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1 Main potential drivers of trout population dynamics in bypassed  
2 stream sections

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9

10 **Short title:** Main drivers of trout population dynamics  
11  
12

13 **ABSTRACT**

14 The key role of hydrological variability in structuring brown trout populations is well-  
15 established. However, the influence of additional drivers is more difficult to identify. The  
16 implementation of long-term monitoring and the development of reliable tools can help reveal  
17 fine local drivers structuring fish populations in contrasted flow regimes. The present study  
18 used data series for nine reaches monitored for nine to nineteen years in four French salmonid  
19 streams. Study reaches were within five bypassed sections influenced by instream flow. A  
20 deterministic trout population dynamics model was applied on each reach, with calibration  
21 and validation procedures. Results revealed that biological drivers structured all reaches  
22 similarly. In addition, seven other drivers were identified. Among these additional drivers,  
23 hydrology mainly explained temporal fluctuations in trout density, regardless of reach. Three  
24 drivers independent of hydrology were also revealed: poor water quality, limited spawning  
25 area, and the effect of power plant operations. All drivers influenced the whole bypassed  
26 section and were never limited to the scale of the reach (sampling area). Further analyses of  
27 each driver are now needed, to regionalize and quantify their respective impact precisely.  
28 Research perspectives include developing a tool that can be used at any location, integrating  
29 temporal variability and most of the controlling drivers for each population type. Thus,  
30 assessment of trout population status would be simplified, enabling implementation of  
31 efficient management rules.  
32

33 **KEY-WORDS:** Trout, population dynamics, structuring drivers, bypassed section  
34

## 35 INTRODUCTION

36 Freshwater ecosystems provide vital natural resources (e.g., clean water and food) and  
37 services (e.g., energy, irrigation, waste assimilation, recreation) that contribute to human well-  
38 being (Vörösmarty et al. 2010). However, such human use of freshwater ecosystems has  
39 resulted in declining biodiversity worldwide (Dudgeon et al. 2006). Balmfort et al. (2002)  
40 estimated that freshwater vertebrates declined at an annual rate of 2.4% over the period 1970–  
41 1999. In the last few decades, 20% of described freshwater fish species worldwide have been  
42 listed as threatened, endangered or extinct (Magurran et al. 2010). Among fish species, brown  
43 trout (*Salmo trutta* L.) is subject to specific human impact because of its economic and  
44 cultural importance. In France, in addition to these pressures, a large majority of hydroelectric  
45 schemes (80%) are located on salmonid streams, where brown trout is the dominant fish  
46 species. Moreover, studies of reference streams revealed a significant decrease in brown trout  
47 distribution area and abundance in recent years (Poulet et al. 2011). Multiple causes were  
48 mentioned: habitat degradation, proliferative kidney disease, angling catch, and water  
49 temperature. Predicted trends for salmonid distribution area under global warming suggest  
50 that trout range will decrease in the future (Comte et al. 2013).

51 In this context, scientists need to develop knowledge and tools to facilitate operational  
52 decisions for ecological and sustainable water management. Above all, precise knowledge of  
53 the driving factors influencing fish population dynamics is required. It is clear that multiple  
54 drivers operating on different space and time scales structure fish population dynamics  
55 (Durance et al. 2006; Jackson et al. 2001; Vincenzi et al. 2012). Trout biology and ecology  
56 have been studied for many years and are now relatively well-documented compared to other  
57 fish species (Baglinière & Maisse 1991; Elliott 1994; Jonsson et al. 2001; Klemetsen et al.  
58 2003). However, few studies have qualified the effects of the various drivers involved in trout  
59 population dynamics. It is well-established that hydrological events during fry, intra-gravel  
60 and post-emergence periods are major drivers of trout recruitment (Cattanéo et al. 2002;  
61 Gouraud et al. 2008; Jensen & Johnsen 1999; Lobón-Cerviá 2004). In addition, recruitment  
62 has often been shown to be the main driver of population size (Lobón-Cerviá 2009; Milner et  
63 al. 2003). Thus, by limiting recruitment, discharge is often one of the main drivers of trout  
64 population dynamics in mountain streams. Beyond hydrology, however, multiple drivers,  
65 abiotic or biotic, can structure trout populations (Milner et al. 2003). The most commonly  
66 cited abiotic factors are temperature (Armstrong et al. 2010; Armstrong et al. 2013; Warren et

67 al. 2012) and water chemistry (Eklöv et al. 1999), while competition for resources seems to be  
68 the major biotic determinant of trout population. Competition is linked to several biotic (such  
69 as food availability, Grant et al. 1998) or abiotic drivers (such as carrying capacity, Lobón-  
70 Cerviá 2008) and can induce density-dependent effects on growth or survival (Elliott 1994).  
71 The various drivers structuring trout populations operate on different space and time scales.  
72 Small-scale studies have highlighted the effects of precise biotic drivers (Einum et al. 2011;  
73 Jenkins et al. 1999; Lobón-Cerviá 2008), and abiotic factors such as flow regime (Lobón-  
74 Cerviá 2004; Vøllestad & Olsen 2008) and temperature (Borgstrøm & Museth 2005).  
75 However, most studies focused on the details of a single site, making large-scale extrapolation  
76 hazardous (Jackson et al. 2001). The present study therefore adopted a local scale analysis of  
77 trout population dynamics in nine different reaches, and summarized the spatial and temporal  
78 incidence of drivers identified at local level so as to assess the generalizability of the local  
79 results.

80 The study focused on nine reaches, located in five bypassed sections of hydroelectric dams in  
81 four geographically remote trout-bearing mountain streams. All the bypassed sections were  
82 under minimum flow, and had been previously studied to assess minimum flow value effects  
83 on trout population dynamics compared with reference sites (Gouraud et al. 2001; Gouraud et  
84 al. 2008). Local trout population dynamics models, calibrated on five of the nine reaches (in  
85 the Beyrède, Pont-Haut and Rory bypassed sections), were previously published (Gouraud et  
86 al. 2001; Gouraud et al. 2008). Long-term monitoring (between nine and nineteen years) then  
87 allowed accurate analysis of the temporal dynamics of the nine trout populations (Waters  
88 1999). The study objective was to provide an update on these trout population dynamics  
89 analyses so as to identify the spatial and temporal incidence of each population driver. A  
90 deterministic population dynamics model was then calibrated for each reach, with local trout  
91 population features. Certain trout population dynamics drivers were implemented in the initial  
92 model and subsequently calibrated for each population (biological characteristics, carrying  
93 capacity, food availability, etc.). In addition, long term monitoring identified further abiotic  
94 drivers which only occasionally influenced trout population, which were then added to the  
95 initial model.

## 96 MATERIAL AND METHOD

### 97 Trout population dynamics model

### 98 *General model*

99 The study used the MODYPOP deterministic trout population dynamics model described by  
100 Gouraud et al. (2001). This model, based on the Leslie matrix, simulates change in a trout  
101 population (i.e., density and biomass of different development stages: 0+, 1+ and >1+) over  
102 time by 1-month time steps. Two mechanisms of population regulation as a function of habitat  
103 are integrated: (1) density-dependent mortality, which tends to push the population toward a  
104 size compatible with local carrying capacity, and (2) adjustment of adult biomass to local  
105 carrying capacity.

### 106 *Trout population dynamics drivers*

107 Several inputs were required for MODYPOP calibration: (1) biological parameters (survival,  
108 fecundity, growth rates, female fertility, sex ratio, number of development stages and initial  
109 density and biomass for each stage) and (2) environmental drivers (carrying capacity, food  
110 availability, and time series of daily discharge and daily temperature). Environmental drivers  
111 contribute to model growth rate and density-dependent effects. These required MODYPOP  
112 inputs were calibrated for each reach, either by monitoring or by knowledge taken from the  
113 literature (detailed in Gouraud et al. (2001).

114 Four non-required drivers (abiotic drivers which may occasionally influence trout population  
115 and which were tested in the study) were added to the MODYPOP model as reach-specific  
116 drivers. The four reach-specific drivers were: flooding (Cattaneo 2005), limited available  
117 spawning area, power plant operations (Gouraud et al. 2008), and water quality. These drivers  
118 were calibrated using the same approach.

### 119 *Model calibration for reach-specific drivers*

120 MODYPOP was calibrated for each reach and each development stage, adding reach-specific  
121 drivers one by one, using the same iterative qualitative approach:

122 (1) Identification of one reach-specific driver: model simulations were compared with  
123 observations to identify whether a reach-specific driver could explain the residual  
124 error for a development stage. We focused at first on the development stage associated  
125 with the highest residual error, then chose an initial reach-specific driver that best  
126 explained deviations in terms of magnitude, direction and frequency.

127 (2) Calibration: the effect of identified reach-specific drivers was calibrated by tuning  
128 mortality rates (testing several rates, by 5% steps, consistent with the accuracy of our

129 data and deterministic approach), while other parameters of the population dynamics  
130 model remained constant. For hydrological drivers, minimum duration and flood  
131 threshold were also tuned: the population was influenced when daily flow exceeded  
132 threshold for a sufficient number of days. Values associated with the minimum  
133 deviation between observation and simulation for the reach (all development stages  
134 and all years) were retained for analysis.

135 (3) Returning to step 1, another driver was identified, with the same approach. The  
136 process stopped when remaining drivers no longer explained any residual deviation.

### 137 *Model validation*

138 MODYPOP validation was based on tests of the significance of each reach model, for each  
139 development stage. The Monte-Carlo randomization test was used with 10,000 permutations  
140 of observed density (Crowley 1992). The aim was to test whether random assignment of data  
141 would be as closely associated with the model's predictions as the original data. The ability of  
142 the model to capture temporal variations was validated for a given reach if less than 5% of  
143 random permutations were associated with (1) a lower sum of squared deviations and (2) a  
144 better prediction of the direction of density fluctuations from one year to another.

### 145 **Data set**

#### 146 *Bypassed sections and reaches*

147 The study focused on five bypassed sections where brown trout (*Salmo trutta* L.) was the  
148 dominant fish species. They were located in four mountain watersheds, geographically remote  
149 from one another except for Fontan and Breil which were at about 10 kilometers' distance  
150 (respectively, upstream and downstream bypassed section) in the same Mediterranean stream  
151 (Fig. 1). The physical characteristics of the bypassed sections differed greatly, with annual  
152 mean flow ranging between 2.7 and 20 m<sup>3</sup>.s<sup>-1</sup>, altitude between 280 and 740 m and slope  
153 between 0.7% and 3.7% (Table 129287). All constituted little reservoirs upstream of a dam  
154 without retention capacity, with high natural flow rates occurring by overtopping.

155 One to three reaches were selected within each bypassed section as being representative of the  
156 mesohabitat assemblage of the whole section (Table 2). When more than one reach was  
157 chosen in a given bypassed section, these reaches showed significantly different mesohabitat  
158 assemblage. We chose to study the population dynamics at reach scale so as to be able to  
159 detect whether driver effects depended on the mesohabitat assemblage.

160 Conducting local modeling in nine reaches, some of which being located within the same  
161 bypassed section, provided an opportunity to investigate the generalizability of the local  
162 approaches: local results were summarized by characterizing the spatial and temporal  
163 incidence of the identified drivers.

### 164 *Monitoring and estimation of model drivers*

165 The study period was from 1990 to 2013. During this period, each reach was monitored in  
166 terms of trout population, habitat, water quality and inter-annual variables (discharge,  
167 temperature and streambed substrate favorable to spawning).

168 Each reach was sampled annually by wading, using two-pass removal electrofishing  
169 sampling, following the recommendations of the European Committee for Standardization  
170 (CEN 2003). Sampling was performed without blocking nets, in summer or early autumn. All  
171 fish caught were identified, measured (total length) and weighed. Histogram analysis  
172 determined size according to development stage (0+, 1+, >1+). Trout abundance for each  
173 stage and for each sample were estimated with the Carle and Strub (1978) method. Densities  
174 (estimated abundance per sampled reach length) and biomasses (total weight per sampled  
175 reach length) were obtained for each development stage and each sample. Mean density and  
176 standard deviation were calculated for each development stage and each reach, based on all  
177 samples taken during the study period.

178 Habitat simulations were obtained for each reach in accordance with the PHABSIM protocol  
179 adapted to French streams (Ginot et al. 1998; Sabaton et al. 1995). Weighted usable area  
180 (WUA, in m<sup>2</sup>) was used to represent habitat availability for the three development stages  
181 (Souchon et al. 1989). The ratio between the maximum adult biomass sampled during the  
182 study period and the WUA for adults at instream flow value (minimum available habitat) was  
183 used to represent the local carrying capacity of the reach. In addition, spawning habitat  
184 availability was calculated almost every year for reaches located in the Fontan, Breil and Rory  
185 bypassed sections; this corresponds to the ratio between the area of streambed displaying  
186 grain sizes between 0.2 and 5 cm in diameter, considered to be favorable to trout spawning  
187 (Baglinière & Maisse 1991; Kondolf & Wolman 1993), and the entire wetted area of the  
188 reach.

189 Daily discharge and temperature time series were determined from recorders deployed within  
190 each monitored bypassed section. When discharge was temporarily unavailable, it was

191 extrapolated using natural daily discharge time series and/or operative data provided by power  
192 plants. Missing water temperature values were estimated using extrapolation models from air  
193 temperature (Bret et al.).

194 Habitat simulations associated to daily discharge time series determined daily WUA time  
195 series for the three development stages for each reach. This dynamic approach is considered  
196 the most appropriate for studying habitat limitation in population dynamics (Capra et al.  
197 1995). It was used in MODYPOP to evaluate local carrying capacity by monthly steps for  
198 each development stage.

199 The date and magnitude of each power plant operation event (overtopping, flushing or plant  
200 shutdown) that occurred during the study period were determined. Water quality was  
201 measured on each reach at the beginning of the study, and then regularly recorded only in  
202 reaches at risk of poor water quality according to the first analysis.

## 203 **RESULTS**

### 204 **Population structure and carrying capacity**

205 Strong temporal fluctuations in trout density were observed in all study reaches (Table  
206 16320). Mean densities and standard deviations were higher for 0+ than for 1+ or >1+. Mean  
207 coefficients of variation for reach development-stage densities were 0.98 for 0+, 0.78 for 1+  
208 and 0.58 for >1+.

209 The population structures were quite similar to each other, except for the Breil reaches.  
210 Comparison of the two trout populations in the Roya River (separated by ~10 km) revealed  
211 differences in biological characteristics. Growth was higher downstream in Breil (26-32 mm  
212 in the third year) than upstream in Fontan (21-24 mm at the third year); trout survived longer  
213 downstream (5 years) than upstream (4 years); and age at first maturity in females was greater  
214 downstream (3 years old) than upstream (2 years old).

215 The carrying capacity of each development stage fluctuated between reaches within a given  
216 bypassed section and between years in a given reach, depending on discharge. Limitation due  
217 to carrying capacity was never observed in any reaches at any time during the study period.

### 218 **Additional reach-specific drivers**

219 The seven additional drivers identified are presented in Bold italic: non-significant test

220



221 Table 4. For the three bypassed sections represented by two or three reaches, the same drivers  
222 were involved for all reaches, and tuned parameters (mortality rates, and flood thresholds and  
223 durations) showed the same values.

224 Four drivers concerned hydrology. Two types of hydrological event induced mortality: (1)  
225 floods during spawning (for the Beyrède bypassed section, represented by three reaches) or in  
226 Spring (for all reaches) induced mortality in 0+ trout, and (2) exceptional floods induced  
227 mortality in all development stages (for two bypassed sections represented by five reaches:  
228 Beyrède and Fontan). Flood thresholds and minimum durations inducing 0+ mortality are  
229 presented in Table 5. Mortality rates could differ greatly depending on the intensity of the  
230 event (between 20% and 90%).

231 In contrast, two hydrological events induced positive effects on mortality: (1) overtopping  
232 was associated with better 1+ survival (when flooding exceeded  $10 \text{ m}^3 \cdot \text{s}^{-1}$  during Spring) and  
233 >1+ survival (whatever the flood value or time of year) in the LIG2 reach, and (2) no floods  
234 during Spring was associated with better 1+ survival in the ROIP2 reach. These survival rates  
235 depended of the number of individuals in the lower development stage the year before.

236 In addition to hydrology, three other abiotic drivers were identified. Limited available  
237 spawning area induced mortality during intra-gravel life in the LIG2 reach. This occurred  
238 almost every year, except in 2000 and 2001 when high floods increased spawning ground. In  
239 the two reaches of the Breil bypassed section, three short-term poor water-quality events were  
240 observed during warm Summers, due to under-sizing of the upstream wastewater treatment  
241 plant, and induced mortality in 0+ trout. Finally, power plant operations induced 0+ and 1+  
242 mortality in the three reaches of the Beyrède bypassed section (three times during the twenty  
243 years of monitoring). The intensities of these drivers differed: power plant operation seemed  
244 to induce less mortality (50% to 75%) in the Beryède reaches than poor water-quality in the  
245 Breil reaches (75%) or limited spawning area in the Rory reach (80%).

### 246 **Final complete models**

247 Model calibration results for each reach underscored the influence of local phenomena on  
248 trout population structure. Observed and simulated density fluctuations for all development  
249 stages in the BEY2 reach are presented Fig. 2 to illustrate these results. Results for all reaches  
250 are proposed as supplementary materials. A synthesis of the temporal and spatial incidence of  
251 each identified driver is shown in Fig. 3. For the three bypassed sections represented by more  
252 than one reach, all identified drivers operated at all reaches of the section. Most of the drivers

253 were observed in any given bypassed section. Temporal occurrence was somewhat dependent  
254 on study period duration, and was more variable than spatial occurrence: between 0.08  
255 times.year<sup>-1</sup> for exceptional flooding and every year for overtopping in the Rory bypassed  
256 section, and for biotic processes (those included in the initial model: survival, fecundity and  
257 growth rate, potential carrying capacity and food availability).

### 258 **Model validation**

259 Validation test results are presented in Table 16320.

260 First, validation tests were performed on reach models with only biotic drivers (without the  
261 seven additional abiotic ones). Results revealed that only 15% of reach models were validated  
262 for the direction of the density fluctuations between years and for the density value.

263 Second, validation tests were performed on final models, integrating all drivers (biotic and  
264 additional abiotic ones). Additional drivers greatly improved the number of validated reach  
265 models: 63% for density fluctuation direction and 70% for density value. All models for the  
266 BREIL1 reach showed poor results. Models for 0+ were validated for all other reaches, except  
267 for direction in the ROIP2 reach (p-value=0.06). Predictions for this development stage were  
268 then successful in seven of the nine reaches. Predictions for other development stages were  
269 less satisfactory (5/9 for 1+ and 6/9 for >1+). The first development stage was better  
270 simulated than the older ones.

### 271 **DISCUSSION**

272 The present study revealed that biotic drivers structured all reaches. In addition, seven other  
273 drivers were identified, four of which concerned hydrology. All drivers operated at bypassed  
274 section rather than reach scale.

### 275 **Biotic processes**

276 The biotic processes originally included in the model (survival, fecundity and growth rates,  
277 carrying capacity and food availability) structured all reaches. They were necessary but not  
278 sufficient to validate reach models in most cases. Gouraud (1999) demonstrated their  
279 importance in population dynamics modeling (for example, a density-dependent effect on 0+  
280 could decrease mortality rate 4-fold in this development stage). Carrying capacity (Ayllón et  
281 al. 2012) and density-dependent mortality (Nicola et al. 2008; Ojanguren et al. 2001) are two  
282 drivers widely documented as structuring trout populations. In the present study, these  
283 processes contributed to achieving validated models, thus confirming that they need to be

284 integrated in population dynamics models. However, no limitation was seen reacted to  
285 carrying capacity for adults, in terms of habitat availability as measured by WUA, during the  
286 study period. Other habitat components, such as shelter availability, may, however, influence  
287 trout dynamics (Dieterman & Hoxmeier 2011).

### 288 **Additional drivers**

289 Among additional drivers, hydrology mainly explained temporal fluctuations in trout density,  
290 regardless of reach. It operated throughout the trout life-cycle, depending on flood intensity.  
291 An effect of flooding during Spring (for all reaches) or spawning (for Beyrède reaches only)  
292 on recruitment was observed regularly during the study period (0.48 times.year<sup>-1</sup> on average).  
293 Hydrological events during spawning show positive or no effect (Hayes 1995; Lobón-Cerviá  
294 1996; Unfer et al. 2011) more often than negative impact (Nelson 1986) on trout density.  
295 These differences may be explained by the timing between the hydrological event and trout  
296 spawning in the study river: a reasonable flood event just before spawning may improve the  
297 potential spawning ground (Poff et al. 1997; Unfer et al. 2011), while high flooding after eggs  
298 have been laid could induce redd scouring and egg mortality (Montgomery 1996). In contrast,  
299 the negative effect of high flow during intra-gravel and post-emergence life on recruitment  
300 has been widely reported in mountain streams (Cattaneo et al. 2002; Jensen & Johnsen 1999;  
301 Lobón-Cerviá 2004). However, comparison of four different geographical contexts revealed  
302 that the threshold value as of which mortality occurred in the first development stage differed  
303 between bypassed sections. The Breil population in the Roya River seemed to have the  
304 highest threshold compared to its low flow magnitude (threshold=4.9\*Q90). This river is  
305 subject to a strong hydrological regime, with regular occurrence of intense floods. The Breil  
306 trout population, which had faster growth, may be less sensitive to floods than the Fontan  
307 population in the same river or other studied populations (Klemetsen et al. 2003).  
308 Furthermore, the present large dataset (in terms of study period and number of monitored  
309 reaches) allowed observation of mortality induced by exceptional floods on two bypassed  
310 sections (Fontan and Beyrède) whenever the event occurred. This driver was also observed in  
311 some other studies (Jowett & Richardson 1989; Young et al. 2010).

312 Usually, hydrology induced negative effects on mortality, but in the present study it was also  
313 associated with a positive impact in the Rory and Pont-Haut reaches, playing a determining  
314 role in maintaining population viability. For the Rory reach, better 1+ and >1+ survival was  
315 likely induced by downstream migration when overtopping occurred (Gouraud et al. 2008).

316 Adult densities were not correctly simulated for this reach (non-significant validation tests:  
317 57% of simulated densities higher than observed values). This driver may be less structuring  
318 for adults than for 1+ trout, and dedicated monitoring will be required to study adult  
319 migration on this reach. Juvenile and adult migration were previously observed in other  
320 streams, occurring regularly over the years, depending on different drivers (Cucherousset et  
321 al. 2006; Frank et al. 2012; Vøllestad et al. 2012). In contrast, populations with little mobility  
322 were also reported (Dieterman & Hoxmeier 2011). The present study revealed an influence of  
323 migration on population dynamics only in the Rory reach. This process need greater attention  
324 and specific monitoring to be precisely modeled. For the Pont-Haut reach, better 1+ survival  
325 was regularly observed (every 0.57 years), due to absence of flooding during Spring. Some  
326 authors reported different effects of hydrology on 0+ trout depending on the timing of the  
327 event (Hayes et al. 2010; Unfer et al. 2011). However, the influence of this driver on 1+ is not  
328 clearly known. Drivers structuring older development stages than 0+ are more difficult to  
329 detect (Cattaneo et al. 2002).

330 Furthermore, three other local drivers, independent of hydrology, were revealed: (1) poor  
331 water quality in the two Breil reaches during warm Summers, (2) limited spawning area in the  
332 Rory reach due to reduced sediment transport, and (3) an impact of power plant operations in  
333 the three Beyrède reaches. These drivers all acted at least on recruitment, with different levels  
334 of influence and frequencies. Limited spawning area by reduced sediment transport in the  
335 Rory reach appeared to be a major structuring driver, occurring every 0.89 years. In contrast,  
336 poor water quality in the Breil reaches and power plant operations in the Beyrède reaches  
337 were rarer, and will require long-term local monitoring. Drivers limiting trout biology (water  
338 quality or spawning area availability) were only observed in one specific bypassed section,  
339 but it could reasonably be supposed that the effect might occur in any bypassed section  
340 affected by the same limitation.

341 Finally, when two or three reaches of the same bypassed section were modeled, no drivers  
342 were identified for only one of them: i.e., all drivers acted at bypassed section scale. This  
343 result is consistent with the spatial scale of influence of the identified drivers (Jackson et al.  
344 2001).

### 345 **Synthesis**

346 We propose to synthesize these results by characterizing the drivers identified in the study:

347 (1) general drivers, observed on more than two bypassed sections: biotic processes  
348 (survival, fecundity and growth rates, potential carrying capacity, food availability),  
349 flooding during Spring or spawning and exceptional floods;

350 (2) specific drivers: downstream migration allowed by overtopping, limited spawning  
351 area, no flooding during Spring, poor water quality, and power plant operation.

352 Complete models were validated: they accurately simulated density and temporal fluctuations  
353 of each development stage in most reaches. The MODYPOP model thus appeared well suited  
354 to simulate trout populations in different geographical contexts. However, 0+ simulations  
355 showed better significance than older stages. Recruitment density was much more variable  
356 than 1+ or >1+ density. This low range of variation explained the lower results of the Monte-  
357 Carlo validation tests for older stages. It was difficult to identify specific drivers structuring  
358 1+ or >1+ trout in these conditions. Most drivers affected recruitment. Monitoring will need  
359 to be maintained to detect drivers for older stages, as the chances of detecting environmental  
360 influences on the population increase with the length of the time series (Vörösmarty et al.  
361 2010), even if older stages were rarely reported to be structured by abiotic drivers (Cattaneo et  
362 al. 2002). Moreover, the studied trout populations were located in bypassed sections. We also  
363 monitored reference reaches and applied this approach to several of them (Gouraud et al.  
364 2004). Results on these reaches were consistent with the drivers presented in this paper, but it  
365 was decided not to include them because they were few in comparison with reaches located in  
366 bypassed sections. Further studies need to be conducted on streams with unregulated flow, to  
367 confirm main the drivers of trout population in various hydrological contexts.

### 368 **Conclusion**

369 The present study used long-term extensive biological and physical monitoring to build  
370 population dynamics models with reach-specific calibration and validation procedures. This  
371 required long and heavy investment, preventing wider analysis. Thus, this reach-based  
372 approach is probably not suited to drawing general conclusions (Armstrong & Nislow 2012).  
373 Our comparative approach revealed drivers operating at different temporal and spatial levels.  
374 Additional analyses need to be conducted for each driver on larger data-sets, to regionalize  
375 and quantify their effects exactly. For example, the influence of hydrological events during  
376 Spring on recruitment may be related to hydraulic conditions (e.g., flow velocity) rather than  
377 of the mean daily flow value. This approach might reveal a global influence of hydraulic  
378 conditions, rather than a site-specific influence of hydrology. Fitting the model through a

379 statistical method would remove the time-consuming calibration procedures and also allow  
380 the combined influence of drivers to be investigated. However, this would need more data, or  
381 else fewer parameters.

382 Research perspectives comprise developing a more global tool that can integrate temporal  
383 variability and controlling drivers for each population. Such a tool is essential to implement  
384 efficient large-scale management measures (Collares-Pereira & Cowx 2004; Jackson et al.  
385 2001). Thus, although long-term monitoring and local analyses will remain crucial,  
386 assessment of trout population status would be simplified.

387

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563

564 **TABLES**

565 Table 1. Physical characteristics of the five bypassed sections. The annual mean flows (AMF)  
 566 are those of the natural part of the river upstream of the dam in the bypassed section. Low  
 567 flow magnitude (Q90) was defined as daily discharge exceeded 90% of the time during the  
 568 study period.

| Bypassed section | River              | Reach               | AMF<br>(m <sup>3</sup> .s <sup>-1</sup> ) | Q90<br>(m <sup>3</sup> .s <sup>-1</sup> ) | Instream flow<br>(m <sup>3</sup> .s <sup>-1</sup> ) | Altitude<br>(m) | Slope<br>(%) |
|------------------|--------------------|---------------------|---|---|---|-----------------|--------------|
| Beyrède          | Neste<br>d'Aure    | BEY1, BEY2,<br>BEY3 | 20.0                                      | 10.5                                      | 1.50  | 688             | 0.7          |
| Fontan           | Roya               | FON2, FON3          | 6.2                                       | 5.2                                       | 0.62  | 522             | 3.6          |
| Breil            | Roya               | BREIL1,<br>BREIL2   | 11.4                                      | 12.2                                      | 1.20  | 280             | 1.4          |
| Pont-Haut        | Roizonne           | ROIP2               | 2.7                                       | 2.5                                       | 0.28  | 740             | 3.7          |
| Rory             | Lignon du<br>Forez | LIG2                | 2.9                                       | 2.2                                       | 0.35  | 560             | 2.4          |

569

570

571 Table 2. Physical characteristics of monitored reaches and bypassed sections.

| Bypassed section | Reach  | Nb of samplings | Dist. water intake (m) | Length (m) | Mean width (m) | Dominant mesohabitat |
|------------------|--------|-----------------|------------------------|------------|----------------|----------------------|
| Beyrède          | BEY1   | 14              | 500                    | 158        | 12.6           | Riffle (51%)         |
|                  | BEY2   | 19              | 2500                   | 149        | 14.8           | Run (43%)            |
|                  | BEY3   | 15              | 3800                   | 195        | 11.1           | Riffle (57%)         |
| Fontan           | FON2   | 13              | 1250                   | 106        | 12.1           | Rapid (54%)          |
|                  | FON3   | 9               | 1700                   | 61         | 10.3           | Run (62%)            |
| Breil            | BREIL1 | 9               | 500                    | 124        | 11.2           | Run (65%)            |
|                  | BREIL2 | 9               | 2800                   | 78         | 11.8           | Pool (65%)           |
| Pont Haut        | ROIP2  | 16              | 700                    | 101        | 7.0            | Rapid (70%)          |
| Rory             | LIG2   | 15              | 1200                   | 148        | 8.8            | Riffle (45%)         |

572

573

574 Table 3. Global statistics on density (mean and standard deviation) and results of validation  
 575 tests of reach models.

| Reach                        | Stage | Observations<br>(ind.100m <sup>-1</sup> ) |     | Validation tests without<br>abiotic drivers |                    | Validation tests of<br>complete models |                    |
|------------------------------|-------|---|-----|---|--------------------|--|--------------------|
|                              |       | Mean                                      | SD  | p-value<br>direction                        | p-value<br>density | p-value<br>direction                   | p-value<br>density |
| BEY1                         | 0+    | 123                                       | 74  | <b>0.40</b>                                 | <b>0.62</b>        | 0.02                                   | 0.00               |
|                              | 1+    | 88  | 59  | <b>0.61</b>                                 | <b>0.71</b>        | <b>0.10</b>                            | 0.00               |
|                              | >1+   | 50  | 24  | <b>0.08</b>                                 | <b>0.50</b>        | 0.00                                   | 0.00               |
| BEY2                         | 0+    | 211                                       | 158 | <b>0.25</b>                                 | <b>0.75</b>        | 0.00                                   | 0.00               |
|                              | 1+    | 91  | 65  | <b>0.05</b>                                 | <b>0.30</b>        | 0.00                                   | 0.00               |
|                              | >1+   | 44  | 26  | <b>0.43</b>                                 | <b>0.59</b>        | 0.03                                   | 0.01               |
| BEY3                         | 0+    | 196                                       | 160 | 0.00  | <b>0.21</b>        | 0.03                                   | 0.00               |
|                              | 1+    | 97  | 65  | 0.00  | 0.03               | 0.00                                   | 0.00               |
|                              | >1+   | 54  | 25  | <b>0.59</b>                                 | <b>0.73</b>        | 0.01                                   | 0.04               |
| FON2                         | 0+    | 113                                       | 93  | <b>0.39</b>                                 | <b>0.14</b>        | 0.01                                   | 0.00               |
|                              | 1+    | 63  | 51  | <b>0.62</b>                                 | <b>0.17</b>        | <b>0.07</b>                            | 0.01               |
|                              | >1+   | 29  | 20  | <b>0.06</b>                                 | 0.02               | 0.00                                   | <b>0.05</b>        |
| FON3                         | 0+    | 181                                       | 168 | <b>0.14</b>                                 | <b>0.05</b>        | 0.02                                   | 0.01               |
|                              | 1+    | 84  | 45  | <b>0.14</b>                                 | <b>0.24</b>        | 0.02                                   | <b>0.05</b>        |
|                              | >1+   | 24  | 11  | <b>0.14</b>                                 | <b>0.10</b>        | 0.00                                   | <b>0.11</b>        |
| BREIL1                       | 0+    | 91  | 118 | <b>0.09</b>                                 | <b>0.57</b>        | <b>0.09</b>                            | <b>0.42</b>        |
|                              | 1+    | 36  | 22  | <b>0.51</b>                                 | <b>0.94</b>        | <b>0.50</b>                            | <b>0.85</b>        |
|                              | >1+   | 16  | 10  | <b>0.50</b>                                 | <b>0.65</b>        | <b>0.19</b>                            | <b>0.38</b>        |
| BREIL2                       | 0+    | 161                                       | 133 | <b>0.11</b>                                 | <b>0.17</b>        | 0.02                                   | 0.03               |
|                              | 1+    | 124                                       | 87  | <b>0.20</b>                                 | <b>0.40</b>        | 0.04                                   | 0.01               |
|                              | >1+   | 48  | 25  | <b>0.73</b>                                 | <b>0.82</b>        | <b>0.27</b>                            | <b>0.39</b>        |
| ROIP2                        | 0+    | 124                                       | 182 | 0.01  | <b>0.07</b>        | <b>0.06</b>                            | 0.00               |
|                              | 1+    | 79  | 68  | <b>0.29</b>                                 | 0.00               | 0.04                                   | 0.00               |
|                              | >1+   | 55  | 28  | 0.04  | 0.01               | <b>0.12</b>                            | 0.00               |
| LIG2                         | 0+    | 50  | 26  | <b>0.50</b>                                 | <b>0.41</b>        | 0.00                                   | 0.00               |
|                              | 1+    | 37  | 17  | <b>0.16</b>                                 | <b>0.16</b>        | <b>0.06</b>                            | 0.00               |
|                              | >1+   | 44  | 12  | <b>0.49</b>                                 | <b>0.72</b>        | <b>0.52</b>                            | <b>0.30</b>        |
| Nb of validated reach models |       |   |     | 4   | 4                  | 17                                     | 19                 |
| % of validated reach models  |       |   |     | 15  | 15                 | 63                                     | 70                 |

576 **Bold italic:** non-significant test

577

578 Table 4. Seven additional drivers identified in the study reaches. Negative values of mortality  
 579 rates correspond to better survivals. Temporal occurrence (N bobs/Nb years) of each driver  
 580 was calculated on the study period on the reach or bypassed section where it was involved.  
 581

| Driver                       | Mortality rate | Stage  | Reach                     | Nb obs/<br>Nb years |
|------------------------------|----------------|--------|---------------------------|---------------------|
| Flood during spring/spawning | 0.20-0.75      | 0+     | All                       | 43/90=0.48          |
| Exceptional flood            | 0.75-0.90      | All    | BEY1, BEY2, BEY3,<br>FON2 | 3/39=0.08           |
| Overtopping                  | -0.6           | 1+     | LIG2                      | 14/18=0.78          |
|                              | -0.2           | >1+    | LIG2                      | 18/18=1.00          |
| No flood during spring       | -0.3           | 1+     | ROIP2                     | 13/23=0.57          |
| Limited spawning area        | 0.80           | 0+     | LIG2                      | 16/18=0.89          |
| Poor water quality           | 0.75           | 0+     | BREIL1, BREIL2            | 3/10=0.30           |
| Power plant operation        | 0.50-0.75      | 0+, 1+ | BEY1, BEY2, BEY3          | 2/20=0.10           |

582

583

584 Table 5. Flood-threshold and number of days for which flow had to exceed threshold to  
 585 induce mortality in 0+ trout for each bypassed section.

| Bypassed section | Period     | Q threshold<br>(m <sup>3</sup> .s <sup>-1</sup> ) | Q Threshold /Q90 | Nb days | Mortality rate |
|------------------|------------|---|------------------|---------|----------------|
| Beyrède          | March-June | 35  | 3.3              | 9       | 75%            |
|                  | March-June | 35  | 3.3              | 4 to 8  | 20%            |
|                  | Nov-Dec    | 60  | 5.7              | 1       | 75%            |
|                  | Whenever   | 94  | 8.9              | 1       | 75%            |
| Fontan           | March-June | 8   | 1.6              | 1       | 75%            |
|                  | Whenever   | 71  | 13.6             | 2       | 90%            |
| Breil            | March-June | 60  | 4.9              | 1       | 75%            |
| Pont-Haut        | March-June | 9   | 3.5              | 1       | 75%            |
| Rory             | March-June | 5.5   | 2.5              | 1       | 75%            |

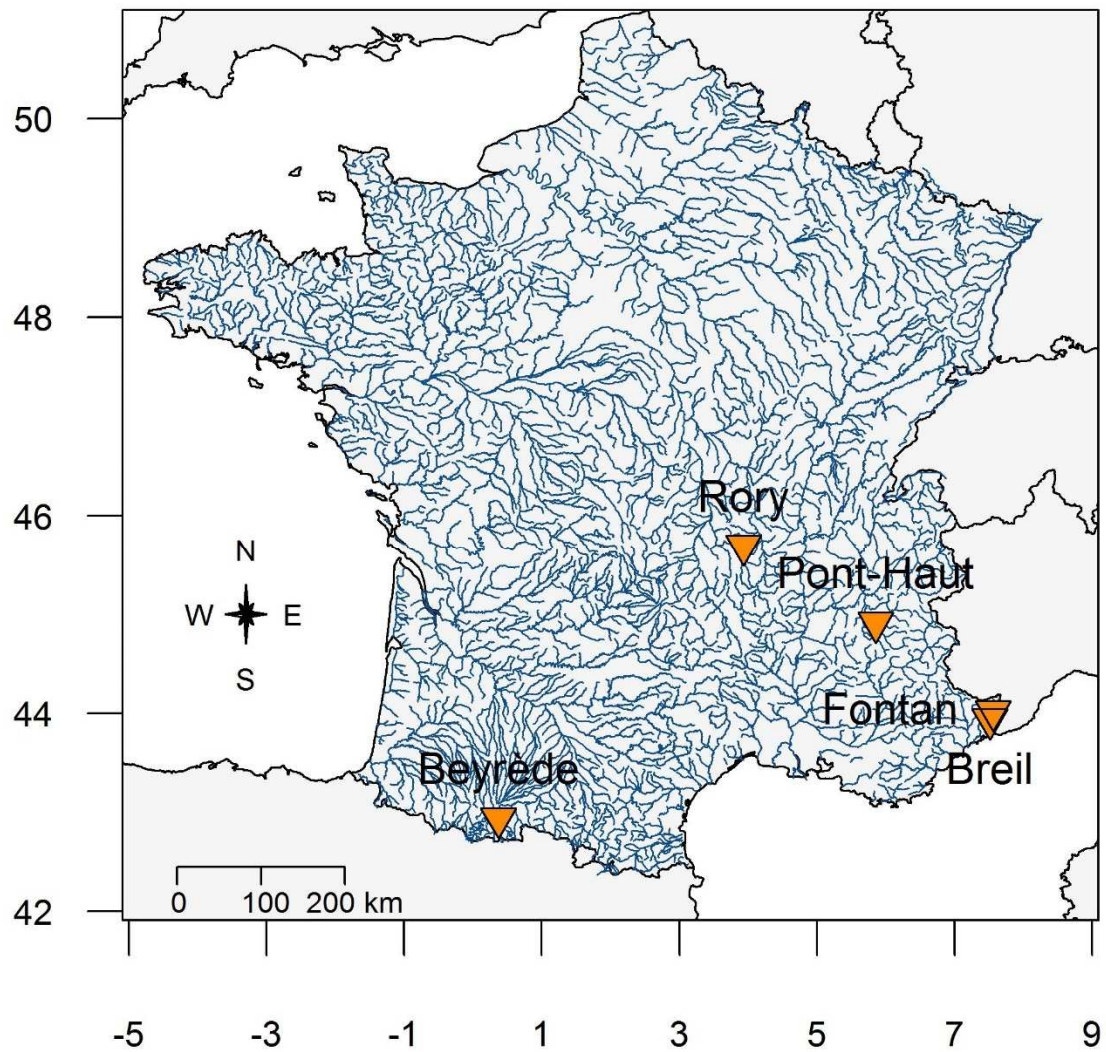
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588 **FIGURES**

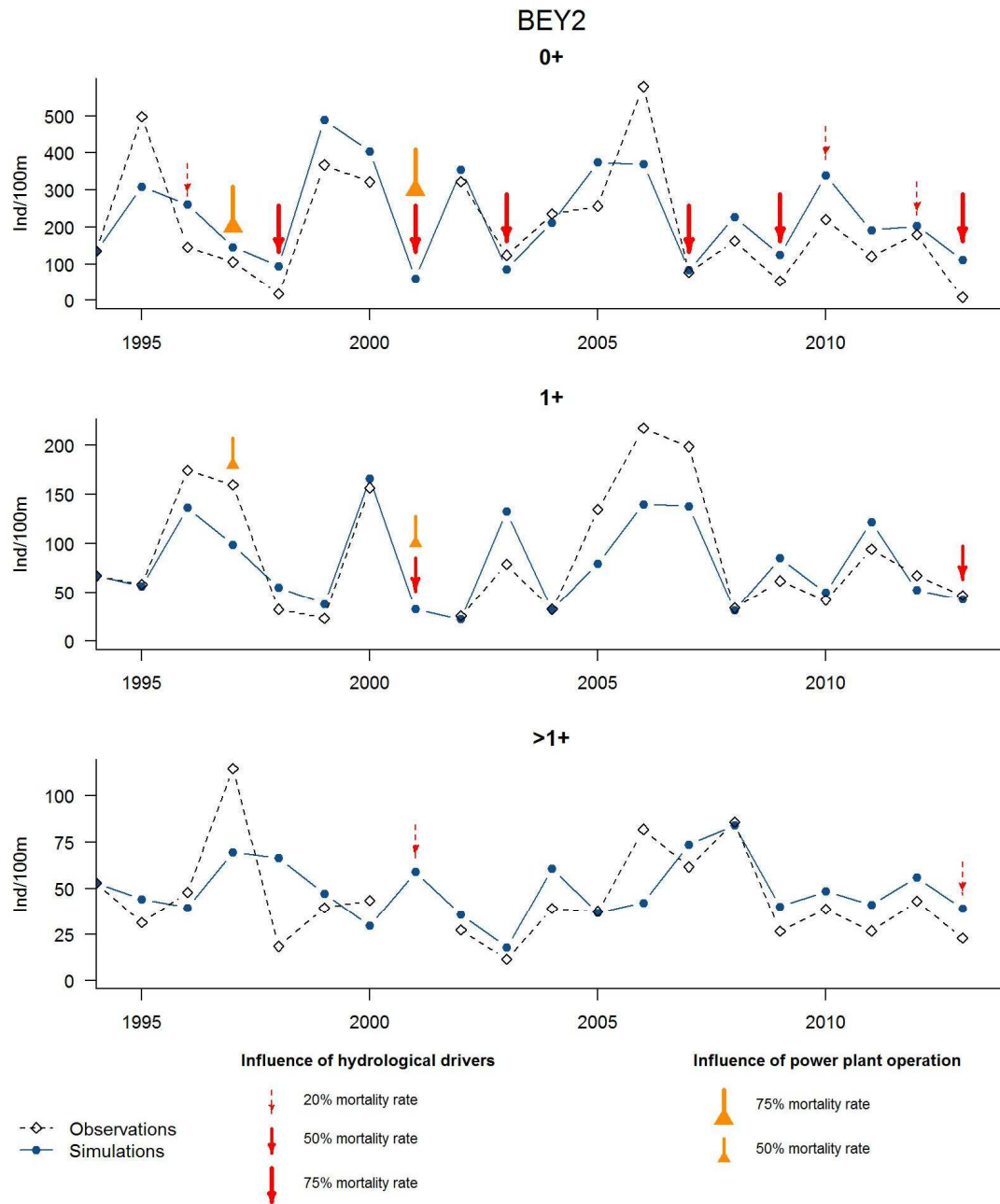
589 Fig. 1. Location of the five bypassed sections.

590  
591





592 Fig. 2. Observed (white squares) and simulated (blue circles) density fluctuations for (a) 0+,  
 593 (b) 1+ and (c) >1+ trout in the BEY2 reach. Results for all reaches are proposed as  
 594 supplementary materials.  
 595



596 Fig. 3. Characterization of temporal and spatial occurrences of each driver structuring trout  
 597 population dynamics. Temporal occurrence was the time frequency of the driver during the  
 598 study period on the reach or bypassed section where it was involved, or the mean time  
 599 frequency when several bypassed sections were involved. The direction of the fluctuation and  
 600 the affected development stage are indicated in brackets. \*Biotic processes were those  
 601 included in the initial model: survival, fecundity and growth rates, carrying capacity and food  
 602 availability.

