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Quantifying the effects of temperature and flow regimes on 0+ cyprinid fish abundance in the upper River Rhone using Bayesian hierarchical modelling.

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SUMMARY

1. Assuming that recruitment variation is one of the main sources of fish population and

    assemblage changes, it is necessary to understand how natural variations in the

environment influence 0+ fish abundance. Temperature regimes play an important role in enhancing both spawning activity and survival during early larval fish development. Flow regime variation, which is a powerful source of stream disturbance, is another factor to be taken into account.

2. Responses to these variables need to be assessed using long-term datasets, since standard statistical approaches fail to provide a causal structure or to quantify the different effects. We therefore used a 26-year dataset to evaluate the respective effects of seven derived independent variables describing the effects of temperature and flow regimes on the 0+ juvenile abundance of eight fish species in the River Rhone.

3. .A clustering procedure using the Kendall tau rank correlation coefficient was implemented and identified three groups of fish according to their synchronic variations in juvenile abundance; i.e. varying with decreasing juvenile abundance, slightly increasing juvenile abundance, and increasing juvenile abundance. These clusters provided the basis for building hierarchical logPoisson Generalized Linear Models. The Bayesian paradigm gives a reliable framework for model selection, and the best model was determined using the Bayes Factor.

4. The posterior distribution of the regression parameters was coherent with what was expected based on knowledge of the biology of the different species. It indicates that temperature regime drives 0+ juvenile abundance but that flow regime also plays an important regulating role. The models thus detected evidence of the consequences of specific flow events such as larval drift and an increase of available habitat during higher flow discharges.

5. Our study illustrates the advantages of using a hierarchical modelling approach to quantify ecological effects by improving discrimination between the different sources of uncertainty, leading to better precision when estimating regression parameters.

Introduction:

The theory of ecological filters has been well demonstrated for fish assemblages (Tonn *et al.*, 1990; Poff, 1997; Quist, Rahel & Hubert, 2005; Chessman, 2006). Regional filters such as temperature and flow (mostly latitude- and altitude-dependent) explain which species are to be found in local situations, where local constraints determine assemblage structure. These local factors can be natural, such as the interannual variations in temperature and flow regimes around general regional regimes, or anthropogenic, such as hydromorphological alterations and organic and chemical pollution (Bayley & Li, 1992).

Assessing the relative importance of these different constraints, determining the effects of anthropogenic pressures on freshwater bodies, and assessing the benefits to be expected from better management of these pressures are challenges that have shaped several national legislations (Clean Water Act USA, 1972; European Water Framework Directive 2000/60/EEC). There is consequently a need to conduct predictive studies, and statistical modelling is considered pivotal to achieving this objective since it can quantify the relationships between anthropogenic pressures and fish assemblages. In addition, climate change and its subsequent effects on flow and temperature regimes could exacerbate these problems (Firth & Fisher, 1992; Poff, 1992; Ficke, Myrick & Hansen, 2007; Schneider *et al.*, 2007).

Individual adult fish are generally more difficult to sample in large rivers than in small rivers, due to the deeper waters. Under these conditions, 0+ fish are probably easier to sample as they preferentially occupy the shallowest zones near banks. The quantitative and physiological assessment of 0+ fish has been shown to be a very useful way of assessing the ecological status of large rivers (Copp *et al.*, 1991; Schiemer *et al.*, 1991). Similarly, assessing the

number of young-of-the-year (YOY) is important as a meaningful indication of the reproductive success of different species, which in turn is a factor of primary importance for establishing self-sustaining populations (Schiemer, 2001). Furthermore, YOY sampling proves a more sensitive indicator of habitat suitability than sampling adult fish (Copp *et al.*, 1991).

Recruitment success depends on many factors: the condition of adult spawners, trophic resources and suitable temperature cycles, the availability of suitable substrate for spawning, the reproduction period during which the number of eggs deposited in the river is determined, the first few months of life that form an initial period of high mortality, and the first winter which is the second period of high mortality (Nunn *et al.*, 2003). In the River Rhone, even a small number of reproducing adult cyprinid individuals can lead to strong 0+ fish cohorts, as the reproductive strategy of these species consists of depositing a large number of eggs (Grenouillet *et al.*, 2001). The main driver of YOY numbers appears to be abiotic conditions (Larkin, 1978). As most fish species are ectothermic, water temperature over the year should be a major factor driving the ecology of species and the survival of YOY individuals, due to its preponderant influence on early growth rates (Nunn *et al.*, 2003). There is a large body of research into the effects of temperature on 0+ fish growth (Mills & Mann, 1985). The influence of flow regimes has also been highlighted (Schlosser, 1985), but it may play a more indirect role as it determines the quantity of available habitat (Souchon, 1994; Lamouroux *et al.*, 1999). However, major floods occurring during critical periods also play an important role. The larval period has been identified as the most vulnerable to floods, which can flush 0+ fish from cover and alter the substrate (Cattanéo *et al.*, 2001). The limited literature examining both thermal and flow effects on freshwater organisms suggests that both the direct and cumulative influences of these factors are critical (Olden & Naiman, 2010).

To a certain extent, the composition of adult fish assemblages results from different abiotic and biological phenomena, making their structures difficult to interpret. For riverine fish it has been shown that year-class-strength is largely determined during the first few months of life, and that a strong cohort of recruits from a given year remains a strong cohort of older fish in succeeding years (Mills & Mann, 1985). This indicates that abundance of YOYs is highly sensitive to the environment. The egg, larval and juvenile periods are the most critical stages in the life history of fish (Copp *et al.*, 1991), and it appears that recruitment variability is one of the main factors governing population variability (Houde, 1997). Many authors have underlined the need for a better understanding of recruitment variability mechanisms (Gulland, 1982; Houde, 1997), stressing the importance of environmental conditions. While Humphries *et al.* (2008) highlighted the need for datasets spanning over 20+ years, these remain rare. This scarcity of long-term datasets is mainly due to monitoring strategies and the structure of research funding (Bayley, 2002).

To quantify the direct effects of human activities on different bodies of water, it is first necessary to assess the effects of natural environmental variation on different species. The links between environmental variations and assemblage structures have been given increasing attention by researchers over the last decade, though mostly through general descriptive methods, such as Principal Components Analysis (PCA). These descriptive methods are based on correlative analysis of dependent and independent variables and are powerful tools for describing and understanding the qualitative structures of phenomena (Tonn *et al.*, 1990; Poff, 1997; Quist *et al.*, 2005; Chessman, 2006). However, they fail to give any formal quantification of the links between the target variables and the different independent variables. Regression models are better in this respect because they inherently assess the linkage strength between a predicted variable and its independent variables. Hierarchical modelling has recently improved our capacity to detect major links in data (Gelman *et al.*,

2004), and the advantages of this approach for analysing the effects of environmental trends on smelt abundance have already been demonstrated (Webb, Stewardson & Koster, 2010). Furthermore, conditional reasoning appears to be a particularly interesting way of developing progressively complex models (Parent & Bernier, 2007).

In this paper we report the use of a Bayesian hierarchical model to perform a quantitative analysis of the effects of annual temperature and flow regimes on the juvenile abundance of eight River Rhone cyprinid fish species forming three functional groups. We then discuss the relative importance of interannual variations in temperature and flow regimes in determining these abundances.

Material and methods

Study site

The upper River Rhone has been transformed since the end of the 19th century by the construction of nine hydropower plants between Geneva (CH) and Lyon (FR), thus tightly regulating the flow regime of the river. The Bugey study site is a 13 km-long segment of the upper River Rhone (45.81N; 5.21E) in France, situated 12.5 km downstream from the Sault-Brénaz hydropower plant (Fig. 1). The segment has a slope of 0.35%, a mean width of 120 m, a mean depth of 3 m and a mean annual flow of 500 $m^3.s^{-1}$ (Daufresne *et al.*, 2003). A nuclear power plant (Bugey CNPE) was built on the segment in 1978. Despite the presence of these power plants, the hydromorphological characteristics of the study site have changed little over time (see the Cassini maps, 1815; http://www.geoportail.fr/5069711/visu2D/afficher-en-2d.htm). The study segment is a mainly morphologically unimpacted single stretch of channel, subjected to seasonal and daily variations of flow regime caused by the regulation of hydropower dams built upstream, and with generally good water quality (Agence de Bassin Rhône Méditerranée Corse, 1999, in Daufresne *et al.*, 2003).

Fish data

The Cemagref has been performing fish surveys by boat electrofishing four times a year since 1979. Fish are sampled at eight fishing sites by continuous electrofishing from a boat drifting downstream along the bank for 30 minutes, so that each site is around 500 metres long and 2-4 metres wide. Electrofishing is performed using a Dream Electronis apparatus (type: Heron DC; 300-400 V; 2-3 A, Pessac, France). Fish are identified to species, measured for total length, and released. For each species, juvenile abundance is expressed as Catch Per Unit Effort (CPUE), meaning the number of fish captured in 30 minutes. The eight sites are distributed from upstream to downstream of the nuclear power plant and between the left and right banks (Fig. 1).

This bank electrofishing method tends preferentially to sample younger fish, including YOY and one-year juveniles. Copp (1989) identified the late summer period as being particularly favourable for sampling YOY. It is a relatively stable biological phase between the larval phase and the winter period, both of which are characterized by high mortality rates. Thus, the fish dataset was limited to a summer (July–August) and autumn (October–November) fishing sessions subset spanning 1980 to 2005 (data for 1988 and 1995 are missing, as are the data for the 1992 and 2004 autumn samples and the 1981 summer sample). In the first trial performed for this study, the juvenile-fish CPUEs were annually and seasonally pooled over the eight sites for each species, so that two counts (summer and autumn) were obtained for each species and each year. By doing this, the effect of warming by water from the nuclear power plant becomes negligible for this study, and thus no nuclear plant effect has been included.

Age class size limits were derived from histograms of size distributions for the different fish species (Persat & Chessel, 1989). Fish measuring strictly less than the size class limits for 0+ fish were considered as 0+ fish for the eight species, each representing more than 5% of total

abundance: bleak (*Alburnus alburnus* Linnaeus, 8 cm), barbel (*Barbus barbus* Linnaeus, 9 cm), chub (*Leuciscus cephalus* Linnaeus, 8 cm), roach (*Rutilus rutilus* Linnaeus, 6 cm), gudgeon (*Gobio gobio* Linnaeus, 10 cm), nase (*Chondrostoma nasus* Linnaeus, 8 cm), stream bleak (*Alburnoides bipunctatus* Bloch, 7 cm) and dace (*Leuciscus leuciscus* Linnaeus, 8.5 cm). Autumnal fish sampling chronologies are given in Fig. 2.

Clustering procedure

Fish species were clustered by the degree of synchrony of their juveniles' CPUEs. The Kendall tau rank correlation coefficient gives a correlation index between the ranks of two samples of fish species. It is computed as:

$$\tau = \frac{n_c - n_d}{\frac{1}{2}n(n-1)} \tag{1}$$

where n is the number of recorded years for the two species. Considering all the possible pairs of years, n_c is the number of concordant pairs (e.g. between years 3 and 7, the two samples either both increased or both decreased), n_d is the number of discordant pairs (during the period of time considered, one sample has increased while the other decreased), and the denominator is the total number of possible pairs.

The Kendall tau expresses the synchrony of two trajectories, and varies between -1 (the changes in reproductive success of the two species are always opposed) and 1 (the changes in reproductive success of the two species are fully synchronised). The Kendall tau was used as distance in a cluster procedure with the Ward method, which minimizes intra-cluster variance (Ward, 1963), to cluster the eight fish species into groups of synchronic interannual CPUE increases or decreases. The clusters are described and discussed below.

Temperature and flow regime data

Mean daily water temperatures and mean daily flow have been recorded since 1 January 1980. In line with Fruget *et al.* (2006), nine synthetic variables describing the annual natural environment of the station between spawning and fishing were derived from these two datasets. Given that temperature is the most important factor in fish ecology management, we set three temperature thresholds (12°C, 18°C, and maximum water temperature; Mills & Mann, 1985) to determine two different time-windows in which to describe the natural variations (i.e. 12-18°C and 18°C-maximum temperature). *C12, C18* and *Cmx* are the number of days between 1 January and the first day to record a 12°C water temperature, 18°C water temperature and maximum water temperature, respectively. Timing of minimum and maximum temperatures are important descriptors of thermal regime (Olden & Naiman, 2010). *S1* and *S2* are the sums of the differences between daytime temperature and the mean daily interannual temperature over each of the two periods, respectively. They express the difference in cumulative degree days between the considered year and the mean year. As temperature is known to play an important role in the early growth of 0+ fish, these two variables indicate whether the period is rather warm or cold compared to the 26-year interannual mean. They are computed using the following formulas, where T_{ij} is the temperature of the day *j* for the ith year:

$$S_1 = \sum_{j=C_{12}}^{C_{18}} (T_j - \frac{\sum_{i=1}^{I} T_{ji}}{I}) \tag{2}$$

and

$$S_2 = \sum_{j=C_{18}}^{C_{mx}} (T_j - \frac{\sum_{i=1}^{I} T_{ji}}{I}) \tag{3}$$

The other four variables describe the annual flow regime, divided between the two periods described earlier: *Qm1* and *Qm2* are the mean daily flows over periods 1 and 2 respectively,

while *Qmx1* and *Qmx2* represent the maximum daily flow discharge observed during periods 1 and 2 respectively.

After checking for correlations between independent variables, the C18 and Qmx1 variables were retrieved from the dataset as they exhibited strong correlations with variable S1 (i.e. Pearson's r = 0.8 or r = -0.8; Oberdorff *et al.*, 2002). A summary of these independent environmental variables is given in Table 1. In the following, we consider seven standardized vectors of length *n*=26: X^1= *C12*; X^2= *Cmx*; X^3= *S1*; X^4= *S2*; X^5= *Qm1*; X^6= *Qm2*; X^7= *Qmx2*. The corresponding regression parameters are then annotated as β_{C12}, β_{Cmx}, β_{S1}, β_{S2}, β_{Qm1}, β_{Qm2}, β_{Qmx2}.

Hierarchical modelling and Bayesian inference

The species groups previously obtained by the clustering method were used to write hierarchical models of Poisson regression (one model for each group) relating the two annual CPUEs to the annual environmental variables. The model's general structure is given as a directed acyclic graph (DAG; Fig. 3). *X* stands for the matrix containing the seven vectors of independent environmental variables. Thus X_j is the line vector of the environmental conditions in the jth year. We define $Z_{i,j,k}$ as a latent variable representing the number of YOY present in the zone the jth year for the ith species (belonging to the kth group of species). A logPoisson was chosen, meaning that the logarithm of $Z_{i,j,k}$ depends on the environmental variables under a linear combination of the independent variables:

$$\log(Z_{i,j,k}) = Z_i^0 + \beta_k \cdot X_{j,k} \tag{4}$$

where β_k is the vector of the coefficients of the regression for the kth group of species and Z_i^0 is the logarithm of the mean annual number of YOY for the ith species. That means that the latent number of YOY for the ith species (belonging to the kth group of species) for the jth year is obtained as the product of a mean interannual number of YOY by the effect of the

environment on the kth group of species. The model is organized into a hierarchy, expressed by the common environmental effect on species belonging to the same group of species. Thus, the β_k parameters are the hyperparameters of the model, which describe (conditional upon environmental conditions $X_{j,k}$) the environmental effects on the exchangeable fish species within each group. The number $Y_{i,j,k,l}$ of YOY observed the jth year in the ith species during the lth fishing event is considered to be a random variable according to a Poisson distribution as a distribution parameter.

$$Y_{i,j,k,l} \sim P(Z_{i,j,k}) \tag{5}$$

This Poisson distribution is justified by the fact that fish are assumed to be randomly distributed in the sample zone, which at first sight is both a simple yet rather realistic hypothesis.

The inference on the regression coefficient of this Generalized Linear Model was conducted using the Bayesian paradigm. Highly-dispersed Zellner Student priors were used on regression parameter priors and on Z^0_i as in Marin & Robert (2008). Priors are probability distributions describing the state of knowledge that scientists have on the possible range of values for their model parameters before carrying out any experiment. There is no single consensus definition of what "non-informative" means in the statistical community (see Bernardo & Smith (1994) for discussion), but using flat priors as we did is a practical and common way of providing vague prior knowledge. The knowledge acquired during the experiment is expressed via the model likelihood [Y|θ] and is used to update the prior probability distributions [θ] of parameters during the inference process to obtain the posterior distribution [θ|Y] using Bayes' formula:

$$[\theta|Y] = \frac{[Y|\theta] \cdot [\theta]}{[Y]} \tag{6}$$

where [Y] is the marginal probability of the data, used to normalize the posterior distribution. [Y] is generally approximated using a Monte Carlo Markov Chain (MCMC) algorithm. The models were written and implemented in the MCMC-based Bayesian analysis software WINBUGS 14 (Lunn *et al.*, 2000). Three independent Markov chains were run simultaneously. A burn-in period of 50,000 iterations was included to permit the Markov Chains to reach stationarity, after which their convergence was checked using the modified Gelman-Rubin diagnosis (Brooks & Gelman, 1998).

Model selection

For each group of species, introducing I=7 possible independent variables means that there are 2^I different possible models (i.e. 128 models resulting from the different possible combinations of independent variables). To make the notations clearer, the model index M is made to appear explicitly in the probability distributions. The Bayes factor (BF) was used to determine which of these models best fitted the data (Kass & Raftery, 1995). BF compares the fit of two different models, M_1 and M_2. It is defined as the ratio of the marginal distributions of the data for both competing models:

$$BF = \frac{[Y|M_1]}{[Y|M_2]} \tag{7}$$

Then, the marginal likelihoods $[Y|M_i]$ of the data relative to a model M_i are computed for each of the $2^7 = 128$ possible models using the importance sampling method described by Marin & Robert (2007). This method does not use WinBUGS parameter outputs, but instead employs samples generated from probability distributions whose mean and standard deviation are the classical logPoisson GLM estimators (see appendix 1 for mathematical development). For each group of species, the model with the highest mean marginal value is selected as the best-fitted model.

Model validation

For each of the three selected models, the Poisson hypothesis was tested using an adjusted Kolmogorov-Smirnov test for discrete random variables. The means of the posterior distributions of the regression parameters of the best-fit models were considered.

A posterior predictive checking method (Gelman *et al.*, 2004) was then used to assess the extent to which the model reflects the natural synchrony between species of the same functional group. Relying on parameter values drawn at random from their posterior joint distribution, a sample containing 10,000 annual predicted catches is generated for each species. This sample is then used to check the synchrony level for each group, as follows. For each $26*25/2=276$ possible pairs of years, the variation signs (positive if the number of juveniles is higher for the latest year than it is for the earliest year; otherwise negative) are calculated for each species. Then, for a given functional group and each pair of years, a score of 1 is given if all the species in the group have the same variation sign, or a score of 0 otherwise. The test statistics associated with the synchrony level are then computed as the sum of the scores over 276. The 10,000 samples make it possible to assess the predictive density of probability of the test statistics for each group, and then to obtain the 0.025 and 0.975 quantiles forming the boundaries of a 95% tolerance interval. The observed synchrony levels are computed for each group of species using the observed number of juveniles, and are then compared to the 95% tolerance intervals previously computed. For a given group of species, if the computed value falls into the interval, then the fit is satisfactory and the model describes the natural synchrony level between species of the same group well. A smaller (resp. higher) observed value than the lower (resp. upper) tolerance interval boundary would indicate that the developed model oversynchronises the species trajectories (resp. little).

Results

Species cluster

The cluster procedure clearly distinguishes three groups of species according to their degree of synchrony (Fig. 4). The first separation (d=1.24) discriminates an initial cluster composed of bleak and dace (hereafter referred to as "decreasing juvenile abundance"). The other branch then divides into two (d = 0.83), isolating a second cluster composed of nase, barbel and gudgeon (hereafter referred to as "slightly increasing juvenile abundance"), while the last cluster encompasses roach, chub and stream bleak (hereafter referred to as "increasing juvenile abundance").

Environmental effects

The independent variables kept in the structure of the selected best-fit model for each group of species are shown in Fig. 5, along with the probability distributions of the regression parameters of these independent variables.

The results have to be interpreted in terms of variations in the values of the independent variables around their means and, logically, the unit of variation to be considered is the standard deviation (Table 1). Thus, the results reported here present the expected effects of one standard deviation unit change in the considered independent variable on 0+ juvenile abundance.

As a logPoisson model was used, the observed distributions have to be transformed by the exponential function in order to measure the expected effects of the independent variables. Considering one independent variable (and thus every other independent variable being taken as the mean), an increase in its mean value equivalent to one standard deviation will have no effect if the posterior predictive distribution of its corresponding regression parameter is centred on 0, but will double the juvenile abundance of the species if the posterior predictive distribution is centred on 0.7 (as $e^{0.7} = 2$), and will divide this species population in two if it is

centred on -0.7 (as $e^{-0.7} = 0.5$). Furthermore, the effect of an increase of n times the standard deviation will raise the exponential of the regression parameter to the power n.

The observed effects are different for the three groups of species. Each group shows a different pattern of response to the environmental variations, and these differences are responsible for the variations in fish assemblage. Nevertheless, some environmental factors seem to have similar effects on different groups of species, revealing possible subtle evolutions.

A late occurrence of the spring temperature threshold has a negative effect on the juvenile abundance of the three groups of species ($\beta_{C12} = -0.275$; -0.138 and -0.159, resp.). Similarly, a summer period warmer than the interannual average is slightly detrimental for the three groups of species ($\beta_{S2} = -0.093$; -0.052 and -0.044, resp.).

The two increasing juvenile abundance species groups show rather similar patterns of response to the environmental variations. Indeed, Cmx, S1 and Qm1 have positive effects on the juvenile abundance of these groups of species ($\beta_{Cmx} = 0.110$, $\beta_{S1} = 0.392$ and $\beta_{Qm1} = 0.129$ for the slightly increasing juvenile abundance species group; $\beta_{Cmx} = 0.372$, $\beta_{S1} = 0.834$ and $\beta_{Qm1} = 0.145$ for the increasing juvenile abundance species group) but have no influence on the group of decreasing juvenile abundance species.

The two environmental variables describing the summer flow conditions, Qm2 and Qmx2, have similar effects on the species of both the decreasing juvenile abundance group and the increasing juvenile abundance group, with Qm2 having a slightly positive effect ($\beta_{Qm2} = 0.119$; 0.043, resp.) while Qmx2 has a strongly negative effect ($\beta_{Qmx2} = -0.514$; -0.498, resp.). Conversely, Qmx2 has no effect and Qm2 has a strong negative effect ($\beta_{Qm2} = 0.681$) on the juvenile abundance of species in the slightly increasing juvenile abundance species group.

Model validation

The posterior predicted levels of synchrony distributions for each group are given in Table 2.

Synchronicity was overpredicted for each group of species (the observed values are lower

than the lower 95% predictive tolerance interval bounds given by the model).

The Poisson hypothesis is too stringent. The data are more dispersed than allowed by a

Poisson probability distribution function, and the Kolmogorov-Smirnov (KS) test of Poisson

adequacy shows that the Poisson distribution fits poorly with the data (KS statistic value =

0.519; KS 95% quantile = 0.071). The implications of this test-of-fit result are discussed

below.

Discussion

Environmental effects

Numerous studies have highlighted the role of water temperature on the growth of fish larvae

(Schiemer *et al.*, 2004) and on the reproductive success of cyprinid fish species (Mills &

Mann, 1985; Grenouillet *et al.*, 2001). It is generally recognized that warmer temperatures (in

the range of physiological tolerance for the species) lead to better growth of cyprinids 0+ fish

(Mills & Mann, 1985; Daufresne *et al.*, 2003; Wolter, 2007). However, our results indicate

that flow conditions also play a major role in determining the juvenile abundances of the

different flow-regulated large river species. Humphries & Lake (2000) suggested that flow

regime variation and regulation had greater impacts on post-spawning factors responsible for

recruitment than on preventing spawning, and it has been shown that in the first weeks of life

YOY fish preferentially inhabit low-flow habitats such as slack waters (Moore & Thorp,

2008), where better temperature, flow, food production and light penetration conditions

ensure better growth during critical life stages (Schiemer *et al.*, 2001; Moore & Thorp, 2008).

However, there is evidence that spawning and YOY development do not occur only in the

flood plain during high waters but also in the main channel (Humphries, Serafini & King,

2002). Our study site, with its regulated flow, contains very little slack water, except during high flows (over 700 m^3.s^{-1}), meaning the YOY have to deal with the conditions of the main channel. The results observed for the early development period seem to confirm this. As mentioned previously, a higher mean flow regime could provide suitable conditions for spawning and growth habitats. Lytle & Poff (2004) highlighted that fish show behavioural adaptations to natural flow regimes, which mostly consist of finding favourable habitats during floods or droughts (Schiemer, Hein & Reckendorfer, 2007). However, Nunn *et al.* (2007) identified the larval period as most vulnerable to increases in river discharge, although the situation was complicated by interannual variations in hatching times and river discharge. Furthermore, several studies have shown that many cyprinid species undergo a larval drift period, especially during their few first weeks of life (Carter & Reader, 2000). This drift could be favoured or intensified by high flow discharges. Although studies have not detected any significant influence of river discharge on the seasonal pattern of juvenile drift densities (Reichard, Jurajda & Ondrakova, 2002; Zitek, Schmutz & Ploner, 2004; Zitek *et al.*, 2004), this kind of effect cannot be totally excluded. The results of this study are in agreement with these general statements, and a coherent hypothesis can be proposed to explain the juvenile abundances.

Overall common effects

Two environmental variables, C12 and S2, have similar effects on the eight species. The negative effect of C12 reveals that the earlier this temperature threshold is reached, the higher the annual juvenile abundance will be. The benefits of this earlier water warming have already been demonstrated for dace (Philippart, 1981; Mills & Mann, 1985). Dace is an early-spring spawner (Teletchea *et al.*, 2009), generally spawning when water temperature reaches 10°C (Tissot & Souchon 2008), and dace larvae benefit from the early water warming as it

enhances growth. Fractional spawning has been reported for bleak (Mackay & Mann, 1969) based on evidence of up to four size groups of eggs in the ovary prior to spawning (Barus & Prokes, 1993). Bleak spawns later than dace when water temperature reaches 15-16°C (Tissot & Souchon 2008), which normally occurs at around day 155 (first week of June). The early water warming may favour better growth of bleak larvae and thus enhance better survival of the successive batches. Teletchea *et al.* (2009) identified nase as an early-spring fractional spawning species, barbel as a late-spring possibly fractional spawning species, and gudgeon as a late-spring fractional spawning species (fractional spawning of gudgeon has also been reported by Mann, 1980). The earlier water warming could then lead to better growth and survival of the nase larvae, as for dace. Concerning the other two species, which are later spawners, earlier water warming probably enhances earlier first spawning and consequently promotes better growth and survival of the different successive batches of larvae. Roach usually spawn once within a 2-4 day period (Mackay & Mann, 1969) when water temperature reaches 15°C (Tissot & Souchon 2008), while chub is a late-spring spawner (Teletchea *et al.*, 2009) that is known to be capable of fractional spawning (Economou, Daoulas & Psarras, 1991; Vriese, Semmekrot & Raat, 1994), and its eggs can be distributed over up to three spawnings (Libosvarsky, 1979), and stream bleak is probably capable of fractional spawning after water temperature reaches 14°C (Tissot and Souchon 2008). Globally, an early spring threshold probably enhances earlier spawning, allowing the larvae and subsequent juveniles better to survive the subsequent environmental conditions.

The overall negative effect of a hotter-than-average summer on juvenile abundance could be explained by both direct and indirect factors. It could reduce the available thermal juvenile niche and provoke increased juvenile mortality if temperature stays higher than the lethal temperature of the species for an excessively long period (Tissot & Souchon, 2008). Higher

water temperature could also be detrimental for aquatic invertebrates and algae, causing higher juvenile mortality due to starvation.

Common environmental drivers for both increasing abundance groups

The three environmental variables Cmx, S1 and Qm1 have positive influences on the species of both groups of increasing abundance but no effect on the species of declining abundance. Thus, the specific responses to these three variables appears to be the main factor driving whether species will belong to the declining abundance group or to one of the two increasing abundance groups. At the same time, Cmx and S1 seem to be the two variables responsible for the particularly high increase in juvenile abundance of roach, chub and stream bleak, as they have a higher positive impact on these three species than on nase, barbel and gudgeon. The very positive effect of S1, which describes the relative sum of degree-days in the spring period, seems to confirm the generally-accepted statement that warmer temperatures lead to better growth of cyprinid juveniles (Mills & Mann, 1985; Daufresne *et al.*, 2003; Wolter, 2007). A high S1 probably decreases the incubation duration of these species and promotes the early development of larvae, which in turn favours survival during the subsequent periods. The positive effect of Cmx on the juvenile abundance of these species indicates the small benefit of a longer summer period. This effect is probably due to the fact that a later water temperature drop lets the early juvenile fish of these three species reach a higher fork length at the end of the summer, thus promoting better subsequent survival. The flow conditions seem to play an important role in determining the juvenile abundance of these groups of species. Qm1 has a positive effect, confirming the importance of the availability of slack waters during spawning. Indeed, slack waters become available if the mean spring flow regime increases from 565 $m^3.s^{-1}$ to 741 $m^3.s^{-1}$.

Benthic vs. pelagic species

The two environmental variables describing the summer flow conditions (Qm2 and Qmx2) have different effects depending on whether they applied to benthic species in the slightly increasing abundance group or pelagic species in the two other groups.

The negative effect of a high maximal flow discharge on pelagic species could be explained by three hypotheses. First, this high flow discharge could promote YOY drift. Carter & Reader (2000) suggested that drift of 0+ fish is probably part of a migratory cycle and has a function in allowing movement from the spawning habitat to nursery areas. They reported that drift of 0+ fish was mostly restricted to the first few weeks of life. In our case, during the defined summer period, YOYs have to be considered as early juveniles or larvae with poor swimming abilities. Secondly, Bolland, Cowx & Lucas (2008) showed that in lowland rivers, vast numbers of under-yearling coarse fish were found in temporary floodplain water bodies created by over-topping of floodbanks, as they were unable to return to the main channel when the floodwaters subsided. These young fish were mainly eurytopic species including bleak and roach, but also included rheophilic species such as dace and chub. Finally, concerning bleak, the summer floods could negatively impact the later reproductive activity of this fractional-spawning species, causing a drop in overall bleak juvenile abundance.

In contrast, a high mean summer flow regime has a detrimental effect on the juvenile abundance of benthic species. This could be due to high water velocities leading to unfavourable benthic feeding conditions, or to higher water depth causing less algae development.

Community structure predictions and human management

The mean annual water temperature at the Bugey study site has increased by 2°C over the last 20 years (Daufresne *et al.*, 2003), accompanied by an increase in the S1 and S2 variables. The

general trend indicates that a shift occurred in the early 1990s, and since 1995 S1 has constantly been higher than its interannual mean. This coincides with the sharp drop in the numbers of juvenile dace and bleak and the significant growth in numbers of juvenile roach, chub and stream bleak. This phenomenon seems to stem from warmer waters strongly favouring the latter three species. Furthermore, the increase in midsummer floods seems to be more detrimental for dace and bleak, probably because these two species do not benefit from water warming. Nevertheless, the system must be appreciated holistically, and certain compensatory mechanisms could be involved, such as juvenile or even adult recolonization from other source sites, thereby slowing down the decrease in some species and preventing their disappearance. Species mobility and spatial connectivity tend to reduce the risk of extinction (Lowe, 2002; Albanese, Angermeier & Peterson, 2009). A study by Phillips & Johnston (2004) suggested that patterns of recovery from disturbances could occur over distances of 20 km or more. The random occurrence of favourable years may act in the same way. Consequently, it is reasonable to think that, if water continues to become warmer, the fish community would continue to evolve toward the overall dominance of roach, chub and stream bleak, with nase, barbel and gudgeon continuing to accompany these species. Dace and bleak should probably remain present due to ecological adaptations and random environmental variations.

This work confirms that juvenile fish assemblages are shaped by the complex interactive effects of flow and thermal regimes (Olden & Naiman, 2010). Even if water temperature plays an important role in determining juvenile abundance, its effects can be significantly modulated by flow conditions. Since these are deeply impacted by human flow management for hydroelectric production, human flow management may be a major factor in structural variations in large river fish assemblages. It follows that readjusting watershed management

to decrease the amplitude of midsummer floods may help slow the decreases in dace and bleak numbers.

Hierarchical modelling

Oberdorff & Porcher (1992) stressed the importance of describing, quantifying and modelling the relationships between assemblages and their habitats. Hierarchical modelling is particularly well-adapted in cases where the structure of the problem pleads for linking certain parameters, making it possible to build a joint probability model for these parameters that reflects their interdependence (Gelman *et al.*, 2004). Here, we assumed the existence of groups of species sharing similar responses to environmental constraints. Bayesian hierarchical modelling proved a reliable method of dealing with our complex system, making it possible to take these similarities into account and thus allowing a better assessment of environmental effects. In fact, by allowing the introduction of hidden variables (Clark, 2005), it becomes possible to separate uncertainty into process uncertainty (here, the environmental effects) and sample uncertainty (the Poissonian error). Furthermore, Bayesian hierarchical models are easy to write, as they directly reflect the way people conceptualize their system, and they are particularly flexible. This is an important advantage when using data from different sources, which leads to different source uncertainties, as is the case when using monitoring datasets (Webb *et al.*, 2010). Although our model has been developed using data from one study site, its structure is robust enough to be completed and then trialled on more general datasets.

Modelling hypothesis

By using a Poisson model, we considered that fish are randomly distributed over the total sampled zone. However, as fish generally form shoals, they may show patchy distributions. It

appears in our study that the Poisson model is not well supported by the data, and that the latter are over-dispersed. This extra variation may, of course, first be imputed to the interannual variation stemming from the non-controlled conditions of the fishing protocol (change of boats, change of operators, changes in river flows between experiments). Technically, but at the cost of estimating an additional parameter, the Poisson distribution could be replaced by a more dispersed alternative such as the negative binomial (a Gamma mixture of Poisson probability distribution functions). The extra variation feature may also be a consequence of pooling all the data from all the sites along the river, and much more refined models can be readily investigated in future research aimed at modelling these extra sources and variations by including fixed seasonal effects as well as random site effects. Nevertheless, it is very likely that the trends in environmental effects (meaning the means of the probability distributions of the regression parameters) will be conserved, despite loss of precision in the coefficient estimators.

Cressie *et al.* (2009) stressed the importance of assessing the model fit using posterior predictive distribution (Gelman *et al.*, 2004), but they also underlined the possible difficulties inherent in such an approach, especially in the case of high-dimensional distributions. Our study includes an example of a simple model test-of-fit, as the statistic used is relatively straightforward and can be directly computed from simulations using the posterior predictive distribution.

Conclusions

Poff & Zimmerman (2010) summarized the latest literature in an attempt to quantify the effects of flow regime alterations on ecological assemblages. They pointed to the lack of studie on the effects of intermediate alterations. Our work combined a hierarchical modelling approach and a simple description of the annual flow regime to provide novel insight into how

0+ fish assemblages react to interannual flow variations in a flow-regulated river, and it points to the importance of flow management in managing fish assemblages. The study identified flow regime as an important driver, in addition to natural temperature regime variations (Daufresne *et al.*, 2003), in determining variations in fish assemblages. Furthermore, introducing the temperature regime confirmed the importance of interannual thermic variations in determining the abundance of species in the different assemblages, and illustrated the effects of water warming over the last two decades.

References

Albanese, B., Angermeier, P.L. & Peterson, J.T. (2009) Does mobility explain variation in colonisation and population recovery among stream fish? *Freshwater Biology*, **54**, 1444-1460.

Barus, V. & Prokes, M. (1993) Fecundity of the bleak (Alburnus alburnus) in the Vestonice reservoir. *Folia Zoologica*, **42**, 281-288.

Bayley, P. & Li, H. (1992) Riverine fishes. In: *The Rivers Handbook, volume 2* (Eds P. Calow & G. Petts), pp. 251-281. Blackwell Scientific Publications, Oxford.

Bayley, P.B. (2002) A review of studies on responses of salmon and trout to habitat change, with potential for application in the Pacific Northwest. Report to the Washington State Independent Science Panel (supplement), Washington.

Bolland, J.D., Cowx, I.G. & Lucas, M.C. (2008) Factors affecting the dispersal of coarse Fish, Environment Agency, UK.

Brooks, S.P. & Gelman, A. (1998) General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, **7**, 434-455.

Carter, K.L. & Reader, J.P. (2000) Patterns of drift and power station entrainment of 0+ fish in the River Trent, England. *Fisheries Management and Ecology*, **7**, 447-464.

Cattanéo, F., Carrel, G., Lamouroux, N. & Breil, P. (2001) Relationship between hydrology and cyprinid reproductive success in the lower Rhône at Montélimar, France. *Archiv für Hydrobiologie*, **151**, 427-450.

Chessman, B.C. (2006) Prediction of riverine fish assemblages through the concept of environmental filters. *Marine and Freshwater Research*, **57**, 601-609.

Clark, J.S. (2005) Why environmental scientists are becoming Bayesians. *Ecology Letters*, **8**, 2-14.

Copp, G.H. (1989) The habitat diversity and fish reproductive function of floodplain ecosystems. *Environmental Biology of Fish*, **26**, 1-27.

Copp, G.H., Olivier, J.M., Penaz, M. & Roux, A.L. (1991) Juvenile fish as functional describers of fluvial ecosystem dynamics: applications on the River Rhone, France. *Regulated Rivers : Research and Management*, **6**, 135-145.

Cressie, N., Calder, C.A., Clark, J.S., Hoef, J.M.V. & Wikle, C.K. (2009) Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. *Ecological Applications*, **19**, 553-570.

Daufresne, M., Roger, M.C., Capra, H. & Lamouroux, N. (2003) Long-term changes within the invertebrate and fish communities of the Upper Rhône River: effects of climatic factors. *Global Change Biology*, **10**, 124-140.

Economou, A.N., Daoulas, C. & Psarras, T. (1991) Growth and morphological development of chub, *Leuciscus cephalus* (L.), during the first year of life. *Journal of Fish Biology*, **39**, 393-408.

Ficke, A.D., Myrick, C.A. & Hansen, L.J. (2007) Potential impacts of global climate change on freshwater fisheries. *Reviews in Fish Biology and Fisheries*, **17**, 581-613.

Firth, P. & Fisher, S.G. (1992) *Global climate change and freshwater ecosystems*, Springer Verlag, Paris.

Fruget, J.F., Bady, P., Olivier, J.M., Carrel, G., Souchon, Y., Villeneuve, B., Daufresne, M. & Capra, H. (2006) Etude thermique globale du Rhône phase III, Lot 2: Etude à l'échelle du Rhône des compartiments biologiques. Cemagref.

Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (2004) *Bayesian Data Analysis*, Chapman & Hall/CRC, Boca Raton, FL.

Grenouillet, G., Hugueny, B., Carrel, G.A., Olivier, J.M. & Pont, D. (2001) Large-scale synchrony and inter-annual variability in roach recruitment in the Rhône River: the relative role of climatic factors and density-dependent processes. *Freshwater Biology*, **46**, 11-26.

Gulland, J.A. (1982) Why Do Fish Numbers Vary. *Journal of Theoretical Biology*, **97**, 69-75.

Houde, E.D. (1997) Patterns and trends in larval-stage growth and mortality of teleost fish. *Journal of Fish Biology*, **51**, 52-83.

Humphries, P., Brown, P., Douglas, J., Pickworth, A., Strongman, R., Hall, K. & Serafini, L. (2008) Flow-related patterns in abundance and composition of the fish fauna of a degraded Australian lowland river. *Freshwater Biology*, **53**, 789-813.

Humphries, P. & Lake, P.S. (2000) Fish larvae and the management of regulated rivers. *Regulated Rivers-Research & Management*, **16**, 421-432.

Humphries, P., Serafini, L.G. & King, A.J. (2002) River regulation and fish larvae: variation through space and time. *Freshwater Biology,* **47***,* 1307-1331.

Kass, R.E. & Raftery, A.E. (1995) Bayes Factors. *Journal of The American Statistical Association*, **90**, 773-795.

Lamouroux, N., Olivier, J.M., Persat, H., Pouilly, M., Souchon, Y. & Statzner, B. (1999) Predicting community characteristics from habitat conditions: fluvial fish and hydraulics. *Freshwater Biology*, **42**, 275-299.

Larkin, P.A. (1978) Fisheries Management - Essay for Ecologists. *Annual Review of Ecology and Systematics*, **9**, 57-73.

Libosvarsky, J. (1979) Gonad weight and egg numbers in chub, *Leuciscus cephalus*, from the Rokytna stream. *Folia Zoologica*, **28**, 35-42.

Lowe, W.H. (2002) Landscape-scale spatial population dynamics in human-impacted stream systems. *Environmental Management*, **30**, 225-233.

Lunn, D.J., Thomas, A., Best, N. & Spiegelhalter, D. (2000) WinBUGS - A Bayesian modelling framework: Concepts, structure, and extensibility. *Statistics and Computing*, **10**, 325-337.

Lytle, D.A. & Poff, N.L. (2004) Adaptation to natural flow regimes. *Trends in Ecology & Evolution*, **19**, 94-100.

Mackay, I. & Mann, K.H. (1969) Fecundity of two cyprinid fish in the River Thames, Reading, England. *Journal of the Fisheries Research Board of Canada*, **26**, 2795-2805.

Mann, R.H.K. (1980) The growth and reproductive strategy of the gudgeon, *Gobio gobio* (L.), in two hard-water rivers in southern England. *Journal of Fish Biology*, **17**, 163-176.

Marin, J.-M. & Robert, C.P. (2007) *Bayesian core: a practical approach to computational Bayesian statistics*, Springer-Verlag, New York.

Mills, C.A. & Mann, R.H.K. (1985) Environmentally-induced fluctuations in year-class strength and their implications for management. *Journal of Fish Biology*, **27**, 209-226.

Moore, S.L. & Thorp, J.H. (2008) Coping with hydrogeomorphic variations in a prairie river: Resiliency in young-of-the-year fish. *River Research And Applications*, **24**, 267-278.

Nunn, A.D., Cowx, I.G., Frear, P.A. & Harvey, J.P. (2003) Is water temperature an adequate predictor of recruitment success in cyprinid fish populations in lowland rivers? *Freshwater Biology*, **48**, 579–588.

Nunn, A.D., Harvey, J.P., Britton, J.R., Frear, P.A. & Cowx, I.G. (2007) Fish, climate and the Gulf Stream: the influence of abiotic factors on the recruitment success of cyprinid fish in lowland rivers. *Freshwater Biology*, **52**, 1576-1586.

Oberdorff, T., Pont, D., Hugueny, B. & Porcher, J.P. (2002) Development and validation of a fish-based index for the assessment of "river health" in France. *Freshwater Biology*, **47**, 1720-1734.

Oberdorff, T. & Porcher, J.P. (1992) Fish assemblage structure in Brittany streams (France). *Aquatic Living Resources*, **5**, 215-223.

Olden, J.D. & Naiman, R.J. (2010) Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology*, **55**, 86-107.

Parent, E. & Bernier, J. (2007) *Le raisonnement bayésien: modélisation et inférence*, Springer, Paris.

Persat, H. & Chessel, D. (1989) Size-Class Ordination - a Useful Method in the Study of Fish and Invertebrate Populations. *Acta Oecologica-Oecologia Generalis*, **10**, 175-195.

Philippart, J.C. (1981) Ecologie d'une population de vandoise, *Leuciscus leuciscus* (L.) dans la rivière Ourthe (bassin de la Meuse, Belgique). *Annales de Limnologie*, **17**, 41-62.

Phillips, B.W. & Johnston, C.E. (2004) Fish assemblage recovery and persistence. *Ecology of Freshwater Fish*, **13**, 145-153.

Poff, N.L. (1992) Regional hydrologic response to climate change: an ecological perspective. In: *Global climate change and freshwater ecosystems* (Eds P. Firth & S.G. Fischer), pp. 88-115. Springer Verlag, New York.

Poff, N.L. (1997) Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, **16**, 391-409.

Poff, N.L. & Zimmerman, J.K.H. (2010) Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology*, **55**, 194-205

Quist, M.C., Rahel, F.J. & Hubert, W.A. (2005) Hierarchical faunal filters: an approach to assessing effects of habitat and nonnative species on native fish. *Ecology of Freshwater Fish*, **14**, 24-39.

Reichard, M., Jurajda, P. & Ondrakova, M. (2002) The effect of light intensity on the drift of young-of-the-year cyprinid fish. *Journal of Fish Biology*, **61**, 1063-1066.

Schiemer, F., Hein, T. & Reckendorfer, W. (2007) Ecohydrology, key-concept for large river restoration. *Ecohydrology and Hydrobiology*, **7**, 101-111.

Schiemer, F., Keckeis, H. & Flore, L. (2001) Ecotones and hydrology: Key conditions for fish in large rivers. *Ecohydrology and Hydrobiology*, **1**, 49-55.

Schiemer, F., Keckeis, H., Nemeschkal, H., Schludermann, E., Winkler, G. & Zweimüller, I. (2004) Ontogenetic patterns in thermal adaptation of fish vs. long-term temperature trends in large rivers. *International Congress Series*, **1275**, 209-217.

Schiemer, F., Spindler, T., Wintersberger, H., Schneider, A. & Chovanec, A. (1991) Fish fry associations: important indicators for the ecological status of large rivers. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **24**, 2497-2500.

Schlosser, I.J. (1985) Flow regime, juvenile abundance, and the assemblage structure of stream fish. *Ecology*, **66**, 1484-1490.

Schneider, S.H., Semenov, S., Patwardhan, A., Burton, I., Magadza, C.H.D., Oppenheimer, M., Pittock, A.B., Rahman, A., Smith, J.B., Suarez, A. & Yamin, F. (2007) Assessing key vulnerabilities and the risk from climate change. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and C.E. Hanson, Eds., Cambridge University Press, Cambridge, UK, 779-810.

Souchon, Y. (1994) Development of Fish Habitat Modelization in French Streams in Recent Years. *Bulletin Français De La Peche Et De La Pisciculture*, **67**, 57-71.

Teletchea, F., Gardeur, J.N., Kamler, E. & Fontaine, P. (2009) The relationship of oocyte diameter and incubation temperature to incubation time in temperate freshwater fish species. *Journal of Fish Biology*, **74**, 652-668.

Tissot, L. & Souchon , Y. (2008) Etat des connaissances sur les préférences thermiques des principales espèces de poissons des eaux continentales françaises. Rapport EDF LNHE/Cemagref.

Tonn, W.M., Magnuson, J.J., Rask, M. & Toivonen, J. (1990) Intercontinental comparison of small-lake fish assemblage: the balance between local and regional processes. *American Naturalist*, **136**, 345-375.

Vriese, F.T., Semmekrot, S. & Raat, A.J.P. (1994) Assessment of spawning and nursery areas in the river Meuse. *Water Science and Technology*, **29**, 297-299.

Ward, J. (1963) Hierarchical Grouping to Optimize an Objective Function. *Journal of The American Statistical Association*, **58**, 236-244.

Webb, J.A., Stewardson, M.J. & Koster, W.M. (2010) Detecting ecological responses to flow variation using Bayesian hierarchical models. *Freshwater Biology*, **55**, 108-126

Wolter, C. (2007) Temperature influence on the fish assemblage structure in a large lowland river, the lower Oder River, Germany. *Ecology of Freshwater Fish*, **16**, 493-503.

Zitek, A., Schmutz, S. & Ploner, A. (2004) Fish drift in a Danube sidearm-system: II. Seasonal and diurnal patterns. *Journal of Fish Biology*, **65**, 1339-1357.

Zitek, A., Schmutz, S., Unfer, G. & Ploner, A. (2004) Fish drift in a Danube sidearm-system: I. Site-, inter-and intraspecific patterns. *Journal of Fish Biology*, **65**, 1319-1338.

Tables

Table 1 Summaries (means and standard deviations) of independent environmental variables used in the model.

Independent variable	mean	Sd
C12	115.4	11.4
Cmx	214.6	16.1
S1	-12.5	88.0
S2	26.4	71.5
Qm1	565.0	176.2
Qm2	580.9	152.7
Qmx2	880.2	221.1

Table 2 Observed degrees of synchrony between species groups and posterior predicted degree of synchrony distributions

	Simulated quantiles			Observed values
	2.5%	50%	97.5%	
Declining juvenile abundance species group	0.764	0.830	0.884	0.641
Slightly increasing juvenile abundance species group	0.721	0.783	0.837	0.652
Increasing juvenile abundance species group	0.754	0.815	0.866	0.558

Figure legends

Fig. 1 Study area showing the locations of the fish sampling sites (1–8) and the temperature

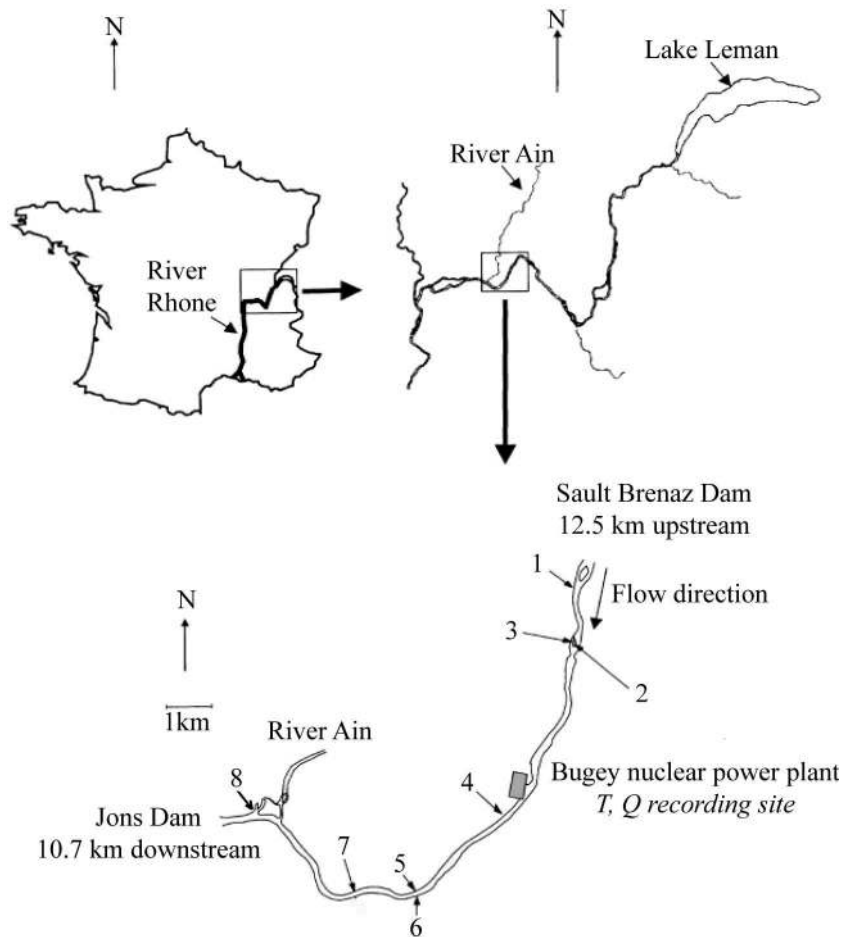(T) and discharge (Q) recording sites (adapted from Daufresne *et al.*, 2003).

Fig. 2 Chronologies of autumn fish sampling results, expressed as Catch Per Unit Effort (CPUE, number of fish caught per 30 minutes), between 1980 and 2005 for the eight most abundant species.
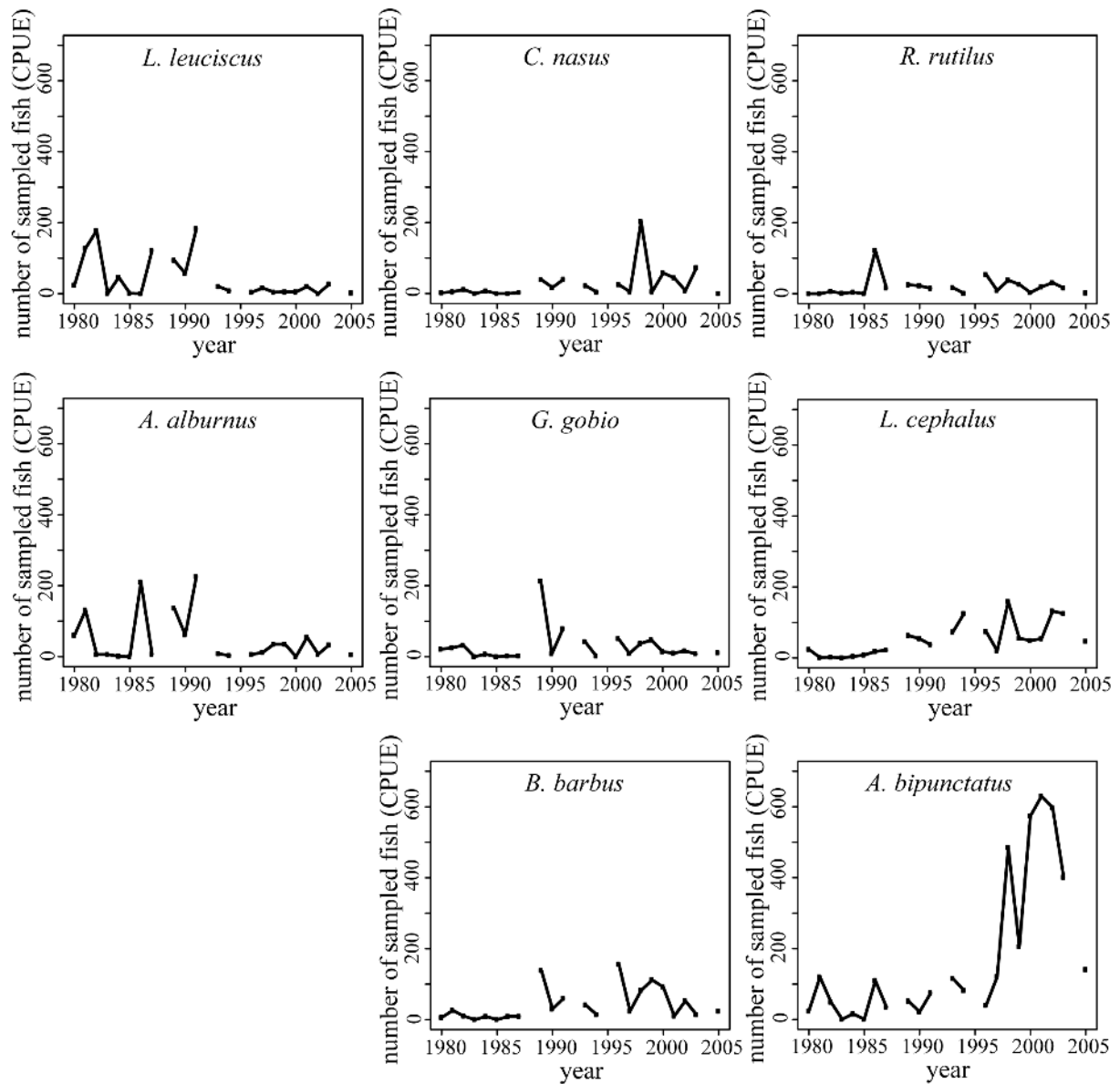
Fig. 3 Directed Acyclic Graph of the model relating the observed annual 0+ fish abundance to the environmental independent variables (square nodes are observed data, circle nodes are latent variables and parameters).
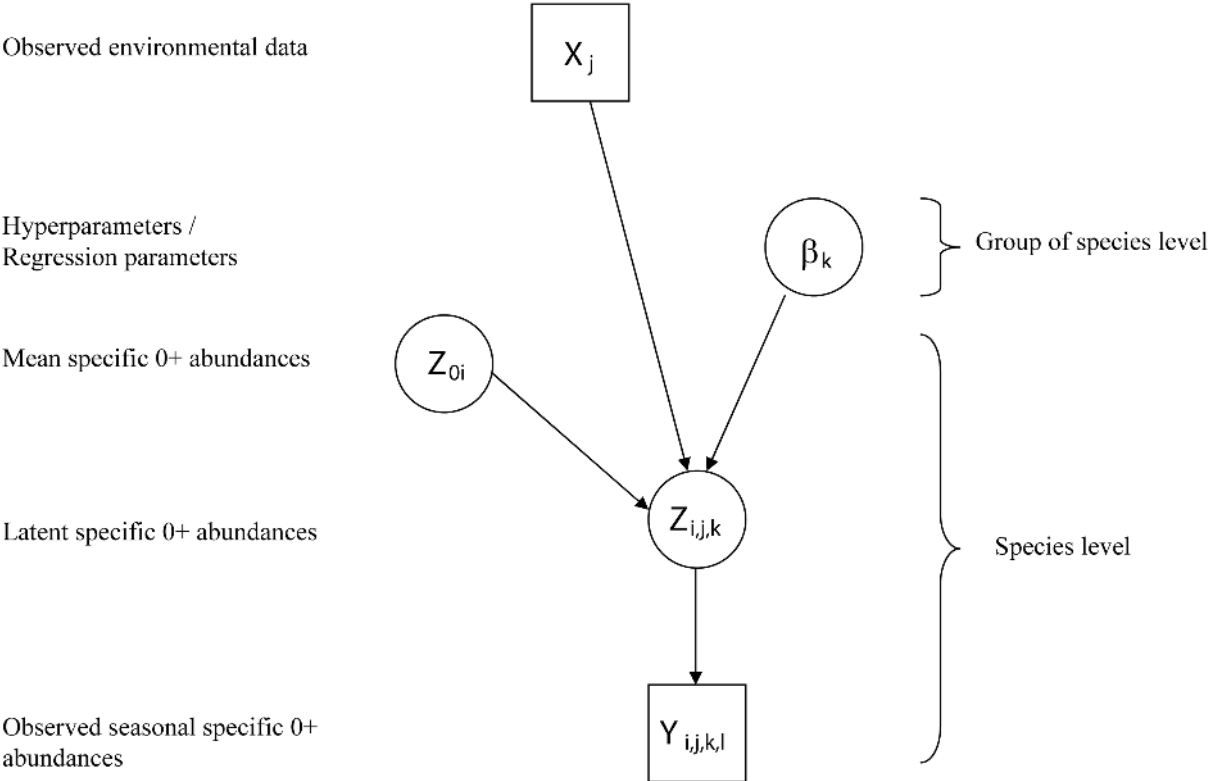
Fig. 4 Cluster dendrogram of fish species. The Kendall tau rank correlation coefficient is used as the distance unit and cluster are computed using Ward's (1963) method.
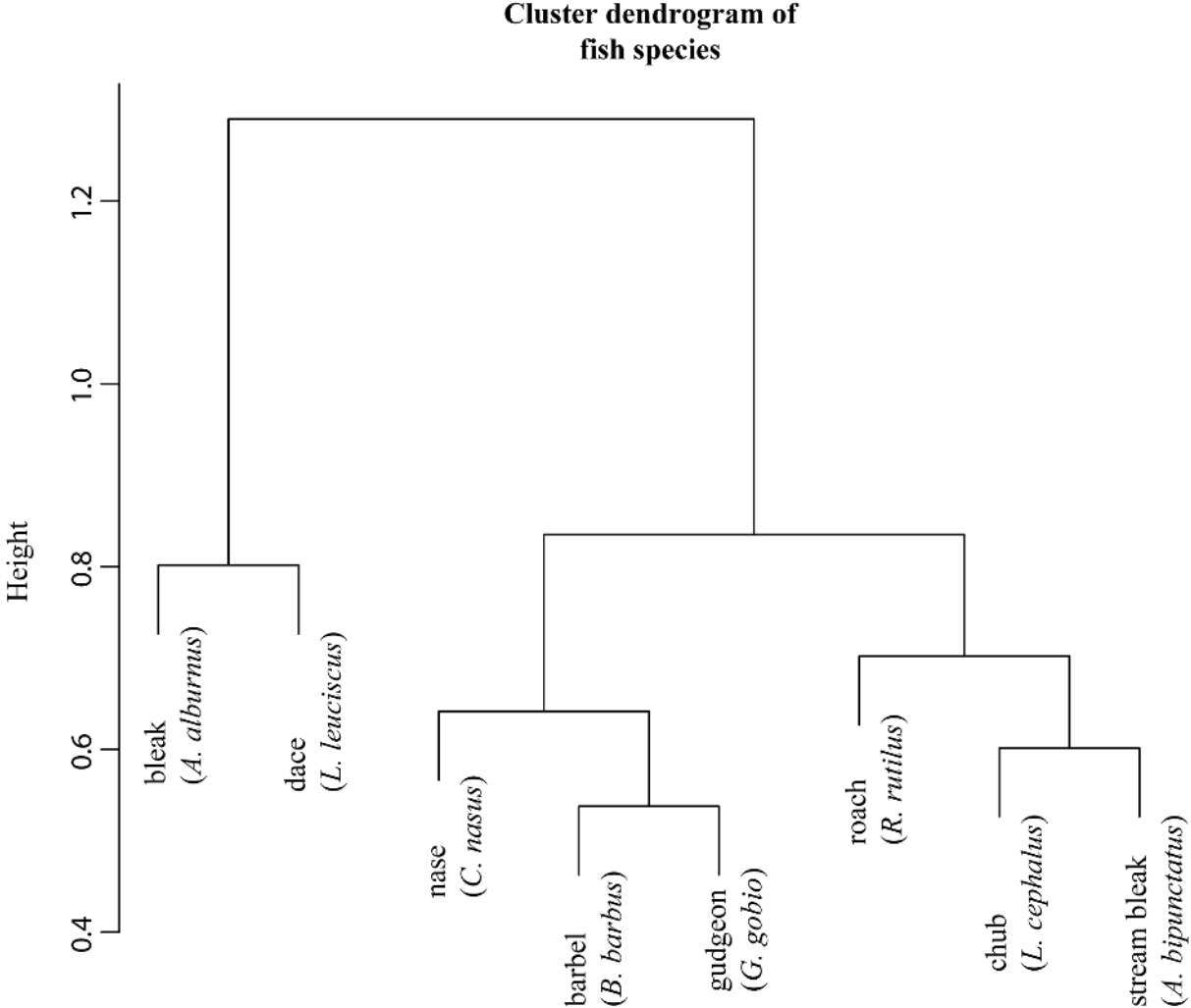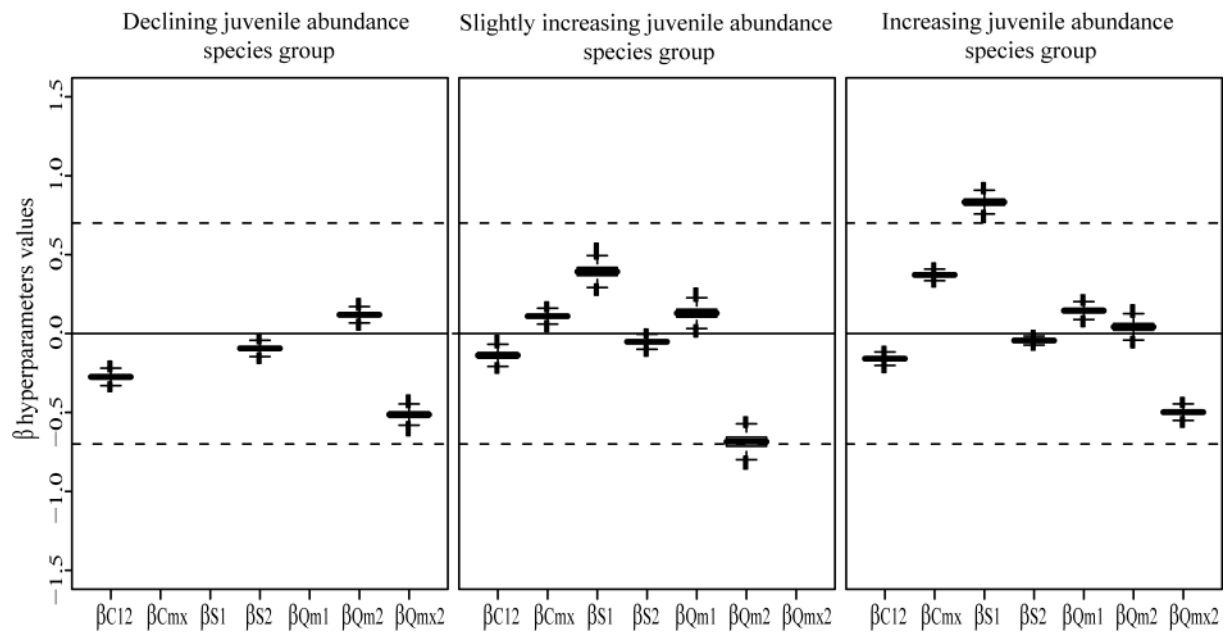

Cluster dendrogram of fish species

Fig. 5 Box plots of the predictive posterior probability distributions of the regression parameters β for the best selected models with a Bayes factor criteria (median, first and third quartiles, 95% credibility intervals). Lines are null effect (plain line), -0.7 and 0.7 effects (dashed lines).

Appendix 1 Implementation of Bayes factor computation.

We denote γ a vector of size 8 with binary digits such as (0,1,1,0,1,0,1,0,1). $\gamma_i = 0$ means that independent variable i is not considered as an explanatory variable. Knowing the dependency on the model γ is equivalent to know the structure of the independent variable matrix X. So, for each model γ, the predictive is expressed as:

$$[Y|X^\gamma] = \iint_{\Sigma B} [Y, \beta^\gamma, \sigma^{\gamma 2}|X^\gamma] \cdot d\beta \cdot d\sigma^2 \tag{1}$$

As we hypothesized an inverse gamma mixture of normal Zellner priors (i.e. a multivariate Student distribution), we can write

$$[Y|X^\gamma] = \iint_{\Sigma B} [Y|\beta^\gamma, X^\gamma][\beta^\gamma|\sigma^{\gamma 2}, X^\gamma][\sigma^{\gamma 2}|X^\gamma] \cdot d\beta \cdot d\sigma^2 \tag{2}$$

The successive conditional distributions are expressed as:

$$[Y|\beta^\gamma, X^\gamma] = \prod_i \frac{\exp(\beta^\gamma . X_i^\gamma)}{Y^i !} \exp(-\exp(\beta^\gamma . X_i^\gamma)) \tag{3}$$

$$[\beta^\gamma|\sigma^{\gamma 2}, X^\gamma] = (2\pi)^{\frac{p}{2}} \cdot \left(\frac{1}{\sigma^{\gamma 2}}\right)^{\frac{p}{2}} \cdot |X^{\gamma^T} X^\gamma|^{\frac{1}{2}} \cdot \exp\left(-\frac{1}{2}\right) \cdot \left(\frac{(\beta^\gamma - \beta_0)^T X^{\gamma^T} X^\gamma (\beta^\gamma - \beta_0)}{\sigma^{\gamma 2}}\right) \tag{4}$$

$$[\sigma^{\gamma 2}|X^\gamma] = \left(\frac{1}{\sigma^{\gamma 2}}\right)^{a-1} \cdot \frac{b^a}{\Gamma(a)} \exp\left(-\frac{b}{\sigma^{\gamma 2}}\right) \tag{5}$$

Once integrated upon the space of $\sigma^{\gamma 2}$, the prior distribution for the coefficients β^γ of X^γ is a multivariate Student distribution and the predictive becomes:

$$[Y|X^\gamma] = \int_B \prod_i \frac{\exp(\beta^\gamma . X^\gamma_i)}{Y^i !} \exp(-\exp(\beta^\gamma . X^\gamma_i)) \cdot \left(\frac{1}{\sqrt{2\pi}}\right)^p |X^{\gamma^T} X^\gamma|^{\frac{1}{2}} \frac{b^a}{\Gamma(a)} \frac{\Gamma(a')}{b'^{a'}} \cdot d\beta \tag{6}$$

With:

$$a' = \frac{p}{2} + a$$

$$b' = b + \frac{(\beta^{\gamma} - \beta_0) X^{\gamma T} X^{\gamma} (\beta^{\gamma} - \beta_0)}{2}$$

(7)

As such, the integral (8) can not be analytically performed and one has to make recourse to a numerical implementation. The importance sampling method described in Marin & Robert (2007) was used. This consists of computing $\hat{\beta}, \hat{\Sigma}$ the classical estimators of β^{γ} and the corresponding covariance matrix of the glm. Then generating a G-sample of $\beta^{(g)}$ following the multivariate normal distribution N($\hat{\beta}, \hat{\Sigma}$). Using this sample, the integral is estimated as via importance sampling:

$$[Y|X^{\gamma}] \approx \frac{1}{G} \sum_{g=1}^{G} \frac{\prod_{i} \frac{\exp(\beta^{(g)}.X^{\gamma}_i)}{Y^i!} \exp(-\exp(\beta^{(g)}.X^{\gamma}_i)).\left(\frac{1}{\sqrt{2\pi}}\right)^p |X^{\gamma T} X^{\gamma}|^{\frac{1}{2}} \frac{b^a}{\Gamma(a)} \frac{\Gamma(a')}{b'^{a'}}}{[\beta^{(g)}|\hat{\beta}, \hat{\Sigma}]}$$

(8)

When computing Bayes factors for different models the determinant term $\left|X^{\gamma T} X^{\gamma}\right|$ will compensate for the various model dimensions. One can see that we can even use an improper prior to compare all models by letting (a,b) going towards zero since the improper inverse gamma probability distribution function will be common to all models.