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Short title: Main drivers of trout population dynamics

ABSTRACT

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

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

INTRODUCTION

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

In this context, scientists need to develop knowledge and tools to facilitate operational decisions for ecological and sustainable water management. Above all, precise knowledge of the driving factors influencing fish population dynamics is required. It is clear that multiple drivers operating on different space and time scales structure fish population dynamics (Durance et al. 2006; Jackson et al. 2001; Vincenzi et al. 2012). Trout biology and ecology have been studied for many years and are now relatively well-documented compared to other fish species (Baglinière & Maisse 1991; Elliott 1994; Jonsson et al. 2001; Klemetsen et al. 2003). However, few studies have qualified the effects of the various drivers involved in trout population dynamics. It is well-established that hydrological events during fry, intra-gravel and post-emergence periods are major drivers of trout recruitment (Cattanéo et al. 2002; Gouraud et al. 2008; Jensen & Johnsen 1999; Lobón-Cerviá 2004). In addition, recruitment has often been shown to be the main driver of population size (Lobón-Cerviá 2009; Milner et al. 2003). Thus, by limiting recruitment, discharge is often one of the main drivers of trout population dynamics in mountain streams. Beyond hydrology, however, multiple drivers, abiotic or biotic, can structure trout populations (Milner et al. 2003). The most commonly cited abiotic factors are temperature (Armstrong et al. 2010; Armstrong et al. 2013; Warren et al. 2012) and water chemistry (Eklöv et al. 1999), while competition for resources seems to be the major biotic determinant of trout population. Competition is linked to several biotic (such as food availability, Grant et al. 1998) or abiotic drivers (such as carrying capacity, Lobón-Cerviá 2008) and can induce density-dependent effects on growth or survival (Elliott 1994). The various drivers structuring trout populations operate on different space and time scales. Small-scale studies have highlighted the effects of precise biotic drivers (Einum et al. 2011; Jenkins et al. 1999; Lobón-Cerviá 2008), and abiotic factors such as flow regime (Lobón-Cerviá 2004; Vøllestad & Olsen 2008) and temperature (Borgstrøm & Museth 2005). However, most studies focused on the details of a single site, making large-scale extrapolation hazardous (Jackson et al. 2001). The present study therefore adopted a local scale analysis of trout population dynamics in nine different reaches, and summarized the spatial and temporal incidence of drivers identified at local level so as to assess the generalizability of the local results.

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

MATERIAL AND METHOD

Trout population dynamics model

General model

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

Trout population dynamics drivers

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

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

Model calibration for reach-specific drivers

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

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

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

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

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

Model validation

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

Data set

Bypassed sections and reaches

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

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

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

Monitoring and estimation of model drivers

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

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

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

Daily discharge and temperature time series were determined from recorders deployed within each monitored bypassed section. When discharge was temporarily unavailable, it was extrapolated using natural daily discharge time series and/or operative data provided by power plants. Missing water temperature values were estimated using extrapolation models from air temperature (Bret et al.).

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

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

RESULTS

Population structure and carrying capacity

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

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

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

Additional reach-specific drivers

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

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

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

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

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

Final complete models

Model calibration results for each reach underscored the influence of local phenomena on trout population structure. Observed and simulated density fluctuations for all development stages in the BEY2 reach are presented Fig. 2 to illustrate these results. Results for all reaches are proposed as supplementary materials. A synthesis of the temporal and spatial incidence of each identified driver is shown in Fig. 3. For the three bypassed sections represented by more than one reach, all identified drivers operated at all reaches of the section. Most of the drivers were observed in any given bypassed section. Temporal occurrence was somewhat dependent on study period duration, and was more variable than spatial occurrence: between 0.08 times.year^{-1} for exceptional flooding and every year for overtopping in the Rory bypassed section, and for biotic processes (those included in the initial model: survival, fecundity and growth rate, potential carrying capacity and food availability).

Model validation

Validation test results are presented in Table 16320.

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

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

DISCUSSION

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

Biotic processes

The biotic processes originally included in the model (survival, fecundity and growth rates, carrying capacity and food availability) structured all reaches. They were necessary but not sufficient to validate reach models in most cases. Gouraud (1999) demonstrated their importance in population dynamics modeling (for example, a density-dependent effect on 0+ could decrease mortality rate 4-fold in this development stage). Carrying capacity (Ayllón et al. 2012) and density-dependent mortality (Nicola et al. 2008; Ojanguren et al. 2001) are two drivers widely documented as structuring trout populations. In the present study, these processes contributed to achieving validated models, thus confirming that they need to be integrated in population dynamics models. However, no limitation was seen reacted to carrying capacity for adults, in terms of habitat availability as measured by WUA, during the study period. Other habitat components, such as shelter availability, may, however, influence trout dynamics (Dieterman & Hoxmeier 2011).

Additional drivers

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

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

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

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

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

Synthesis

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

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

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

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

Conclusion

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

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

REFERENCES

Armstrong, J.B., Schindler, D.E., Omori, K.L., Ruff, C.P. & Quinn, T.P. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. *Ecology* 91: 1445-1454.

Armstrong, J.B., Schindler, D.E., Ruff, C.P., Brooks, G.T., Bentley, K.E. & Torgersen, C.E. 2013. Diel horizontal migration in streams: Juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology* 94: 2066-2075.

Armstrong, J.D. & Nislow, K.H. 2012. Modelling approaches for relating effects of change in river flow to populations of Atlantic salmon and brown trout. *Fisheries Management and Ecology* 19: 527-536.

Ayllón, D., Almodóvar, A., Nicola, G.G., Parra, I. & Elvira, B. 2012. Modelling carrying capacity dynamics for the conservation and management of territorial salmonids. *Fisheries Research* 134–136: 95-103.

Baglinière, J.L. & Maisse, G. 1991. *La truite - Biologie et écologie*: INRA Editions. 303 pp.

Balmford, A., Bruner, A., Cooper, P., Costanza, R., Farber, S., Green, R.E., Jenkins, M., Jefferiss, P., Jessamy, V., Madden, J., Munro, K., Myers, N., Naeem, S., Paavola, J., Rayment, M., Rosendo, S., Roughgarden, J., Trumper, K. & Turner, R.K. 2002. Economic Reasons for Conserving Wild Nature. *Science* 297: 950-953.

Borgstrøm, R. & Museth, J. 2005. Accumulated snow and summer temperature – critical factors for recruitment to high mountain populations of brown trout (*Salmo trutta* L.). *Ecology of Freshwater Fish* 14: 375-384.

Bret, V., Bergerot, B., Capra, H., Gouraud, V. & Lamouroux, N. in press. Influence of discharge, hydraulics, water temperature and dispersal on density synchrony in brown trout populations (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* 0.

Capra, H., Breil, P. & Souchon, Y. 1995. A new tool to interpret magnitude and duration of fish habitat variations. *Regulated Rivers: Research & Management* 10: 281-289.

Carle, R.T. & Strub, M.R. 1978. A new method for estimating population size from removal data. *Biometrics* 34: 621-630.

Cattanéo, F. 2005. Does hydrology constrain the structure of fish assemblages in French streams? Regional scale analysis. *Archiv für Hydrobiologie* 164: 367-385.

Cattanéo, F., Lamouroux, N., Breil, P. & Capra, H. 2002. The influence of hydrological and biotic processes on brown trout (*Salmo trutta*) population dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 12-22.

CEN. 2003. Water quality - Sampling of fish with electricity. *European Standard*.

Collares-Pereira, M.J. & Cowx, I.G. 2004. The role of catchment scale environmental management in freshwater fish conservation. *Fisheries Management and Ecology* 11: 303-312.

Comte, L., Buisson, L., Daufresne, M. & Grenouillet, G. 2013. Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. *Freshwater Biology* 58: 625-639.

Crowley, P.H. 1992. Resampling Methods for Computation-Intensive Data Analysis in Ecology and Evolution. *Annual Review of Ecology and Systematics* 23: 405-447.

Cucherousset, J., Ombredane, D. & Bagliniere, J. 2006. Linking juvenile growth and migration behaviour of brown trout (*Salmo trutta*) using individual PIT-tagging. *Cahiers de biologie marine* 47: 73.

Dieterman, D.J. & Hoxmeier, R.J.H. 2011. Demography of Juvenile and Adult Brown Trout in Streams of Southeastern Minnesota. *Transactions of the American Fisheries Society* 140: 1642-1656.
Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J. & Sullivan, C.A. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81: 163-182.
Durance, I., Lepichon, C. & Ormerod, S.J. 2006. Recognizing the importance of scale in the ecology and management of riverine fish. *River Research and Applications* 22: 1143-1152.
Einum, S., Robertsen, G., Nislow, K., McKelvey, S. & Armstrong, J. 2011. The spatial scale of density-dependent growth and implications for dispersal from nests in juvenile Atlantic salmon. *Oecologia* 165: 959-969.
Eklöv, A.G., Greenberg, H.M., Brönmark, C., Larsson, P. & Berglund, O. 1999. Influence of water quality, habitat and species richness on brown trout populations. *Journal of fish biology* 54: 33–43.
Elliott, J.M. 1994. *Quantitative ecology and the brown trout*. Oxford GBR: Oxford University Press. 286 pp.
Frank, B.M., Gimenez, O. & Baret, P.V. 2012. Assessing brown trout (*Salmo trutta*) spawning movements with multistate capture–recapture models: a case study in a fully controlled Belgian brook. *Canadian Journal of Fisheries and Aquatic Sciences* 69: 1091–1104.
Ginot, V., Souchon, Y., Capra, H., Breil, P. & Valentin, S. 1998. Logiciel EVHA 2.0. Evaluation de l'habitat physique des poissons en rivière. Cemagref BEA/LHQ et Ministère de l'Aménagement du Territoire et de l'Environnement, 130 pp.
Gouraud, V. 1999. *Etude de la dynamique de populations de truites communes (Salmo trutta L.) à l'aide d'un modèle déterministe*: ENGREF. 302 pp.
Gouraud, V., Baglinière, J.L., Baran, P., Sabaton, C., Lim, P. & Ombredane, D. 2001. Factors regulating brown trout populations in two french rivers: Application of a dynamic population model. *Regulated Rivers : Research & Management* 17: 557-569.
Gouraud, V., Capra, H., Sabaton, C., Tissot, L., Lim, P., Vandewalle, F., Fahrner, G. & Souchon, Y. 2008. Long-term simulations of the dynamics of trout populations on river reaches bypassed by hydroelectric installations - Analysis of the impact of different hydrological scenarios. *River Research and Applications* 24: 1185-1205.
Gouraud, V., Sabaton, C. & Capra, H. 2004. Role of habitat variability in trout population dynamics: Application of a dynamic population model to three French rivers. *Hydroécologie appliquée* 14: 221-244
Grant, J., Steingrímsson, S.Ó., Keeley, E.R. & Cunjak, R.A. 1998. Implications of territory size for the measurement and prediction of salmonid abundance in streams. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 181-190.
Hayes, J.W. 1995. Spatial and temporal variation in the relative density and size of juvenile brown trout in the Kakanui River, North Otago, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 29: 93-407.
Hayes, J.W., Olsen, D.A. & Hay, J. 2010. The influence of natural variation in discharge on juvenile brown trout population dynamics in a nursery tributary of the Motueka River, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 44: 247-269.

Jackson, D.A., Peres-Neto, P.R. & Olden, J.D. 2001. What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 157-170.

Jenkins, T.M., Diehl, S., Kratz, K.W. & Cooper, S.D. 1999. Effects of population density on individual growth of brown trout in streams. *Ecology* 80: 941-956.

Jensen, A.J. & Johnsen, B.O. 1999. The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Functional Ecology* 13: 778-785.

Jonsson, B., Jonsson, N., Brodtkorb, E. & Ingebrigtsen, P.J. 2001. Life-history traits of Brown Trout vary with the size of small streams. *Functional Ecology* 15: 310-317.

Jowett, I.G. & Richardson, J. 1989. Effects of a severe flood on instream habitat and trout populations in seven New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research abstracts* 23: 11-17.

Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F. & Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* 12: 1-59.

Kondolf, G.M. & Wolman, M.G. 1993. The sizes of salmonid spawning gravels. *Water Resources Research* 29: Pages: 2275-2285.

Lobón-Cerviá, J. 1996. Response of a Stream Fish Assemblage to a Severe Spate in Northern Spain. *Transactions of the American Fisheries Society* 125: 913-919.

Lobón-Cerviá, J. 2004. Discharge-dependent covariation patterns in the population dynamics of brown trout (*Salmo trutta*) within a Cantabrian river drainage. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 1929-1939.

Lobón-Cerviá, J. 2008. Habitat quality enhances spatial variation in self-thinning patterns of stream-resident brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* 65: 2006-2015.

Lobón-Cerviá, J. 2009. Recruitment as a driver of production dynamics in stream-resident brown trout (*Salmo trutta*). *Freshwater Biology*: 1-13.

Magurran, A.E., Baillie, S.R., Buckland, S.T., Dick, J.M., Elston, D.A., Scott, E.M., Smith, R.I., Somerfield, P.J. & Watt, A.D. 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends in Ecology and Evolution*: 574-582.

Milner, N.J., Elliott, J.M., Armstrong, J.D., Gardiner, R., Welton, J.S. & Ladle, M. 2003. The natural control of salmon and trout populations in streams. *Fisheries Research* 62: 111-125.

Montgomery, D. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 1061-1070.

Nelson, F.A. 1986. Effect of Flow Fluctuations on Brown Trout in the Beaverhead River, Montana. *North American Journal of Fisheries Management* 6: 551-559.

Nicola, G.G., Almodovar, A.N.A., Jonsson, B. & Elvira, B. 2008. Recruitment variability of resident brown trout in peripheral populations from southern Europe. *Freshwater Biology* 53: 2364-2374.

Ojanguren, A.F., Reyes-Gavilán, F.G. & Braña, F. 2001. Thermal sensitivity of growth, food intake and activity of juvenile brown trout. *Journal of Thermal Biology* 26: 165-170.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E. & Stromberg, J.C. 1997. The natural flow regime : a paradigm for river conservation and restoration. *BioScience* 47: 769-784

Poulet, N., Beaulaton, L. & Dembski, S. 2011. Time trends in fish populations in metropolitan France: insights from national monitoring data. *Journal of fish biology*: 1-17.

Sabaton, C., Valentin, S. & Souchon, Y. 1995. La méthode des microhabitats. Protocoles d'application. EDF Direction des Etudes et Recherches and Cemagref BEA/LHQ, 33 pp.

Souchon, Y., Trocherie, F., Fragnoud, E. & Lacombe, C. 1989. Les modèles numériques des microhabitats des poissons : application et nouveaux développements. *Revue des Sciences de l'Eau* 2: 807-830.

Unfer, G., Hauer, C. & Lautsch, E. 2011. The influence of hydrology on the recruitment of brown trout in an Alpine river, the Ybbs River, Austria. *Ecology of Freshwater Fish* 20: 438-448.

Vincenzi, S., Satterthwaite, W.H. & Mangel, M. 2012. Spatial and temporal scale of density-dependent body growth and its implications for recruitment, population dynamics and management of stream-dwelling salmonid populations. *Reviews in Fish Biology and Fisheries* 22: 813-825.

Vøllestad, L.A. & Olsen, M.E. 2008. Non-additive effects of density-dependent and density-independent factors on brown trout vital rates. *Oikos* 117: 1752-1760.

Vøllestad, L.A., Serbezov, B., Bass, A., Bernatchez, L., Olsen, E.M. & Taugbøl, A. 2012. Small-scale dispersal and population structure in stream-living brown trout (*Salmo trutta*) inferred by mark–recapture, pedigree reconstruction, and population genetics. *Canadian bulletin of fisheries and Aquatic Sciences* 69: 1513–1524.

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R. & Davies, P.M. 2010. Global threats to human water security and river biodiversity. *Nature* 467: 555-561.

Warren, D.R., Robinson, J.M., Josephson, D.C., Sheldon, D.R. & Kraft, C.E. 2012. Elevated summer temperatures delay spawning and reduce redd construction for resident brook trout (*Salvelinus fontinalis*). *Global Change Biology* 18: 1804-1811.

Waters, T.F. 1999. Long term trout production dynamics in valley creek, Minnesota. *Transactions of the American Fisheries Society* 128: 1151-1162.

Young, R.G., Hayes, J.W., Wilkinson, J. & Hay, J. 2010. Movement and Mortality of Adult Brown Trout in the Motupiko River, New Zealand: Effects of Water Temperature, Flow, and Flooding. *Transactions of the American Fisheries Society* 139: 137-146.

TABLES

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

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%)

Table 3. Global statistics on density (mean and standard deviation) and results of validation 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	***0.40***	***0.62***	0.02	0.00
	1+	88	59	***0.61***	***0.71***	***0.10***	0.00
	>1+	50	24	***0.08***	***0.50***	0.00	0.00
BEY2	0+	211	158	***0.25***	***0.75***	0.00	0.00
	1+	91	65	***0.05***	***0.30***	0.00	0.00
	>1+	44	26	***0.43***	***0.59***	0.03	0.01
BEY3	0+	196	160	0.00	***0.21***	0.03	0.00
	1+	97	65	0.00	0.03	0.00	0.00
	>1+	54	25	***0.59***	***0.73***	0.01	0.04
FON2	0+	113	93	***0.39***	***0.14***	0.01	0.00
	1+	63	51	***0.62***	***0.17***	***0.07***	0.01
	>1+	29	20	***0.06***	0.02	0.00	***0.05***
FON3	0+	181	168	***0.14***	***0.05***	0.02	0.01
	1+	84	45	***0.14***	***0.24***	0.02	***0.05***
	>1+	24	11	***0.14***	***0.10***	0.00	***0.11***
BREIL1	0+	91	118	***0.09***	***0.57***	***0.09***	***0.42***
	1+	36	22	***0.51***	***0.94***	***0.50***	***0.85***
	>1+	16	10	***0.50***	***0.65***	***0.19***	***0.38***
BREIL2	0+	161	133	***0.11***	***0.17***	0.02	0.03
	1+	124	87	***0.20***	***0.40***	0.04	0.01
	>1+	48	25	***0.73***	***0.82***	***0.27***	***0.39***
ROIP2	0+	124	182	0.01	***0.07***	***0.06***	0.00
	1+	79	68	***0.29***	0.00	0.04	0.00
	>1+	55	28	0.04	0.01	***0.12***	0.00
LIG2	0+	50	26	***0.50***	***0.41***	0.00	0.00
	1+	37	17	***0.16***	***0.16***	***0.06***	0.00
	>1+	44	12	***0.49***	***0.72***	***0.52***	***0.30***
Nb of validated reach models				4	4	17	19
% of validated reach models				15	15	63	70

Bold italic: non-significant test

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

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

Table 5. Flood-threshold and number of days for which flow had to exceed threshold to 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%

FIGURES

Fig. 1. Location of the five bypassed sections.

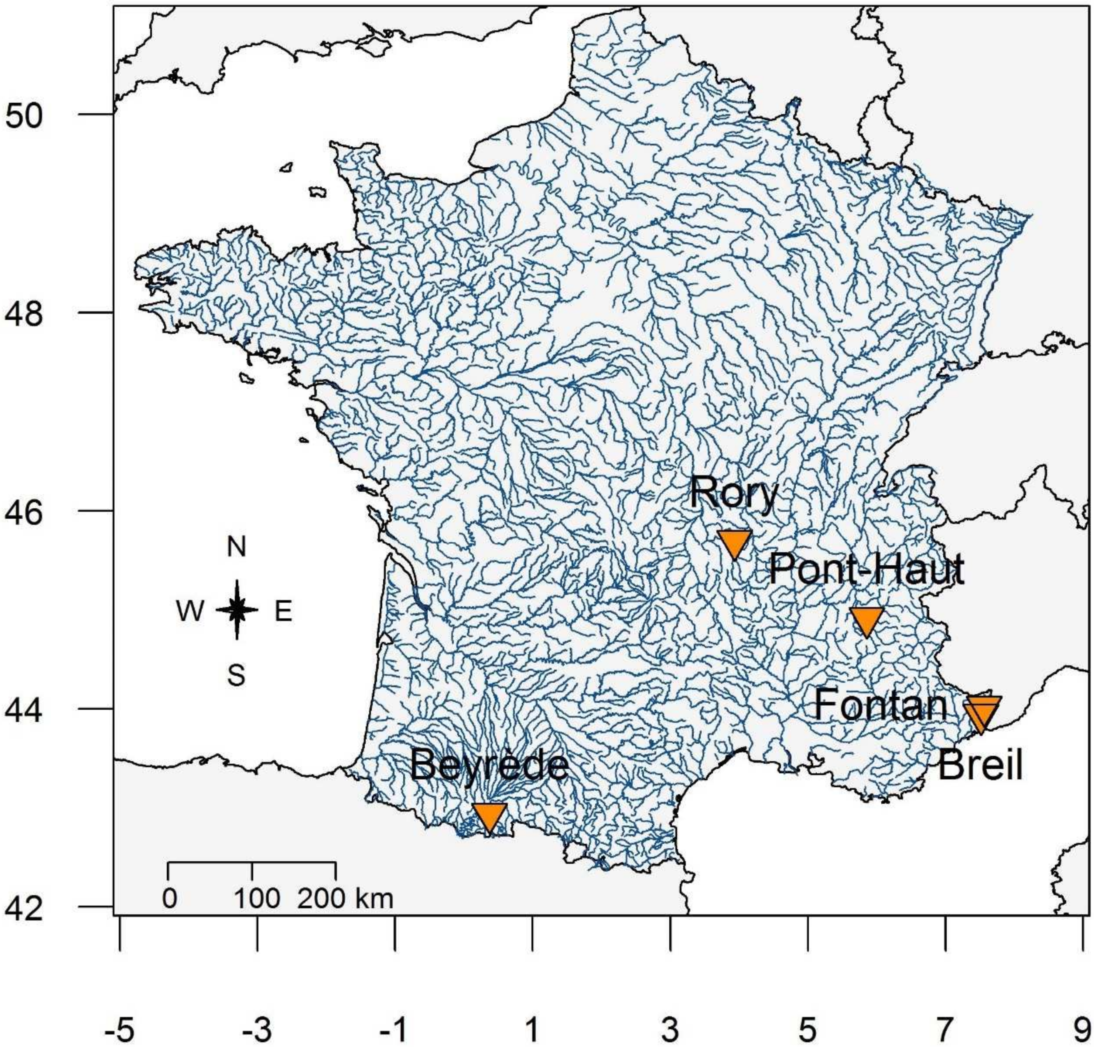

Fig. 2. Observed (white squares) and simulated (blue circles) density fluctuations for (a) 0+, (b) 1+ and (c) >1+ trout in the BEY2 reach. Results for all reaches are proposed as supplementary materials.

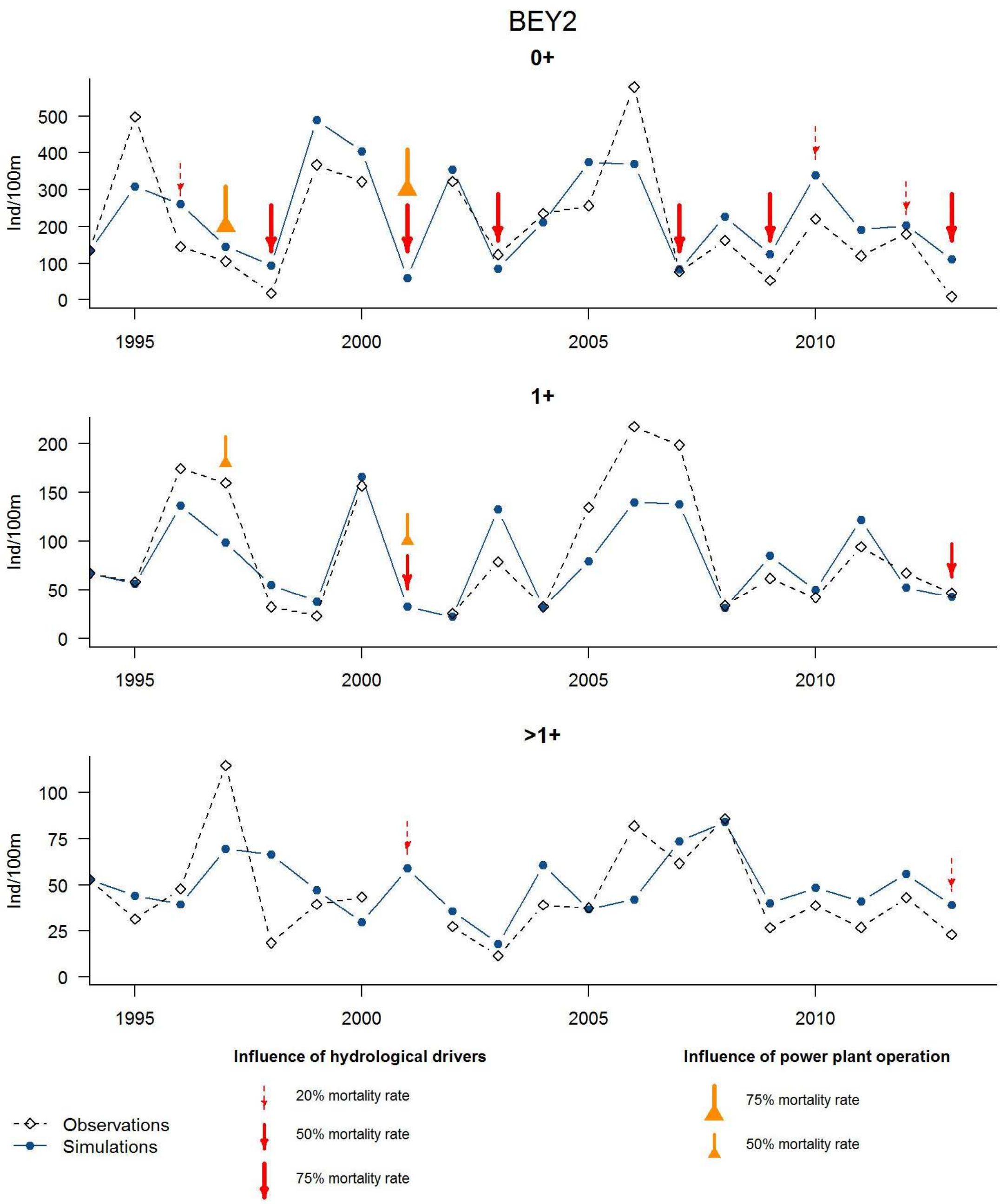

Fig. 3. Characterization of temporal and spatial occurrences of each driver structuring trout population dynamics. Temporal occurrence was the time frequency of the driver during the study period on the reach or bypassed section where it was involved, or the mean time frequency when several bypassed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