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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 (Cattanéo 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 m³.s⁻¹, 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 m²) 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⁻¹ 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⁻¹ on average).
293 Hydrological events during spawning show positive or no effect (Hayes 1995; Lobón-Cervía
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-Cervía 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 (Cattanéo 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 (Cattanéo 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.

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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 (m ³ .s ⁻¹)	Q90 (m ³ .s ⁻¹)	Instream flow (m ³ .s ⁻¹)	Altitude (m)	Slope (%)
Beyrède	Neste d'Aure	BEY1, BEY2, 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, 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 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 (ind.100m ⁻¹)		Validation tests without abiotic drivers		Validation tests of complete models	
		Mean	SD	p-value direction	p-value density	p-value direction	p-value density
BEY1	0+	123	74	<i>0.40</i>	<i>0.62</i>	0.02	0.00
	1+	88	59	<i>0.61</i>	<i>0.71</i>	<i>0.10</i>	0.00
	>1+	50	24	<i>0.08</i>	<i>0.50</i>	0.00	0.00
BEY2	0+	211	158	<i>0.25</i>	<i>0.75</i>	0.00	0.00
	1+	91	65	<i>0.05</i>	<i>0.30</i>	0.00	0.00
	>1+	44	26	<i>0.43</i>	<i>0.59</i>	0.03	0.01
BEY3	0+	196	160	0.00	<i>0.21</i>	0.03	0.00
	1+	97	65	0.00	0.03	0.00	0.00
	>1+	54	25	<i>0.59</i>	<i>0.73</i>	0.01	0.04
FON2	0+	113	93	<i>0.39</i>	<i>0.14</i>	0.01	0.00
	1+	63	51	<i>0.62</i>	<i>0.17</i>	<i>0.07</i>	0.01
	>1+	29	20	<i>0.06</i>	0.02	0.00	<i>0.05</i>
FON3	0+	181	168	<i>0.14</i>	<i>0.05</i>	0.02	0.01
	1+	84	45	<i>0.14</i>	<i>0.24</i>	0.02	<i>0.05</i>
	>1+	24	11	<i>0.14</i>	<i>0.10</i>	0.00	<i>0.11</i>
BREIL1	0+	91	118	<i>0.09</i>	<i>0.57</i>	<i>0.09</i>	<i>0.42</i>
	1+	36	22	<i>0.51</i>	<i>0.94</i>	<i>0.50</i>	<i>0.85</i>
	>1+	16	10	<i>0.50</i>	<i>0.65</i>	<i>0.19</i>	<i>0.38</i>
BREIL2	0+	161	133	<i>0.11</i>	<i>0.17</i>	0.02	0.03
	1+	124	87	<i>0.20</i>	<i>0.40</i>	0.04	0.01
	>1+	48	25	<i>0.73</i>	<i>0.82</i>	<i>0.27</i>	<i>0.39</i>
ROIP2	0+	124	182	0.01	<i>0.07</i>	<i>0.06</i>	0.00
	1+	79	68	<i>0.29</i>	0.00	0.04	0.00
	>1+	55	28	0.04	0.01	<i>0.12</i>	0.00
LIG2	0+	50	26	<i>0.50</i>	<i>0.41</i>	0.00	0.00
	1+	37	17	<i>0.16</i>	<i>0.16</i>	<i>0.06</i>	0.00
	>1+	44	12	<i>0.49</i>	<i>0.72</i>	<i>0.52</i>	<i>0.30</i>
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/ 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, 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 (m ³ .s ⁻¹)	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%

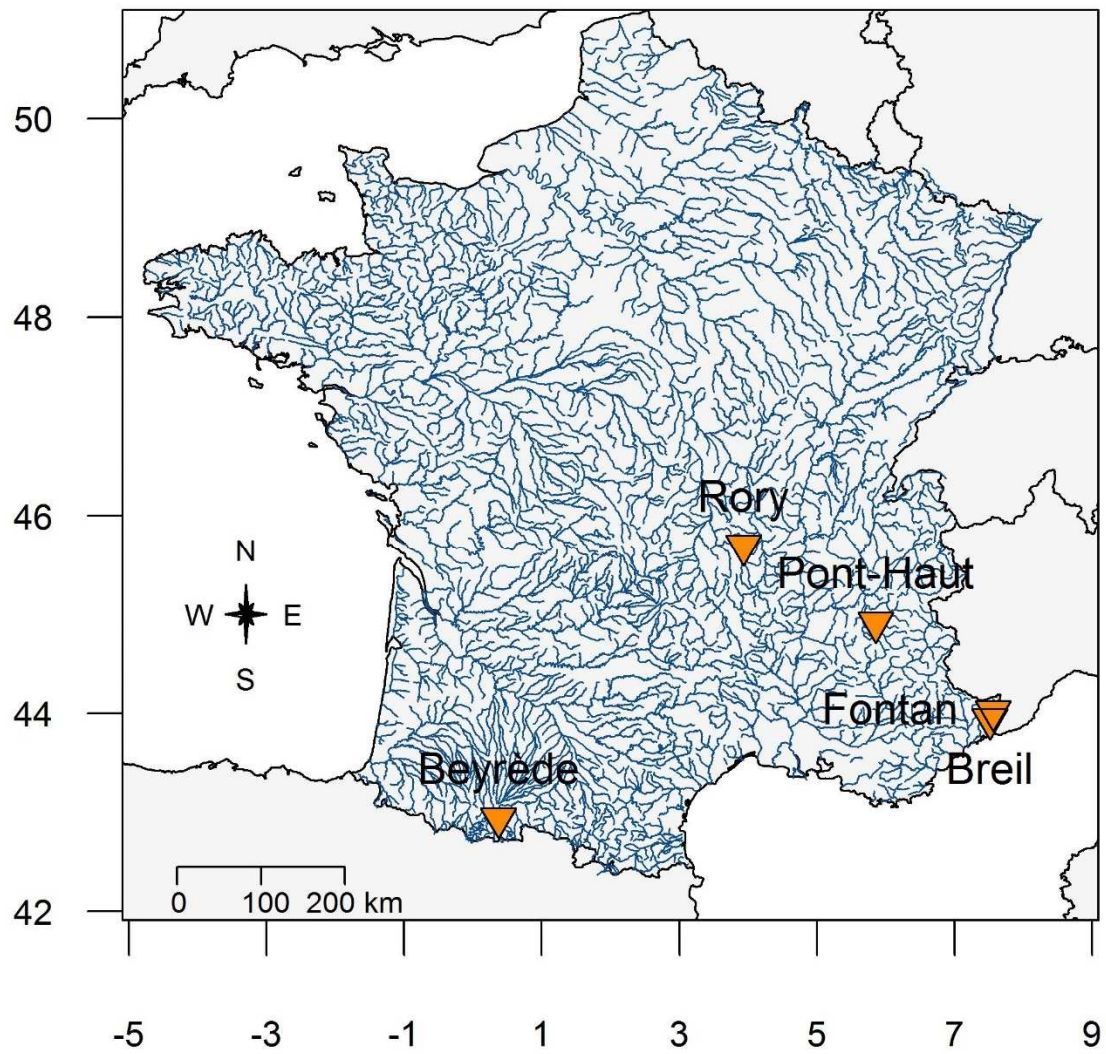
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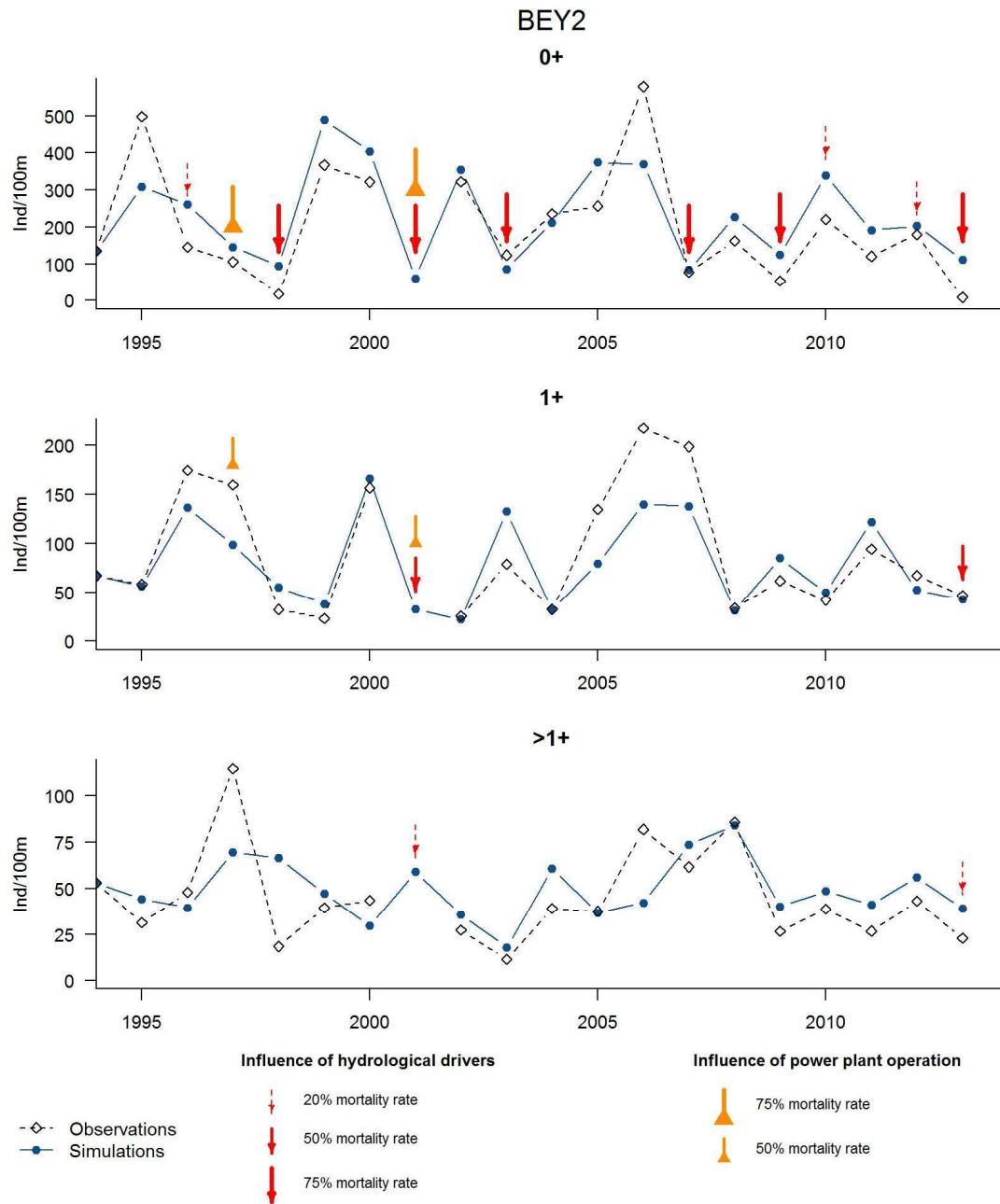
588 **FIGURES**

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.

