



**Modelling the factors influencing ontogenetic dietary shifts
in stream-dwelling brown trout (*Salmo trutta* Linnaeus,
1758)**

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1 **Modelling the factors influencing ontogenetic dietary shifts in**
2 **stream-dwelling brown trout (*Salmo trutta* Linnaeus, 1758)**

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20

21 **Abstract**

22 Biotic and abiotic variables shape ontogenetic trajectories of animals. This study
23 modelled (i) the body length-related timing of the ontogenetic switch from aquatic to
24 surface prey, and (ii) the impacts of habitat characteristics, prey availability, and fish
25 densities on the relative contribution of surface prey to the overall diet of native brown
26 trout. We used individual-based models of dietary data for 170 fish (length range: 48-
27 343 mm). There was a high degree of individual variation in the use of surface prey, but
28 logistic regression suggested that the shift from aquatic to surface prey was established
29 at a body length of 81 mm (range: 36-127 mm). Results of linear mixed-effects models
30 highlighted the importance of fish length, benthic invertebrates, brown trout density and
31 water current velocity to the switch to surface prey by riverine brown trout, with fish
32 length being the most influential variable. Our study provides evidence of the
33 importance of ontogeny (intrinsic features of individuals linked to fish length) and
34 individual differences in feeding behaviour to understand water-column use for feeding
35 by stream-dwelling salmonids.

36

37 **Keywords:** among-individual variation, dietary shifts, foraging, mixed modelling,
38 ontogenetic trajectories

39 Introduction

40 Ontogenetic dietary shifts are frequent and widespread across the animal kingdom.
41 Understanding these is an important issue in animal ecology with implications for niche
42 theory and animal bioenergetics, because dietary shifts influence body growth and
43 competition through resource partitioning (e.g. Jensen et al. 2012; Sánchez-Hernández
44 et al. 2013a; Nakazawa 2015). While most studies have focused on the nature of
45 ontogenetic niche shifts of animals, information is scarce about the mechanisms driving
46 these shifts. Ontogenetic niche shifts usually vary among individuals (e.g. Post 2003),
47 and they are determined by competitive interactions between sympatric species, prey
48 availability, predation risk, and internal mechanisms (Sánchez-Hernández et al. 2017a
49 and references therein).

50

51 Diet and habitat use can vary considerably during ontogeny of salmonids (e.g. Ayllón et
52 al. 2010; Hasegawa et al. 2012; Sánchez-Hernández et al. 2013a). For example, during
53 their life history, stream-dwelling brown trout (*Salmo trutta* L.) undergo ontogenetic
54 dietary shifts from aquatic to terrestrial invertebrates as principal prey (e.g. Kelly-Quinn
55 and Bracken 1990; Montori et al. 2006; Sánchez-Hernández and Cobo 2016). Small
56 brown trout typically consume aquatic invertebrates, whereas larger brown trout also
57 may forage on terrestrial invertebrates, rodents, amphibians and fish (Kelly-Quinn and
58 Bracken 1990; Jensen et al. 2012; Sánchez-Hernández et al. 2013a; Milardi et al.
59 2016). Similarly, larger brown trout more often use upper the water column to forage on
60 surface-drifting prey than smaller brown trout, which typically remain feeding on
61 aquatic drift prey close to the substratum (Gustafsson et al. 2010), but individual
62 reliance of brown trout on terrestrial invertebrates may vary considerably (Sánchez-
63 Hernández and Cobo 2016). Thus, brown trout show ontogenetic dietary shifts from

64 aquatic to surface prey (drifting terrestrial invertebrates and imagos of emerged aquatic
65 insects, probably caught at the surface). This shift facilitates the use of brown trout as a
66 model species to explore the factors influencing the ontogenetic switch from aquatic to
67 surface prey.

68

69 The annual and daily feeding rhythm of brown trout can be highly synchronized with
70 insect activities (Neveu 1980). The availability of terrestrial resources peaks during
71 summer, when aquatic invertebrate biomass is usually low (Nakano and Murakami
72 2001). Thus, patterns of reliance on surface prey can vary considerably among seasons
73 and during ontogeny (e.g. Jonsson and Gravem 1985; Kelly-Quinn and Bracken 1990;
74 Milardi et al. 2016; Sánchez-Hernández et al. 2016a). Kelly-Quinn and Bracken (1990)
75 observed that surface prey is only taken in small numbers by young of the year (YOY)
76 brown trout during the summer. This dietary shift (from aquatic to surface prey) is
77 gradual in YOY brown trout, starting in summer, and does not include all individuals of
78 the age group (Jonsson and Gravem 1985). A similar pattern is exhibited for other
79 salmonids for example Arctic charr *Salvelinus alpinus* (L.) (Sanchez-Hernandez et al.
80 2016a). The amount of prey caught at the water surface by fish is thought to be related
81 to prey characteristics (e.g. size, morphology and availability), fish characteristics (e.g.
82 prior experience, prey preferences, locomotor abilities and sensory capabilities) and
83 physical habitat characteristics (e.g. flow patterns and structural complexity) (Gerking
84 1994; Sánchez-Hernández and Cobo 2013; Giller and Greenberg 2015). For example
85 Giller and Greenberg (2015), showed that riverine salmonids foraging in pool habitats
86 usually consume more surface prey than individuals in riffles do.

87

88 Stream-dwelling salmonids are drift feeders (Rader 1997) that typically ‘sit-and-wait’ to
89 ambush prey from short distances in lotic habitats (Tunney and Steingrimsson 2012). In
90 contrast, they tend to adopt a cruising behaviour for searching food resources in lentic
91 areas of riverine systems (Hasegawa and Yamamoto 2010). As predicted by optimal
92 foraging theory (OFT), fish should select prey resources that maximize their net rate of
93 energy gain (Pyke et al. 1977; Gerking 1994). Successful prey detection and capture are
94 usually related to water current velocity, as prey capture probability and fish mobility
95 decrease with increasing water velocity (Piccolo et al. 2008; Tunney and Steingrimsson
96 2012). Stream-dwelling salmonids usually select areas of high energy gain for feeding
97 based on hydraulic and drift characteristics. Thus, brown trout tend to feed in slower
98 and deeper pool habitats in streams (Guensch et al. 2001; Booker et al. 2004).

99
100 Swimming ability in riverine salmonids changes during development as fish grow this
101 enables ontogenetic habitat shifts and thus the foraging opportunities available (e.g.
102 Ayllón et al. 2010; Gustafsson et al. 2010; Hasegawa et al. 2012). A number of
103 controlled studies have identified factors influencing the pattern of drift-feeding in
104 salmonids (Dunbrack and Dill 1983; Nakano et al. 1999a; Guensch et al. 2001; Booker
105 et al. 2004; Gustafsson et al. 2010). For example, at least some salmonids are able to
106 adapt their foraging mode (i.e. from drift to benthos foraging or *vice versa*) according to
107 the availability of drifting prey, i.e., the frequency of benthos foragers increases as the
108 abundance of drifting prey declines, and *vice versa* (Nakano et al. 1999a). Despite the
109 intuitive expectation that foraging shifts (e.g. from benthos to water surface feeding) can
110 be highly influenced by prey abundance, water depth and water current velocity
111 (Nakano et al. 1999a; Booker et al. 2004), the extent to which these parameters
112 influence the foraging mode of riverine salmonids is unexplored. Understanding the

113 causative mechanisms behind individual differences in feeding behaviour is an
114 emergent field of study in animal ecology (e.g. Bolnick et al. 2003). Few studies have
115 investigated the link between individual differences in feeding and ontogeny in fish
116 species, although some notable exceptions exist (Svanbäck et al. 2015; Nakayama et al.
117 2017; Sánchez-Hernández et al. 2017a). Thus, elucidating the mechanisms behind
118 ontogenetic niche shifts requires a framework that includes the interplay between
119 individual differences in feeding and environmental heterogeneity.

120

121 The aims of this paper are to (i) investigate the body length-related timing of the
122 ontogenetic shift from aquatic to surface prey, i.e. dietary shift associated with the
123 development of individual fish, and (ii) assess the most influential variables influencing
124 this ontogenetic dietary shift of a stream-dwelling model species, the brown trout. We
125 hypothesised that the relative abundance of surface prey in the diet of individual brown
126 trout (i.e. individuals capable to adopt a drift foraging behaviour) would increase with
127 increasing abundance of surface invertebrates irrespective of other site-specific
128 characters such as benthic invertebrates availability, habitat characteristics (riparian
129 canopy cover, water depth, river width and water current velocity) and fish densities.
130 We expected that the relative abundance of surface prey in the diet of brown trout
131 would increase gradually with fish length (Montori et al. 2006; Sánchez-Hernández and
132 Cobo 2016). This study will provide novel insights into whether habitat features (above-
133 mentioned variables), prey availability (benthic and drifting invertebrates), fish densities
134 (as a proxy of inter- and intraspecific competition) or fish length (as a proxy of
135 ontogenetic mechanisms) have the most influence on the foraging mode (benthic or drift
136 foraging) adopted by stream-dwelling salmonids.

137

138 **Material and methods**

139 Study area

140 The sampling sites are located in four rivers of Galicia (NW Spain), situated in a region
141 that includes a mixture of farmed and relatively undisturbed areas, interspersed by small
142 urban areas (Figure 1). The vegetation structure comprises a series of extended grazing
143 lands with Monterey pine (*Pinus radiata* D. Don 1836) and Tasmanian blue gum
144 (*Eucalyptus globulus* Labill.) forests. Thus, agriculture, livestock farming and domestic
145 sewage effluents are the primary human impacts on the catchments. The fish
146 community of the rivers is mainly composed of brown trout and northern straight-mouth
147 nase *Pseudochondrostoma duriense* (Coelho, 1985), although other fish species such as
148 European eel *Anguilla anguilla* (L.), and less frequently sea lamprey *Petromyzon*
149 *marinus* L., are also present in the River Anllóns (Appendix 1). Moreover, Eurasian
150 otter (*Lutra lutra* L.), common kingfisher [*Alcedo atthis* (L.)], grey heron (*Ardea*
151 *cinerea* L.) and great cormorant [*Phalacrocorax carbo* (L.)], are the top predators of the
152 studied aquatic ecosystems.

153

154 Data collection

155 The study was replicated spatially (three replicates) in each four neighbouring rivers in
156 September 2007 (Figure 1). Sampling was carried out on three consecutive days in each
157 river, and all samples (fish, habitat, benthos and drifting invertebrates) for a specific
158 location (replicate) were carried out the same day. Sample was in late summer because:
159 (i) the density of surface invertebrates vary seasonally with peaks during summer and is
160 positively correlated with temperature (Bridcut 2000; Nakano and Murakami 2001), (ii)
161 summer is the time when the aquatic food resource supply is lowest and thus the period
162 when competitive interactions should be strongest among sympatric stream-dwelling

163 fish species (e.g. Gabler and Amundsen, 2010; Sánchez-Hernández et al. 2016b), (iii)
164 September is the month when the seasonal contribution of surface prey to the diet of
165 YOY salmonids is highest (Jonsson and Gravem 1985; Sánchez-Hernández et al.
166 2016a), and (iv) feeding during summer, because of the energetic input of surface prey,
167 is largely responsible for gonadal development, fish growth and bioenergetics (energy
168 and reserves gain) (Sweka and Hartman 2008; Erős et al. 2012; McBride et al. 2015),
169 and consequently for overwinter survival and spawning success.

170

171 Habitat conditions were controlled as much as possible to avoid biased results. To avoid
172 any differences in fish feeding behaviour of individuals between pools and riffles (Giller
173 and Greenberg 2015), sites were visually selected to ensure habitat similarity among
174 sampling sites. Thus, we attempted to survey the same substratum types at all sampling
175 sites, and samples were collected from riffle sections with cobble and small boulders as
176 the main substratum. The minimum distance between two sampling sites was 1 km
177 (River Furelos) and the maximum distance was 5 km (River Lengüelle). We assumed
178 that fish and insect movements between sampling sites would be negligible during the
179 timeframe of the study (three consecutive days in each river system), and thus that the
180 study sites were therefore deemed independent.

181

182 We established a transect perpendicular to the direction of the flow in the middle of
183 each of 12 sampling sites (lengths between 70 m and 100 m), and measured water depth
184 (m) and current velocity (m/s) at five equally spaced intervals across the transect. A
185 water current meter (Flowwatch, JDC Electronic) was used to measure velocity, and
186 depths were measured with a metre stick (see Appendix 1 for habitat details). Riparian
187 canopy cover (%) (i.e. the percentage of the river that is overhung by vegetation) was

188 measured with a concave spherical densiometer as described in Bain and Stevenson
189 (1999). Riparian vegetation was composed of deciduous vegetation including alder
190 [*Alnus glutinosa* (L.) Gaertner 1791], oak (*Quercus robur* L.) and willow (*Salix* spp.) at
191 all sampling sites, but with different levels of riparian cover (Appendix 1).

192

193 At each sampling site a stretch of the river was delineated by upstream and downstream
194 stop nets, and prior to electrofishing, samples of potential prey (benthic and drifting
195 invertebrates) were collected at each site to study their availability. To ensure
196 representativeness of benthic invertebrates among sampling sites, a combination of three
197 habitats (sand, cobbles and macrophytes) were always sampled. Thus, three replicates
198 (one for each habitat type) were collected at each sampling site. Benthic invertebrates
199 were collected using a 0.1 m² Surber sampler (mesh size = 250 µm). Because surface
200 prey is expected to be more abundant at the water surface than close to the bottom and
201 rather the opposite for aquatic drifting invertebrates, we surveyed two different depths
202 in the water column to ensure representativeness of both types of invertebrates in our
203 drift sample. Two Brundin nets (250 µm mesh size, 1 m long, 30 cm mouth diameter)
204 were used to simultaneously collect two drift samples (one set at the water surface and
205 the other on the substratum). Because the abundance of drifting invertebrates is high at
206 night and in the early morning (e.g. Neveu 1980), Brundin nets were set at sunrise and
207 retrieved after approximately 3 hours (ranging between 179 min and 200 min). The
208 samples were fixed in 4% formalin solution. We estimated drift density (ind/m³ per
209 hour) according to Allan and Russek (1985). The filtered water was estimated based
210 upon the dimensions of the net and the water velocity. Drifting invertebrates were
211 classified as either aquatic (henceforth termed “aquatic drifting prey”) or surface prey
212 (henceforth termed “surface drifting prey”) (values in Appendix 1).

213 Brown trout were captured and their stomachs examined to evaluate dietary
214 composition. To reduce the risk that the invertebrate surveys disturbed the fish, fish
215 sampling were carried out 30 minutes after the sampling of potential prey. Brown trout
216 were collected using pulsed D.C. backpack electrofishing equipment (Hans Grassl
217 GmbH, ELT60II). Three-pass removal electrofishing was conducted at each sampling
218 site with 30 min between passes following the standardized procedures described for the
219 EU Water Framework Directive by the CEN directive on fishing with electricity in
220 wadeable rivers (CEN 2003). Fishes were identified to species level, counted and
221 returned to the river except for brown trout, which were immediately killed using an
222 overdose of anaesthetic (benzocaine), measured (fork length) to the nearest 1 mm and
223 transported in cooler boxes (approx. 4°C) to the laboratory, where they were frozen at
224 -30°C until processing. We attempted to collect at least ten brown trout individuals
225 from each sampling site (sampling size range: 10-42). In total, 170 brown trout (48-343
226 mm) were used for stomach content analyses. The density (fish/m²) of each fish species
227 was calculated using the Zippin multiple-pass depletion method (Zippin 1956).

228

229 Diet analysis

230 Prey items in each brown trout stomach were identified to the same taxonomic level as
231 the invertebrate samples, and counted. When fragmented or partially digested, the
232 number of items was estimated by counting body parts resistant to digestion. No empty
233 stomachs were observed. Prey taxa were classified as either aquatic or surface prey, and
234 fish remains were omitted from diet analysis (no rodents and amphibians were found).
235 For each individual, diet was presented as the relative abundance (%) of each prey
236 category. Using previously described foraging modes of salmonids (Nakano et al.
237 1999a), individual fish were categorised by their prime foraging mode (benthic or drift

238 feeding) according to which prey category that was dominant (>50% contribution) in
239 the diet (Knudsen et al. 2010). Benthos foragers (benthic foraging) included
240 individuals feeding mainly on aquatic prey, whereas individuals feeding mainly on
241 surface prey were assigned as drift foragers (drift foraging).

242

243 Statistics

244 Statistical analyses and graphical outputs were performed using R 3.2.2 (R Core Team
245 2015). Logistic regression models were fitted using the “popbio” package in R (Stubben
246 and Milligan 2007) to examine the ontogenetic shift of brown trout from aquatic
247 prey/benthic foraging to surface prey/drift foraging as a function of fish length, based on
248 presence/absence data (1 = surface prey consumed, 0 = no surface prey consumed). The
249 shift to a specific prey category can be assumed to occur when, according to the fitted
250 curve of a logistic regression model, the probability of the category occurring in the diet
251 is 50% (Kahilainen and Lehtonen 2003). Hence, a 50% probability level was employed
252 to investigate the body length-related timing of the dietary shift (from aquatic to surface
253 prey) by brown trout. 25% and 75% probability levels were considered as threshold
254 values for the range of sizes that the shift from aquatic to surface feeding occurs. To
255 increase the accuracy of predictions on the body length-related timing of this dietary
256 shift, nearby riverine data on the diet composition of newly emerged (20-44 mm) brown
257 trout collected in March and April (Sánchez-Hernández et al. 2011a) as well as
258 juveniles and adults of brown trout collected in June (Cobo et al. 2013), August
259 (Sánchez-Hernández et al. 2013b; Sánchez-Hernández 2016) and October (Sánchez-
260 Hernández et al. 2011b) were included in the logistic regression models to account for
261 the absence of earlier developmental stages and fish diet surveys in months other than
262 September (see Appendix 2). Although, brown trout may tend to prey on benthos in

263 early spring (March and April) and late summer (October) because surface invertebrates
264 are not usually abundant, surface invertebrates may represent a significant part of the
265 drift during those months in northern Iberian rivers (Cobo and González 1990; Rincón
266 and Lobón-Cerviá 1997), and also as indicated by stomachs contents (Sánchez-
267 Hernández et al. 2011a, 2011b). We also ran sensitivity analyses to test whether logistic
268 regression models changed after excluding additional data (i.e. using only data collected
269 in September). Additionally, the strength of association between fish length and surface
270 prey was tested using Pearson's rank correlation. This analysis allowed us to test
271 ontogenetic changes in surface prey use by brown trout.

272

273 The relationships between the abundance of surface prey in the diet and the twelve
274 explanatory variables (riparian vegetation cover, water depth, river width, water current
275 velocity, benthic density, aquatic drifting prey, surface drifting prey, brown trout length,
276 brown trout density, northern straight-mouth nase density, European eel density and sea
277 lamprey density) were investigated with linear-mixed effects models using sampling
278 site as a random factor. By including sampling site as a random factor, we attempted to
279 include components that allow for heterogeneity of variables among sampling sites
280 (Zuur et al. 2009). Because the consumption of surface prey (e.g. Montori et al. 2006;
281 Sánchez-Hernández and Cobo 2016) and swimming capacity (Ojanguren and Braña
282 2003) increases with brown trout length, fish length was included as an explanatory
283 variable to account for intrinsic features, such as swimming capacity and dietary shifts,
284 linked to the ontogeny of the species. Our linear-mixed modelling was individual-based,
285 using diet data for each fish. Modelling was performed using the “nlme” package
286 (Pinheiro et al. 2016), with model selection by model comparison using the “MuMIn”
287 library (Bartoń 2016). First, we set the full model (i.e. including all explanatory

288 variables as fixed part and sampling site as a random factor) using the maximum
289 likelihood (ML) procedure. In comparison to restricted maximum likelihood (REML),
290 ML procedure should be used to compare models with different number of fixed factors
291 (Crawley 2007) as in this study. Then, we used a model selection method (Burnham and
292 Anderson 2002) to compare all possible combinations of fixed factors and ranked
293 candidate models according to the Akaike information criterion (AIC), with the model
294 with the lowest AIC value deemed the most satisfactory. It should be noted that when
295 sample size is small or the number of parameters is large, AIC_c (AIC corrected for
296 small-sample bias) or $QAIC_c$ (AIC_c for overdispersed data) should be used instead of
297 AIC (Anderson and Burnham 2002). In the present study AIC_c was used for model
298 selection. Additionally, models with AIC values within 1-2 units of the best model have
299 also substantial support (Burnham and Anderson 2002). Hence, we considered models
300 within 1-2 units of the best model to have equally strong support for a given set of
301 model parameters. To identify the importance of the variables belonging to the best
302 model, the t -statistics (obtained with the *summary* command) or the F -statistic (obtained
303 with the *anova* command) can be used (Zuur et al. 2009). Because the *anova* command
304 applies sequential testing, and changing the order of model parameters may trigger
305 different p -values (Zuur et al. 2009), we used the t -statistic. Finally, the residuals of the
306 most satisfactory model were inspected for deviations from normality and
307 heteroscedasticity without finding evidence of violation of the model assumptions
308 (Appendix 3). A significance level of $p = 0.05$ was used for all analyses.

309

310 **Results**

311 Benthic invertebrate densities varied by a factor of seven among sampling sites (2245.2
312 ind/m² to 14573 ind/m², Appendix 1). Drift densities varied among sampling sites

313 (Appendix 1). Except for one location on the River Lengüelle (L1), aquatic
314 invertebrates dominated the drift samples in terms of abundance.

315

316 With the exception of one sampling site (A2, River Anllóns), aquatic prey tended to
317 constitute an important food source in all brown trout populations with a high degree of
318 inter-individual variation in resource use (Figure 2). Indeed, overall individually
319 categorised as benthos foragers were more abundant than drift foragers (76.5% and
320 18.2%, respectively). The remaining fish (5.3%) were not assigned a specific feeding
321 mode (equal abundance of aquatic and surface prey). The observed minimum size of an
322 individual with surface prey in its stomach was 25 mm. The logistic regression model
323 conducted across all sites indicated that the ontogenetic shift from aquatic to surface
324 prey occurs at a body length of 81 mm (Table 1 and Figure 3), with threshold values
325 between 36 mm (25%) and 127 mm (75%). Our sensitivity analyses indicated that this
326 shift occurs at a body length of 51 mm. The percentage of surface prey in the diet
327 increased with fish length (Pearson's rank correlation, $R = 0.492$; $p < 0.001$).

328

329 All selected model simulations had strong support (AIC_c values within 1-2 units of the
330 best model) (Table 2). There was a strong positive influence of fish length, water
331 current velocity, river width, riparian canopy cover and water depth, but a negative
332 influence of benthic invertebrate density, brown trout density and eel density, on the
333 proportion of surface prey in the diet of brown trout (Table 2). Fish length seemed to be
334 the most influential variable of the most satisfactory model (Table 3), which is also
335 present in all selected model simulations (Table 2).

336

337

338 **Discussion**

339 Our key finding is that individual differences in feeding behaviour and ontogenetic
340 stage (i.e. intrinsic features of fish individuals linked to fish length) operate as a strong
341 modulator of foraging mode (benthic vs. drift) of riverine brown trout. A number of
342 studies under controlled conditions have identified that foraging shifts (e.g. from the
343 benthos to the water surface) of riverine salmonids can be highly influenced by
344 competition, prey abundance, water depth and water current velocity (Nakano et al.
345 1999a; Booker et al. 2004). Using empirical data, our results provide important
346 advances on these previous studies by contributing new evidence of the importance of
347 individual variation in feeding behaviour and ontogenetic stage, rather than prey
348 availability, habitat characteristics and fish densities (as a proxy for inter- and
349 intraspecific competition), in the switch from benthic to drift foraging of stream-
350 dwelling salmonids. This dietary shift can reduce intraspecific competition in wild
351 populations through food resource partitioning and promote brown trout bioenergetics
352 (e.g. increase in somatic growth and body reserves). While seasonal shifts in benthic
353 invertebrate community structure do not force fish individuals to shift to drift foraging
354 (Sánchez-Hernández et al. 2016b), it is reasonable to posit that seasonality of surface
355 invertebrates, which peaks during summer (Bridcut 2000; Nakano and Murakami 2001),
356 in combination to individual variation in feeding behaviour and ontogenetic stage shape
357 foraging mode shifts of wild stream-dwelling salmonids. As a caveat, caution should be
358 exercised regarding our conclusions because our analyses did not include seasonal data,
359 and need to be tested in future studies.

360

361 Our study supports the view that the use of the water surface for feeding has a strong
362 ontogenetic component. This is in agreement with previous works demonstrating that

363 the consumption of surface prey increases with fish size and age (e.g. Montori et al.
364 2006; Syrjänen et al. 2011; Sánchez-Hernández and Cobo 2016). As in other studies
365 (Johnson and Ringler 1980; Sánchez-Hernández et al. 2011*a*, 2016*a*), we found that
366 foraging by YOY individuals at the water surface is common. We provided novel
367 insights into the predicted length (~80 mm, with threshold values between 36 mm and
368 127 mm) of the body length-related timing of the dietary shift from aquatic to surface
369 prey, but this ontogenetic dietary shift may occur earlier as the observed minimum size
370 of an individual with surface prey in its stomach was 25 mm. The observed variability
371 in the described body length-related timing of the ontogenetic switch from aquatic to
372 surface prey seems to be best explained by individual differences in feeding behaviour
373 and ontogenetic stage in combination to environmental gradients (here mainly benthic
374 invertebrate density, brown trout density and water current velocity, but see all selected
375 model simulations with strong support in Table 2). Inter-individual variation in feeding
376 behaviour is common in nature (Bolnick et al. 2003; Nakayama et al. 2017), and this
377 variation promotes ecological success of populations and species (Forsman and
378 Wennersten 2016). Our understanding of the consequences of the observed ontogenetic
379 switch by brown trout can be summarised as a beneficial trade-off between different
380 ontogenetic feeding strategies in riverine environments because, for example, the
381 dietary shifts during fish life stage transitions are usually accompanied by a marked
382 increase of the somatic growth and reduction of intra-specific competition through
383 resource partitioning (Jensen et al. 2012; Sánchez-Hernández et al. 2013*a*; Nakazawa
384 2015).

385

386 We suggest that the capacity of brown trout to switch their foraging behaviour from
387 aquatic to surface resources may be partly related to the development of locomotor

388 abilities during ontogeny. We assume that the body length-related timing of this shift is
389 strongly connected to the lower swimming capacity of smaller individuals (Ojanguren
390 and Braña 2003). Moreover, predation risk can impact on the foraging behaviour of
391 salmonids (e.g. Metcalfe et al. 1987). Tentatively high predation risk of YOY
392 individuals (here mainly by grey heron and common kingfisher) when foraging at the
393 water surface combined with their comparatively low swimming capacity may influence
394 the decision to forage at the surface (Nislow et al. 1998; García de Leániz et al. 2000).
395 Because our analyses did not include individuals from pools where they usually
396 consume more surface prey than in riffles (Giller and Greenberg 2015), additional work
397 will be needed to explore whether or not a similar predicted length for the dietary shift
398 from aquatic to surface prey may occur in lentic areas of riverine systems where
399 swimming ability is presumably less important.

400

401 This study does not support the hypothesis that the relative abundance of surface prey in
402 the diet of individual stream-dwelling fish would increase with increasing availability of
403 surface invertebrates irrespective of other site-specific characters. The feeding mode
404 (benthic or drift) of stream-dwelling salmonid species is usually established in response
405 to site-specific prey accessibility and energy gain (Nakano et al. 1999a; Booker et al.
406 2004; Sánchez-Hernández and Cobo 2013). For example, Nakano et al. (1999a) found
407 that decreases in the abundance of drifting prey led to increases in the proportion of
408 individuals foraging on benthic organisms. However, our results emphasise the
409 importance of the abundance of benthic invertebrates, in addition to the abundance of
410 surface prey, in explaining the use of the water surface for feeding. Because stream-
411 dwelling salmonids typically 'sit-and-wait' to ambush prey from short distances in lotic
412 areas (Tunney and Steingrimsson 2012) or they adopt a cruising behaviour for searching

413 food resources in more lentic areas (Hasegawa and Yamamoto 2010), it is pertinent to
414 take into account prey proximity and local abundance to fully understand the switch
415 from aquatic to surface prey by stream-dwelling salmonids. The outcome of our study
416 supports the view that if aquatic invertebrates are more abundant and accessible than
417 surface invertebrates, it is possible that individuals will not switch to surface prey (drift
418 foraging). It is possible that this is because benthic invertebrates and aquatic drifting
419 invertebrates are more accessible than surface prey to brown trout individuals.

420

421 Water depth may be of paramount importance to explain the position in the water
422 column chosen by drift-feeding salmonids through its influence on prey detection and
423 capture (e.g. Guensch et al. 2001; Piccolo et al. 2007). For example, Piccolo et al.
424 (2007) observed that prey capture probabilities are always lower at the water surface
425 than near the substratum. Thus, it can be hypothesised that individuals located in deep
426 areas of riverine systems may have difficulty detecting prey at the surface of the water
427 column. Our results did not support this, as water depth had a positive effect on the
428 relative abundance of surface prey in the diets. One explanation might be that deeper
429 sites probably were less turbulent than shallow sites and surface prey thus easier to
430 detect and capture. However, this view should be treated with some caution because the
431 sites in this study (riffles with mean depths of between 0.3 m and 0.6 m) prevented a
432 robust assessment of the influence of water depth on the consumption of surface prey
433 and the foraging mode of riverine brown trout.

434

435 Factors other than water depth, such as water current velocities, may also be a major
436 determinant of successful prey detection and interception (Piccolo et al. 2008; Tunney
437 and Steingrimsson 2012). It can be expected that surface invertebrates are easier to

438 detect and capture in pools than in the more turbulent riffles. Individuals in pools
439 usually catch more prey at the water surface than do individuals in riffles because pools
440 usually offer high-quality drift-foraging stations for brown trout (Giller and Greenberg
441 2015). Kerr et al. (2017) observed that swimming costs are affected by water current
442 velocity and turbulence, and fish individuals spend more energy as hydrodynamic
443 conditions increase. Our study supports the view that the relative consumption of
444 surface prey is positively connected with water current velocity. This could be related to
445 the range of water current velocities observed in this study (range: 0.02-0.10 m/s),
446 which were considerably lower than the maximum swimming speed (between 1 m/s and
447 2 m/s), critical swimming speed (6.95 ± 0.94 body lengths per second) and velocity
448 preference curves (usually between 0.3 m/s and 0.4 m/s) of brown trout (Ojanguren and
449 Braña 2003; Ralph et al. 2012; Kerr et al. 2017), and therefore likely unable to impose a
450 limitation on foraging at the surface of the water column. However, brown trout
451 individuals tended to consume more aquatic invertebrates in sampling sites with higher
452 water current velocities (>0.06 m/s, as observed in F1, F3, L1 and T1), which also
453 highlights that wild individuals might avoid foraging at the water surface to evade
454 energetic cost associated with flows.

455

456 Although deciduous riparian vegetation was similar among localities, our study
457 demonstrates the importance of riparian canopy cover for the relative contribution of
458 surface prey to the diet of wild brown trout. This is in agreement with several authors,
459 who provided evidence that terrestrial input to riverine systems depends greatly on
460 riparian canopy cover (Edwards and Huryn 1996; Ryan and Kelly-Quinn 2015). For
461 example, streams running through forest supply more biomass of terrestrial
462 invertebrates to salmonids than do those running through pasture (Edwards and Huryn

463 1996). Thus, alterations to the landscape, and specifically riparian land use, have an
464 important influence on the availability of terrestrial invertebrates to stream-dwelling fish
465 species (Edwards and Huryn 1996; Erős et al. 2012), and thereby fish production, fish
466 bioenergetics and ecosystem functioning (Edwards and Huryn 1995; Nakano et al.
467 1999*b*; Sweka and Hartman 2008; Erős et al. 2012). This underpins the interface
468 between terrestrial and aquatic ecosystems, which, in turn, has a direct impact on
469 stream-dwelling fish species in the biological processes derived of feeding such as
470 growth and competition.

471

472 Fish abundance, assumed to be a principal mediator of intra- and interspecific
473 competition, can play a role in governing stream positions of and foraging modes
474 adopted by salmonids (e.g. Fausch and White 1981, 1986; Nakano et al. 1999*a*;
475 Sánchez-Hernández et al. 2017*b*). Theoretical considerations, that address relationships
476 between drift, foraging behaviour and competition, posit that ambush drift is the key
477 variable that forces subordinate individuals to shift to benthic foraging (Nakano et al.
478 1999*a*). The present study reveals that there was a negative influence of brown trout
479 density on the proportion of surface prey in the diet of brown trout. Thus, our results
480 support the view that higher fish abundances may trigger individuals to shift to benthic
481 foraging as Nakano et al. (1999*a*) previously indicated for subordinate individuals in
482 fish assemblages.

483

484 In summary, we conclude that the dietary shift from aquatic to surface prey in riverine
485 salmonids may occur early in their ontogeny (YOY individuals), but this shift is largely
486 influenced by a number of inter-related factors. The fundamental mechanisms driving
487 the drift foraging of stream-dwelling brown trout are intrinsic features (individual

488 feeding behaviour and ontogenetic stage), environmental variation (mainly benthic
489 invertebrate density and water current velocity) and fish densities (as a proxy of
490 competition).

491

492

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502

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733

734 **Tables**

735 Table 1. Summary of logistic regression model explaining the probability of surface
 736 prey/drift foraging over the ontogeny of brown trout. Statistically significant differences
 737 ($p < 0.05$) are marked in bold. S.E. = standard error.

	Model parameters					Probability		
	Variable	Coefficient	S.E.	<i>z</i> value	<i>p</i> value	25%	50%	75%
Surface prey	Intercept	-1.976	0.282	-7.010	<0.001	36 mm	81 mm	127 mm
	Fish length	0.243	0.025	9.531	<0.001			

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741 Table 2. Summary table for the ten best model simulations explaining the contribution of surface prey of stream-dwelling brown trout according
 742 to AIC_c values (the best model is the model with the lowest AIC_c values).

Model	Intercept	Predictor variables								Model statistics					
		Fish length	Benthic density	River width	Brown trout (density)	Water depth	Water current velocity	Riparian cover	Eel (density)	R ²	df	logLik	AIC _c	delta	weight
1	23.509	1.444	-0.002	–	-47.989	–	1.383	–	–	0.20	7	-795.036	1604.763	0	0.015
2	-28.660	1.412	-0.001	2.327	–	–	–	0.164	–	0.20	7	-795.052	1604.795	0.032	0.015
3	28.051	1.407	-0.002	–	-46.002	–	–	–	–	0.19	6	-796.272	1605.060	0.297	0.013
4	-35.370	1.491	–	2.124	–	–	–	0.191	–	0.19	6	-796.333	1605.182	0.419	0.012
5	-41.447	1.481	–	1.851	–	52.567	–	–	–	0.19	6	-796.392	1605.299	0.536	0.012
6	-40.009	1.507	–	2.313	–	–	–	0.252	-133.516	0.20	7	-795.429	1605.550	0.787	0.010
7	-33.324	1.432	-0.001	2.050	–	42.190	–	–	–	0.20	7	-795.441	1605.573	0.809	0.010
8	28.466	1.510	-0.001	–	-51.848	–	–	–	-122.779	0.20	7	-795.458	1605.607	0.844	0.010
9	-41.588	1.428	-0.001	2.024	–	51.902	1.301	–	–	0.20	8	-794.407	1605.709	0.946	0.009
10	8.627	1.491	-0.002	0.967	-29.703	–	–	–	–	0.20	7	-795.527	1605.746	0.983	0.009

743

744

745 Table 3. Estimated parameters of the best model simulation (model 1 of Table 2)
746 explaining the contribution of surface prey of stream-dwelling brown trout. S.E. =
747 standard error.

	Value	S.E.	<i>t</i> value	<i>p</i> value
Intercept	23.509	9.277	2.534	0.012
Benthic density	-0.002	0.001	-2.507	0.036
Fish length	1.444	0.335	4.310	<0.001
Brown trout (density)	-47.989	11.679	-4.109	0.003
Water current velocity	1.383	0.889	1.555	0.159

748

Draft

749 **Figure legends**

750

751 Figure 1. Maps of the Iberian Peninsula and north-western Spain showing the sampling
752 sites.

753

754 Figure 2. Abundance of aquatic and surface prey in the stomach contents of brown
755 trout. Data are presented for each river [Anllóns = A, Furelos = F, Lengüelle = L and
756 Tambre = T] and for each sampling site within each river system [sampling sites
757 labelled from the upper part (1) to lower part (3)].

758

759 Figure 3. Probability of the ontogenetic shift from aquatic to surface prey as a function
760 of fork length of stream-dwelling brown trout. Grey bars represent histograms of relative
761 frequencies based on presence/absence data (1 = surface prey consumed, 0 = no surface
762 prey consumed). Red line represents the fitted curve of the logistic regression model.

763

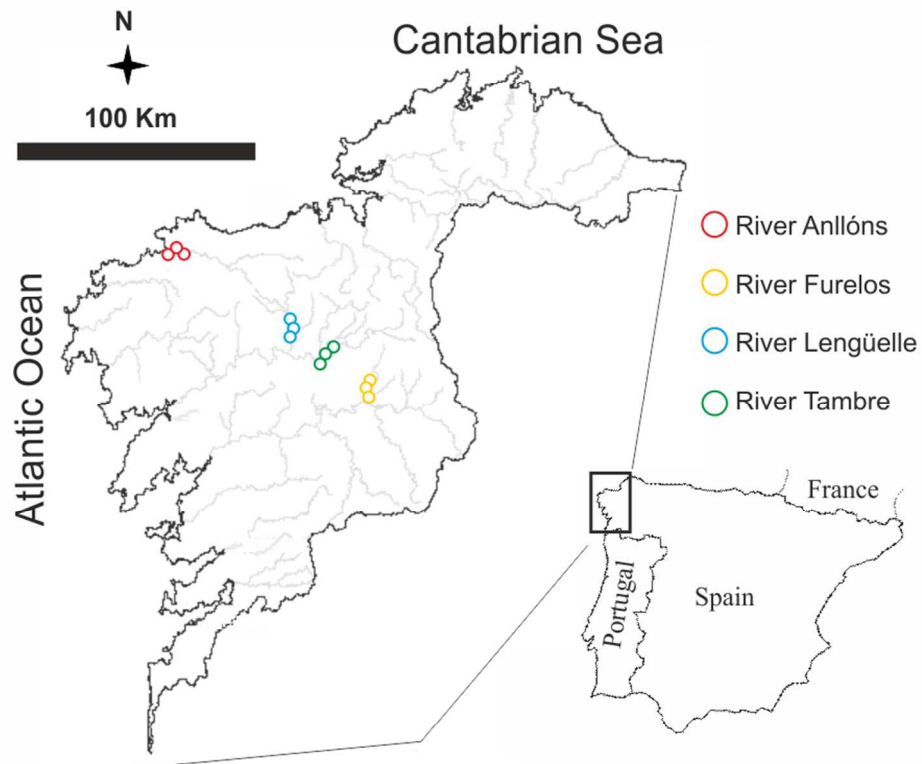


Figure 1.

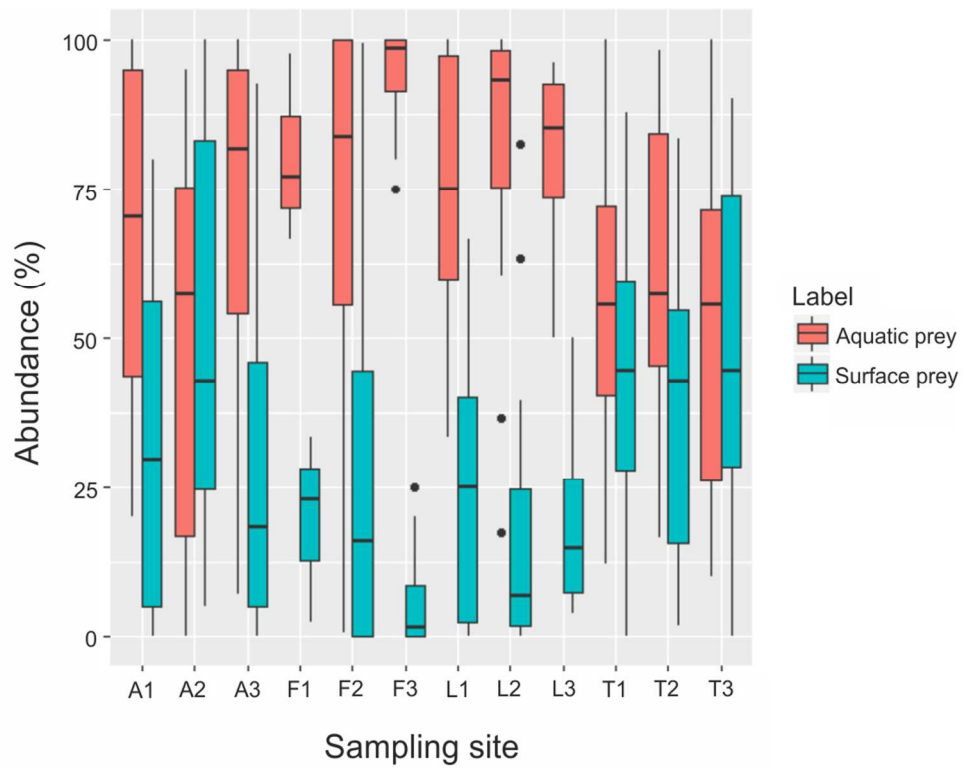


Figure 2.

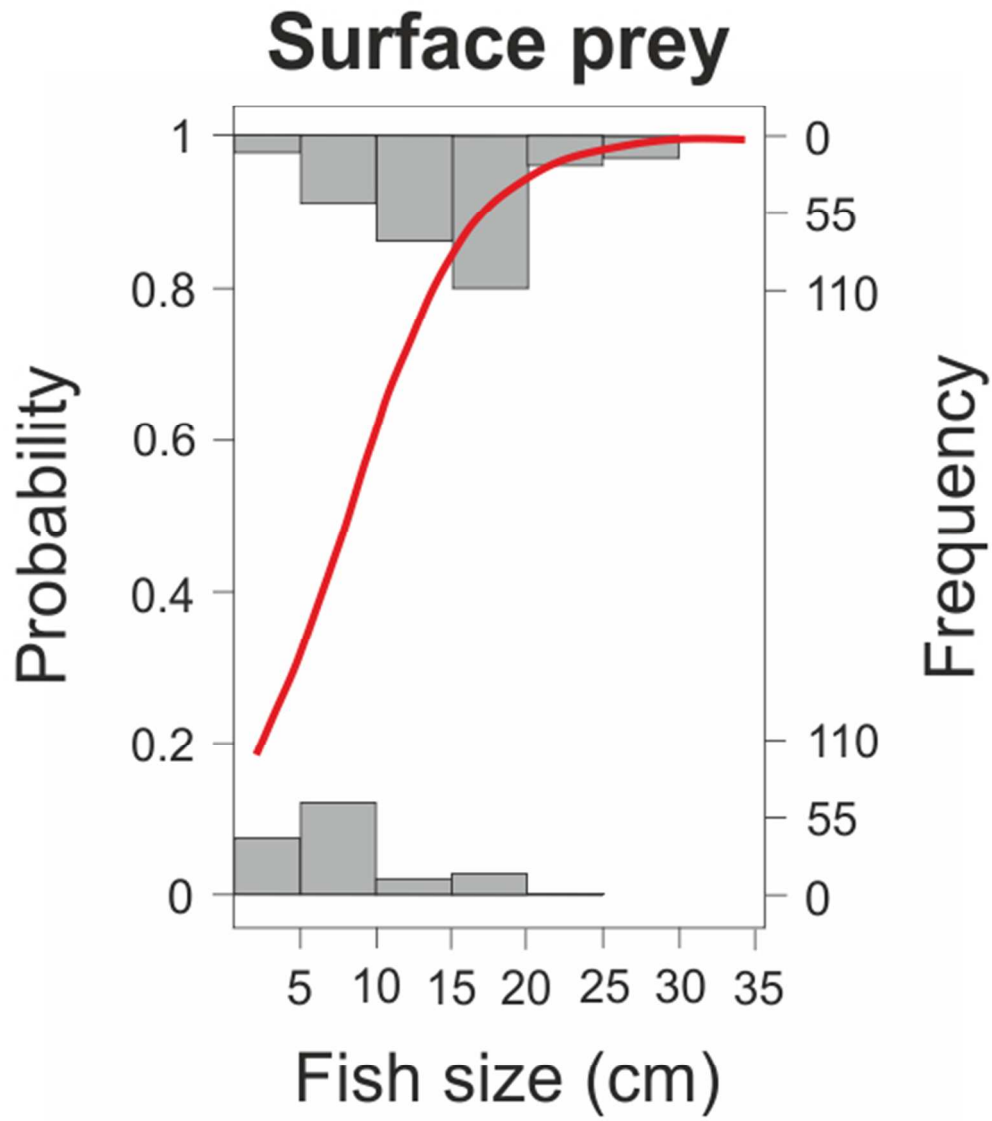


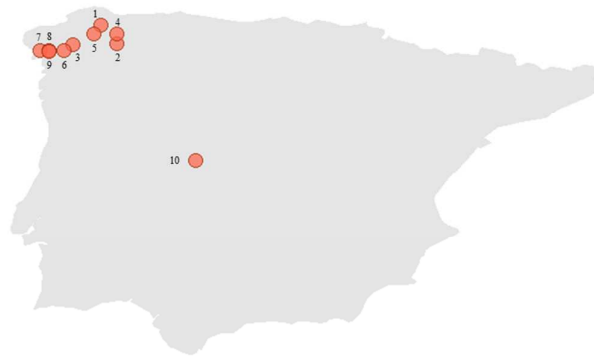
Figure 3.

Appendix 1. Environmental characteristics of sampling sites. Sampling sites are labelled from the upper part (1) to lower part (3). Nase = northern straight-mouth nase. * larval sea lamprey (ammocoetes).

River/location	River morphometric and hydrodynamic conditions				Riparian vegetation	Prey availability			Fish densities			
	River width (m)	River length (m)	Water depth (m)	Water current velocity (m/s)	Riparian cover (%)	Benthic density (ind/m ²)	Aquatic drifting prey (ind/m ³ *hour)	Surface drifting prey (ind/m ³ *hour)	Brown trout (ind/m ²)	Nase (ind/m ²)	European eel (ind/m ²)	Sea lamprey* (ind/m ²)
Anllóns/A1	16.95	70	0.51	0.03	85.5	7789.3	1547.4	15.9	0.053	0.010	0.068	-
Anllóns/A2	17	85	0.47	0.06	71.9	8650.1	1172.5	96.4	0.026	0.008	0.015	0.005
Anllóns/A3	14.6	80	0.35	0.02	64	7892.6	837.2	12.9	0.028	0.011	0.067	0.060
Furelos/F1	7.68	83	0.59	0.06	72.4	8519.2	2178.8	799.3	0.363	0.298	-	-
Furelos/F2	19.8	85	0.33	0.03	12.2	7417.4	850.7	52.1	0.115	0.528	-	-
Furelos/F3	15.27	95	0.19	0.09	20.6	14573.0	410.0	8.1	0.259	0.670	-	-
Lengüelle/L1	15	83	0.30	0.07	61.6	6584.0	25.4	51.9	0.398	0	-	-
Lengüelle/L2	9.3	100	0.39	0.03	58.5	2575.8	1905.9	24.6	0.444	0.098	-	-
Lengüelle/L3	7	91	0.36	0.03	40	3099.2	955.8	251.8	0.693	1.247	-	-
Tambre/T1	17.92	80	0.32	0.10	61.6	2245.2	303.6	275.9	0.192	0.294	-	-
Tambre/T2	12.76	85	0.57	0.04	100	3884.3	1647.3	223.1	0.090	0.083	-	-
Tambre/T3	20	90	0.39	0.05	50	5392.6	473.9	60.9	0.079	0.103	-	-

Appendix 2. Information about the additional data sources used in the logistic regression models.

Code	Reference	River	Geographical coordinates		Date of survey	Sampling size (<i>n</i>)	Fish size (range, mm)
			Latitude	Longitude			
1	Sánchez-Hernández et al. (2011a)	Castromaior	43.3444	-7.5369	March and April 1996	19	21-25
2	Sánchez-Hernández et al. (2011a)	Xemil	42.9281	-7.2040	March and April 1996	25	19-26
3	Sánchez-Hernández et al. (2011a)	Iso	42.9107	-8.1497	March and April 1996	29	20-44
4	Sánchez-Hernández et al. (2011a)	Eo	43.1583	-7.2039	March and April 1996	26	24-27
5	Sánchez-Hernández et al. (2011b)	Ladra	43.1474	-7.6905	October 1996	31	67-88
6	Sánchez-Hernández et al. (2013b)	Ulla	42.7946	-8.3362	August 2011	21	55-81
7	Cobo et al. (2013)	Traba	42.7944	-8.8558	June 2003	31	106-179
8	Cobo et al. (2013)	Sar	42.7795	-8.6593	June 2003	30	133-198
9	Cobo et al. (2013)	Rois	42.7706	-8.6623	June 2003	34	119-183
10	Sánchez-Hernández (2016)	Tormes	40.3167	-5.4833	August 2010	43	59-286



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Appendix 3. Residual plot of the best model explaining the contribution of surface prey of stream-dwelling brown trout.

