Sea (see Rovira et al. 2012 for more details). A

107   tributary of the Segre River is the Noguera Pallaresa River (154 km of length and 37.1

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

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

110   59'E, FLM) and the Noguera Vallferrera (42° 34'N, 1° 19'E, NV). The three reaches had

111   a mean stream width less than 10 m, showed a high gradient, and channel morphology

112   consisted primarily of pool-run-riffle sequences under a forest canopy. Physical

113   characteristics of study reaches are shown in Table 1. The hydrological regime is snow-

114   fed, thus, the highest flows generally occurs in spring after snowmelt (Ebro Water

115   Authority; http://www.chebro.es/). Brown trout was the only fish species present and

116   populations belong to the Mediterranean lineage (Aparicio et al. 2005). During the

117   study, sport fishing was closed in the study area.

118

119   Sampling design

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

121   the FLM and to 1200 m long in the FLM and in the NV, respectively[A2]. The reaches

122   were selected on the basis of being wadeable and the absence of barriers to fish

123   movement or significant tributaries within the study boundaries. Each reach was divided

124   into 25-40 m-long sections (mean length: 30.6 m ± 4.3 SD), the boundaries of which

125   usually coincided with habitat discontinuities in the channel morphology (pool-run-

126   riffle sequence). Brown trout were marked in October 1992 in NP and in March 1993 in

127   NV and FLM. Four subsequent mark-recapture sampling events were conducted in each

128   reach: NP was sampled in 1993 (May and October) and 1994 (July and October), and

129   both NV and FLM reaches were sampled in 1993 (July and October) and 1994 (July and

130   October). Autumn surveys (October) were performed just prior or at the beginning of

131   the spawning season, which in the study area occurs from the end of October to early

132   December. Therefore, movement data from October samplings included the possible

133   fish displacements related to spawning. Sampling sections were isolated with block nets

134   (mesh size 5 mm) and three-pass electrofishing removal were was conducted in an

135   upstream direction (500 V, 1.0 A pulsed DC). Captured fish were anaesthetised (MS-

136   222 solution), measured for fork length (FL, mm), and weighed (g). Sex was determined

137 externally for mature individuals in autumn (*i.e.* October) surveys by the production of

138 milt or visible evidence of eggs beneath the body wall. The adipose fin was clipped on

139 all captured fish, which constituted a permanent batch mark to distinguish recaptured

140 individuals.

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

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

143 tags; Northwest Marine Technology, Shaw Island, Washington, USA) in the adipose

144 tissue posterior to eye. Fish smaller than 120 mm were not tagged, because the tissue

145 available for placing the tag was too thin, thus leading to extremely low retention rates

146 (Niva 1995). After handling, fish were allowed to recover from anaesthesia and released

147 into the mid-point of the capture section. In recapture surveys, each fish's VI-tag code

148 was read, and those un~~not~~ tagged fish larger than 120 mm FL (*i.e.* captured for the first

149 time or having lost the VI-tag) were tagged following the above procedure.

150   Habitat variables were measured along transects perpendicular to the flow at 10-m

151 intervals. Water depth and mean water velocity (at 0.6 times total water depth) were

152 measured every 1m along transects, and averaged for each section. For each transect,

153 the percent cover of each substrate category (Table 1) was visually estimated, averaged

154 per section and an index of substrate coarseness was derived for each section following

155 Bain et al. (1985). Fish cover was estimated as the percentage area of a section covered

156 by woody debris, rocks or undercut banks.

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

158 the competent authorities: Departament de Medi Ambient i Habitatge de la Generalitat

159 de Catalunya (current Departament d'Agricultura, Ramaderia, Pesca, Alimentació i

160 Medi Natural) (SF/602) of the regional authorities of Catalonia.

161

162

163   Data analyses

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

165   recapture section to the midpoint of its previous capture section. A movement distance

166   of 0 m was assigned to individuals captured and recaptured in the same section. Thus,

167   the minimum detectable movement was the distance between two or more sections (*i.e.*

168   larger than 25-40 m). Movement patterns were quantified using frequency distributions

169   (two-tailed) of distances moved. Positive and negative values were assigned to upstream

170   and downstream movements, respectively. Mark-recapture studies are generally biased

171   since long movements are less frequently measured than short distances (Albanese et al.

172   2003). To assess this source of bias, all movement observations were weighted by

173   determining the total possible movements sampled for each distance and weighting the

174   under-sampled distances (Porter and Dooley 1993; Albanese et al. 2003). The

175   movement distributions were not significantly different after adjustment (Kolmogorov-

176   Smirnov test, $P > 0.40$ for all comparisons), suggesting a good study design (Porter and

177   Dooley 1993). Therefore, unweighted distributions were used for all analyses.

178   Trout were classified as ~~mobile~~ moving (individuals leaving the home section

179   between sampling events) and non-moving~~mobile~~ (sedentary individuals not leaving the

180   home section) individuals. Differences in distance covered~~moved~~ by moving~~bile~~ fish

181   among streams and sampling events were analysed with analysis of variance (two-way

182   ANOVA). The ~~lepto~~kurtosis and skewness of the frequency distribution of distances

183   moved by brown trout were obtained with the package *moments* (version 0.14) for

184   program R, and w~~ere~~as used as an indicator of individual level variation in movement

185   behaviour (Skalski and Gilliam 2000). Dispersal range was estimated as the distance

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

187 fish captured at least in three sampling _events_ (elapsed time between first and last

188 capture was 7 to 24 months) were included in the analyses. The frequency distribution

189 of dispersal range was fitted to a two-group exponential function (Rodriguez 2002):

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

191 where x is the distance covered, λ_s and λ_m correspond to the inverse of mean dispersal

192 distance for both the s_tationary_~~edentary~~ and mobile components, respectively, p is the

193 proportion of s_tationary_~~edentary~~ individuals, and thus, 1- p is the proportion of mobile

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

195 2002). Estimated movement parameters were then compared to the expected movement

196 parameters for stream-resident brown trout obtained with the package _fishmove_ (version

197 0.3-3) for program R, which models dispersal in relation to species, fish length, aspect

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

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

200 specific growth rate (SGR, in % day^{-1}) for a given fish in the summer period was

201 calculated as SGR = (ln(final fork length) – ln(initial fork length)) × 100 / (days

202 between captures). Differences in the growth rate–fork length relationship between

203 mo_ving_~~bile~~ and non-mo_ving_~~bile~~ individuals were tested with analysis of covariance

204 (ANCOVA), for each stream. Software Pop/Pro 1.0 (Kwak 1992) was used to estimate

205 population size~~s~~ per section _and capture probability per size class (i.e. trout smaller and_

206 _larger than 120 mm)_ from _the three-pass_ electrofishing ~~removal~~ data. Fish density

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

208 and weight by the area sampled. Variations in fish density and biomass among streams

209 were analysed with multiple analysis of variance (MANOVA). MANOVA is used when

210 several dependent variables are measured on each sampling unit. MANOVA compares

211 the mean vectors of k groups; whereas equality of the mean vector implies that the k

212   means are equal for each variable, if two means differ for just one variable then we

213   conclude that the mean vectors of the k groups are different (Sokal and Rohlf 1995). We

214   used η^2 (eta squared) as a measure of effect size (i.e. importance of factors). Similarly to

215   r^2, η^2 is the proportion of variation explained for a certain effect.

216   The effects of biotic and abiotic stream features of sampling sections on trout

217   departure ratio (defined as the proportion of individuals leaving section i from the total

218   number of recaptures of trout initially marked in section i) were analysed with

219   Generalized Linear Models (GLMs). We performed a global analysis including the three

220   different streams, and then streams were analysed separately. In each case, an

221   information-theoretic approach was used to find the best approximating models

222   (Burnham and Anderson, 2002). GLMs were built including all possible combinations

223   of environmental and biotic variables, excluding interactions, due to the large number of

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

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

226   inflation factor ≤ 5, in order to avoid multicollinearity effects. The second order Akaike

227   Information Criterion (AICc) was used to assess the degree of support for each

228   candidate model. AICc was rescaled to obtain ΔAICc values (ΔAICc = AICc$_i$ −

229   minimum AICc), since models with ΔAICc ≤ 2 have the most substantial support. The

230   relative plausibility of each candidate model was assessed by calculating Akaike's

231   weights (w_i), which range from 0 to 1, and can be interpreted as the probability that a

232   given model is the best model in the candidate set. Because no model was clearly the

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

234   the relative importance of each independent variable (Burnham and Anderson 2002).

235   Model-averaged coefficients were compared with those from the full model to assess

236   the impact of model selection bias on parameter estimates. All data analyses were

237   performed with R software version 3.3.2.

238

239   **Results**

240   Recapture rates and VI-tag retention

241   A total of 13340 individuals were captured and fin-clipped during the study period,

242   and 7050 of them were larger than 120 mm FL and tagged (NP: 2201; FLM: 1181; NV:

243   3668). Mean FL of tagged fish was 165.1 mm ± 34.7 SD in the NP, 162.8 mm ± 38.1

244   SD in the FLM and 183.0 mm ± 42.1 SD in the NV. ~~Estimated c~~Capture probabilities

245   estimated from electrofishing depletion surveys ranged from 0.40 to 0.88 ($\mu = 0.65$) for

246   trout larger than 120 mm, and from 0.14 to 0.49 ($\mu = 0.38$) for individuals smaller than

247   120 mm. The proportion of the new trout individuals (*i.e.* fish not fin-clipped) larger

248   than 120 mm FL captured for the first time was similar among streams and decreased

249   sharply until the end of the study, with a maximum reduction of about 60 % between the

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

251   individuals smaller than 120 mm FL captured in the second survey was less pronounced

252   (Figure 2), probably because of recruitment and reduced capturability. Despite the high

253   recapture rates, the recovery percentage of VI-tag (*i.e.* fish larger than 120 mm) was

254   relatively low due to tag loss. Overall, mean VI-tag retention rate was 45.0 % but varied

255   in relation to fish size. Trout smaller than 180 mm FL at tagging showed mean retention

256   rates of 32.4 % whereas the rate was 74.9 % for trout larger than 240 mm FL.

257

258   Movements and dispersal patterns

259   Overall, movements of brown trout between consecutive sampling events were

260   relatively short since the 53.4 ~~per cent~~% (ranging between 48.1 and 54.4 %) of the total

261 recaptures *(N = 3073)* were in the same stream section of previous capture. When fish

262 mov~~ed~~ing out from home section were analysed separately, most of the displacements

263 were between contiguous sections, and long-range movements were infrequent; for

264 instance, only the 2.18 ~~percent~~ % of the movements were over 400 m in NV, being 2.37

265 and 3.35 % in NP and FLM, respectively. Distance covered by fish moving out from

266 home section was not significantly related to fork length (ANCOVA, $P > 0.29$ in all

267 rivers) or length × season interaction ($P > 0.15$), so an ANOVA was used. Distance

268 covered by fish showed significant temporal variations in both the NP (ANOVA, $F_{3, 426}$

269 $= 4.49$, $P = 0.004$, $\eta^2 = 0.24$) and NV ($F_{3, 795} = 9.45$, $P < 0.0001$, $\eta^2 = 0.26$) streams,

270 with trout covering larger distances in autumn (Figure 3), but ~~not significant differences~~

271 ~~were observed~~ seasonal differences were not significant in the FLM stream ($F_{3, 198} =$

272 1.08, $P = 0.36$).

273   In the three streams the distance-frequency distributions were highly leptokurtic

274 and skewed to the right, the Kurtosis values were 28.9, 19.6 and 144.6 for FLM, NV

275 and NP, respectively. The two-group exponential model provided a good fit to the

276 frequency distributions of dispersal range (Figure 4). Based on the estimates of *p*, the

277 proportion of s~~edentary~~tationary individuals in the three streams ranged from 71.1 to

278 87.5 % and, thus, the percentage of mobile individuals varied from 12.5 to 28.9 %

279 (Table 2). The mean dispersal range, calculated as $1/\lambda$ (see methods), ranged from 20.7

280 to 45.4 m for the s~~edentary~~tationary group and from 229.4 to 540.5 m for the mobile

281 group (Table 2). These dispersal ranges were similar to that expected by the general

282 model for stream resident brown trout estimated with *fishmove* package, which

283 calculates a mean movement distance for the s~~edentary~~tationary and mobile groups of

284 25.1 and 428.3 m, respectively.

285

286 Influence of biotic and abiotic factors on movements

287 Several biotic and abiotic factors were associated ~~to~~ with brown trout movement

288 patterns. Overall, the information theoretic analysis of the candidate set of GLMs

289 selected eight plausible models (*i.e.* ΔAICc < 2) to explain variability in departure rat~~e~~io

290 (*i.e.* proportion of individuals leaving section *i* from the total number of recaptures of

291 trout initially marked in section *i*) in relation to stream features. The best explanatory

292 variables (SP values in Table 3), were water depth, fish cover and fish biomass.

293 Interestingly, fish biomass was preferentially selected over density, despite the high

294 correlation between them (Pearson's $r = 0.94$, $N = 246$, $P < 0.0001$)[A3]. All three

295 variables (water depth, cover and biomass) were negatively related to departure rat~~e~~io;

296 in contrast, organic substrate, water velocity, substrate coarseness and fish density had a

297 positive relationship with departure rat~~e~~io. Season had the weakest relationship with

298 trout departure rat~~e~~io. However, the lower correlation between observed and predicted

299 values and larger parameters bias indicated some differences among streams (Table 3,

300 Supplementary Table 1). When analysed separately by streams, similar patterns were

301 observed, with some variations linked to specific stream habitat characteristics (Table 1,

302 Table 3). For instance, in the FLM stream where higher departure rat~~es~~ios (ANOVA, $F_{2,}$

303 $_{243} = 11.67$, $P < 0.0001$) and lower biomass and density values (MANOVA, Wilks's $\lambda =$

304 0.513; $F_{4, 484} = 47.92$; $P < 0.0001$) were reported, physical features (*i.e.* fish cover,

305 substrate coarseness and water depth) and fish biomass were the best explanatory

306 variables. Seasonal variation in departure rat~~e~~io confirmed previous observed results

307 (Figure 3); thus, while no seasonal differences were observed in the FLM stream, ~~pre-~~

308 ~~spawn~~autumn departure rat~~e~~io (*i.e.* pre-spawn movements) was higher in the NV

309 stream, and lower in the NP stream. In the NV stream, ~~together to~~along with fish

310 biomass and season, the most important variable was water velocity, ~~both~~ all negatively

311 related to departure rat~~ioe~~. In the NP stream, fish density and biomass showed a

312 contrasting pattern (Table 3), which might be explained by differences in fish length,

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

314 Mo~~ving~~bile brown trout were significantly larger than ~~non- mobile~~ non-moving

315 individuals in the three study streams ($P < 0.029$ and $\eta^2 > 0.16$, in all cases), but

316 distances moved were not significantly correlated with trout fork length ($P > 0.15$, in all

317 cases). In both FLM and NV streams, specific growth rate of mo~~ving~~bile trout ($\mu \pm$

318 standard error: 0.132 ± 0.006 and 0.057 ± 0.002 % day^{-1}, in the FLM and NV

319 respectively) was significantly higher than non-mo~~ving~~bile trout (0.103 ± 0.005 and

320 0.050 ± 0.001 % day^{-1}) (ANCOVA, $F_{1, 242} = 5.73$, $P < 0.05$, $\eta^2 = 0.19$, in FLM, and $F_{1,}$

321 $_{1262} = 6.07$, $P < 0.05$, $\eta^2 = 0.28$ in NV), but no significant differences were observed in

322 the NP stream (0.048 ± 0.002 and 0.052 ± 0.002 % day^{-1}, for mo~~ving~~bile and non-

323 moving fish respectively) ($F_{1, 327} = 1.06$, $P = 0.31$).

324

Discussion

326 Movements and dispersal patterns

327

328 Brown trout exhibited limited mobility and few fish performed long-range

329 movements. Between successive sampling events, a significant proportion of fish ~~leave~~

330 moved ~~out~~ from their home section, but most of them moved less than 100 m and settled

331 in contiguous sections (*i.e.* adjacent channel units). ~~Movement of i~~Individuals move in

332 response ~~are responses~~ to changing resource abundance and quality, thus movement

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

334 longer movement distances presumably occurring when suitable habitats are widely

335 spaced (Wiens 2001). Therefore, the low mobility exhibited by brown trout from this

336 study could indicate that the different habitats required to complete its life cycle are in

337 spatial proximity (Northcote 1992; Gowan et al. 1994; Albanese et al. 2004). Spatial

338 habitat heterogeneity is usually higher in small streams than in larger rivers, where

339 habitat units are more widely spaced (Gorman and Karr 1978), and habitat

340 heterogeneity reduces territory size and mobility (Heggenes et al. 2007). Consequently,

341 limited movements of no more than a few hundred meters are frequently reported for

342 trout populations in small streams (Heggenes 1988; Knouft and Spotila 2002) when

343 compared to those from large and long rivers, where longer movements, up to several

344 kilometres, have been observed (Clapp et al. 1990; Young 1994; Zimmer et al. 2010).

345 Therefore, the size of the study streams could have influenced the limited range of

346 movements observed (Woolnough et al. 2009).

347 ~~Movement of brown trout followed a leptokurtic distribution, thus indicating a~~

348 Although there was substantial intra-population variation in movement behaviour, ~~*i.e.*~~

349 ~~populations include both stationary~~edentary~~ and mobile individuals. T~~the studied

350 populations were dominated by stationary~~edentary~~ individuals, in concordance with

351 most of the studies on movement in stream salmonids (Rodriguez 2002 and references

352 therein). Our results also match the estimated movement parameters [A4]provided by

353 predictive models for stream-resident brown trout (Radinger & Wolter 2014), for both

354 the stationary~~edentary~~ and the mobile component. The displacement range of the

355 stationary~~edentary~~ component was less than 50 meters, and thus, is considered as a

356 restricted movement (Rodriguez 2002). Despite being in low proportion, ~~the~~ mobile

357 individuals are importan~~ce~~t ~~of mobile individuals is decisive~~ since they are responsible

358 for exchange between populations and successful colonization of new habitats (Vera et

359 al. 2010; Kennedy et al. 2012).

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

361   mobility due to upstream spawning migration and downstream movement for

362   overwintering (Clapp et al. 1990; Meyers et al. 1992; Ovidio et al. 1998). Our results

363   showed temporal differences in the distance covered by mo~~ving~~bile fish, thus

364   suggesting that seasonal changes in environmental conditions or the reproductive cycle

365   of fish affected trout movements. There was an increase in distances moved in autumn

366   surveys in both the NP and the NV stream, just before the spawning period, although

367   this cannot be considered a true spawning migration because movement did not involve

368   most of the population nor were distances moved ~~were of~~ long-range. In streams where

369   spawning sites are located in or near the rearing habitats, as occurred in the studied

370   reaches where gravel beds were widely distributed, spawning-related movements may

371   be minimal or involve short distances (Northcote 1992; Nakamura et al. 2002).

372   Movement data ~~was~~ were based on recaptured (*i.e.* surviving) tagged fish, thus several

373   potential sources of bias could have affected our results. For instance, VI-tag insertion

374   and adipose fin clipping may result in different behaviour or mortality rate compared to

375   the non-tagged fish. However, studies on salmonid species suggest that adipose fin

376   clipping and VI tag insertion do not affect condition, growth or survival (*e.g.* Coombs et

377   al. 1990; Bryan & Ney 1994; Shepard et al. 1996), thus the behaviour of tagged fish is

378   representative of the population. Another potential source of bias could be related to the

379   relatively low percentage of VI-tags recovered, not only due to tag loss but also to

380   natural mortality, which is expected in a nearly two years study. Although it was not

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

382   Pyrenean rivers (Gouraud et al. 1999). Tag loss may bias abundance estimates from

383   mark-recapture methods (Frenette & Bryant, 2011), but movement estimates are not

384   biased since differences in behaviour between tagged and tag-loss fish are not expected.

385   Therefore, both mortality and tag loss only affect movement estimates by reducing total

386   data gathered, but this was avoided by maximizing sample size increasing the number

387   of fish tagged. Trout leaving the sampling area probably also accounted for a percentage

388   of missed recaptures, thus leading to an underestimation of long-range movements

389   (Gowan et al., 1994). However, our results agree with those obtained from the

390   predictive model included in the *fishmove* [A5]package; thus, the possible

391   underestimation of true dispersal distances did not appear to greatly affect our results.

392   Furthermore, the high proportion of recaptures of fin-clipped fish suggests that the

393   emigration from the study area was proportionally low compared to the trout population

394   monitored (Gowan et al. 1994).

395

396   Relationship of habitat and biotic factors with brown trout movements

397

398   Fish movements are mediated by biotic and abiotic factors affecting individual

399   fitness (Gowan et al. 1994; Railsback et al. 1999; Bélanger and Rodríguez 2002). Our

400   results showed that departure ratioe was not consistently linked to particular habitat

401   features, which suggestsing that movement behaviour probably does not depend on a

402   single parameter but on a complex combination and availability of several factors. For

403   instance, fish inhabiting shallower sections in the FLM stream showed higher departure

404   ratioses than those from deeper waters. Among the study streams, the FLM had the

405   lowest mean water depth, therefore deeper waters, which confer greater protection

406   against predators (Lonzarich and Quinn 1995), were a valuable resource motivating

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

408   stream showed lower departure ratioses, probably because of the refugia provided from

409   predators and fast currents (Harvey et al. 1999; Ayllón et al. 2014). Finally, the negative

410   effect of water velocity on departure rat~~io~~<u>io</u> in the NV stream could be mediated by an

411   increase in prey delivery rate in high velocity areas (Leung et al. 2009), thus promoting

412   residency.

413   Movements of stream fishes have been associated with fish size and growth rates.

414   There is evidence from previous studies that movement distances increase with fish

415   length, particularly for trout larger than 300-400 mm FL (Meyers et al. 1992; Young

416   1994; Quinn and Kwak 2011). In the three study streams mo<u>ving</u>~~bile~~ fish were larger

417   than non-<u>moving</u>~~mobile~~ trout, but there was no relationship between distance moved

418   and fish size. Results are probably skewed by the scarcity of large fish, since only few

419   individuals (< 0.5 %) exceeded 300 mm FL, or the fact that large dominant fish could

420   displace subordinate individuals, thus leading a movement cascade of fish of all sizes

421   and obscuring length-related patterns (Gowan and Fausch 2002; Railsback and Harvey

422   2002). Mobility is energetically expensive and increases risk of predation since fish

423   have to move through unfamiliar space (Pépino et al. 2015). Nevertheless, mobility

424   appeared to confer an advantage on trout growth rate. Several authors have reported

425   that, when resources are scattered, mobile fish maximize food supply and compensate

426   energetic costs of movement, thus increasing growth rate (e.g. Hilderbrand and

427   Kershner 2004; Závorka et al. 2015).

428

429   Management implications

430

431   Most of the remnant brown trout populations of the Mediterranean lineage are confined

432   to streams where many artificial in-stream barriers have been built for hydropower

433   generation. For example, more than 400 weirs and dams are distributed in the Spanish

434   Pyrenean rivers (Espejo & García, 2010), mainly for small-scale hydropower

435   production. Barriers can restrict movement pathways among critical habitats for

436   spawning, feeding or refuge (Dunham et al. 2011), thus stream longitudinal connectivity

437   is a key consideration in the management and conservation of the brown trout. The low

438   rate of average movement at population level reported here suggests that management

439   of brown trout populations in headwater streams, similar to those studied here, should

440   focus on the conserving high quality habitats, whereas stream connectivity may not be

441   as critical since relatively small stream length may provide sufficient habitat to meet all

442   life-history needs. However, connectivity could become important when other

443   anthropogenic impacts are present or the population verges the threshold of the

444   minimum viable size (Hilderbrand & Kershner, 2011). Then, the importance of medium

445   and long distance movements may be higher for population persistence, by allowing

446   fish to withstand locally unfavourable conditions or favouring the recolonization after

447   the disturbance (Fausch et al. 2009).

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

449   dispersal fishing regulations could exert a high influence on trout abundance.

450   Overfishing and depletion of fishery stocks seem more probable in stream reaches

451   inhabited by trout populations with low mobility because substantial immigration of

452   new individuals or eventual displacement of fish to safer areas (*i.e.* closed fishing

453   reaches) are infrequent. To improve native trout abundance in streams with significant

454   fishing pressure, no-kill regulations are advised or, at least, hardening existing

455   regulations to avoid overexploitation[A6].

456

460   are grateful to the anonymous reviewers for their feedback which was very helpful in

461   improving the manuscript.

462

463   **References**

464   Albanese, B., Angermeier, P.L. & Gowan, C. 2003. Designing mark–recapture studies

465   to reduce effects of distance weighting on movement distance distributions of

466   stream fishes. Transactions of the American Fisheries Society 132:925–939.

467   DOI:10.1577/T03-019

468   Albanese, B., Angermeier, P.L. & Dorai-Raj, S. 2004. Ecological correlates of fish

469   movement in a network of Virginia streams. Canadian Journal of Fisheries and

470   Aquatic Sciences 61: 857–869. DOI: 10.1139/f04-096

471   Almodóvar, A. & Nicola, G.G. 2004. Angling impact on conservation of Spanish

472   stream-dwelling brown trout *Salmo trutta*. Fisheries Management and Ecology 11:

473   173–182. DOI: 10.1111/j.1365-2400.2004.00402.x

474   Almodóvar, A., Nicola, G. G., Ayllón, D. and Elvira, B. 2012. Global warming

475   threatens the persistence of Mediterranean brown trout. Global Change Biology, 18:

476   1549–1560. DOI:10.1111/j.1365-2486.2011.02608.x

477   Aparicio, E., García-Berthou, E., Araguas, R.M, Martínez, P. & García-Marín, J.L.

478   2005. Body pigmentation pattern to assess introgression by hatchery stocks in

479   native *Salmo trutta* from Mediterranean streams. Journal of Fish Biology 67: 931–

480   949. DOI: 10.1111/j.1095-8649.2005.00794.x

481   Ayllón, D., Nicola, G. G., Parra, I., Elvira, B. and Almodóvar, A. (2014), Spatio-

482   temporal habitat selection shifts in brown trout populations under contrasting

483   natural flow regimes. Ecohydrology, 7: 569–579. DOI:10.1002/eco.1379

484   Bain, M.B., Finn, J.T. & Booke, H.E. 1985. Quantifying stream substrate for habitat

485   analysis studies. North American Journal of Fisheries Management 5: 499–500.

486   DOI: 10.1577/1548-8659(1985)5<499:QSSFHA>[A7]2.0.

487   Bélanger, G. & Rodríguez, M.A. 2002. Local movement as a measure of habitat quality

488   in stream salmonids. Environmental Biology of Fishes 64: 155-164. DOI:

489   10.1023/A:1016044725154.

490   Benejam, L., Saura-Mas, S., Bardina, M., Solà, C., Munné, A. and García-Berthou, E.

491   2016. Ecological impacts of small hydropower plants on headwater stream fish:

492   from individual to community effects. Ecology of Freshwater Fish, 25: 295–306.

493   DOI:10.1111/eff.12210

494   Bernatchez, L. 2001. The evolutionary history of brown trout (*Salmo trutta* L.) inferred

495   from phylogeographic, nested clade and mismatch analyses of mitochondrial DNA

496   variation. Evolution 55, 351–379. DOI: 10.1554/0014-

497   3820(2001)055[0351:TEHOBT]2.0.CO;2

498   Burnham, K.P. & Anderson D.R. 2002. Model Selection and Multimodel Inference: A

499   Practical Information-Theoretic Approach. New York: Springer-Verlag.

500   Burrell, K.H., Isely, J.J., Bunnell Jr, D.B., Van Lear, D.H. & Dolloff, C.A. 2000.

501   Seasonal movement of brown trout in a southern Appalachian river. Transactions of

502   the American Fisheries Society 129: 1373–1379. DOI: 10.1577/1548-

503   8659(2000)129<1373:SMOBTI>2.0

504   Clapp, D.F., Clark Jr, R.D. & Diana, J.S. 1990. Range, activity, and habitat of large,

505   free-ranging brown trout in a Michigan stream. Transactions of the American

506   Fisheries Society 119: 1022–1034. DOI: 10.1577/1548-

507   8659(1990)119<1022:RAAHOL>2.3.CO;2

508   Cortey, M., Pla, C., & Garcia-Marin, J. L. 2004. Historical biogeography of

509   Mediterranean trout. Molecular Phylogenetics and Evolution 33: 831–844.

510   DOI:10.1016/J.YMPEV.2004.08.012

511   Espejo, C. & García, R. 2010. Agua y energía: producción hidroeléctrica en España.

512   Investigaciones Geográficas 51: 107–129.

513   Fausch KD, Torgersen CE, Baxter CV, Li HW. 2002. Landscapes to riverscapes:

514   bridging the gap between research and conservation of stream fishes. BioScience.

515   52:483498

516   Fausch, K.D., Rieman, B.E., Dunham, J.B., Young, M.K. & Peterson, D.P. 2009.

517   Invasion versus isolation: trade-offs in managing native salmonids with barriers to

518   upstream movement. Conservation Biology 23: 859–870. DOI: 10.1111/j.1523-

519   1739.2008.01159.x

520   Gorman, O.T. & Karr, J.R. 1978. Habitat structure and stream fish communities.

521   Ecology 59: 507–515. DOI: 10.2307/1936581

522   Gowan, C., Young, M.K., Fausch, K.D. & Riley, S.C. 1994. Restricted movement in

523   resident stream salmonids: A paradigm lost? Canadian Journal of Fisheries and

524   Aquatic Sciences 51: 2626–2637. DOI: 10.1139/f94-262

525   Gowan, C. & Fausch, K.D. 2002. Why do foraging stream salmonids move during

526   summer? Environmental Biology of Fishes 64:139-153. DOI:

527   10.1023/A:1016010723609

528   Harcup, M.F., Williams, R. & Ellis, D.M. 1984. Movements of brown trout, *Salmo*

529   *trutta* L., in the River Gwyddon, South Wales. Journal of Fish Biology 24: 415–

530   426. DOI: 10.1111/j.1095-8649.1984.tb04812.x

531   Harvey, B.C., Nakamoto, R.J. & White. J.L. 1999. Influence of large woody debris and

532   a bankfull flood on movement of adult resident coastal cutthroat trout

533   (*Oncorhynchus clarki*) during fall and winter. Canadian Journal of Fisheries and

534   Aquatic Sciences 56: 2161-2166. DOI: 10.1139/f99-154

535   Hasegawa, K. 2017. Displacement of native white-spotted charr *Salvelinus leucomaenis*

536   by non-native brown trout *Salmo trutta* after resolution of habitat fragmentation by

537   a migration barrier. Journal of Fish Biology, 90: 2475–2479.

538   DOI:10.1111/jfb.13320

539   Heggenes, J. 1988. Effect of experimentally increased intraspecific competition on

540   sedentary adult brown trout (*Salmo trutta*) movement and stream habitat choice.

541   Canadian Journal of Fisheries and Aquatic Sciences 45: 1163-1172. DOI:

542   10.1139/f88-139

543   Heggenes, J., Omholt, P.K., Kristiansen, J.R., Sageie, J., Økland, F., Dokk, J.G. &

544   Beere, M.C. 2007. Movements by wild brown trout in a boreal river: response to

545   habitat and flow contrasts. Fisheries Management and Ecology 14: 333–342. DOI:

546   10.1111/j.1365-2400.2007.00559.x.

547   Hesthagen, T. 1988, Movements of brown trout, *Salmo trutta*, and juvenile Atlantic

548   salmon, *Salmo salar*, in a coastal stream in northern Norway. Journal of Fish

549   Biology 32: 639-653. DOI:10.1111/j.1095-8649.1988.tb05404.x

550   Hilderbrand, R.H. & Kershner, J.L. 2004. Are there differences in growth and condition

551   between mobile and resident cutthroat trout? Transactions of the American

552   Fisheries Society 133:1042-1046. DOI: 10.1577/T03-015.1

553   Hilderbrand, R.H. & Kershner, J.L. 2011. Conserving Inland Cutthroat Trout in Small

554   Streams: How Much Stream is Enough?, North American Journal of Fisheries

555   Management, 20: 513-520, DOI: 10.1577/1548-

556   8675(2000)020<0513:CICTIS>2.3.CO;2

557   Dunham, J.B., Vinyard G.L. & Rieman, B.E. 2011. Habitat Fragmentation and

558   Extinction Risk of Lahontan Cutthroat Trout. North American Journal of Fisheries

559   Management, 17: 1126-1133. DOI: 10.1577/1548-

560   8675(1997)017<1126:HFAERO>2.3.CO;2

561   Kennedy, R. J., Rosell, R. and Hayes, J. 2012. Recovery patterns of salmonid

562   populations following a fish kill event on the River Blackwater, Northern Ireland.

563   Fisheries Management and Ecology, 19: 214–223. doi:10.1111/j.1365-

564   2400.2011.00819.x

565   Knouft, J.H. & Spotila, J.R. 2002. Assessment of movements of resident stream brown

566   trout, *Salmo trutta* L., among contiguous sections of stream. Ecology of Freshwater

567   Fish 11: 85–92. DOI: 10.1034/j.1600-0633.2002.110203.x

568   Kwak, T.J. 1992. Modular microcomputer software to estimate fish population

569   parameters, production rates and associated variance. Ecology of Freshwater Fish

570   1:73-75. DOI: 10.1111/j.1600-0633.1992.tb00009.x

571   Leung, E.S., Rosenfeld, J.S. & Bernhardt, J.R. 2009. Habitat effects on invertebrate drift

572   in a small trout stream: implications for prey availability to drift-feeding fish.

573   Hydrobiologia, 623: 113-125. DOI: 10.1007/s10750-008-9652-1

574   Lonzarich, D.G. & Quinn, T.P. 1995. Experimental evidence for the effect of depth and

575   structure on the distribution, growth, and survival of stream fishes. Canadian

576   Journal of Zoology 73: 2223–2230. DOI: 10.1139/z95-263

577   Lucas, M.C. & Baras, E. 2001. Migration of Freshwater Fishes. Oxford: Blackwell

578   Science.

579   Meyers, L.S., Thuemler, T.F. & Kornely, G.W. 1992. Seasonal movements of brown

580   trout in northeast Wisconsin. North American Journal of Fisheries Management 12:

581   433–441. DOI: 10.1577/1548-8675(1992)012<0433:SMOBTI>2.3.CO;2

582 Nakamura, T., Maruyama, T. & Watanabe, S. 2002. Residency and movement of

583   stream-dwelling Japanese charr, *Salvelinus leucomaenis*, in a central Japanese

584   mountain stream. Ecology of Freshwater Fish 11: 150–157. DOI: 10.1034/j.1600-

585   0633.2002.00014.x

586 Niva, T. 1995. Retention of visible implant tags by juvenile brown trout. Journal of Fish

587   Biology, 46: 997–1002. DOI:10.1111/j.1095-8649.1995.tb01404.x

588 Northcote, T. 1992. Migration and residence in stream salmonids-some ecological

589   considerations and evolutionary consequences. Nordic Journal of Freshwater

590   Research 67: 5–17.

591 Ovidio, M., Baras, E., Goffaux, D., Birtles, C. & Philippart, J.C. 1998. Environmental

592   variability rules the autumn migration of brown trout (*Salmo trutta*) in the Belgian

593   Ardennes. Hydrobiologia 371/372: 263–274. DOI: 10.1023/A:1017068115183

594 Pépino M., Rodríguez M.A., Magnan, P. 2015. Shifts in movement behavior of

595   spawning fish under risk of predation by land-based consumers, Behavioral

596   Ecology, 26: 996–1004. DOI: 10.1093/beheco/arv038

597 Porter, J.H. & Dooley, J.L. 1993. Animal dispersal patterns: a reassessment of simple

598   mathematical models. Ecology 74: 2436-2443. DOI: 10.2307/1939594

599 Quinn, J.W. & Kwak, T.J. 2011. Movement and survival of brown trout and rainbow

600   trout in an Ozark Tailwater river. North American Journal of Fisheries Management

601   31: 299–304. DOI: 10.1080/02755947.2011.576204

602 Radinger, J. & Wolter, C. 2014. Patterns and predictors of fish dispersal in rivers. Fish

603   and Fisheries, 15: 456–473. DOI:10.1111/faf.12028

604 Railsback, S.F., Lamberson, R.H., Harvey, B.C. & Duffy, W.E. 1999. Movement rules

605   for individual-based models of stream fish. Ecological Modelling 123: 73–89.

606   DOI:10.1016/S0304-3800(99)00124-6

607   Railsback, S.F. & Harvey, B.C. 2002. Analysis of habitat-selection rules using an

608   individual-based model. Ecology 83: 1817-1830. DOI: 10.1890/0012-

609   9658(2002)083[1817:AOHSRU]2.0.CO;2

610   Rasmussen J.E. & Belk, M.C. 2017. Individual Movement of Stream Fishes: Linking

611   Ecological Drivers with Evolutionary Processes. Reviews in Fisheries Science &

612   Aquaculture, 25: 70-83. DOI: 10.1080/23308249.2016.1232697

613   Rodríguez, M. 2002. Restricted movement in stream fish: the paradigm is incomplete,

614   not lost. Ecology 83: 1–13. DOI: 10.2307/2680115

615   Rovira, A., Alcaraz, C. & Ibanez C.2012. Spatial and temporal dynamics of suspended

616   load at-a-cross-section: The lowermost Ebro River (Catalonia, Spain). Water

617   research 46: 3671–3681. DOI: 10.1016/j.watres.2012.04.014

618   Skalski, G.T. & Gilliam, J.F. 2000. Modelling diffusive spread in a heterogeneous

619   population: A movement study with stream fish. Ecology 81:1685-1700. DOI:

620   10.1890/0012-9658(2000)081[1685:MDSIAH]2.0.CO;2

621   Sokal, R.R. & Rohlf F.J. 1995. Biometry: the principles and practice of statistics in

622   biological research. Freeman, New York

623   Van Houdt, J.K.J., Pinceel, J., Flamand, M.C., Briquet M., Dupont, E., Volckaert,

624   F.A.M & Baret P.V. 2005. Migration barriers protect indigenous brown trout

625   (*Salmo trutta*) populations from introgression with stocked hatchery fish.

626   Conservation Genetics 6: 175-191. DOI: 10.1007/s10592-004-7822-x

627   Vatland, S. & Caudron, A. 2015. Movement and early survival of age-0 brown trout.

628   Freshwater Biology, 60: 1252–1262. DOI:10.1111/fwb.12551

629   Vera, M, Sanz, N, Hansen, MM, Almodóvar, A & García-Marín, JL. 2010. Population

630   and family structure of brown trout, *Salmo trutta*, in a Mediterranean stream.

631   Marine and Freshwater Research, 61: 672-681. DOI: 10.1071/MF09098

632   Wiens, J.A. 2001. The landscape context of dispersal. *In* Dispersal. Edited by J. Clobert,

633   E. Danchin, A.A. Dhondt, and J.D. Nichols. Oxford University Press, New York.

634   pp. 97–109.

635   Woolnough, D.A., Downing, J.A. & Newton, T.J. 2009. Fish movement and habitat use

636   depends on water body size and shape. Ecology of Freshwater Fish 18: 83–91.

637   DOI: 10.1111/j.1600-0633.2008.00326.x

638   Young, M.K. 1994. Mobility of brown trout in southcentral Wyoming streams.

639   Canadian Journal of Zoology 72:2078–2083. DOI: 10.1139/z94-278

640   Závorka, L., Aldvén, D., Näslund, J., Höjesjö, J. & Johnsson, J.I. 2015. Linking lab

641   activity with growth and movement in the wild: explaining pace-of-life in a trout

642   stream. Behavioral Ecology, 26: 877-884. DOI: 10.1093/beheco/arv029

643   Zimmer, M., Schreer, J.F. & Power, M. 2010. Seasonal movement patterns of Credit

644   River brown trout (*Salmo trutta*). Ecology of Freshwater Fish, 19: 290–299. DOI:

645   10.1111/j.1600-0633.2010.00413.x

646