HIERARCHICAL BAYESIAN MODELING OF BROWN TROUT POPULATION DYNAMICS

BRET, VICTOR

LNHE, EDF R&D, 6, quai Watier
78401 Chatou, France

CAPRA, HERVE

UR MALY, IRSTEA Lyon, 5, rue de la Doua
69626 Villeurbanne, France

GOURAUD, VERONIQUE

LNHE, EDF R&D, 6, quai Watier
78401 Chatou, France

LAMOUROUX, NICOLAS

UR MALY, IRSTEA Lyon, 5, rue de la Doua
69626 Villeurbanne, France

PIFFADY, JEREMY

UR MALY, IRSTEA Lyon, 5, rue de la Doua
69626 Villeurbanne, France

TISSOT, LAURENCE

LNHE, EDF R&D, 6, quai Watier
78401 Chatou, France

RIVOT, ETIENNE

UMR 0985, INRA-Agrocampus Ouest, Ecologie et Santé des Ecosystèmes,
Agrocampus Ouest, 65, route de Saint-Brieuc
35042 Rennes, France

Managing brown trout (*Salmo trutta fario*) populations is of high concerns for many stakeholders (e.g. angling associations or hydropower companies). However, building trout life cycle models remains challenging. Here, we describe a general hierarchical Bayesian model of brown trout population dynamics that combines global (e.g. an average value of age-class annual survival) and local parameters (e.g. shelter availability influencing local carrying capacity). To fit the model, we used annual fish samplings (i.e., two-pass electrofishing followed by density estimation) conducted at 40 reaches. Reaches were located in natural (n=21) or bypassed (i.e. downstream dam; n=19) stream sections across France, thus offering different habitat characteristics. Habitat characteristics were measured at each reach, including daily flow, daily hydraulics conditions, daily temperature and shelter availability.

This study (1) allowed us to understand between-reach differences in survival processes, (2) was consistent with previous studies and explained spatial variations in resident brown trout population dynamics and (3) offers a promising framework for future developments.

1   INTRODUCTION

Successful management and protection of wild animal populations relies on a good comprehension of their life-cycle. Models of population dynamics can be developed locally (i.e. in one or few close sites; [1]) or at a larger scale (i.e. in many distant sites studied together; [2]). If local studies can precisely model local processes, their results are often difficult to generalize at larger scale. By contract, results of large scale studies are easier to generalize, but often have a low predictive capacity as they do not integrate local conditions. New population dynamics models, accounting for spatial variability in demographic processes, need to be developed (e.g. [3]). They should use long-term and large scale data to capture the global processes (shared by all populations), while

handling local variations to avoid misleading management decision at a local scale. The hierarchical setting offers the possibility to account for site-specific variations among species-level processes [4], and has therefore been used to model processes occurring over multiple spatial scales . Quantifying uncertainties is critical in the modeling process, especially when predictions derived from the model are used to inform decision making [5]. The Bayesian setting offers a consistent framework to quantify and propagate uncertainties in models [6].

The flexible framework of Hierarchical Bayesian Models (HBM) has been widely used to model ecosystems. Such methods were particularly applied by fisheries scientists to model stage-structured marine fish population dynamics (e.g. [3]; [7]). However, fewer studies have been carried out on freshwater species.

In this paper, we developed a HBM for a resident brown trout life cycle described using a monthly time-step. We used a large dataset combined with local information at the reach scale (e.g. discharge data, flow depth and velocity, water temperature and shelter availability). We identified the local survival processes responsible for between-reach variations in population dynamics. The approach also allowed the identification of habitat characteristics that were linked to variations in mortality rates.

2   MATERIALS & METHODS

2.1   Local samplings at 40 reaches

Data were available for 40 reaches selected from 23 French rivers distributed across continental France (Figure 1). A total of 19/40 reaches were bypassed for hydroelectricity production. They experienced flow regulation (minimal instream flow) and therefore showed decreased low-flows. They were selected based on the availability of trout and environmental data and covered a wide range of environmental characteristics.
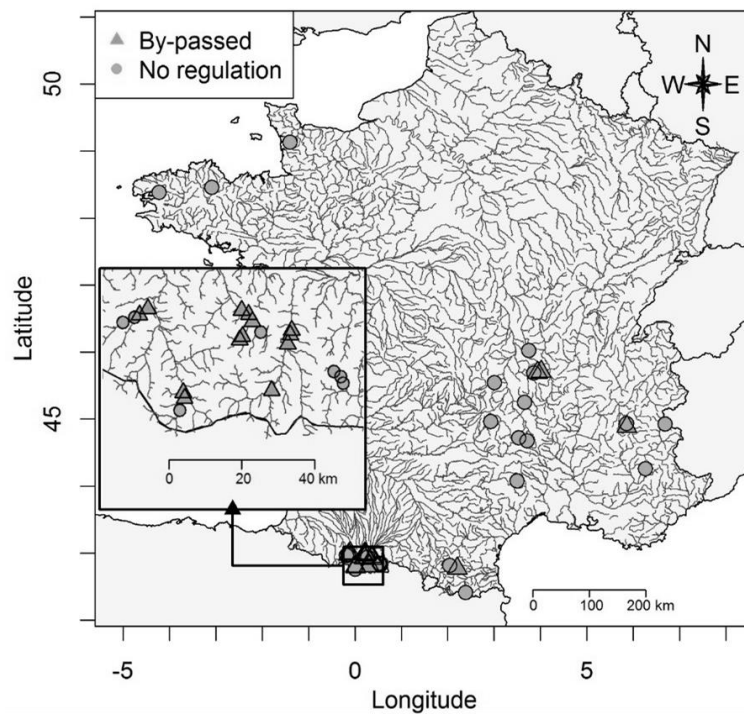

Figure 1. Location of the 40 reaches (19 in by-passed section)

Populations were sampled at all reaches in autumn over 4 to 20 years (mean of 10.7 years) between 1990 and 2013. Reaches were sampled using two-pass removal electrofishing sampling techniques based on the European Committee for Standardization guidelines ([8]). Fish densities were estimated by the Carle and Strub [9] method. Sampled area (between 175 and 2,902 m²) was computed as sampled length × reach width at median flow. All fish were measured (to the nearest 1mm total length) and annual length-frequency histograms were used to distinguish three age-groups: 0+ (young-of-the-year), 1+ (older than one year, generally juveniles) and adult (all fish older than two years).

We collected mean daily discharge and daily water temperature in most reaches and we used predictive relationships and models to calculate missing values (method detailed in [10]). For water temperature, extrapolation models indicated errors of the order of 1°C. Hydraulic conditions (width, flow velocity) were derived from numerical hydraulic models or detailed hydraulic measurements (N>100) made throughout each reach at different flows. They were then averaged for the whole studied reach.

These regimes were summarized by environmental descriptors such as the median value of water temperature and the 10th percentile of flow velocity ($V_{10,E}$, defined as daily flow velocity exceeded 10% of the time, $m^3.s^{-1}$) during trout emergence (March 1st to April 30th; [11]). We also measured the percent of reach surface that could be used as a shelter for brown trout (wider than 200 cm² and located under the river bank or under streambed rock).

2.2   Hierarchical Bayesian model of brown trout life-cycle

We built a stage-based life cycle model that consisted in five stages: under-gravel development, emergence, end of 0+ life stage, 1+ life stage and adult age-stage. Several processes were modeled:

- Spawning depended on sex-ratio and number of eggs per kg of female. These parameters were estimated based on the literature (no site-specific data was available for these processes).
- Survival linked to biotic processes: we proposed an alternative formulation of the Beverton-Holt (BH) relation [12] (following Quinn & Deriso [13]) to model trout survival after emergence on a monthly time-step. The survival during an age-stage k depended upon a density-independent mortality rate δ_k and a density-dependent mortality rate γ_k. Both parameters were estimated (except for mortality rates during eggs incubation, which were based on the literature).
- Survival linked to abiotic processes: we assumed that, when an environmental descriptor was higher than a threshold value during the year before the sampling, a fraction of the population died or emigrated downstream. This was modeled as an exponential decay in survival above this threshold. Both the threshold and the decay rate were estimated.

Samplings were considered as observations of intermediate states for three age-stages (end of 0+ life, 1+ life and adult). The monthly time-step of the modified BH function allowed the integration of variations in sampling dates. The residual error was split into process stochasticity (unpredictable variability) and measurement errors [7].

A hierarchical structure was used to model mortality that showed between-reach variations ($\gamma_1, \delta_{Ad}, \gamma_{Ad}$) and we identified reach-specific characteristics that could explain observed variations.

Non-informative prior distributions were set on all parameters, except for those involved in spawning and under-gravel survival. Posterior distribution were estimated via Markov Chain Monte Carlo (MCMC) simulations methods using the JAGS (http://mcmc-jags.sourceforge.net) and R [14] software through the package R2jags [15]. Convergence of MCMC chains was tested using the Gelman-Rubin diagnostic [16]. Cross-validation was used to check the stability of all estimations.

3   MAIN RESULTS AND PROSPECTS

Results revealed high mortality rates during emergence, nearly negligible mortality rates during the following months, and higher mortality for adults. Density-dependent mortality rate for 1+ decreased with shelter availability and median water temperature. Density-dependent mortality rate for adults decreased with shelter availability and increased with median water temperature. No reach-characteristics significantly explained the variations in δ_{Ad}. By-passed river sections did not show an increase in mortality rates.

Estimated values were consistent with survival rates observed in previous studies (e.g. [17]; [18]; [19]). Relationships explaining between-reach variations in survival are also consistent with the variability of mortality rates observed among previous studies.

Results also highlight a strong influence of high flows on recruitment. Mortality of emergent fry is higher when mean channel velocity was higher than 37cm.s⁻¹. Previous studies had identified similar threshold (50cm.s⁻¹ in [20]). Our results can be tested in a wide range of context, because they involve environmental variables directly related to fish habitats (flow velocity rather than flow, water temperature rather than air temperature).

Our extensive dataset allowed us to build a robust hierarchical Bayesian state-space model for resident brown trout life-cycle. Using the model to derive predictions would need some improvements. Adding other abiotic

processes, growth or density-dependent dispersal are promising developments. Finally, adding data from more contrasted reaches could help confirming the trends observed in this study.

The state-space model was shown to be suitable for analyzing environmental data: it can handle missing years, measurement error and variation in sampling dates. Moreover, the Bayesian framework allowed the direct consideration of uncertainty, which is a key tool for management decision.

REFERENCES

[1]   J. W. Hayes, D. A. Olsen and J. Hay, "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*, Vol. 44, No. 4, (2010), pp 247-269.

[2]   C. Alonso, D. García de Jalón, J. Álvarez and J. Gortázar, "A large-scale approach can help detect general processes driving the dynamics of brown trout populations in extensive areas", *Ecology of Freshwater Fish*, Vol. 20, No. 3, (2011), pp 449-460.

[3]   S. Rochette, O. Le Pape, J. Vigneau and E. Rivot, "A hierarchical Bayesian model for embedding larval drift and habitat models in integrated life cycles for exploited fish", *Ecological Applications*, Vol. 23, No. 7, (2013), pp 1659-1676.

[4]   E. Prevost, "Setting biological reference points for Atlantic salmon stocks: transfer of information from data-rich to sparse-data situations by Bayesian hierarchical modelling", *ICES Journal of Marine Science*, Vol. 60, No. 6, (2003), pp 1177-1193.

[5]   S. Lek, "Uncertainty in ecological models", *Ecological Modelling*, Vol. 207, No. 1, (2007), pp 1-2.

[6]   J. S. Clark, "Why environmental scientists are becoming Bayesians", *Ecology Letters*, Vol. 8, No. 1, (2005), pp 2-14.

[7]   E. Rivot, E. Prévost, E. Parent and J. L. Baglinière, "A Bayesian state-space modelling framework for fitting a salmon stage-structured population dynamic model to multiple time series of field data", *Ecological Modelling*, Vol. 179, No. 4, (2004), pp 463-485.

[8]   CEN, "*Water quality – sampling of fish with electricity. European Standard*", B. E. C. f. Standardization, (2003),

[9]   R. T. Carle and M. R. Strub, "A new method for estimating population size from removal data", *Biometrics*, Vol. 34, No. 4, (1978), pp 621-630.

[10]   V. Bret, B. Bergerot, H. Capra, V. Gouraud and N. Lamouroux, "Influence of discharge, hydraulics, water temperature and dispersal on density synchrony in brown trout populations (*Salmo trutta*)", *Canadian Journal of Fisheries and Aquatic Sciences*, *in press* (2015)

[11]   V. Gouraud, P. Baran, A. Bardonnet, C. Beaufrère, H. Capra, A. Caudron, M. Delacoste, J. M. Lescaux, M. Naura, M. Ovidio, N. Poulet, L. Tissot, C. Sebaston and J.-L. Baglinière, "Sur quelles connaissances se baser pour évaluer l'état de santé des populations de truite commune (*Salmo trutta*)?", *Hydroécologie Appliquée*, Vol. No. (2014), pp 1-28.

[12]   R. J. H. Beverton and S. J. Holt, "*On the dynamics of exploited fish populations*", (1957),

[13]   T. J. Quinn and R. B. Deriso, "*Quantitative fish dynamics*", (1999),

[14]   R Core Team, "*R: A language and environment for statistical computing.*", (2014), http://www.R-project.org/

[15]   M. Plummer, A. Stukalov and M. Denwood, "*rjags 3-15*", (2015), http://cran.r-project.org/web/packages/rjags/index.html

[16]   S. P. Brooks and A. Gelman, "General Methods for Monitoring Convergence of Iterative Simulations", *Journal of Computational and Graphical Statistics*, Vol. 7, No. 4, (1998), pp 434-455.

[17]   J. M. Elliott, "*Quantitative ecology and the brown trout*", (1994),

[18]   L. A. Vøllestad and E. M. Olsen, "Non-additive effects of density-dependent and density-independent factors on brown trout vital rates", *Oikos*, Vol. 117, No. 11, (2008), pp 1752-1760.

[19]   J. Lobon-Cervia, "Density-dependent mortality in adults, but not juveniles, of stream-resident brown trout (*Salmo trutta*)", *Freshwater Biology*, Vol. 57, No. 10, (2012), pp 2181-2189.

[20]   J. Heggenes, "Habitat selection by brown trout (*Salmo trutta*) and young atlantic salmon (*S. salar*) in streams : Static and dynamic hydraulic modelling", *Regulated rivers*, Vol. 12, No. 2-3, (1996), pp 155-169.