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ENVIRONMENTAL FLOW REGIMES BASED ON NATURAL FLOW REGIME: MYTH OR REALITY FOR TROUT POPULATION DYNAMICS?

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Before and after relicensing of Pont-Haut hydropower station on the Roizonne (in the French Alps), fish monitoring surveys were conducted over a fifteen-year period, complemented by measurement of discharge and characterization of habitat. A model of the dynamics of the trout population (MODYPOP) was calibrated for the period to analyze the fluctuations in the different age classes upstream and downstream of the power plant. Several hydrological scenarios were developed over a twenty-year period on the basis of random picking from the available daily natural discharge time series. For the bypassed reach, four management modes were reconstituted, with MIF(i) constant throughout the year, (ii) varying in accordance with the discharge upstream of the water intake, and (iii) varying in accordance with the season (high in winter and low in summer, or the opposite). The corresponding habitat time series were reconstituted and compared. The response of the population to these different scenarios and dam operation options was tested with the aid of MODYPOP simulations, combining two hypotheses of population regulation as a function of the habitat: i) density-dependent mortality, which tends to push the population toward a size compatible with the local carrying capacity in a hydrologically typical year under low-flow conditions, and ii) adjustment of the adult biomass to the local carrying capacity using a one-month time step. The results of the simulations of population dynamics are compared with the results obtained on the upstream reach under natural flow conditions. This comparison is helpful to a discussion of the natural flow regime paradigm adopted in global instream flow methodologies that are based essentially on hydrology.

INTRODUCTION

The richness and productivity of aquatic ecosystems are largely dependent on natural hydrological variability (Poff *et al.* [1]; Pyron and Lauer [2]). Many studies based essentially on hydrological factors (Richter *et al.* [3]; Arthington *et al.* [4]; Richter *et al.* [5] ; Tharme [6]) advocate a return to quasi natural hydrological regimes. It is true that all of the components of the hydrological regime of a river (discharge values, rhythm, frequency, duration, stability) can influence the dynamics of an aquatic ecosystem (Poff *et al.* [1]). Recommendations are based on this concept of hydrological regime, which

enables preserving the variability of the minimum instream flow (MIF) and supporting the ecological processes in aquatic systems (protection of the biodiversity and resilience of the ecosystems) (Richter *et al.* [5] [7]; Poff *et al.* [8]; Baran and Leroyer-Gravet [9]).
While it is relatively easy to evaluate the degree to which hydropower installations change the hydrological regime of a river, it is considerably more complex to identify the impact on the biological communities of such a change in regime. Indeed, the links between biodiversity, population dynamics and hydrology are not simple. On the one hand, the hydrological regime involves indirect relationships. It is determined by the full set of all modifications in discharge, habitat, morphology, nature of substrate, degree of armoring or silting, water quality and temperature. On the other, correlation between biological communities and the hydrological regime is not instantaneous, as the physical environment and the living organisms continue to be affected by past events. Here again, all of the components in the regime can play a role (intensity, duration, frequency, season). Lastly, biological communities can develop various strategies to deal with fluctuations in the hydrological regime. Some authors have already shown that the entire range of discharges is not always necessary for restoration of a viable salmonid population (Jowett and Biggs [10]). Moreover, studies by Stalnaker [11] and Bovee [12] have demonstrated the influence of hydraulic characteristics on fish communities and their functional structure. What has not yet been determined is the relative influence of fluctuations in MIF compared to other regulating factors.

Biological monitoring data must now be acquired over the long term, linked to the hydrological operating modes of power installations or to experimental situations in which the management mode is modified (Souchon *et al.* [13]), in order to better understand the impact on biological communities of such changes in instream flow. This type of experimentation is unfortunately far too rare (Bayley [14]; Jowett and Biggs [10]; Lamouroux *et al.* [15]; Sabaton *et al.* [16]). A study in France from 1994 to 2002 (Sabaton *et al.* [17], [16]) in the framework of the “Minimum Instream Flow” Working Group pointed up the important role of multiple regulating factors, on the one hand, and the need for a long monitoring period to detect a positive response on the part of the population to an increase in instream flow, on the other. Therefore, to incorporate these two aspects in the response of a population, we shall analyze the long-term dynamics of a trout population in an Alpine stream (France) with the help of a deterministic population dynamics model (MODYPOP). Having calibrated the model, we shall then analyze the response of the population to different methods of managing instream flow combined with different possible hydrological scenarios.

MATERIALS AND METHODS

Study site and monitoring of the ecosystem

The Roizonne is a river found at an altitude of 1100 m in the Alps. It is characterized by a nival regime with annual mean flow of 2.9 m^3/s, a slope of 3 to 4 % and a mean width of 6 m. The geology is predominantly crystalline terrain. A dammed lake at an altitude of

792 m enables diverting a maximum discharge of 4.4 m3/s to a hydropower plant located at Pont Haut. Following a relicensing procedure, discharge through the bypassed reach of the Roizonne rose by a factor of 3 (from 0.11 m^3/s to 0.33 m^3/s in March 1999). The bypassed reach (BPR) is 3 km in length. A site representative of the BPR and a control site on the upstream reach were selected in accordance with recognized geomorphologic principles (Simonson *et al.* [18]; Ginot *et al.* [19]). Habitat measurements were taken in accordance with the Phabsim protocol adapted to French streams (Sabaton *et al.* [20]; Ginot *et al.* [19]). Daily discharge and temperature time series were obtained from sensors installed at each study site. We also have curves for Weighted Usable Area (WUA) as a function of discharge, for all three stages in the life cycle of the brown trout (0+, 1+, >1+). WUA time series for each of the two reaches were then built up from the monthly discharge time series over the entire period of monitoring.

The same sites were also sampled by means of electrofishing, using a standard protocol (successive removal with 2-pass - Carle and Strube [21]), once a year in the autumn, to study the structure of the trout communities (numbers in each life stage as defined above) and year-to-year change. Scale measurement coupled with a study of the histograms of total length of trout captured enabled estimation of abundance and biomass for each life stage (0+, 1+, >1+) and for each year of monitoring.

Modeling of population dynamics

We used the MODYPOP trout population dynamics model described by Sabaton *et al.* [22] and Gouraud *et al.* [23]. This model, based on the Leslie matrix (Leslie [24]), simulates change in a trout population using biological parameters which are dependent on environmental conditions. The population is broken down into age classes, and the abundance of each age class is calculated over time with a one-month time step. Two mechanisms of population regulation as a function of the habitat are integrated: i) density-dependent mortality, which tends to push the population toward a size compatible with the local carrying capacity in a typical hydrological year under mean-flow conditions, and ii) adjustment of the adult biomass to the local carrying capacity using a one-month time step. In the bypassed reach, the carrying capacity is linked to the value of the MIF, which determines the amount of available habitat (WUA).

The biological characteristics of the population were based on data acquired in fishing surveys. The model was calibrated using inventories available between 1990 and 2007. The impact of flooding in the post-emergence stage (Cattanéo *et al.* [25]; Capra *et al.* [26]) was simulated by adding 75% mortality in this cohort whenever daily discharge exceeded a given threshold (8.5 m^3/s, which is indeed exceeded 2% of the time). Downstream migration of juveniles was simulated in the years following a year with no flooding (years with a high potential for recruitment). The number of 1+ individuals immigrating was assumed proportional to the number of individuals recruited in the preceding year (30% of total recruitment). The values of the parameters for mortality linked to higher discharge (75%) and rate of immigration (30%) were calibrated by

comparing simulations of trout stocks obtained from models and numbers of trout actually observed in the inventory month (September or October).

Long-term simulation with different management modes and hydrological scenarios

In order to determine what, in the longer term, might have been the effect of a modulation in MIF, simulations were run until 2030 (i.e. for 23 years) comparing different hydrological scenarios for the bypassed reach and the natural flow reach. To test the importance of sequences of theoretically structuring hydrological events (flooding and low-flow periods), ten hydrological scenarios covering periods of some twenty years were built, taking care to (i) retain the same seasonal frequency of hydrological episodes influencing the fish population dynamics as that observed during the period of monitoring, and (ii) to have contrasted sequences of hydrological events. For each of the ten hydrological scenarios, 4 management modes were simulated, in the bypassed reach only. The choice of theses modes was based on the requirements of the new French Water Law of December 2006 and in order to obtain contrasted fluctuations in the MIF. Whatever the management mode tested, the MIF in one day was always greater than or equal to $1/20^{th}$ of the annual mean flow over the period, and the mean flow for the year was greater than or equal to $1/10^{th}$ of the annual mean flow over the period. The mode 1 corresponded to a MIF equal to $1/10^{th}$ of the annual mean flow (a value taken from the work of Tennant [27]); the mode 2 to a MIF equal to $1/5^{th}$ of the discharge upstream of the water intake; the mode 3 to a MIF equal to $1/20^{th}$ of the annual mean flow from April to September and to $1/5^{th}$ of the discharge upstream of the water intake from October to March ; the mode 4 to a MIF equal to $1/5^{th}$ of the discharge upstream of the water intake from April to September and to $1/20^{th}$ of the annual mean flow from October to March.

For each management mode, the level of equilibrium in the population (the numbers toward which the population will tend) was calculated from the local carrying capacity, corresponding to the WUA in a summer low-flow period in an average year ($1.95 m3.s^{-1}$). This carrying capacity was expressed in m² of habitat favorable for adults per 100 m.

For each hydrological scenario, the response of the population to the different management modes was simulated with MODYPOP (this corresponded to 40 simulations). The results of the simulations of population dynamics were compared, analyzing only the results relating to numbers of adults (>1+). The mean number of adults obtained with the 10 hydrological scenarios was represented as a function of the year for each of the 4 management modes. The change was compared with that found on the upstream reach. Finally, a class of abundance was attributed to each simulated number of adults in a year, in the bypassed reach and in the natural flow reach. These classes, from 1 to 4, were defined on the basis of the highest carrying capacity for the ecosystem (CC), obtained in a low-flow period at mean hydrological conditions between the upstream and downstream reaches, with different management modes. The thresholds of the 4 classes of abundance were defined as the number of individuals in 100 m of the

reach, as follows: [0 – 0.25]*CC, [0.25 – 0.5]*CC, [0.5 – 0.75]*CC, [0.75 – 1]*CC, where CC is expressed as the number of individuals per 100m.

RESULTS

Monitoring of the environment and model calibration

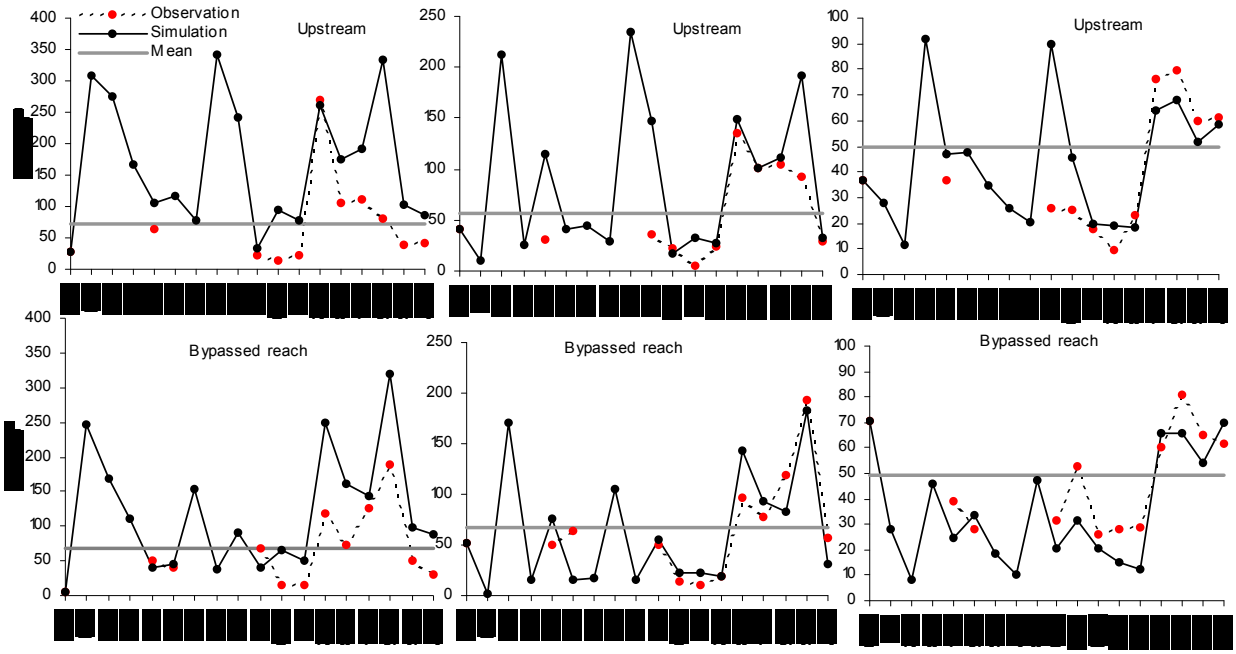

Figure1. Calibration of the MODYPOP model with observed trout abundance in the upstream reach (natural flow) and in the downstream reach (instream flow).

Figure 1 shows the changes in simulated and observed densities, together with the mean year-to-year density for the upstream reach and for the bypassed reach and for all 3 life stages. There is considerable year-to-year variability in abundance for all 3 stages. Upstream, the mean year-to-year densities drop as age increases (0+ to >1+). In the bypassed reach, these values are virtually the same for the 0+ and the 1+ cohorts. The sampled years in which the 0+ densities were lower than the mean year-to-year value correspond to years with higher spring discharge (exceeding 8.5m3.s^{-1}): 1994, 1995, 1999, 2000, 2001, 2006 and 2007. These years are identical upstream and downstream of the power plant. Hydrological conditions during the spring were different in the upstream and bypassed reaches only in 1996 and 1997 (when there was no sampling). The simulated recruitment data therefore diverge between upstream and downstream in those years, whereas it is synchronous in the other years. Fluctuations in 0+ stocks combined with immigration of 1+ individuals in years with no high-discharge episodes have a

repercussion on the other cohorts (1+ and >1+). The fluctuations in 0+ and 1+ stocks are quite well reproduced by the model.

Habitat response to the different management modes in a typical year

While the low summer discharge value is much higher in the upstream reach, the carrying capacity is quite similar upstream and downstream. In the bypassed reach, the highest carrying capacities ($m^2.100m^{-1}$) are found with mode 2 (imitating natural flow) and mode 4 (higher discharge in summer and low in winter – table 1). The lowest carrying capacity is found with mode 3 (low discharge in summer and higher in winter). The carrying capacity with mode 1 (discharge equal to $1/10^{th}$ of the annual mean flow) is intermediate.

Reach	Upstream reach	Bypassed reach			
Flow regime	Natural flow	Mode 1	Mode 2	Mode 3	Mode 4
Flow ($m3.s^{-1}$)	2.1	0.3	0.5	0.2	0.5
WUA ($m2.100m^{-1}$)	64.2	59.3	69.8	49	69.8

Table 1. Value of the low summer discharge flowing through the upstream reach and in the bypassed reach, and the carrying capacities (CC) corresponding to 4 modes

Results from long-term simulations

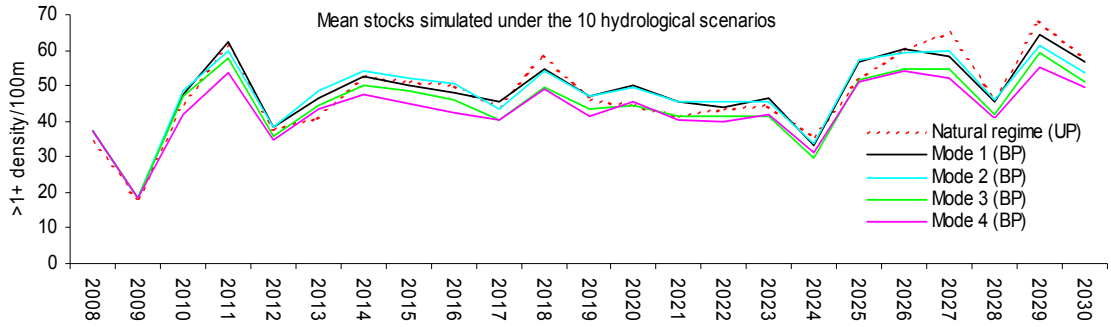

Figure 2: Results for the upstream (UP) and bypassed (BP) reaches for the 4 modes

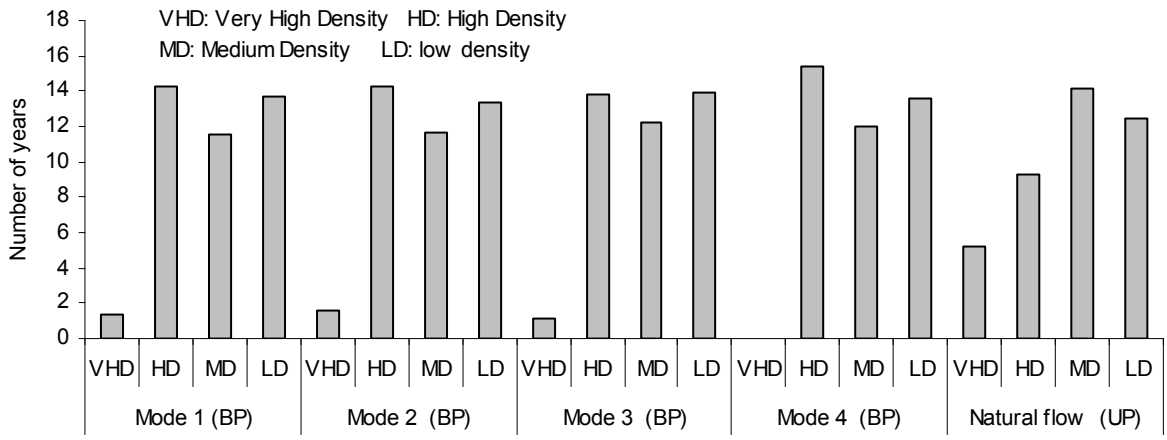

Figure 3: Distribution of the number of years in the 4 classes of abundance as related to the management mode in the bypassed reach (BP) and in the upstream reach (UP).

Figure 2 represents the mean simulated densities of adults for the 10 hydrological scenarios from 2008 to 2030. Adult stocks simulated with modes 1 and 2 are greater than with modes 3 and 4 throughout the period. Densities simulated upstream varied in ranges close to those of the stocks in the bypassed reach (regardless of the management mode), and depend on the year (values slightly higher or lower in certain years). Despite a higher level of equilibrium in the population, mode 4 gives mean densities lower than those found with the other scenarios. In any event, the simulated numbers vary within very similar ranges, no matter what the management mode. If we look at the results on a larger scale (analysis by class of abundance rather than exact level of abundance), the results obtained are identical, whatever the hydrological scenario. In other words, the distribution of the number of years in the 4 classes of abundance as a function of the management mode is the same, no matter what the hydrological scenario. Figure 3 shows this distribution for the 4 management modes tested in the bypassed section and with a natural flow regime in the upstream reach. The response of the population to the different management modes is very similar. The bypassed reach shows many years with high densities whereas the upstream reach shows more years with very high densities.

DISCUSSION

Significant variability in densities for all 3 life stages is found over the monitoring period. This great variability has been observed by numerous authors (Crisp [28]; Elliott [29]; Cattanéo *et al.* [25]; Sabaton *et al.* [16]). Despite this variability, synchronous trends are found in the communities upstream and downstream of the power plant. These synchronisms can be explained by density-dependent mechanisms (such as dispersion of individuals) as well as by density-independent mechanisms (e.g. climatic factors) (Bjornstad *et al.* [30]). These regulating factors were represented in the population dynamics model used here and their calibration helps to explain the trends in the densities observed.

The immigration simulated in the model, for example, enables obtaining densities in the 0+ stage close to the 1+ levels and therefore approaching the structure of the population actually observed. This imbalanced structure of the population points up the open nature of the system studied. The importance of immigration in structuring communities has been pointed out by many authors (Riley and Fausch [31]; Gouraud *et al.* [23], [32]). The fluctuations in habitat availability observed upstream of the study zone might encourage immigration, most particularly by juveniles because of the dry areas in the Roizonne basin.

The simulated effect of higher spring discharge allows for a good representation of the years with low recruitment. The impact of higher discharge is represented in the model by an added mortality in the 0+ cohort together with density-dependent mortality

in this same age class. This effect of fluctuations in discharge on density is pointed up by various authors (Lobon-Cervia and Rincon, [33]; Einum, [34]; Daufresne and Renault, [35]). The capacity for recovery modeled here is therefore greater or lesser depending on the stocks still in place after the hydrological event, in relation to the local carrying capacity. The higher this local capacity, the greater the capacity for recovery on the part of the population. This hypothesis is confirmed by the work of Hilderbrand [36], who shows that the risk of extinction of a population drops as the carrying capacity increases. Carrying capacity was estimated here using the amount of available habitat in low-flow periods. The structuring effect of this low discharge has been demonstrated by a number of authors (Souchon *et al.* [37]; Bell *et al.* [38]). Jowett *et al.* [39] further demonstrated, in 3 years of monitoring of a fish community in a small New Zealand river, that the 2 principal hydrological factors that explain variations in abundance of fish are flood periods, on the one hand, and the amplitude and duration of low-flow periods, on the other.

Furthermore, simulating a limitation of the adult biomass by the local carrying capacity, on a one-month time step, produces a better match between a simulated population and a monitored population when levels of abundance are high. The same is not true when densities are low. This phenomenon of adjustment of the population has been demonstrated by Baran [40], Gouraud *et al.* [23] on rivers in the Pyrenees, and by Souchon *et al.* [37].

All of the regulating factors described here affect the response of the population to the different management modes. The densities simulated were essentially arrived at by combining the value for the low summer discharge (which determines the level of balance in the population), the frequency of hydrological episodes, and monthly limitation of the population by the carrying capacity. Despite a higher level of balance in the population, mode 4 gives mean densities lower than those found with the other scenarios. They illustrate the fact that the differences observed among the 4 management modes are the result of restoration of the communities during periods not limited by hydrological events. The years with higher spring discharge, however, do show declines in 0+ cohorts which are later reflected in the other life stages; these limitations are the same, regardless of the management mode. This is due to the greater limitation of the biomass by the carrying capacity in spring than that simulated for the other management modes. In any event, the simulated numbers vary within very similar ranges, no matter what the management mode. The multiplicity and combinability of these regulating factors make the response of the population to the different management modes quite complex. The adopted hypotheses concern only the effects on the demography of the population and not the effect on the diversity and productivity of macroinvertebrates. Therefore, with these hypotheses, the results obtained seem to indicate that adopting a flow regime closer to the natural regime would not necessarily produce a positive response of the trout population.

These results are conditioned, however, by the different processes chosen for the model, given our current understanding of these processes. The influence of the

management mode on population response is represented in the model first via the capacity of the population to return to a level of equilibrium (assuming the equilibrium determined by the amount of available habitat in low-flow periods), and second, via limitation of the population by the carrying capacity, using a one-month time step. The impact of the management mode on other key regulating factors could also be represented. Mortality of the 0+ class, for example, due to greater or lesser flooding, compared with the base discharge above which flooding is considered to occur, could be integrated. Similarly, varying levels of immigration in response to the hydrological signal and the local carrying capacity might be represented. Generally speaking, the issue is to identify, on a seasonal cycle, the relative or combined influence on the different life stages of the fish of a) habitat, b) the timeframes for different life cycles, and c) hydrological episodes (flooding, low-flow). Given that objective, long-term monitoring of the living organisms and the physical environment before and after introduction of a minimum-flow regime would enable better identification of the influence of such regimes on the ecological mechanisms in play. Finally, the response of the population to the different management modes was examined here using frequencies of hydrological episodes in line with what has been observed in the past. The question of climate change and global trends should also be explored to analyze a population's response to different scenarios that integrate the changes which are now to be expected.

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