

This is a post-peer-review, pre-copyedit version of an article published in Ichthyological Research. The final authenticated version is available online at: https://doi.org/10.1007/s10228-022-00866-1

Springer Nature terms of use for archived accepted manuscripts (AMs) of subscription articles at:

https://www.springernature.com/gp/open-research/policies/accepted-manuscript-terms

Document downloaded from:



1	Life history traits of Mediterranean brown trout (Salmo trana complex) in Pyrenean
2	headwater streams
3	
4	Enric Aparicio ¹ · Rafel Rocaspana ² · Antoni Palau-Ibars ³ · Adolfo de Sostoa ⁴ · Carles
5	Alcaraz ⁵
6	
7	¹ GRECO, Institute of Aquatic Ecology, University of Girona, E-17071 Girona, Catalonia,
8	Spain
9	² Gesna Estudis Ambientals, S.L., Linyola, Catalonia, Spain
10	³ Department of Environment and Soil Sciences, University of Lleida, Lleida, Catalonia,
11	Spain
12 13	⁴ Department of Animal Biology and Biodiversity Research Institute (IRBIO), University of Barcelona, Barcelona, Catalonia, Spain
14	⁵ IRTA Marine and Continental Waters, Carretera Poble Nou Km 5.5, E-43540 La Ràpita,
15	Catalonia, Spain
16	
17	⊠ Carles Alcaraz
18	carles.alcaraz@gmail.com // carles.alcaraz@irta.cat
19	
20	Enric Aparicio (Co-corresponding Author)
21	enric.aparicio@gmail.com
22	
23	
24	
25	Running head: Trout life history in Pyrenean streams

Abstract

26

27

28

29

30

31

32

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47

The Mediterranean brown trout (Salmo trutta complex) is native to basins draining to the Western Mediterranean Sea, and natural populations are currently declining in abundance and distribution due to habitat degradation and introgression with stocked trout of the Atlantic lineage. Data on its life history traits is limited, although is an essential first step in developing effective conservation and management strategies. We studied age, growth and reproduction of Mediterranean brown trout from three headwater streams in northeast Iberian Peninsula. The maximum observed fork length was 382 mm in males and 322 mm in females, and six age groups (from 1+ to 6+) were identified. There was large variation in the backcalculated lengths for individual fish within ages. The von Bertalanffy growth curves were similar among streams and comparable to other European populations from small streams, but growth rate was lower when compared to larger and more productive rivers. Overall, sexual maturation began at age 1+, and the estimated L_{50} was 136 mm for males and 150 mm for females. Monthly variations in the gonadosomatic index showed that spawning occurred between late autumn and early winter, mainly in November and December. Mean fecundity and egg diameter were positively correlated with fish length, and values were within the typical range reported in other brown trout populations. Most of the differences among streams can be explained by differences in water temperature. This results constitute a contribution to better understanding of key aspects Mediterranean brown trout biology, and to develop conservation and management strategies for preserving their populations.

Keywords: Size at maturity · Growth rate · Fecundity · Age determination · Salmonidae

Introduction

48

49

50

51

52

53

54

55

56

57

58

59

60

61

62

63

64

65

66

67

68

69

70

71

72

The brown trout Salmo trutta L. 1758 is a polytypic species of Salmonidae family distributed over a wide geographic range, spanning Europe, Western Asia and North Africa (Jonsson and Jonsson 2011). The species is distributed as a mosaic of at least five evolutionary lineages. which evolved in geographic isolation and remained largely allopatric since the Pleistocene (Bernatchez 2001). Furthermore, the evolutionary history of brown trout is characterized by the different latitudinal impact of paleoclimatic events (e.g., glaciations) on population isolation, colonization events and secondary contacts between lineages (Bernatchez 2001; Rossi et al. 2019). Because of the complex evolutionary history of brown trout, its taxonomic status is still unclear and needs further revision (Kottelat and Freyhof 2007); in recent taxonomic revisions Salmo trutta is considered a species complex (e.g., Rossi et al. 2019; Splendiani et al. 2019). Originally, brown trout from the western Mediterranean basins (eastern Spain and southern France) are considered of Mediterranean lineage (Berrebi et al. 2000; Sanz 2017). However, in the last century, the genetic integrity has been compromised due to massive restocking for angling, mainly with individuals of the Atlantic lineage (Araguas et al. 2017). Both Mediterranean and Atlantic lineages differ in many aspects, not only genetic but also behavioural, reproductive, and phenotypic characteristics such as ornamentation (e.g., Aparicio et al. 2005; Benhaim et al. 2013; Gil et al. 2015). Mediterranean lineage populations are strictly riverine and complete their entire life-cycle in freshwater (Doadrio et al. 2011). The biology of brown trout has been largely studied because of its value as a recreational fishing resource and the diversity of life-history traits, but most research has focused on Atlantic lineage (e.g., Jonsson 1985; Jonsson and L'Abée-Lund 1993; Elliott 1994; Crisp 2000; Nicola and Almodóvar 2002). Consequently, information on the life history characteristics of Mediterranean brown trout populations is still limited, and only some

ecological data are available (e.g., Champigneulle et al. 2003; Larios-López et al. 2015;
Aparicio et al. 2018; Rocaspana et al. 2019). Mediterranean brown trout populations are
currently declining mainly due to habitat degradation (Benejam et al. 2016), overfishing, and
hybridization with non-native trout of the Atlantic lineage (Berrebi et al. 2000; Aparicio et al.
2005). In addition, an increase in water temperature due to climate change is likely to reduce
its distributional range (Almodóvar et al. 2012). Hence, a better understanding of life history
traits is an essential first step in developing effective conservation and management strategies
(Wootton et al. 2000). The main aim of this paper is therefore to study and provide estimates
of life history characteristics of Mediterranean brown trout populations, and specific
objectives are to determine growth parameters and reproductive traits (i.e., size and age at first
maturity, fecundity and spawning period).

Material and methods

86 Study area.

The study was conducted in three headwaters tributaries (Noguera Pallaresa, Flamisell and Noguera Vallferrera) of the Segre River (NE Iberian Peninsula; Fig. 1). The Segre River is the largest catchment in the Southern Pyrenees (265 km long, 22,580 km² of basin area and ca. 100 m³ s⁻¹ of average water flow), and is the main tributary of the Ebro River (426 m³ s⁻¹ of annual mean flow) (for more details see Rovira et al. 2012). Three different reaches were selected (Fig. 1) in the Noguera Pallaresa River (154 km long and 37.1 m³ s⁻¹ of average flow); the main stream (hereafter NP) and two tributaries, the Flamisell (FLM) and the Noguera Vallferrera (NV). The three reaches were similar, channel morphology consisted primarily of pool-run-riffle sequences under a forest canopy. Physical and hydromorphological characteristics of study reaches are shown in Table 1. Streams originate in the Pyrenees, at an altitude above 2,000 m, and run through narrow valleys with steep

slopes. The hydrological regime is snow-fed, thus, the highest flows generally occur in spring after snowmelt (Ebro Water Authority; http://www.chebro.es/), and summers are relatively dry. Brown trout was the only fish species present. Headwater streams in the area support abundant trout populations of the Mediterranean lineage with high genetic integrity (Araguas et al. 2017).

Sampling procedures and data analysis.

Brown trout were sampled monthly (with the same sampling effort and spatial design) by electrofishing from December 1991 to November 1993. All fish collected were counted, measured (FL, fork length to the nearest mm), weighed (W, total weight to the nearest g), and a sample of scales was taken from each fish above the lateral line at the insertion of the dorsal fin. All fish were returned alive to the same location from where they were captured, except those for life history traits analysis which were euthanized *in situ* by overdose with tricaine methanesulfonate (MS-222), fixed in formaldehyde solution (4%) and transported to the laboratory.

The relationship between the fork length and total weight was fitted using the logarithmic form of the allometric growth equation proposed by Fuiman (1983): $\log(W) = \log(a) + b \log(FL)$, where a is the intercept, and b is the allometric growth coefficient. The parameters a and b were estimated by linear regression analysis, allometric growth is positive when b is larger than the isometric value and negative when b is lower than this threshold value. Student's t test was used to analyse divergences in the regression slope (b) from isometric growth (i.e., b = 3). Differences among streams, seasons, and sexes analysed with the Package FSA (Ogle 2017) in R 3.6.3 (R Core Team 2020). Brown trout were aged from scales; scales were cleaned (5% KOH solution), rinsed in water and dry-mounted between two glass slides. Scale circuli (i.e., age) were counted and the distance between circuli were

measured by two independent readers using a microfilm projector. Count or measurement divergences (< 10%) were re-examined and resolved, thus a single data set was generated. Growth was back-calculated from scale readings. Back-calculated fork length at a given age was estimated by using the Fraser-Lee equation (Francis 1990; Ricker 1992): $L_i = a + (L - a)$ (S_i/S) ; where FL_i , is the back-calculated fork length at age i, L is the fork length at capture, S_i is the scale radius at capture, S, is the annulus radius for age i, and a is the standard intercept constant (a = 19.27, 19.23, 28.26 for NP, NV, and FLM, respectively). Back-calculated fork lengths were used to estimate von Bertalanffy growth function (Ricker 1975): $L_t = L_{\infty}(1 - e^{-k})^{t}$ ^{-t0)}); where L_t is the mean fork length at age t, L_{∞} is the theoretical maximum fork length, k is a growth rate parameter, and t_0 is the theoretical age at a fork length of 0. The growth function was fitted for each stream separately with the function "growth" in the package fishmethods (Nelson 2019) in R 3.6.3 (R Core Team 2020). Model parameters differences among streams were estimated through likelihood ratio tests with the function "vblrt" in fishmethods (Nelson 2019). A total of 265 individuals (N = 83, 91 and 89 from NP, NV, and FLM, respectively) were examined for life history analysis, fish were collected in September-October, prior to the start of the spawning period. In the laboratory, sex and maturity stage were determined by examining the gonads under a stereoscope. Males were considered mature when their testes were large and white, and immature otherwise (e.g., filiform testes restricted to the dorsal surface of the body cavity). Females were classified as mature when their ovaries contained well developed eggs occupying much of the abdominal cavity, and as immature when their ovaries were small and translucent. The gonads were weighed (GW) to the nearest 0.1 g, and ovaries were fixed in Gilson's fluid (Bagenal and Braum 1978) to determine fecundity and egg diameter. Mature probability, for both males and females, was determined using a logistic regression models with fork length and stream as independent variables and maturity stage (juvenile/immature or mature) as response variable. Size-at-maturity (L_{50}) of a population, is

123

124

125

126

127

128

129

130

131

132

133

134

135

136

137

138

139

140

141

142

143

144

145

146

147

the fork length at which 50% of the individuals are mature and was estimated from the fit of logistic regression. The reproductive cycle and spawning season were determined from the gonadosomatic index (GSI), calculated as the percentage of gonadal mass of total mass GSI = $100 \times (GW/TW)$. Fecundity was determined from 18 mature-rip females collected before the spawning period, only the yolky eggs were counted for fecundity estimates, and the diameter of 20 yolky eggs per female were measured with a digital micrometer. The relationship between fecundity and egg diameter with fork length was assessed through linear regression analysis (Bagenal and Braum 1978). Relative fecundity was calculated by dividing fecundity by TW. Variation in fecundity among streams were analysed with analysis of covariance (ANCOVA) using fish length as the covariate.

158

159

148

149

150

151

152

153

154

155

156

157

Results

- 160 *Mediterranean brown trout growth and age.*
- A total of 2,859 trout were captured; the maximum recorded fork length for males and
- 162 females was 382 mm and 322 mm, respectively; mean fork length was 161.2 ± 1.06 mm ($\mu \pm$
- SE), being similar for both adult males (202.0 \pm 3.60) and females (208.9 \pm 3.13). The overall
- length-weight relationship was: $\log(W) = -4.774 + 2.923 \times \log(FL)$ ($R^2 = 0.989$; $F_{1.2857} =$
- 165 125,234, P < 0.0001), and $b (2.923 \pm 0.008)$ was significantly different from 3 (Student's t-
- test, P < 0.0001), thus indicating a slightly negative allometric relationship. The length-weight
- relationships did not differed significantly between sexes (ANCOVA, P = 0.54), but varied
- among streams ($F_{2,2853} = 26.52$, P < 0.0001); see equations in Fig. 2. The overall length-
- weight relationship also differed significantly among seasons (P < 0.0001), b was lowest in
- winter (2.777) and highest in spring (3.067).
- A total of 1,114 trout were aged by examining scales (293, 369 and 452 from FLM, NP
- and NV, respectively). Age ranged from 1+ to 6+ but two large individuals could not be aged

because of crowded annuli on the scale margins. The majority of fish were age 1+ (39.0%) or age 2+ (33.3%), 90.5 percent of the fish aged 3+ or younger, and only 9.5% of the trout aged over 4+ (7.0, 1.8, and 0.7% of individuals in age class 4+, 5+ and 6+, respectively). Lengthat-age plot showed a faster growth for younger individuals (Fig. 3). The length-at-age plots also indicated that our sample did not include the asymptote of the von Bertalanffy growth curve for either stream, thus our data probably did not include the largest (i.e., oldest) fish of the stream populations (Fig. 3). Overall, the variance in back-calculated length-at-age increased with age, but the estimated CV was highest at age 1+ (20.1%), decreasing to 9.23% by age 6+; however, it should be noted that the sample sizes for older ages were rather small. This variability is explained by differences in length and growth rates among streams. Overall, brown trout length significantly increased with age (ANOVA; $F_{5,1096} = 1307$, P <0.0001), being largest in FLM stream ($F_{2,1096} = 74.78$, P < 0.0001). However, differences in length-at-age among streams were more pronounced in the younger age groups, and reduced in older individuals (age \times stream interaction; $F_{10,1096} = 4.818$, P < 0.0001), thus suggesting a relatively faster growth rate in the NV stream (Fig. 3). The contrast of the size-specific growth rates in the three streams is summarized by the von Bertalanffy growth curves (Fig. 3). In NV, growth rate was higher and asymptotic fork length was larger; however, the von Bertalanffy growth curves were similar, and the estimated parameters did not vary among streams (likelihood ratio test, P = 0.91, 0.96, and 0.62 for L_{∞} , k, and t_0 , respectively). Reproductive variables. Overall sex ratio did not deviate significantly from the expected 1:1 (G = 1.83, df = 1, P =0.18), and was not different among the three streams (G = 3.95, df = 2, P = 0.14). Overall, both sexes began to mature at age 1+, males at 119 mm fork length, and females at 145 mm

173

174

175

176

177

178

179

180

181

182

183

184

185

186

187

188

189

190

191

192

193

194

195

196

197

fork length; the L_{50} for both sexes (estimated from the logistic models) was 136.4 mm and

198 150.1 mm for males and females respectively (Fig. 4). However, size-at-maturity differed significantly among streams in males (Wald χ^2 : stream, P = 0.038; fork length, P < 0.0001; 199 Nagelkerke's $R^2 = 0.53$), but not in females (Wald χ^2 : stream, P = 0.39; fork length, P <200 0.0001; Nagelkerke's $R^2 = 0.83$). Males from NP stream matured at larger sizes (153.4 mm 201 202 FL, P = 0.022) than in FLM (129.0 mm) and NV (131.2 mm) streams (Fig. 4). 203 The gonadosomatic index (GSI) values for both male and female brown trout showed strong 204 similarity in onset and amplitude, with minor variations among streams (Fig. 5). The timing 205 of testis development closely coincided with that of ovary development. Three periods were 206 identified based on the GSI variation. For both male and female brown trout, the reproduction 207 cycle started in July, when gonads began to develop (Fig. 5). The increase in testis weight 208 occurred sharply, the maximum monthly GSI values for males was reached in August-209 September, prior to the spawning period, and then decreased gradually until February. 210 However, ovary weight and hence GSI values for females reached a peak in October-211 November, then reduced sharply and in January all analysed females were considered spent. 212 In the field, spawning activity was first observed in early November, peaking in late 213 November, and decreasing gradually until the end of December. 214 Fecundity, prior to the start of the spawning period, ranged from 148 to 561 eggs and 215 was positively related to female fork length (Fig. 6). After accounting for fish length 216 (ANCOVA, P < 0.0001), females from NP stream had lower fecundity ($F_{2.14} = 14.83$, P < 0.0001) 217 0.0001) than females from both FLM and NV streams (Fig. 6). Overall, relative fecundity ranged from 1,822 to 4,966 ($\mu \pm SE = 3,172 \pm 189$) eggs kg⁻¹ of body weight. Relative 218 219 fecundity was not significantly related to total weight (ANCOVA, $F_{1,14} = 3.138$, P = 0.098), but was significantly lower (ANCOVA, $F_{2.14} = 13.07$, P = 0.001) in NP (2,370 ± 226 eggs kg⁻¹ 220 1) than in FLM $(3.288 \pm 188 \text{ eggs kg}^{-1})$ and NV $(3.858 \pm 232 \text{ eggs kg}^{-1})$. The mean diameter 221 222 of eggs ranged from 3.2 to 5.0 mm (mean 3.9 ± 0.08). After accounting for fish size

(ANCOVA, P < 0.0001), which as expected had a positive effect (Fig. 7), there was no significant differences among streams (P = 0.23).

225

226

227

228

229

230

231

232

233

234

235

236

237

238

239

240

241

242

243

244

245

246

247

223

224

Discussion

Overall, brown trout showed a negative isometric growth, however the allometric coefficient (b) of the length-weight relationship varied among streams and seasons. The length-weight relationship in fish is influenced by different factors, such as age, sex, maturity, temperature, habitat, and diet (Wootton 1998; Froese 2006). The allometric coefficient (b) was higher in spring and minimum in winter. During winter months, when water temperature is lowest, trout reduces activity and feeding activity (Cunjak and Power 1987), hence reducing growth rate. In contrast, in spring months, following an increase in water temperature, feeding activity increases (Arslan et al. 2004). Brown trout populations were characterized by medium life spans, 90.5% of the fish aged 3+ or younger and the maximum recorded age was 6+ years, found in the three sampled streams. However, older fish may be present since some of the larger individuals could not be aged because of scale anomalies. It has been previously reported that harsh environmental conditions in high altitude streams reduce the growth rate of large trout, thus leading to the apparition of crowded annuli on the scale edges (Bohlin et al. 2002). Our results agree with previous studies on brown trout growth in most European waters, where trout live up to five or six years reaching a maximum length of 30–35 cm (Almodóvar and Nicola 2004; Parra et al. 2009 and references therein). However, in some Iberian populations of the Atlantic basins, observed length-at-age and growth increments were higher. For instance, in an aquifer-fed stream of central Spain trout ranged between 25.3 and 27.8 cm in standard length (SL) at age 3, and 31.8–34.8 cm at age 4 (Lobón-Cerviá et al. 1986). These differences can be related to stream characteristics since the growth rate of stream-resident salmonids is influenced by environmental factors, such as water temperature,

which affects positively (Elliott 1994; Vøllestad et al. 2002; Réalis-Doyelle et al. 2018). Our fish sample did not include the asymptote ($L_{\infty} = 427$ mm) of the von Bertalanffy growth curve (age 6+ mean FL = 254.5 ± 8.5 mm), thus older fish (i.e., larger) may exist in the population. The results of the von Bertalanffy growth model showed similar growth rates among streams, although interpopulation differences in length-at-age, particularly by the presence of smaller fish, for a given age, in NP stream. According to Parra et al. (2009), the growth rate of 0+ individuals determines the length at older ages. The size of the first year is positively related to the extent of the age 0+ (i.e., larvae and alevins stages) growing period. In colder streams, such as NP when compared to NV and FLM, the fry emergence from the stream bed occurs later, thus reducing the growing period (Ojanguren and Braña 2003), and also reducing adult fish length for a given length. Overall, length at maturity of Mediterranean brown trout differed between sexes, with females reaching maturity at large sizes ($FL_{50} = 150.1 \text{ mm}$) than males (136.4 mm), but there were some differences among streams, NP males matured at larger sizes (153.4 mm) than FLM and NV (129.0 and 131.2 mm, respectively) males. Furthermore, due to differences in length-at-age and growth rate, both males and females from NP stream reached sexual maturity at older age; in colder waters, brown trout mature at older ages and larger sizes (Jonsson et al. 1991). Our results are similar to those reported in the literature, with age and length at maturity also differing between sexes, with trout males maturing at younger age and shorter length than females (Johnson 1985; Olsen and Vøllestad 2005). Previous studies have also shown great plasticity in age and length at maturity among different brown trout populations of the Atlantic lineage. For instance, in rivers of North of Spain, both males and females start to mature at lengths ranging between 10.5 and 11 cm at age 1+ (Lobón-Cerviá et al. 1997); while in Norway, resident brown trout males reach maturity at lengths between 141

248

249

250

251

252

253

254

255

256

257

258

259

260

261

262

263

264

265

266

267

268

269

270

271

and 187 mm at age 1+ to 3+, and females at 147–188 mm in length at age 2+ to 4+ (Olsen and Vøllestad 2005).

272

273

274

275

276

277

278

279

280

281

282

283

284

285

286

287

288

289

290

291

292

293

294

295

296

The spawning season was relatively short, beginning in late autumn-early winter, lasted for two months according to the GSI values. Brown trout spawning period usually occurs during the autumn-winter period (e.g., Klemetsen et al. 2003; Rubin et al. 2005; Riedl and Peter 2013). Several factors, such water temperature and photoperiod, have been proposed to modulate the timing and the duration of the spawning season (e.g., Jonsson and L'Abée-Lund 1993; Elliott 1994; Ojanguren and Braña 2003). In colder regimes (due to latitude and/or altitude) spawning occurs earlier, because of longer incubation period (Crisp 1994; Elliott and Hurley 1998; Klemetsen et al. 2003). Despite being located in the southern range of brown trout, the high altitude of the study sites and hence water temperature regimes (Table 1) explain the relatively early spawning season. In other Iberian populations located at similar latitude but in streams with higher mean water temperature, the peak of the spawning season is between February and March (García and Braña 1988; Gortázar et al. 2007). Furthermore, the short spawning season contrasts with that of trout populations from the south of Iberian Peninsula, where the spawning season is extended from October to April, which is considered an adaptation to environmental variability of the Mediterranean climate (Gortázar et al. 2007; Larios-López et al. 2015).

Fork length of female trout was positively correlated with fecundity and egg diameter, as reported elsewhere (e.g., Nicola and Almodóvar 2002). Previous studies worldwide, including Central and North Europe (Maisse et al. 1987; L'Abée-Lund et al. 1989; Crisp 1994), Southern Europe (Lobón-Cerviá et al. 1986; Nicola and Almodóvar 2002; Champigneulle et al. 2003), Asia (Arslan and Aras 2007; Rasool and Jan 2013), and USA (Avery 1985), have shown that fecundity for a standard female of 200 mm FL ranges between 208 and 347 eggs. A standard female of 200 mm FL from our study populations had an estimated fecundity of

209, 307 and 326 for NP, NV and FLM, respectively. Therefore, both NV and FLM females are in the upper part of the range, and similar to those values reported in rivers of Central Spain (Lobón-Cerviá et al. 1986). However, NP females are in the lower part of the range, which could be explained by differences in water temperature and productivity among streams (see Lobón-Cerviá et al. 1997). The results reported in this study represent a contribution to better understanding of key aspects of the biology of Mediterranean brown trout populations, for which limited information is currently available, although it is necessary to develop sound conservation and management strategies for preserving their populations. **Acknowledgments** This research was supported by the Biodiversity Conservation Plan of ENDESA through the project PIE 121043-00-FECSA. Carles Alcaraz also acknowledge support from CERCA Programme (Generalitat de Catalunya). We want to thank F Casals, JM Olmo and MJ Vargas for field assistance. All appropriate ethics and permissions required for the realization of this manuscript were obtained, previously, by the authors. The Departament de Medi Ambient i Habitatge de la Generalitat de Catalunya (current Departament d'Agricultura, Ramaderia, Pesca, Alimentació i Medi Natural) of the regional authorities of Catalonia provided authorization to conduct the research (SF/602). References Almodóvar A, Nicola GG (2004) Angling impact on conservation of Spanish stream-dwelling brown trout Salmo trutta. Fish Manag Ecol 11:173–182 Almodóvar A, Nicola GG, Ayllón D, Elvira B (2012) Global warming threatens the persistence of Mediterranean brown trout. Glob Chang Biol 18:1549–1560

297

298

299

300

301

302

303

304

305

306

307

308

309

310

311

312

313

314

315

316

317

318

319

320

321

322	Aparicio E, Garcia-Berthou E, Araguas RM, Marinez P, Garcia-Marin JL (2005) Body
323	pigmentation pattern to assess introgression by hatchery stocks in native brown trout
324	(Salmo trutta) from Mediterranean streams. J Fish Biol 67:931-949
325	Aparicio E, Rocaspana R, de Sostoa A, Palau-Ibars A, Alcaraz C (2018) Movements and
326	dispersal of brown trout (Salmo trutta Linnaeus, 1758) in Mediterranean streams:
327	influence of habitat and biotic factors. PeerJ 6:e5730
328	Araguas RM, Vera M, Aparicio E, Sanz N, Fernández-Cebrián R, Marchante C, García-Marín
329	JL (2017) Current status of the brown trout (Salmo trutta) populations within eastern
330	Pyrenees genetic refuges. Ecol Freshw Fish 26:120–132
331	Arslan M, Aras NM (2007) Structure and reproductive characteristics of two brown trout
332	(Salmo trutta) populations in the Çoruh River Basin, North-eastern Anatolia, Turkey.
333	Turk J Zool 31:185–192
334	Arslan M, Yildirim A, Bekta S (2004) Length-weight relationship of brown trout, Salmo
335	trutta L., Inhabiting Kan Stream, Çoruh Basin, North-Eastern Turkey. Turk J Fish Aquat
336	Sci 4:45–48
337	Avery E (1985) Sexual maturity and fecundity of brown trout in central and northern
338	Wisconsin streams. Technical Bulletin no. 154. Department of Natural Resources,
339	Madison, Wisconsin
340	Bagenal TB, Braum E (1978) Eggs and early life history. In: Bagenal TB (ed) Methods for
341	assessment of fish production in fresh waters. IBP Handbook No. 3. Blackwell Scientific
342	Publications, London, pp 165–201
343	Benejam L, Saura-Mas S, Bardina M, Sola C, Munne A, García-Berthou E (2016) Ecological
344	impacts of small hydropower plants on headwater stream fish: from individual to
345	community effects. Ecol Freshw Fish 25:295–306
346	Benhaim D, Guyomard R, Chatain B, Quillet E, Begout ML (2013) Genetic differences for

34/	behaviour in juveniles from two strains of brown trout suggest an effect of domestication
348	history. Appl Anim Behav Sci 147:235–242
349	Bernatchez L (2001) The evolutionary history of brown trout (Salmo trutta L.) inferred from
350	phylogeographic, nested clades, and mismatch analysis of mitochondrial DNA variation.
351	Evolution 55:351–379
352	Berrebi P, Poteaux C, Fissier M, Cattaneo-Berrebi G (2000) Stocking impact and allozyme
353	diversity in brown trout from Mediterranean southern France. J Fish Biol 56:949-960
354	Bohlin T, Sundström LF, Johnsson JI, Höjesjö J, Pettersson J (2002) Density dependent
355	growth in brown trout: effects of introducing wild and hatchery fish. J Anim Ecol 71:683-
356	692
357	Champigneulle A, Largiader CR, Caudron A (2003) Reproduction de la truite (Salmo trutta
358	L.) dans le Torrent de Chevenne, Haute-Savoie.un fonctionnement original? Bull Fr
359	Pêche Piscic 369:41–70
360	Crisp DT (1994) Reproductive investment of female brown trout, Salmo trutta L., in a stream
361	and reservoir system in northern England. J Fish Biol 44:343-349
362	Crisp DT (2000) Trout and salmon: ecology, conservation and rehabilitation. Fishing News
363	Books, Blackwell Science, Oxford
364	Cunjak RA, Power G (1987) The feeding and energetics of stream-resident trout in winter. J
365	Fish Biol 31:493–511
366	Doadrio I, Perea S, Garzón-Heydt P, González JL (2011) Ictiofauna Continental Española.
367	Bases para su seguimiento. Ministerio de Medio Ambiente y Medio Rural y Marino,
368	Madrid
369	Elliott JM (1994) Quantitative ecology and the brown trout. Oxford Series in Ecology and
370	Evolution, Oxford
371	Elliott JM, Hurley MA (1998). Predicting fluctuations in the size of newly emerged sea-trout

372	fry in a Lake District stream. J Fish Biol 53:1120–1133
373	Francis RI (1990). Back-calculation of fish length: a critical review. J Fish Biol 36:883–902
374	Froese R (2006) Cube law, condition factor and weight-length relationships: history, meta-
375	analysis and recommendations. J Appl Ichthyol 22:241-253
376	Fuiman LA (1983) Growth gradients in fish larvae. J Fish Biol 23:117-123
377	Garcia A, Braña F (1988). Reproductive biology of brown trout (Salmo trutta L) in the Allen
378	River (Austurias, Spain). Pol Arch Hydrobiol 35:361–373.
379	Gil J, Caudron A, Labonne J (2015) Can female preference drive intraspecific diversity
380	dynamics in brown trout (Salmo trutta, L.)? Ecol Freshw Fish 25:352-359
381	Gortázar J, García de Jalón D, Alonso-González C, Vizcaíno P, Baeza D, Marchamalo M
382	(2007) Spawning period of a southern brown trout population in a highly unpredictable
383	stream. Ecol Freshw Fish 16: 515–527
384	Jonsson B (1985) Life-history patterns of freshwater resident and sea-run trout migrant brown
385	trout in Norway. Trans Am Fish Soc 114:182–194
386	Jonsson B, Jonsson N (2011) Ecology of Atlantic salmon and brown trout: habitat as a
387	template for life histories. Springer, New York
388	Jonsson B, L'Abée-Lund JH (1993) Latitudinal clines in life-history variables of anadromous
389	brown trout in Europe. J Fish Biol 43(Suppl A):1–16
390	Jonsson B, L'Abée-Lund JH, Heggberget TG, Jensen AJ, Johnsen BO, Næsje TF, Sættem LM
391	(1991) Longevity, body size, and growth in anadromous brown trout (Salmo trutta). Can J
392	Fish Aquat Sci 48:1838–1845
393	Klemetsen A, Amundsen PA, Dempson JB, Jonsson B, Jonsson N, O'Connell MF, Mortensen
394	E (2003) Atlantic salmon Salmo salar L., brown trout Salmo trutta L. and Arctic charr
395	Salvelinus alpinus (L.): a review of aspects of their life histories. Ecol Freshw Fish 12:1-
396	59

397	Kottelat M, Freyhof J (2007) Handbook of European freshwater fishes. Publications Kottelat
398	Cornol, Switzerland
399	L'Abee-Lund JH, Jonsson B, Jensen AJ, Saettem LM, Heggberget TG, Johnsen BO, Naesje
400	TF (1989) Latitudinal variation in life-history characteristics of sea-run migrant brown
401	trout Salmo trutta. J Anim Ecol 58:525-542
402	Larios-López JE, Tierno de Figueroa JM, Galiana-García M, Gortázar J, Alonso C (2015)
403	Extended spawning in brown trout (Salmo trutta) populations from the southern Iberian
404	Peninsula: the role of climate variability. J Limnol 74:394–402
405	Lobón-Cerviá J, Montañés C, de Sostoa A (1986) Reproductive ecology and growth of a
406	population of brown trout (Salmo trutta L.) in an aquifer-fed stream of Old Castile
407	(Spain). Hydrobiologia 135:81–94
408	Lobón-Cerviá J, Utrilla C, Rincón P, Amezcua F (1997) Environmentally induced spatio-
409	temporal variations in the fecundity of brown trout Salmo trutta L.: trade-offs between
410	egg size and number. Freshw Biol 38:277–288
411	Maisse G, Bagliniere JL, Le Bail PY (1987) Dynamique de la population de Truite commune
412	(Salmo trutta) d'un ruisseau breton (France): les géniteurs sédentaires. Hydrobiologia
413	148:123–130
414	Nelson GA (2019) fishmethods: Fishery Science Methods and Models. R package version
415	1.11-1. https://cran.r-project.org/web/packages/fishmethods/
416	Nicola GG, Almodóvar A (2002) Reproductive traits of stream-dwelling brown trout Salmo
417	trutta in contrasting neighbouring rivers of central Spain. Freshw Biol 47:1353–1365
418	Ogle DH (2017) FSA: Fisheries Stock Analysis. R package version 0.8.17. https://cran.r-
419	project.org/web/packages/FSA/
420	Ojanguren AF, Braña F (2003) Thermal dependence of embryonic growth and development
421	in brown trout. J Fish Biol 62:580–590

422	Olsen EM, Vøllestad LA (2005) Small-scale spatial variation in age and size at maturity of
423	stream-dwelling brown trout, Salmo trutta. Ecol Freshw Fish 14:202–208
424	Parra I, Almodóvar A, Nicola GG, Elvira B (2009) Latitudinal and altitudinal growth patterns
425	of brown trout Salmo trutta at different spatial scales. J Fish Biol 74:2355–2373
426	R Core Team (2020). R: A language and environment for statistical computing. R Foundation
427	for Statistical Computing, Vienna, Austria
428	Rasool N, Jan U (2013) Study on the fecundity of Salmo trutta fario (Brown trout) in
429	Kashmir. J Biol Life Sci 4:181–193
430	Réalis-Doyelle E, Gisbert E, Alcaraz C, Teletchea F, Pasquet A (2018) Temperature affects
431	growth allometry and development patterns in brown trout (Salmo trutta) fry: a multitrait
432	approach. Can J Fish Aquat Sci 75:714–722
433	Ricker WE (1975) Computation and interpretation of biological statistics of fish populations.
434	Bulletin of the Fisheries Research Board of Canada. Bulletin 191. Department of the
435	Environment, Fisheries and Marine Service, Ottawa
436	Ricker WE (1992) Back-calculation of fish lengths based on proportionality between scale
437	and length increments. Can J Fish Aquat Sci 49:1018-1026
438	Riedl C, Peter A (2013) Timing of brown trout spawning in Alpine rivers with special
439	consideration of egg burial depth. Ecol Freshw Fish 22:384–397
440	Rocaspana R, Aparicio E, Palau-Ibars A, Guillem R, Alcaraz C (2019). Hydropeaking effects
441	on movement patterns of brown trout (Salmo trutta L.). River Res Appl 35: 646–655
442	Rossi AR, Petrosino G, Milana V, Martinoli M, Rakaj A, Tancioni L (2019) Genetic
443	identification of native populations of Mediterranean brown trout Salmo trutta L.
444	complex (Osteichthyes: Salmonidae) in central Italy. Eur Zool J 86:424-431
445	Rovira A, Alcaraz C, Ibáñez C (2012) Spatial and temporal dynamics of suspended load at-a-
446	cross-section: the lowermost Ebro River (Catalonia, Spain). Water Res 46:3671–3681

447	Rubin JF, Glimsäter C, Jarvi T (2005) Spawning characteristics of the anadromous brown
448	trout in a small Swedish stream. J Fish Biol 66:107-121
449	Sanz N (2017) Phylogeographic history of brown trout. In: Lobón-Cerviá J, Sanz N (eds)
450	Brown trout: biology, ecology and management. John Wiley & Sons Inc., Hoboken
451	Splendiani A, Palmas F, Sabatini A, Caputo-Barucchi V (2019) The name of the trout:
452	considerations on the taxonomic status of the Salmo trutta L., 1758 complex
453	(Osteichthyes: Salmonidae) in Italy. Eur Zool J 86:432-442
454	Vøllestad LA, Olsen EM, Forseth T (2002) Growth-rate variation in brown trout in small
455	neighbouring streams: evidence for density-dependence? J Fish Biol 61:1513-1527
456	Wootton RJ (1998) The ecology of teleost fishes. Fish and Fisheries Series 24. Kluwer,
457	Dordrecht
458	Wootton RJ, Elvira B, Baker JA (2000) Life-history evolution, biology and conservation of
459	stream fish: introductory note. Ecol Freshw Fish 9:90-91

Figure legends

Fig. 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

Fig. 2 Weight-length relationship for Mediterranean brown trout per stream. *FLM* Flamisell, *NP* Noguera Pallaresa, *NV* Noguera Vallferrera

Fig. 3 Top: von Bertalanffy growth curves for Mediterranean brown trout per stream based on back-calculated lengths-at-age. *The box* corresponds to standard deviation, *the dark line inside the box* is the mean, and *the error bars* are the range. Bottom: back-calculated lengths-at-age per stream. *Error bar* is the standard error of the mean. *FLM* Flamisell, *NP* Noguera Pallaresa, *NV* Noguera Vallferrera

Fig. 4 Relationship between maturity stage of both male (top) and female (bottom) Mediterranean brown trout with fork length per stream (0, immature and 1, mature). *Bars* show length frequency distribution. *FLM* Flamisell, *NP* Noguera Pallaresa, *NV* Noguera Vallferrera

Fig. 5 Mean values of gonadosomatic index (GSI) by month and stream of male (top) and female (top) Mediterranean brown trout. *FLM* Flamisell, *NP* Noguera Pallaresa, *NV* Noguera Vallferrera

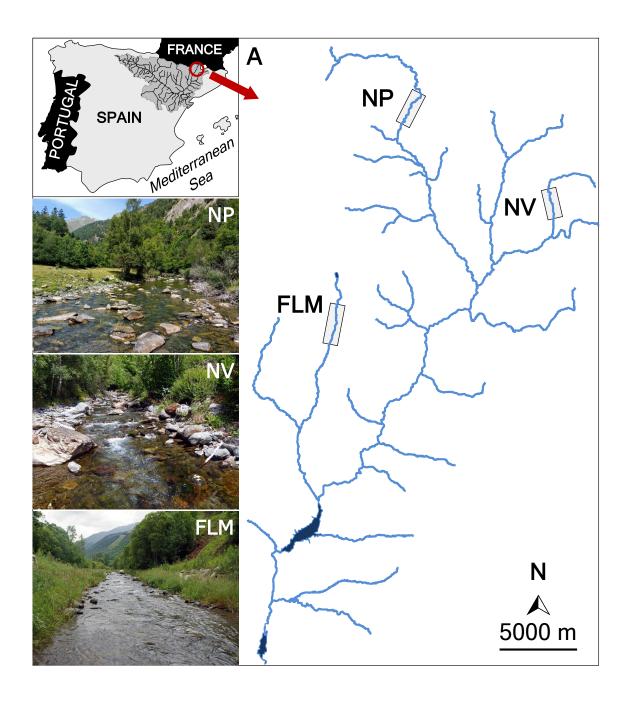
Fig. 6 Relationship of fecundity per stream with fork length. *FLM* Flamisell, *NP* Noguera Pallaresa, *NV* Noguera Vallferrera

Fig. 7 Relationship of egg diameter (ED) with female body weight

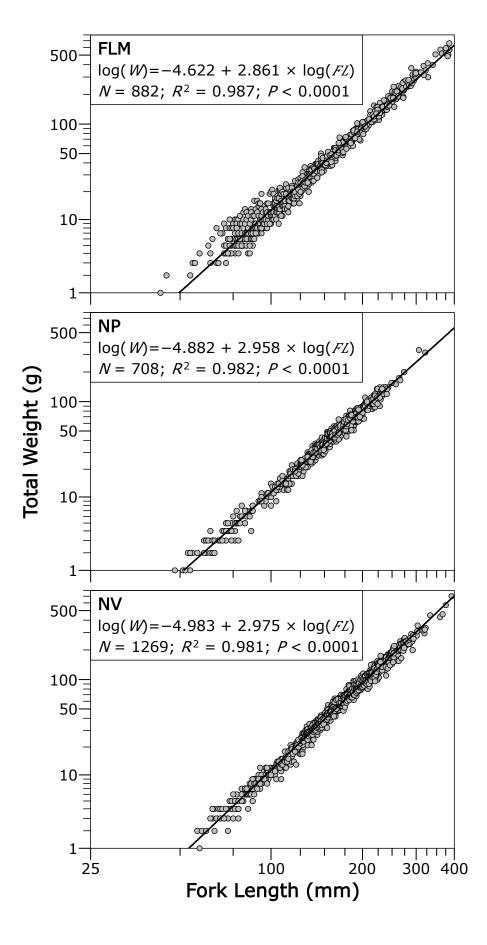
 Table 1 Stream features during the study period

Variable	Stream		
v ariable	FLM	NP	NV
Latitude	42°23'40.92"N	42°44'1.68"N	42°34'3.36"N
Longitude	0°58'0.84"E	1°6'27.36"E	1°19'42.60"E
Mean elevation (m)	917	1,387	1,127
Mean slope (m km ⁻¹)	31.8	21.5	50.2
Mean base flow (m ³ s ⁻¹)	1.52	0.95	1.29
Mean stream width (m)	5.9	10.2	6.1
Mean water depth (cm)	15.4	21.1	22.1
Water temperature (°C)	8.8	5.8	7.9
Water temperature range (°C)	4.2-15.7	0.0 - 15.1	3.6-15.4
Mean pH	7.8	8.1	7.3
pH range	6.5-8.5	6.7-8.8	6.7-8.1
Conductivity (µs cm ⁻¹)	120.8	103.4	45.8
Conductivity range (µs cm ⁻¹)	78–171	46–157	17–94
Dissolved oxygen (mg l ⁻¹)	10.6	11.8	11.5
Dissolved oxygen range (mg l ⁻¹)	3.2–12.9	5.3–14.3	4.4–13.5

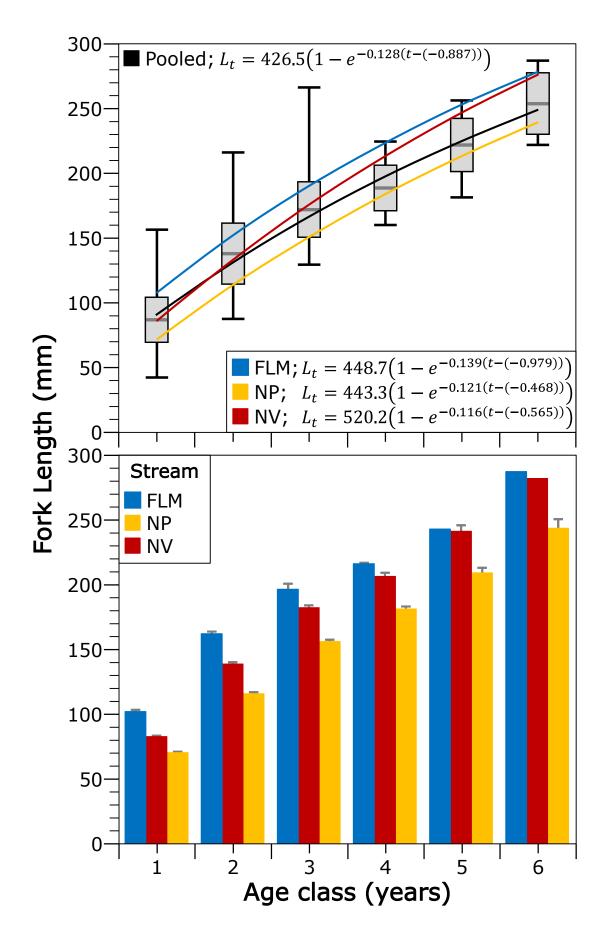
FLM Flamisell, NP Noguera Pallaresa, NV Noguera Vallferrera

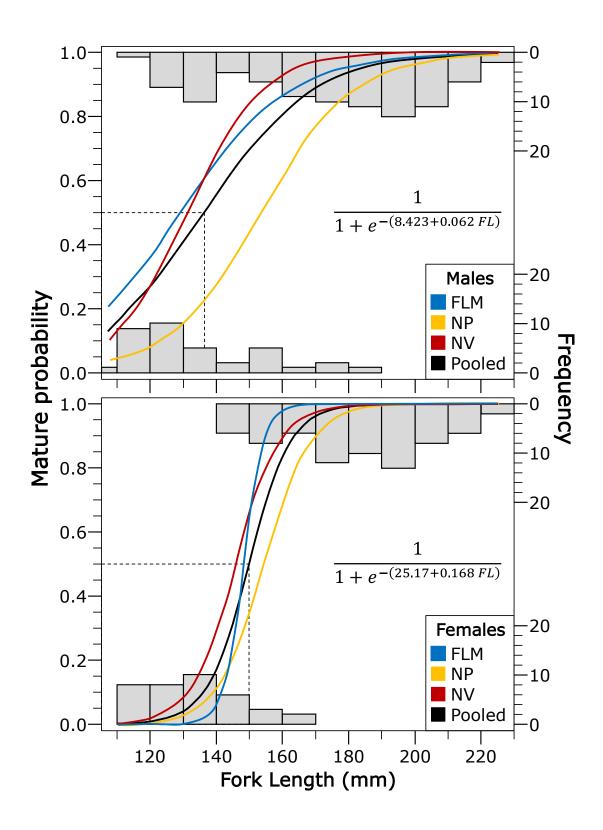


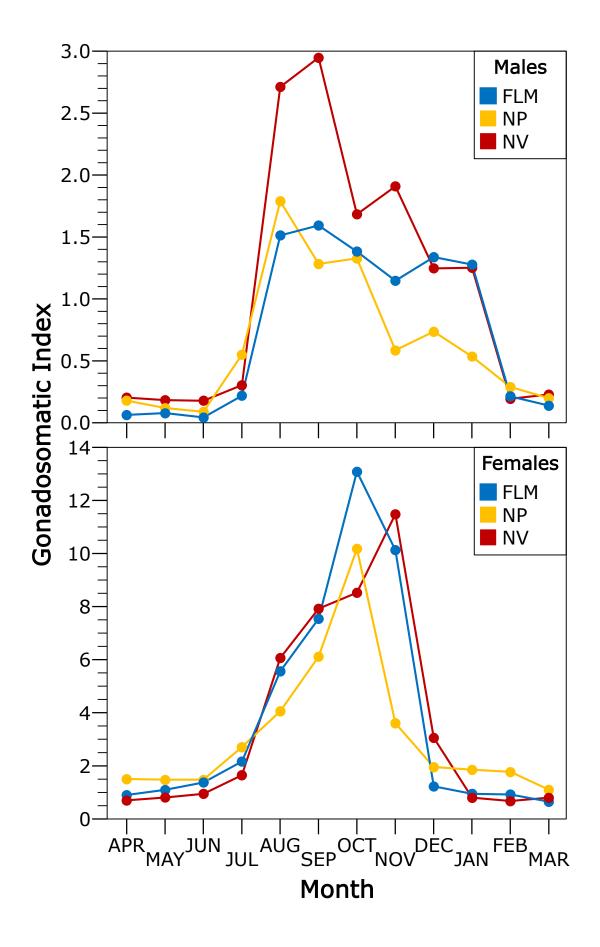












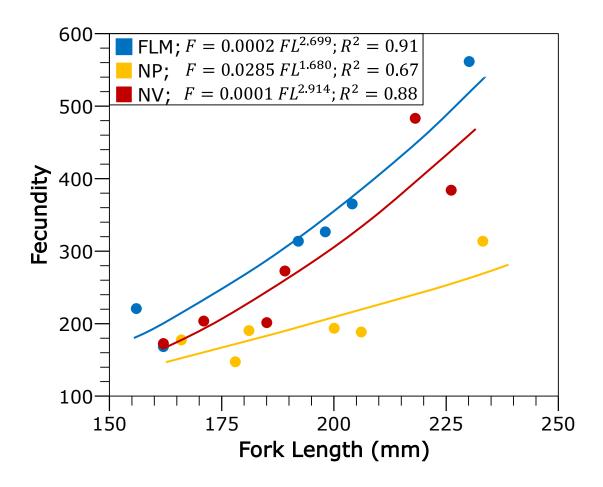


Figure 7. Aparicio et al.

