

Simulating brown trout demogenetics in a river/nursery brook system: The individual-based model DemGenTrout

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ABSTRACT

The brown trout (*Salmo trutta* L.) is among the most biologically diverse vertebrate species. Human activities are threatening this biodiversity, and many endemic populations now face a medium-term risk of extinction. An individual-based model called DemGenTrout was developed to improve the management of these populations. The model was parameterized, optimized and validated with demographic, genetic, and environmental data collected over 7 years on the Lesse River drainage (Belgium). The sensitivity of the model to its parameters was analysed. The model was then used to assess how the demogenetics of a wild trout population might be affected by anthropogenic disturbances. From the sensitivity analysis, we found that modifications in survival and spawning parameters could lead to important changes in the demogenetics of the studied brown trout population. Two parameters were identified as the most influential in the DemGenTrout model, the survival rate of fry in the brook, and the mean of the spawner condition factor distribution. Two scenarios were simulated over 35 years and compared: (i) a barrier to upstream spawning migration, (ii) stocking with hatchery-reared trout during a 10-year period. Both of them appeared to have a strong short-term impact on the demogenetic structure of the wild trout population. The migration barrier mostly impacted abundance, while genetic issues arose when a significant number of stocked fish survived in the wild. Stocking also appeared to act on a longer time frame if hatchery and wild trout had similar survival and spawning probabilities.

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1. Introduction

The brown trout (*Salmo trutta* L.) possesses a great adaptability to diverse ecological conditions and a high tolerance to habitat changes. These factors have contributed to its success as an introduced species worldwide (Baglinière and Maisse, 2002; Klemetsen et al., 2003). However, due to the relatively narrow range of physico-chemical habitat requirements, particularly for migration and reproduction, the brown trout is environmentally sensitive. It is also one of the vertebrate species presenting the highest degree of intraspecific biological diversity, including strong genetic and phenotypic variation among populations (Laikre, 1999; Bernatchez, 2001). Human activities such as environmental degradation and stocking from hatcheries have induced a loss in brown trout genetic diversity, and many endemic populations are now faced with a medium-term risk of extinction (Laikre, 1999; Dudgeon et al., 2006; Caudron et al., 2011).

Geographic barriers to brown trout migration fragment populations into smaller breeding units, resulting in both demographic and genetic deleterious effects. On the one hand, the trout production is reduced to some extent, changing the age structure within the population and decreasing its size (Almodovar and Nicola, 1999; Wofford et al., 2005). On the other hand, fragmentation of trout populations can limit gene flow among them, leading to a higher genetic differentiation and to an increased effect of genetic drift (Arthington et al., 2004; Van Houdt et al., 2005). Both effects will eventually induce an accelerated loss in the genetic diversity of these populations, which could lead to their extinction (Frankham, 2003).

Stocking with hatchery fish is used for both increasing production for fisheries and for conservation and restoration of wild populations (Laikre, 1999; Arthington et al., 2004). However, if a significant number of stocked fish survive in the wild, ecological and genetic issues may arise. Stocking tends to reduce vital rates (growth, survival, reproduction) of wild fish and may also increase the transmission of infectious diseases (Arthington et al., 2004). Furthermore, direct genetic impacts can occur when wild and stocked trout reproduce together. First, the consequence of hybrid production is a reduction in the reproductive potential of wild populations (Allendorf and Luikart, 2007). Second, when offspring

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resulting from these hybridizations are fertile and backcross to one or both parental populations (Rhymer and Simberloff, 1996), there is introgression (i.e., introduction of genes from hatchery individuals into wild populations). This phenomenon is responsible for a loss of genetic variability in natural fish populations, which could ultimately lead to their extinction (Ruzzante et al., 2001; Madeira et al., 2005).

Different techniques can be used to study the impacts of anthropogenic disturbances on brown trout population dynamics and genetics. Among them, *in silico* approaches using modelling techniques are better suited than are *in situ* experiments because both short and long temporal scales need to be integrated: short temporal scales (i.e., every year) for demographic studies, and longer scales (i.e., 10 years) for genetic studies. The development of ecological models for brown trout has followed four separate trajectories over the past 30 years (Frank et al., 2011): population dynamics, population genetics, habitat preferences, and spatial distribution. Recently, efforts have been made to integrate demographic and genetic approaches through the use of individual-based simulation techniques. A new field called demogenetics has begun to integrate two paradigms (Crawford, 1984; Waples, 2006): the ecological paradigm, which emphasizes co-occurrence in space and time of individuals and relates to conservation biology or management, and the evolutionary paradigm, which emphasizes reproductive interactions between individuals and studies the interplay of micro-evolutionary processes such as natural selection, genetic drift, gene flow and mutation.

The use of individual-based techniques has greatly facilitated the development of demogenetic models. Such techniques treat individuals as unique and autonomous discrete entities and enable the joint generation and analysis of demographic and genetic data (Grimm and Railsback, 2005; Palsboll et al., 2007). Individual-based models explore how population-level properties can emerge from interactions of individuals with each other and their environment (Grimm and Railsback, 2005). They allow accounting for three types of individual variability: demographic, genetic and spatial.

Although some individual-based models combining these three dimensions already exist (e.g., KERNELPOP; Strand and Niehaus, 2007), no comprehensive, spatially explicit, demogenetic model has been proposed for a fish species. Indeed, only a few individual-based models have been specifically developed for or applied to salmonids, and they can be divided into two categories (Frank et al., 2011). On the one hand, nonspatial demogenetic models such as VORTEX (Lacy, 2000) incorporate more genetic realism into population dynamics models, and are often used for population viability analysis. Such models predict the likelihood of the persistence of an endangered species for a given time (DeSalle and Amato, 2004). On the other hand, spatially explicit bioenergetic models such as inSTREAM (Railsback et al., 2009) integrate both demographic and spatial dimensions. These models evaluate behavioural responses (e.g., individual growth, habitat choice) by quantifying the balance between energy gained through feeding, and energy lost through swimming, digestion, food capture, growth, reproduction, urine and faeces (Fausch, 1984; Rosenfeld, 2003; Booker et al., 2004). Also of note are individual-based eco-genetic models, which evaluate the relative importance of genetic and ecological effects on life-history traits and population dynamics, accounting for inheritance of quantitative genetic traits (Dunlop et al., 2009). To our knowledge, three eco-genetic models were developed and applied to salmonids (Thériault et al., 2008; Wang and Hook, 2009; Piou and Prévost, 2012).

In the present work, a model called DemGenTrout was designed to study medium-term impacts of human activities on the brown trout population of a Belgian watershed, constituted by a main river section and its headwater tributary. Among the factors that may affect the demogenetic (i.e., demographic and genetic) structure

of a brown trout population, only those identified as crucial for fulfilling the modelling purpose were integrated into the model. Demographic data were extensive and precise for the studied hydrological system, allowing us to thoroughly model the trout life cycle (survival, growth, reproduction, movement). First, several sources of mortality such as predation by other fish or high water temperatures were accounted for in survival rates. Second, we used the equations of von Bertalanffy (1957) and Le Cren (1951) to model trout growth. Third, the selection of spawners was based on their body condition, which was considered an indirect measure of fitness. Fourth, movements of individuals between the two streams were modelled to mimic the behaviour of the brown trout species, which uses main stems to grow and mature (Jonsson and Jonsson, 1993; Forseth et al., 1999) and first-order streams as spawning and nursery areas (Elliott, 1994; Armstrong et al., 2003). We decided to keep this part as simple as possible. For instance, hydrological conditions were supposed homogeneous within each stream and environmental factors were not directly integrated in the growth and survival processes, as the model was not designed to predict how changes in habitat may affect the demogenetics of a brown trout population. Genetic data available for the hydrological system consisted of trout genotype obtained from the analysis of microsatellite genetic markers, which are selectively neutral by nature (i.e., they are not affected by natural selection). Therefore, the DemGenTrout model is not suitable for predicting the dynamics of genes under selection. However, the effect of natural selection can still be indirectly evaluated by studying the genetic structure of the population.

This paper first presents the study area and field data collected over 7 years on the river/nursery brook system, before describing in detail the structure of the DemGenTrout model. These data were used to optimize and validate the model within the pattern-oriented modelling framework (Grimm et al., 1996, 2005; Wiegand et al., 2003), formally defined as the multi-criteria design, selection, and calibration of models of complex systems (Grimm and Railsback, 2012). A sensitivity analysis followed by a comparison of simulation scenarios were performed on the DemGenTrout model. This last step consisted of determining how a brown trout population might respond to migration barriers and stocking with hatchery trout. The impacts were measured by the following demogenetic output indicators: annual evolution of trout abundances, inbreeding coefficients F_{IS} , and fixation index F_{ST} . For both scenarios, it was expected that trout abundance in the nursery brook would decrease over time, leading to a significant rise of trout F_{IS} in this stream, and that the genetic differentiation among trout of both streams, measured by F_{ST} , would increase.

2. Material and methods

2.1. Study area

The study was conducted in a small stream network in the Lesse River, a tributary to the Meuse River, which occupies an area of 1343 km² and is located in southern Belgium (Fig. 1). The study area consisted of a 1.1 km-long section of a main river (Lesse River, fourth-order) with one 1.2 km-long tributary (Chicheron Brook, first-order).

The Lesse River flows through a wide forested area, offers excellent water quality, and is located at the boundary between the trout and the grayling fish assemblage zones. The river has a slope of 0.8‰, is between 13 and 27 m wide, has an average depth of 0.5 m, and a mean flow of 3.5 m³ s⁻¹. Water temperature varies between -0.03 °C and 21.4 °C, annual mean is 10.2 °C. The Lesse River is known as a moderately stocked site for recreational fishing with annual stocking coefficient between 50 and 100% (De Meyer, 2006).

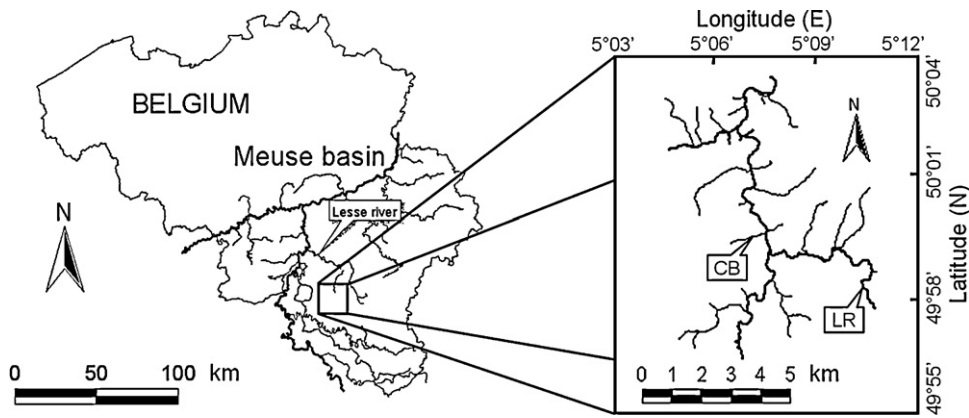


Fig. 1. Situation plan of the study area comprising a section of the Lesse River (LR), located in the Meuse basin, and one of its tributaries, the Chicheron Brook (CB).

Analysis of 5 years of stocking records showed that, on average, 77 hatchery trout (or 13.3 kg) were restocked each year in 830 m of the studied section. Current regulations involve a quota per fisherman limited to 5 catches per day and a minimum legal fishing size of 24 cm.

The Chicheron Brook has a slope of 4.7%, an average width of 1.4 m, and a depth varying from 2 to 15 cm with several deeper pools. The brook is populated only with wild brown trout, and has low water flow during summer ($0.013 \text{ m}^3 \text{ s}^{-1}$ on average) and especially during autumn ($0.008 \text{ m}^3 \text{ s}^{-1}$ on average), which prevents large individuals from living in this narrow, shallow habitat. Water flow increases in late autumn ($>0.05 \text{ m}^3 \text{ s}^{-1}$), and the brook becomes a well-functioning spawning and nursery habitat. Mean water temperature is 5°C during winter, and increases to a maximum of about 20°C in summer.

2.1.1. Brown trout population and samplings

Trout movements between the Chicheron Brook and the Lesse River were monitored by a trapping facility built 20 m upstream from the confluence of the tributary (98.14% average catch efficiency; Frank et al., 2012), and capture–recapture experiments were conducted over a time period of 7 years (from 2004/10/06 to 2011/08/02) on trout of both streams, using passive integrated transponder tags to mark each fish: (i) captures at the trapping facility (5252 individuals), (ii) electrofishing in autumn in the Chicheron Brook (3941 individuals), (iii) electrofishing in autumn in the Lesse River (4844 individuals). All captured fish were measured for total length (mm), and most of them were weighed (g). The numbers of upswimming and downswimming individuals caught at the trapping facility during 2004–2011 are presented in Table A.1 of Appendix A.

2.1.2. Genetic analyses

Tagged individuals were gathered into three groups according to their place of birth and their behaviour: (i) CR, residents born in the Chicheron Brook, (ii) CM, migrants born in the Chicheron Brook, (iii) EX, native to the Lesse River or another tributary with unknown behaviour. For each group, 48 individuals caught in 2003–2004 (time a) were selected. The number of trout selected in the CR and EX groups was doubled by samples of 48 individuals captured in 2008 (time b). Thus, we ended up with 240 individuals belonging to five different groups (CRa, CMa, EXa, CRb, EXb).

Adipose fins of these 240 individuals, as well as those of 48 hatchery-reared trout sampled in 2008 in the Mirwart Hatchery (Saint-Hubert, Belgium), were removed. DNA was extracted from fin tissue using an adapted version of the Doyle and Doyle (1990) CTAB protocol. Three tetranucleotide and nine dinucleotide microsatellite loci were analysed: Str15, Str60, Str73 (Estoup

et al., 1993), Str85 (Presa and Guyomard, 1996), Ssa85, Ssa171 (tetranucleotide), Ssa197 (tetranucleotide) (O'Reilly et al., 1996), Ssa408 (tetranucleotide) (Cairney et al., 2000), SsoSL85, SsoSL417 (Slettan et al., 1995), SsoSL438 (Slettan et al., 1996), and T3-13 (Estoup et al., 1998). Microsatellites were amplified at 55°C in two multiplexes following the recommendations of the Qiagen simultaneous amplification kit. Electrophoresis was performed on an ABI Prism 3100 genetic analyser (Applied Biosystems). A molecular size marker (GeneScan 400HD [Rox] size standard ABS) was added to the samples, and information at the exit of the capillary was then transformed into electrophoregrams using programs GeneScan and GeneMapper.

2.2. Model description

The description of DemGenTrout follows the ODD (Overview, Design concepts, Details) protocol for individual- and agent-based models (Grimm et al., 2006, 2010). The model was implemented in NetLogo (Wilensky, 1999). We used R (R Development Core Team, 2012) for testing and analysing the model, taking advantage of the RNetLogo package (Thiele et al., 2012) that allows the integration of NetLogo in R.

2.2.1. Overview

2.2.1.1. Purpose. The DemGenTrout model was designed to understand how anthropogenic disturbances can affect a brown trout population living in a river/nursery brook system of the Lesse River network (Belgium). In particular, we investigated the demogenetic structure of the population, and the subsequent medium-term changes caused by migration barriers and stocking with hatchery trout.

2.2.1.2. Entities, state variables, and scales. Two types of entities are comprised in the DemGenTrout model: two streams, representing the studied hydrological system, and trout agents. Each stream has three state variables and trout agents are characterised by 15 state variables (Table 1). The spatial resolution and extent of the model are defined by the two possible locations for trout in the system (Fig. 1): the Chicheron Brook (referred hereafter as stream C), and a section of the Lesse River (stream L). One time step represents one week and simulations last 35 years, corresponding to 10 trout generations (the average generation interval being 3.52 years, as computed from trapping observations on 263 individuals of the studied system over the years 2004–2009).

2.2.1.3. Process overview and scheduling. Nine processes are considered in the model (Fig. 2; see Section 2.2.3.3 for details): the update of hydrological conditions for each stream agent; survival, growth, reproduction, ageing, hatching, moving downstream,

Table 1

List of agents intervening in the DemGenTrout individual-based model, with their state variables and corresponding status or measure unit (C: Chicheron Brook, L: Lesse River, F: female, M: male). Fry are trout of age 0, juveniles are of age 1 and 2, and adults are of age ≥ 3 .

Agent	State variable	Description	Status/unit of measure
Stream	<i>stream</i>	Stream code	C, L
	<i>temperature</i>	Water temperature	Numeric ($^{\circ}\text{C}$)
	<i>flow</i>	Flow rate	Numeric ($\text{m}^3 \text{s}^{-1}$)
Trout	<i>sex</i> ^a	Sex	F, M
	<i>genotype</i> ^a	Genotype	List of lists
	<i>natal-stream</i> ^a	Natal stream	C, L
	<i>week-of-birth</i> ^a	Week of birth	Numeric (-)
	<i>current-stream</i>	Current stream	C, L
	<i>age</i>	Age	0, 1, 2, 3, 4, 5, 6
	<i>stage</i>	Stage	Fry, juvenile, adult
	<i>status</i>	Status	Non-spawner, spawner, migrant
	<i>body-length</i>	Body length	Numeric (mm)
	<i>body-weight</i>	Body weight	Numeric (g)
	<i>condition-factor</i>	Body condition factor	Numeric (-)
	<i>num-offspring</i>	Number of offspring	Numeric (-)
	<i>spawned?</i>	Spawned this year	Boolean
<i>moved-to-spawn?</i>	Moved to spawn this year	Boolean	
<i>returned?</i>	Returned to previous stream after spawning this year	Boolean	

^a Fixed state variables.

post-spawning homing, and leaving the system forever for each trout agent.

All actions occur in the same predetermined order (Fig. 3). Each time step, stream agents first update their water temperature and flow. Second, trout agents challenge their survival. If alive, they update their length, weight, and condition factor. Third, if spawning conditions are met, trout possibly produce offspring that will hatch ten weeks later. Fourth, trout update their age and stage one week before the beginning of the hatching period. Fifth, if conditions for movement are met, trout of the tributary have the possibility to move downstream (i.e., to the Lesse River). Sixth, alive spawners return to their previous stream one week after the spawning process (post-spawning homing behaviour). The last week of the year, some juveniles living in stream L do not settle in this stream and disappear from the system to search for more suitable locations.

2.2.2. Design concepts

Objectives, Learning, Prediction, and Collectives concepts do not apply to the DemGenTrout individual-based model.

Basic principles: The model is underpinned by demogenetics, an emerging field in ecology that integrates both population dynamics and population genetics. Population abundance and structure can be influenced by density-dependent or density-independent

processes. In the model, we considered both types of processes at the submodel-level: on the one hand, the downstream migration of young trout is density-dependent and is expected to have a strong effect on the regulation of abundance in the brook; on the other hand, environmental variability may affect the behaviour of individuals such as their decision of moving between streams which in turn shapes the demographic structure. Individuals inhabiting large rivers usually move into first-order tributaries to spawn (Elliott, 1994; Armstrong et al., 2003), and return to their original territory once reproduction is complete (i.e., post-spawning homing behaviour; Stuart, 1957). Homing to natal rivers is particularly strong in salmonids (Belica, 2007). However, some individuals might decide to not reproduce in their home river (i.e., straying behaviour; Rieman and Dunham, 2000; Castric and Bernatchez, 2004). Natural selection is the key micro-evolutionary process of population genetics considered in the model. Its effect is evaluated indirectly through the use of microsatellite markers, which allow describing the genetic structure of the population with *F*-statistics (Wright, 1969).

Emergence: Survival, growth, spawning, and movements of individuals are imposed behaviours that are empirically described in the model using real data. Spawning and downstream movement processes are affected by hydrological variables. Population dynamics and genetics (i.e., demogenetics) emerge from these

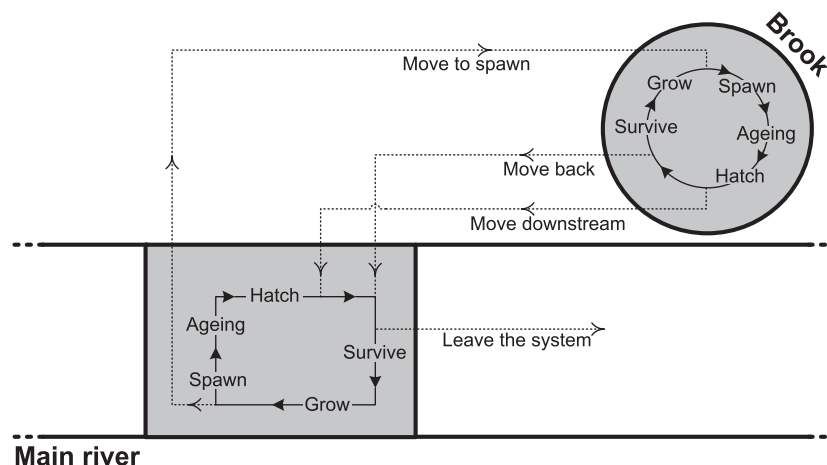


Fig. 2. Conceptual diagram of the DemGenTrout individual-based model. Life cycle of brown trout, including movements of individuals between a main river section (stream L) and a brook (stream C), was implemented to mimic the behaviour of a population living in a Belgian hydrological system.

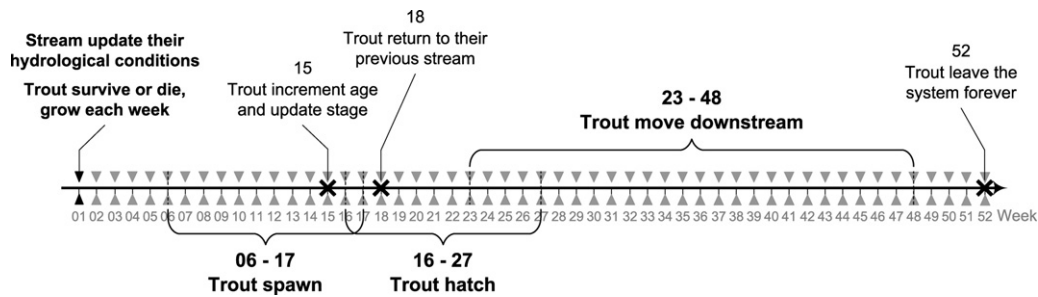


Fig. 3. Fixed scheduling of the DemGenTrout individual-based model, as parameterized for the Lesse River/Chicheron Brook hydrological system. The update of stream conditions, trout survival and growth are actions executed once per time step. Spawning, hatching and downstream movement processes happen at specific time steps. Trout ageing, post-spawning homing, and the disappearance of some trout from the Lesse River are actions that occur only once a year.

behaviours acting at the individual level: on the one hand, the demographic structure of the population (fry, juveniles and adults proportions) is shaped by the number of reproducing individuals; on the other hand, the number of produced offspring is determined by the female length and new genotypes emerge as a result of genetic adaptation and natural selection.

Adaptation: Juvenile and mature adult movements are the adaptive traits in the model. They are modelled as indirect fitness-seeking, in which individuals make decisions of life history tactics that indirectly contribute to future success at passing genes on. Juveniles decide whether and when they migrate to the main stream, and this decision affects their growth. Mature adults decide whether, when and where they spawn each year, and this decision affects the offspring production in each stream. The selection of spawners is based on their body condition factor, and offspring length is inherited from their parents.

Sensing: No sensing mechanisms are explicitly represented. Individuals are assumed to know the status or value of all their state variables, which affect their survival, growth, spawning and movements. They also have access to information about their current stream, such as water temperature and flow.

Interaction: Individuals do not directly interact together, but competition for shared resources is taken into account in the downstream movement process of juveniles. The probability of moving depends on the number of similar age trout present in the tributary (density-dependent population regulation).

Stochasticity: Most processes of the model are drawn from empirical probability distributions in order to include individual variability. The model incorporates environmental variability through the hydrological variables (i.e., input data, see Section 2.2.3.2), for which additional stochasticity was introduced using random floating point numbers. Survival and downstream dispersal are stochastic events. Whether a trout actually dies or moves to the main stream is determined by comparing a random number to the survival rate or the movement probability. Stochasticity is also used in the spawning process for the selection of spawners, the production of offspring and the definition of their state variables.

Observation: The following demographic and genetic outputs were recorded to follow the changes through time of the brown trout population demogenetic structure: the number of migrant juveniles and the number of spawners moving between both streams over each year and, for each stream, the total number of individuals, the number of individuals with a body length >70 mm, the number of offspring, and the genotypes of 48 randomly chosen individuals. Three genetic outputs were derived from genotypes using the adegenet (Jombart et al., 2008) and pegas (Paradis, 2010) R packages: (i) the effective number of alleles, E_A , to measure the genetic diversity for trout of each stream, (ii) the inbreeding coefficient, F_{IS} , to measure the extent of genetic inbreeding within trout of each stream, and (iii) the fixation index, F_{ST} , to measure the degree of genetic differentiation between trout of both streams.

2.2.3. Details

2.2.3.1. Initialisation. Each simulated year starts on October 1, and lasts 52 weeks. There are 40 initialisation variables in total (Table 2). Observations made in autumn 2004 on the Lesse River/Chicheron Brook system were used to specify the state of hydrological variables (water temperature and flow), which are input data values corresponding to the first week of simulation. Values of initial trout abundance and age-class repartition of individuals in each stream were obtained by calibration (Section 2.3.1).

Means and standard deviations of the age-specific trout length and condition factor random normal distributions in both streams were also derived from 2004 field observations. Length distributions are truncated at ± 4 standard deviations.

Trout condition factor corresponds to Fulton's coefficient K , which assumes that the standard weight W of a fish is proportional to the cube of its length L , i.e., $K = W/L^3$ (Ricker, 1975). The value of this factor is 1 when an individual has a healthy weight for its length; a value >1 indicates an overweight, and a value <1 a poor condition.

Each trout genotype is constituted of twelve loci, with two alleles at each locus randomly assigned in accordance with observed allelic frequencies. In the Chicheron Brook, initial trout genotypes were assigned from results obtained for the 48 individuals of group CRa, while for the Lesse River, they were derived from the 96 trout belonging to the CMa and EXa groups (see Section 2.1.2 and Table A.2 of Appendix A).

Trout current and natal stream are assigned according to the location of the individual or to its stream of birth. As the presence of natal homing behaviour was demonstrated for trout of the studied system (Frank et al., 2012), some randomly selected individuals living in stream L change their natal-stream state variable from L to C. Their proportion was obtained by calibration (Section 2.3.1).

The other trout variables are initialised as follows: each trout weight is calculated as its body condition factor times its length cubed according to Fulton's formula; trout sex is randomly assigned with even probability of being female or male; age of adults is drawn from a uniform integer distribution between 3 and 6; stage is set according to age (see point 5 of Section 2.2.3.3); trout status is set to 'non-spawner'; the week of birth is set to the trout age multiplied by -52 ; the number of offspring is set to 0; and the Boolean variables *spawned?*, *moved-to-spawn?* and *returned?* are set to false.

2.2.3.2. Input data. The following time series of observations were available for the Lesse River/Chicheron Brook hydrological system: water temperatures ($^{\circ}\text{C}$) in both streams, flow rates ($\text{m}^3 \text{s}^{-1}$) in stream L, and water heights (m) in stream C. Water temperatures in both streams were automatically measured and recorded every hour with loggers, from years 2004 to 2009. For the Lesse River, daily flow rates were available from a nearby permanent gauging station located in Daverdisse (Q_D) for the years 2004–2009. We used the following equation to compute the flow at the study

Table 2
Initial values for stream and trout variables of the DemGenTrout individual-based model, with their corresponding measure units (C, Chicheron Brook; L, Lesse River).

Variable name	Description	Value	Unit
Stream			
<i>streamC-temperature</i>	Water temperature in stream C	9.8	°C
<i>streamL-temperature</i>	Water temperature in stream L	12.1	°C
<i>streamC-discharge</i>	Flow rate in stream C	0.004	m ³ s ⁻¹
<i>streamL-discharge</i>	Flow rate in stream L	1.324	m ³ s ⁻¹
Trout			
<i>init-N</i>	Trout abundance in both streams	4500 ^a	trout
<i>prop-C</i>	Trout proportion in stream C	0.73 ^a	–
<i>prop-L</i>	Trout proportion in stream L (= 1 – <i>prop-C</i>)	0.27	–
<i>prop-age0-C</i>	Proportion of age-0 trout in stream C	0.76 ^a	–
<i>prop-age1-C</i>	Proportion of age-1 trout in stream C	0.21 ^a	–
<i>prop-age2-C</i>	Proportion of age-2 trout in stream C	0.02 ^a	–
<i>prop-age3-C</i>	Proportion of trout of age 3–6 in stream C (= – (<i>prop-age0-C</i> + <i>prop-age1-C</i> + <i>prop-age2-C</i>))	0.01	–
<i>prop-age0-L</i>	Proportion of age-0 trout in stream L	0.10 ^a	–
<i>prop-age1-L</i>	Proportion of age-1 trout in stream L	0.22 ^a	–
<i>prop-age2-L</i>	Proportion of age-2 trout in stream L	0.37 ^a	–
<i>prop-age3-L</i>	Proportion of trout of age 3–6 in stream L (= – (<i>prop-age0-L</i> + <i>prop-age1-L</i> + <i>prop-age2-L</i>))	0.31	–
<i>propC-inL</i>	Proportion of trout living in stream L that change their natal stream from L to C	0.67 ^a	–
<i>meanl-birth-C</i>	Mean of the normal distribution for length of trout at birth in stream C	1.01	mm
<i>meanl-age0-C</i>	Mean of the normal distribution for length of age-0 trout in stream C	59.00	mm
<i>meanl-age1-C</i>	Mean of the normal distribution for length of age-1 trout in stream C	106.40	mm
<i>meanl-age2-C</i>	Mean of the normal distribution for length of age-2 trout in stream C	150.60	mm
<i>meanl-age3-C</i>	Mean of the normal distribution for length of trout of age 3–6 in stream C	191.70	mm
<i>sdl-birth-C</i>	Standard deviation of the normal distribution for length of trout at birth in stream C	0.85	mm
<i>sdl-age0-C</i>	Standard deviation of the normal distribution for length of age-0 trout in stream C	6.48	mm
<i>sdl-age1-C</i>	Standard deviation of the normal distribution for length of age-1 trout in stream C	12.90	mm
<i>sdl-age2-C</i>	Standard deviation of the normal distribution for length of age-2 trout in stream C	13.49	mm
<i>sdl-age3-C</i>	Standard deviation of the normal distribution for length of trout of age 3–6 in stream C	22.53	mm
<i>meanl-birth-L</i>	Mean of the normal distribution for length of trout at birth in stream L	1.04	mm
<i>meanl-age0-L</i>	Mean of the normal distribution for length of age-0 trout in stream L	82.28	mm
<i>meanl-age1-L</i>	Mean of the normal distribution for length of age-1 trout in stream L	132.42	mm
<i>meanl-age2-L</i>	Mean of the normal distribution for length of age-2 trout in stream L	178.27	mm
<i>meanl-age3-L</i>	Mean of the normal distribution for length of trout of age 3–6 in stream L	220.20	mm
<i>sdl-birth-L</i>	Standard deviation of the normal distribution for length of trout at birth in stream L	0.87	mm
<i>sdl-age0-L</i>	Standard deviation of the normal distribution for length of age-0 trout in stream L	6.36	mm
<i>sdl-age1-L</i>	Standard deviation of the normal distribution for length of age-1 trout in stream L	17.12	mm
<i>sdl-age2-L</i>	Standard deviation of the normal distribution for length of age-2 trout in stream L	15.55	mm
<i>sdl-age3-L</i>	Standard deviation of the normal distribution for length of trout of age 3–6 in stream L	16.73	mm
<i>mean-bcf-C</i>	Mean of the normal distribution for condition factor of trout in stream C	0.98	–
<i>mean-bcf-L</i>	Mean of the normal distribution for condition factor of trout in stream L	0.99	–
<i>sd-bcf-C</i>	Standard deviation of the normal distribution for condition factor of trout in stream C	0.13	–
<i>sd-bcf-L</i>	Standard deviation of the normal distribution for condition factor of trout in stream L	0.09	–

^a Calibrated values.

site (Q_L), in which A_L and A_D are the watershed areas of the study site and the Daverdisse station, respectively, expressed in square kilometres: $Q_L = (A_L/A_D) \times Q_D = (195/302) \times Q_D = 0.65 \times Q_D$. For the Chicheron Brook, flow rates Q were estimated from water heights H recorded at a rectangular weir, on days when the trapping facility was checked over the years 2004–2009. We used the following calibration equation provided by E. Dupont (Earth and Life Institute, Croix du Sud 2 Box L7.05.14, 1348 Louvain-la-Neuve, Belgium, personal communication, 2009): $Q = \sqrt{2g} \times 0.2 \times \sqrt{H^3}$ for $H < 0.22$ m and $Q = \sqrt{2g} \times (0.2 \times \sqrt{H^3} + 0.368 \times \sqrt{(H - 0.22)^3})$ for $H \geq 0.22$ m, where g is the gravitational constant.

Each time series was transformed into a weekly time series using the xts R package (Ryan and Ulrich, 2010). Holt-Winters method implemented in R (R Development Core Team, 2011) was used to apply a multiplicative seasonal model to each weekly time series in order to predict 29 years of data (2010–2039) from the 6 years of field data (2004–2009), and then use all 35 years of data as input in the DemGenTrout model. This exponential smoothing technique separates the time series t into three components, a level L_t , a trend T_t , and a seasonal index S_t : $X_t = (L_t + T_t \times t)S_t$, where X_t is an observation on the time series, $L_t = \alpha \times (X_t/S_{t-p}) + (1 - \alpha) \times (L_{t-1} + T_{t-1})$, $T_t = \beta \times (L_t - L_{t-1}) + (1 - \beta) \times T_{t-1}$, and $S_t = \gamma \times (X_t/L_t) + (1 - \gamma) \times S_{t-p}$ (α , β and γ are the smoothing parameters of level, trend, and seasonal index). The prediction function on h periods is given by: $X_{t+h} = (L_t + h \times T_t) \times S_{t-p+1+(h-1) \bmod p} + e_t$, where p is the period

length equal to 52 weeks, and e_t is the random error component. For water temperatures in streams C and L, parameters were: $\alpha = 0.9076$ and 0.6360 , $\beta = 0.0000$ and 0.0000 , $\gamma = 1.0000$ and 0.0033 , e_t was a normal random number with mean and standard deviation equal to 0.00 and 0.44, and to 0.00 and 1.22, respectively. For flow rates in streams C and L, parameters were: $\alpha = 0.0734$ and 0.0010 , $\beta = 0.0072$ and 0.0000 , $\gamma = 0.3670$ and 0.0000 , e_t was a log-normal random number with mean and standard deviation equal to 1.00 and 3.00, and to 0.01 and 0.03, respectively.

2.2.3.3. Submodels. The model contains 51 parameters, which are listed in Table 3 according to the submodel they are involved in: survival, growth, spawning, hatching, downstream movement, and leaving stream L forever. The values of 38 of them were obtained from field studies conducted on the Lesse River/Chicheron Brook hydrological system, and the value of one parameter was derived from the literature. Four parameters were guestimated (i.e., we had only an idea of what would be a realistic value for each of them) and 8 parameters were calibrated (Section 2.3.1).

The model comprises nine submodels or processes, and their description follows the fixed scheduling presented in Section 2.2.1.3. We used the following conventions when a parameter name is referring to either both streams or several age classes: *streamX*, where X corresponds to C or L; *ageY*, where Y corresponds to age class 0, 1, 2 or ≥ 3 ; *ageZ*, where Z corresponds to age class 1 or 2.

Table 3
List of parameters involved in the DemGenTrout individual-based model. Fry are trout of age 0, and juveniles are of age 1 and 2 (C, Chicheron Brook; L, Lesse River). The reference value of each parameter was either calibrated (C), estimated (E), guestimated (G), or came from an observation (O). For E and O, data sources are specified in footnotes.

Parameter name	Description	Value	Unit	Source
Survival				
<i>streamC-age0-survival</i>	Survival rate for age-0 trout in stream C	0.39	year ⁻¹	E ^a
<i>streamC-age1-survival</i>	Survival rate for age-1 trout in stream C	0.37	year ⁻¹	E ^a
<i>streamC-age2-survival</i>	Survival rate for age-2 trout in stream C	0.85	year ⁻¹	E ^a
<i>streamC-age3-survival</i>	Survival rate for trout of age 3–6 in stream C	0.70	year ⁻¹	G
<i>streamL-age0-survival</i>	Survival rate for age-0 trout of in stream L	0.38	year ⁻¹	E ^a
<i>streamL-age1-survival</i>	Survival rate for age-1 trout of in stream L	0.74	year ⁻¹	E ^a
<i>streamL-age2-survival</i>	Survival rate for age-2 trout of in stream L	0.87	year ⁻¹	E ^a
<i>streamL-age3-survival</i>	Survival rate for trout of age 3–6 in stream L	0.69	year ⁻¹	E ^a
<i>predation-factor</i>	Division factor for survival rate of spawners moving from stream L to stream C	2	–	G
Growth				
<i>streamC-parK</i>	von Bertalanffy growth coefficient for trout in stream C	0.012	week ⁻¹	E ^b
<i>streamL-parK</i>	von Bertalanffy growth coefficient for trout in stream L	0.011	week ⁻¹	E ^b
<i>streamC-max-length</i>	Asymptotic length for trout in stream C	179.80	mm	E ^b
<i>streamL-max-length</i>	Asymptotic length for trout in stream L	267.00	mm	E ^b
<i>streamC-parA</i>	Parameter a of the length-weight relationship for trout in stream C	14E–06	–	E ^c
<i>streamL-parA</i>	Parameter a of the length-weight relationship for trout in stream L	13E–06	–	E ^c
<i>streamC-parB</i>	Parameter b of the length-weight relationship for trout in stream C	2.95	–	E ^c
<i>streamL-parB</i>	Parameter b of the length-weight relationship for trout in stream L	2.96	–	E ^c
Spawning				
<i>spawn-start</i>	Start of the spawning period	6	week	O ^d
<i>spawn-end</i>	End of the spawning period	17	week	O ^d
<i>spawn-min-age</i>	Minimum age at which trout spawn	3	year	O ^d
<i>spawn-mean-length</i>	Mean of the normal distribution for length of spawners	222.90	mm	O ^d
<i>spawn-sd-length</i>	Standard deviation of the normal distribution for length of spawners	33.82	mm	O ^d
<i>spawn-mean-cond</i>	Mean of the normal distribution for condition factor of spawners	0.936	–	O ^d
<i>spawn-sd-cond</i>	Standard deviation of the normal distribution for condition factor of spawners	0.108	–	O ^d
<i>moved-prop</i>	Proportion of trout born in stream L moving to stream C for spawning	0.45	–	O ^d
<i>spawn-mean-flow</i>	Mean of the log-normal distribution for flow rate in stream L	6.85	m ³ s ⁻¹	O ^d
<i>spawn-sd-flow</i>	Standard deviation of the log-normal distribution for flow rate in stream L	5.15	m ³ s ⁻¹	O ^d
<i>offprod-min-length</i>	Minimum length at which trout spawn in both streams	120.00	mm	O ^d
<i>offprod-max-length</i>	Maximum length at which trout spawn in both streams	388.00	mm	O ^d
<i>offprod-min</i>	Minimum number of offspring produced in both streams	0	–	E ^e
<i>offprodC-max</i>	Maximum number of offspring produced in stream C	168	–	C
<i>offprodL-max</i>	Maximum number of offspring produced in stream L	5	–	C
<i>length-heritability</i>	Heritability of length at age for fry	0.18	–	E ^f
Hatching				
<i>hatch-start</i>	Start of the hatching period	16	week	G
<i>hatch-end</i>	End of the hatching period	27	week	G
Downstream movement				
<i>move-start</i>	Start of the migration period for juveniles	23	week	O ^d
<i>move-end</i>	End of the migration period for juveniles	48	week	O ^d
<i>move-min-age</i>	Minimum age at which trout of stream C move downstream	1	year	O ^d
<i>move-max-age</i>	Maximum age at which trout of stream C move downstream	2	year	O ^d
<i>move-mean-length</i>	Mean of the normal distribution for length of juveniles	88.49	mm	O ^d
<i>move-sd-length</i>	Standard deviation of the normal distribution for length of juveniles	20.98	mm	O ^d
<i>move-age1-varA</i>	Variable A of the logistic function for the probability of moving for age-1 juveniles	0.0026	–	C
<i>move-age1-varB</i>	Variable B of the logistic function for the probability of moving for age-1 juveniles	–4.8	–	C
<i>move-age2-varA</i>	Variable A of the logistic function for the probability of moving for age-2 juveniles	–0.0007	–	C
<i>move-age2-varB</i>	Variable B of the logistic function for the probability of moving for age-2 juveniles	0.1	–	C
<i>move-mean-temperature</i>	Mean of the normal distribution for water temperature in stream C	9.72	°C	O ^d
<i>move-sd-temperature</i>	Standard deviation of the normal distribution for water temperature in stream C	3.72	°C	O ^d
<i>move-mean-flow</i>	Mean of the log-normal distribution for flow rate in stream C	0.040	m ³ s ⁻¹	O ^d
<i>move-sd-flow</i>	Standard deviation of the log-normal distribution for flow rate in stream C	0.038	m ³ s ⁻¹	O ^d
Leaving stream L forever				
<i>leaving-propC</i>	Proportion of juveniles migrated from stream C that do not settle in stream L	0.57	–	C
<i>leaving-propL</i>	Proportion of juveniles born in stream L that do not settle in stream L	0.07	–	C

^a Capture–recapture data (2003–2009) with age classes fitted by Bayesian hierarchical Cormack–Jolly–Seber models; WinBUGS codes modified from Schofield et al. (2009).

^b Capture–recapture data (2003–2009) with age classes fitted by Bayesian hierarchical growth models; WinBUGS codes modified from Zhang et al. (2009).

^c Weight and length measurements from capture–recapture data (2003–2009).

^d Egg counting experiment conducted on female spawners caught at the trapping facility (2008).

^e Observations at the trapping facility (2004–2009).

^f Length heritability for age-0 brown trout of the Bellbekken Brook (Norway), as estimated by Serbezov et al. (2010b).

1. *Update stream hydrological conditions*: Each week, the flow and water temperature of each stream are updated from the input data (see Section 2.2.3.2). They are assumed uniform throughout a stream.
2. *Kill trout in each stream*: Each week, a random number between 0 and 1 is drawn for each trout. If this number is higher than the survival rate corresponding to the trout current age and stream location (*streamX-ageY-survival* parameters), then the trout dies.

Probability density functions were used to get annual trout survival rates, which were transformed into weekly values in the model (i.e., survival rates exponent 1/52). The value of *streamC-age3-survival* was guestimated from *streamL-age3-survival*.

Three mortality sources were indirectly taken into account when the survival functions were drawn: predation by spawners for young trout of the brook during the reproduction period, high temperatures in summer for all trout, predation by grey

herons (*Ardea cinerea* L.) in autumn for trout of age ≥ 2 . For brown trout, the upper lethal temperature in fresh water is at 24.7 °C (Jonsson and Jonsson, 2009). Trout frequently eat eggs or smaller conspecifics (Vik et al., 2001; Aymes et al., 2010), while birds have been observed to remove large numbers of individuals from small shallow streams (Larsson, 1985; Feunteun and Marion, 1994; Hodgens et al., 2004). As a high mortality was observed in the brook for spawners during winter, mainly due to predation by herons (E. Dupont and P.V. Baret, unpublished data), the survival rate of trout moving from stream L to stream C for reproduction (i.e., individuals for which the *moved-to-spawn?* state variable is true) was divided by 2 (*predation-factor*; guestimated value).

3. *Update trout length, weight and condition factor in each stream:* Growth in length is modelled with the von Bertalanffy equation (1957), for which the parameters differ between both streams. Each week, each trout length is updated according to its previous length: $L_{t+1} = L_t + k(L_\infty - L_t)$, where k is the growth coefficient (*streamX-parK* parameter) and L_∞ is the asymptotic length (*streamX-max-length*). Then, the trout new length is used to calculate its healthy weight W_h , using parameters a and b of the length–weight relationship (*streamX-parA* and *streamX-parB*), which also vary between streams: $W_h = a \times L_{t+1}^b$. Finally, the weight W of each trout is computed as its relative condition factor (K_r ; corresponding to the *condition-factor* state variable) multiplied by its healthy weight according to Le Cren's formula (1951): $W = K_r \times W_h$. An inter-individual variability is randomly generated for the condition factor, which value can vary by ± 0.008 (a conditional statement avoids values < 0.5).
4. *Reproduce trout in each stream:* Trout are iteroparous; spawning only occurs during the breeding season each year, but individuals can spawn several times during their life (Belica, 2007). Trout adapt their reproductive behaviour to external conditions and their own state, and the location and time of spawning are influenced by both their physical state and hydrological conditions (e.g., Nelson et al., 1987; Nicola et al., 2002).

Each week of the spawning period (i.e., week 6–17; *spawn-start* and *spawn-end* parameters), each trout first determines if it belongs to the group of candidates for reproduction. Then, when hydrological conditions in stream L are suitable, each candidate spawner determines if it moves upstream. Eventually, candidates of each stream become spawners when they produce offspring.

4.1 *Identify candidate spawners:* Each trout determines whether it meets a series of criteria: adequate age (≥ 3 ; *spawn-min-age* parameter), length (normal distribution of mean and standard deviation equal to *spawn-mean-length* and *spawn-sd-length*) and condition factor (normal distribution of mean and standard deviation equal to *spawn-mean-cond* and *spawn-sd-cond*), not spawned or moved to spawn the current year. If it does, its status is changed from 'non-spawner' to 'candidate-spawner'. Then, candidate spawners living in stream L are randomly selected to move upstream for reproduction, among which 55% (1 – *moved-prop*) of individuals born in stream C (natal-homing behaviour) and 45% (*moved-prop*) of individuals born in stream L (straying behaviour).

4.2 *Move candidate spawners upstream:* The upstream movement of candidate spawners occurs when flow rate in stream L follows a log-normal distribution of mean and standard deviation equal to *spawn-mean-flow* and *spawn-sd-flow* parameters. On weeks meeting this criterion, the current location of each selected candidate spawner as well as each candidate spawner born in stream C and currently living in stream L is changed from 'L' to 'C'.

4.3 *Create offspring:* Each week of the spawning period and for each stream, the number of crosses is computed as half the total number of candidate spawners. Females can reproduce only once each year, while several small subordinate males can contribute to the fertilization of the eggs of one female (polygamous mating strategy; Garcia-Vazquez et al., 2001). For each cross, the female is selected among the list of candidate female spawners ranked in descending order by condition factor. The number of males per female (n) is randomly drawn from a uniform distribution from 1 to 4 (Serbezov et al., 2010a). Then, the n males are randomly selected among a list containing all the candidate male spawners minus n males having the highest condition factor. Upstream spawners are prioritized over other spawners of stream C by a statement that first identifies the candidate spawners that have moved (*moved-to-spawn?* state variable is true), and then selects them before the others.

The number of offspring produced per female per week in each stream depends on its length (Fleming, 1996) and follows a linear function, with a slope α equal to $(F_2 - F_1)/(L_+ - L_-)$ and an intercept β given by $F_1 - \alpha \times L_-$. Values of L_- and L_+ (*offprod-min-length* and *offprod-max-length* parameters) were derived from observations at the trapping facility during 2004–2009 (lower and upper bounds of the 95% confidence interval of the length distribution of upswimming spawners, respectively). Values of α and β were obtained by linear regression of produced offspring vs female length, and were then used to derive the value of F_1 (*offprod-min*), which was considered identical for both streams. F_2 corresponds to *offprodX-max* and was set to 168 for stream C and 5 for stream L (calibrated values; see Section 2.3.1). For the regression, we used data from a field experiment of egg counting conducted on female spawners in 2008 (E. Dupont, Earth and Life Institute, Croix du Sud 2 Box L7.05.14, 1348 Louvain-la-Neuve, Belgium, personal communication, 2010). The mean number of eggs observed by female was translated into number of fry, by assuming that only 10% of the eggs survived to the next stage (Baglinière and Maisse, 1991; Elliott, 1994).

The process continues until the precomputed number of crosses is reached. After each cross, the *num-offspring* state variable of females and males that have effectively spawned is updated. The state variables of each offspring are set as follows. Genotype is given by a random combination of the parental genotypes (the female genotype and a random genotype constructed from the genotypes of the n males), with equal probability of getting each parent allele; age and stage are set to –1 and 'fry', respectively; sex is randomly assigned with even probability of being female or male; current and natal streams are assigned according to the location where the reproduction occurs; birth week is set to the current week; body condition factor is drawn from the same stream-specific normal distributions used for model initialisation and weight is calculated as condition factor times length cubed according to Fulton's formula (see Section 2.2.3.1).

Offspring lengths L^{off} are modelled as being inherited from their parents, following the equation of Kempthorne (1957): $L^{\text{off}} = \mu^{\text{par}} + \text{dev}_p^{\text{off}} = \mu^{\text{par}} + \text{dev}_G^{\text{off}} + \text{dev}_E^{\text{off}}$, where μ^{par} is the parental population mean, $\text{dev}_p^{\text{off}}$ is the total phenotypic deviance of the offspring population, $\text{dev}_G^{\text{off}}$ and $\text{dev}_E^{\text{off}}$ are the genetic and environmental contributions to the total phenotypic deviance, respectively. First, μ^{par} and σ^{par} are derived from the distribution of the parents lengths at the fry stage, L_0^{par} , known from the reverse von Bertalanffy

growth equation: $L_0^{\text{par}} = L_\infty - ((L_\infty - L_t^{\text{par}})/(1 - k)^t)$, where k and L_∞ correspond to the *streamX-parK* and *streamX-max-length* parameters, and t is the time elapsed since the birth of the trout (k and L_∞ are set according to the natal stream). Second, dev_G^{off} is given by $\sqrt{h^2} \times (dev_\mu^{\text{par}1} + dev_\mu^{\text{par}2})$, where h^2 is the narrow-sense heritability, $dev_\mu^{\text{par}1}$ and $dev_\mu^{\text{par}2}$ are the deviation of each parents length from the population mean μ^{par} . The value of h^2 (*length-heritability* parameter) is set to 0.18 (Serbezov et al., 2010b). Third, dev_E^{off} is drawn from a random normal distribution with mean 0 and variance $(1 - h^2)^2 \times \sigma^{\text{par}}$. To avoid negative lengths, each L^{off} value not included in a trout length distribution defined for each stream by the *mean1-birth-X* and *sdl-birth-X* initial conditions (see Table 2), truncated at ± 4 standard deviations and rounded to 1 mm when negative values are drawn, are set to a random value drawn from this distribution.

5. *Increment age and update stage of trout in each stream*: One week before the beginning of the hatching period (i.e., week 15; *hatch-start - 1*), the age of each trout is incremented by one. The stage is updated as follows: if the age is < 1 , the stage is set to 'fry'; if the age is equal to 1 or 2, it is set to 'juvenile'; if the age is > 2 , it is set to 'adult'. All individuals die once they reach the age of 7.
6. *Reveal offspring in each stream*: Offspring that have been previously created during reproduction have an age equal to -1 and are hidden until a 10-week delay is reached. When it does, offspring progressively set their age to 0 and become visible in the system. This action occurs once a week during the hatching period (i.e., week 16–27; *hatch-start* and *hatch-end* parameters). Values chosen for the *hatch-start* and *hatch-end* parameters were based on the hypothesis that the mean number of degree-days for brown trout to complete the egg stage was equal to 444 (Elliott, 1994). As we observed an average water temperature of 6°C in both streams during the spawning period, we supposed there was a delay of 10 weeks between the spawning and hatching periods.
7. *Move trout of stream C downstream*: Each week during the migration period (i.e., week 23–48; *move-start* and *move-end* parameters), each trout determines if it belongs to the group of candidate migrants. Then, if the flow in stream C is adequate, the candidate migrants that actually move to stream L become migrants.
 - 7.1 *Identify candidate migrants*: Trout are candidate migrants if they are born in stream C and currently live in stream C, if their age is equal to 1 or 2 (*move-min-age* and *move-max-age* parameters), and if their length follows a normal distribution of mean and standard deviation equal to *move-mean-length* and *move-sd-length*. The status of trout meeting these criteria is set to 'candidate-migrant'.
 - 7.2 *Move candidate migrants*: Young individuals often leave their home tributary to large rivers for feeding (Baglinière et al. (1987), Forseth et al. (1999)). It appears there is an apparent advantage in form of increased growth, size and thereby reproductive potential by moving instead of remaining resident in the nursery area (Jonsson and Sandlund, 1979; Baglinière et al., 1994). Several factors can trigger these movements, such as the physical state of the individuals and hydrological criteria. This migration can also be explained by density-dependent mechanisms (Jonsson and Jonsson, 1993; Milner et al., 2003). Juveniles that are unable to establish a territory in the nursery brook may be displaced by competition with dominant individuals (Elliott, 1994; Landergren, 2004; Skoglund and Barlaup, 2006).

In the model, the downstream movement of candidate migrants occurs when water temperature and flow rate in stream C follow distributions of means and standard

deviations equal to *move-mean-temperature*, *move-mean-flow*, *move-sd-temperature* and *move-sd-flow*, respectively. On weeks meeting these criteria, a random number between 0 and 1 is drawn for each candidate migrant. If this number is lower than the probability of moving downstream, then the current location of the candidate is changed from 'C' to 'L' and its status is set to 'migrant'. The migration of individuals is age-specific and follows a density-based logistic function given by: $P = \exp(A \times X + B) / (1 + \exp(A \times X + B))$, where A and B correspond to parameters *move-ageZ-varA* and *move-ageZ-varB*, respectively. Their values were obtained by calibration (see Section 2.3.1).

8. *Move upswimming spawners back to stream L*: One week after the end of the spawning period (i.e., week 18; *spawn-end + 1*), candidate and effective spawners that have moved to spawn return to their original stream (post-spawning homing behaviour). Their current location is changed from 'C' to 'L'.
9. *Remove young trout of stream L from the system*: The last week of the year (i.e., week 52), trout are randomly selected among (i) migrants from stream C currently living in stream L, with a proportion of 57% corresponding to the *leaving-propC* parameter (calibrated value; see Section 2.3.1), (ii) juveniles born in stream L and currently living in stream L, with a proportion equal to 7% (*leaving-propL* parameter; calibrated value). These selected trout are assumed to leave the system to search for more suitable locations, owing to their territorial behaviour (Elliott, 1994).

2.3. Simulation experiments

The exploration and verification of the DemGenTrout individual-based model was conducted at three levels: (i) a visual debugging (i.e., locating/correcting errors using the visual interface of NetLogo) was performed while writing the code, and separate implementations of each submodel were tested and analysed, (ii) the code was peer-reviewed, i.e., it was thoroughly compared with the written formulation of the model by other scientists, (iii) several controlled simulation experiments were performed, in which the model or its parts were simplified so that the outcome of each experiment could be predicted and verified.

We followed the pattern-oriented modelling strategy for developing and calibrating the model (Grimm et al., 1996, 2005; Wiegand et al., 2003). After identifying the submodels to consider as key processes, parameter values of the model were first determined directly to reduce the parameter space (Table 3). Second, the model was optimized by selecting the most appropriate representation of the mating mode for the spawning process, which required an extra calibration step (Section 2.3.1). Third, the model was validated (Section 2.3.2).

In each case, we defined a set of characteristic patterns observed in the real system over the years 2004–2011, keeping the values of the 2 last years as independent data for validation. To evaluate the agreement between the observed and predicted patterns, a quantitative measure, named SSSE, was defined as the sum of standardized squared errors between the observed and simulated values: $\sum_i (sim_i - obs_i)^2 / obs_i$. Simulations were run for 5 and 7 years for the optimization and validation steps, respectively. The random seed was fixed to 1223251200 during calibration, but we performed 50 replicates in the submodel selection and validation steps to account for model stochasticity.

2.3.1. Model optimization

The influence of the mating mode on the genetic structure of the brown trout population was tested by submodel selection. Salmonids exhibit a wide diversity of breeding systems (Fleming, 1998), and both monogamous and polygamous matings have been observed (Serbezov et al., 2010b). Monogamy, in which each cross

involves two parents, and polygamy, in which each cross involves one female and several satellite males, are the most commonly described mating strategies for brown trout (Garcia-Vazquez et al., 2001).

Alternative models corresponding to both strategies were first calibrated using standard genetic algorithms implemented in BehaviorSearch (Stonedahl and Wilensky, 2010). The calibration was conducted on 9 initial conditions (Table 2) and 8 parameters (Table 3). These latter were selected because of their influence on the two key processes of the model, the downstream movement of young trout, and the spawning (Table 4). Five field patterns were used: population size in stream C (C1), population size in stream L (C2), number of upswimming spawners (C3), number of age-1 migrants (C4), number of age-2 migrants (C5). Patterns C1 and C2 were estimated by fitting Jolly-Seber models to capture–recapture data of trout electrofished and tagged in autumn in both streams, using the POPAN formulation in program MARK (White and Burnham, 1999) (Table A.3 of Appendix A). Patterns C3 to C5 were derived from observations at the trapping facility (Table A.1 of Appendix A). Annual observations of each pattern were compared to simulated numbers of (i) trout with a length >70 mm in both streams, (ii) upswimming spawners, (iii) age-1 migrants, (iv) age-2 migrants, monitored over 5 years (at week 1 in the first case, during the year otherwise). The search process was performed three times, with 2000 model runs. The purpose was to find the best set of initial condition and parameter values that minimizes the SSSE.

After their calibration, both alternative models were tested against a set of three field patterns derived from a genetic analysis conducted on five groups of trout (i.e., CRa, CMa, EXa, CRb and EXb; see Section 2.1.2): effective number of alleles E_A in each group of trout (S1), inbreeding coefficients F_{IS} in each group of trout (S2), fixation index F_{ST} between groups of trout (S3). Values of patterns S1 to S3 (available in Table A.4 of Appendix A) were compared to outputs of the model computed from genotypes of 48×5 randomly selected individuals, which were recorded at different moments in time to match field samplings. The model with the lowest SSSE was selected.

2.3.2. Model validation

The validation of the DemGenTrout model corresponds to the last step of the pattern-oriented modelling strategy. We applied the same method used for submodel selection to the whole model, which was evaluated by comparing simulated outputs with four field patterns: ratio of trout abundances in both streams (V1), return rate of spawners to stream L after reproduction (V2), number of age-1 and age-2 migrants (V3), trout length distributions in both streams (V4). Values of V1 and V2 were computed from Tables A.3 and A.1 of Appendix A, as the ratio of population size in stream L to population size in stream C and the ratio of the number of downswimming spawners to the number of upswimming spawners, respectively. Values of V3 were derived from observations at the trapping facility (Table A.1 of Appendix A). Values of V4 were derived from length measurements of trout electrofished in autumn in both streams (Table A.3 of Appendix A).

Demographic outputs, corresponding to the number of trout with a length >70 mm in both streams, the number of upswimming and downswimming spawners, the number of migrants, and the length of trout in each stream, were recorded annually during 7 years. The annual SSSE values were computed by pattern to quantify the performance of the model of reproducing each of them.

2.4. Sensitivity analysis

The sensitivity analysis conducted on the DemGenTrout individual-based model served two purposes: (i) screening

non-influential and influential parameters in the model, and (ii) among the most influential parameters, identifying those that would lead to the greatest reduction in the output variance when fixed to their reference values. In both cases, we used the sensitivity R package (Pujol, 2008) to automatically generate the design of experiments, and to estimate the sensitivity measures. The following outputs were chosen as indicators of model behaviour: trout abundance in each stream (N_C and N_L), trout inbreeding coefficients in each stream to measure the extent of genetic inbreeding (F_{IS}^C and F_{IS}^L) and fixation index between trout of both streams to measure the degree of genetic differentiation (F_{ST}), recorded the last week of the year after all processes have occurred and averaged over a 7-year period.

First, we used an improved version of the elementary effects method (Morris, 1991; Campolongo et al., 2007) to identify the parameters to which the DemGenTrout model was particularly insensitive or sensitive. All 51 parameters (k) of the model were varied over five levels according to predefined ranges, the central values being those presented in Table 3 and the other four their corresponding lower extreme, lower median, upper median and upper extreme. The number of tested settings is given by $r \times (k + 1)$, where r is the number of elementary effects or trajectories computed per parameter. As we chose 50 trajectories, this leads to $50 \times (51 + 1) = 2600$ runs. We used the estimate of the mean of the distribution of the absolute values of the elementary effects, μ^* , as a sensitivity measure to ascertain the importance of each parameter. It can be considered as a proxy of the total sensitivity index, which itself is a measure of the overall effect of a parameter on the output, including interactions (Cariboni et al., 2007; Saltelli et al., 2008).

Second, using the results of the Morris method as a starting point, we applied the variance decomposition method of Sobol (1993). The number of tested settings was given by $m \times (p + 1)$, where m is the size of the Monte Carlo sample matrix and p is the number of parameters to analyse. We chose a sample matrix of size 500, and Sobol first-order indices were computed for each parameter. These indices represent the main effect of each parameter contribution to the variance of the output (Saltelli et al., 2008).

2.5. Scenarios comparison

Two simulation scenarios were explored with the DemGenTrout model: (i) the presence of an obstacle preventing spawners to access the nursery brook (stream C), (ii) stocking with age-2 hatchery trout in the main river (stream L), resulting in hybridization between wild and stocked trout. We recorded the same five indicators as the ones used in the sensitivity analysis (Section 2.4) to evaluate impacts of both scenarios on the demogenetic structure of the population. Demographic outputs and genotypes were yearly recorded at week 1 before all processes have occurred and were followed during 35 simulated years. Evolution of trout abundance, fixation index, and trout inbreeding coefficients was also monitored for the validated model not implementing any scenarios, to serve as a reference (i.e., baseline situation). A demographic explosion was observed in the baseline and stocking scenarios at the end of the 35 simulated years. Consequently, we decided to limit offspring production in stream C by dividing *offprodC-max* by 10 whenever trout abundance in this stream reaches a capacity of 6700 individuals (minimum value at which simulations remained unchanged over the first 7 years).

We predicted that both indirect and direct genetic impacts should occur, i.e., (i) the trout abundance in stream C should decrease over time, leading to a significant increase of trout F_{IS} in this stream, and (ii) the genetic differentiation between trout of both streams, measured by F_{ST} , should increase.

Table 4
Initial conditions and parameters identified for the calibration step performed on the DemGenTrout individual-based model, and their corresponding influence on model processes. For each of them, the range of tested values and the best final value are specified.

Initial condition/parameter	Main influence on	Tested range	Best value
<i>init-N</i>	Juvenile downstream migration	[4000 100 6000]	4500
<i>prop-C</i>	Juvenile downstream migration	[0.60 0.01 0.80]	0.73
<i>prop-age0-C</i>	Juvenile downstream migration	[0.70 0.01 0.85]	0.76
<i>prop-age1-C</i>	Juvenile downstream migration	[0.12 0.01 0.27]	0.21
<i>prop-age2-C</i>	Juvenile downstream migration	[0.01 0.01 0.05]	0.02
<i>prop-age0-L</i>	Spawner upstream migration	[0.01 0.01 0.15]	0.10
<i>prop-age1-L</i>	Spawner upstream migration	[0.10 0.01 0.30]	0.22
<i>prop-age2-L</i>	Spawner upstream migration	[0.25 0.01 0.50]	0.37
<i>propC-inL</i>	Spawner upstream migration	[0.20 0.05 0.80]	0.67
<i>offprodC-max</i>	Offspring production	[50 1 170]	168
<i>offprodL-max</i>	Offspring production	[1 1 20]	5
<i>move-age1-varA</i>	Juvenile downstream migration	[0.0000 0.0001 0.0100]	0.0026
<i>move-age1-varB</i>	Juvenile downstream migration	[-5.3 0.1 2.0]	-4.8
<i>move-age2-varA</i>	Juvenile downstream migration	[-0.0100 0.0001 0.0000]	-0.0007
<i>move-age2-varB</i>	Juvenile downstream migration	[-1.0 0.1 1.0]	0.1
<i>leaving-propC</i>	Spawner upstream migration	[0.05 0.01 0.90]	0.57
<i>leaving-propl</i>	Spawner upstream migration	[0.02 0.01 0.90]	0.07

Tested ranges are expressed in the form [start increment stop]. For instance, the *init-N* parameter was varied from 4000 up to 6000, by increments of 100.

2.5.1. Scenario 1: migration barrier

The presence of an obstacle at the confluence of stream C was simulated in the model by simply preventing any upstream movement during the spawning process. All candidate spawners thus stayed in their current stream during the reproduction period. The modelling of the young trout downstream movement process remained unchanged.

2.5.2. Scenario 2: stocking with hatchery trout

To study the stocking impacts on wild brown trout, several modifications of the model structure were needed. More specifically, one submodel, two breeds, and five parameters (*stocking-coefficient*, *num-stocked*, *trout-spawning-prob*, *stocked-spawning-prob*, *hybrid-spawning-prob*) were added. Both spawning and survival submodels were adapted to include phenotypic and genetic differences between hatchery-reared and wild trout.

First, a submodel that simulates the introduction of hatchery individuals in the Lesse River was created. Each year at week 27 (i.e., the end of March, corresponding to the beginning of the fishing season) and during 10 years, a fixed number of stocked trout (*num-stocked* parameter) was introduced in stream L. This number was calculated once, at week 27 of year 1, as the product of the stocking coefficient by the number of wild trout in stream L. The value of *stocking-coefficient* was sequentially set to 0.50, 0.70 and 0.90 to reflect the fact that the river is moderately stocked. The state variables of each stocked trout were defined as follows. Their length was drawn from a random normal distribution with a mean of 248.47 mm and a standard deviation of 26.71 mm, determined using 477 length measurements of individuals reared in the Ochamps hatchery (Libin, Belgium). Their condition factor was set to 1.1, as hatchery fish are often larger and heavier than wild fish (e.g., Bohlin et al., 2002). The weight of each individual was calculated as its condition factor times its length cubed according to Fulton's formula. For the genotype state variable, we used analyses of individuals from the Mirwart hatchery to get the different alleles and the corresponding allelic frequencies (see Section 2.1.2 and Table A.5 of Appendix A). All stocked individuals were of age 2.

Second, the spawning submodel was modified to incorporate the new breeds, which correspond to stocked trout and hybrids. Both breeds had the same state variables as those previously defined for wild trout (Section 2.2.1). Breed attribution to each offspring depends of the mating. A thirteenth locus was added in trout genotypes for breed tracking, with homozygous alleles

arbitrarily fixed to "000" and "999" for wild and hatchery trout, respectively. Hybrids were identified as individuals having heterozygous alleles (i.e., either "000/999" or "999/000"). Phenotypes were thus inherited the same way as genotypes. We hypothesised that stocked trout had reduced reproductive success in comparison with wild trout, as previously has been shown (e.g., Jonsson, 1997; Berejikian and Ford, 2004). The probability of spawning was set to 0.10 for hatchery trout (*stocked-spawning-prob* parameter) and to 1.00 for wild trout (*trout-spawning-prob*). The spawning probability for hybrids (*hybrid-spawning-prob*) was given by $trout-spawning-prob \times (1 - ((1 - stocked-spawning-prob)/2))$ and is thus equal to 0.55.

Third, the survival process of trout was adapted. Many studies have reported high mortality of hatchery-reared fish soon after their release in comparison with wild fish, due to their lower adaptation capability (e.g., Miller, 1953; Deverill et al., 1999; Bohlin et al., 2002). As phenotypic differences between hatchery and wild fish often disappear after 1 year in nature (Fleming et al., 1994), the survival rate of age-2 hatchery trout released in stream L was set 10 times lower than the rate normally used for wild trout. Stocked trout of age >2 and hatchery trout born in the system had the same age-specific survival rates than wild trout. Survival of hybrids was computed from survival of wild (S_W) and hatchery trout (S_S): $S_H = S_W \times (1 - ((1 - S_S)/2))$.

3. Results

3.1. Model optimization and validation

The model including a polygamous mating mode showed the lowest SSSE computed over all patterns, with a value equal to 0.31 (against 1.42 for the alternative model implementing monogamy). This model was also the best one identified during the calibration step, as a SSSE value lower than the one computed for the alternative model was found (i.e., 602 vs 630).

The model appears to reproduce all the validation patterns relatively well. Considering each year, the highest discrepancies were found in 2006–2007 (16% of the global SSSE), 2009–2010 (12%) and 2010–2011 (36%). Considering pattern V1 (Fig. 4(a)), we observed small discrepancies for years 2007–2008 (9% of the SSSE for this pattern) and 2008–2009 (10%), and a higher one in 2009–2010 (49%). This latter year was also an issue for V2 (Fig. 4(b)) along with 2005–2006, since they contributed to the SSSE computed for this pattern in an amount of 31% and 32%, respectively. For V3 (Fig. 4(c)),

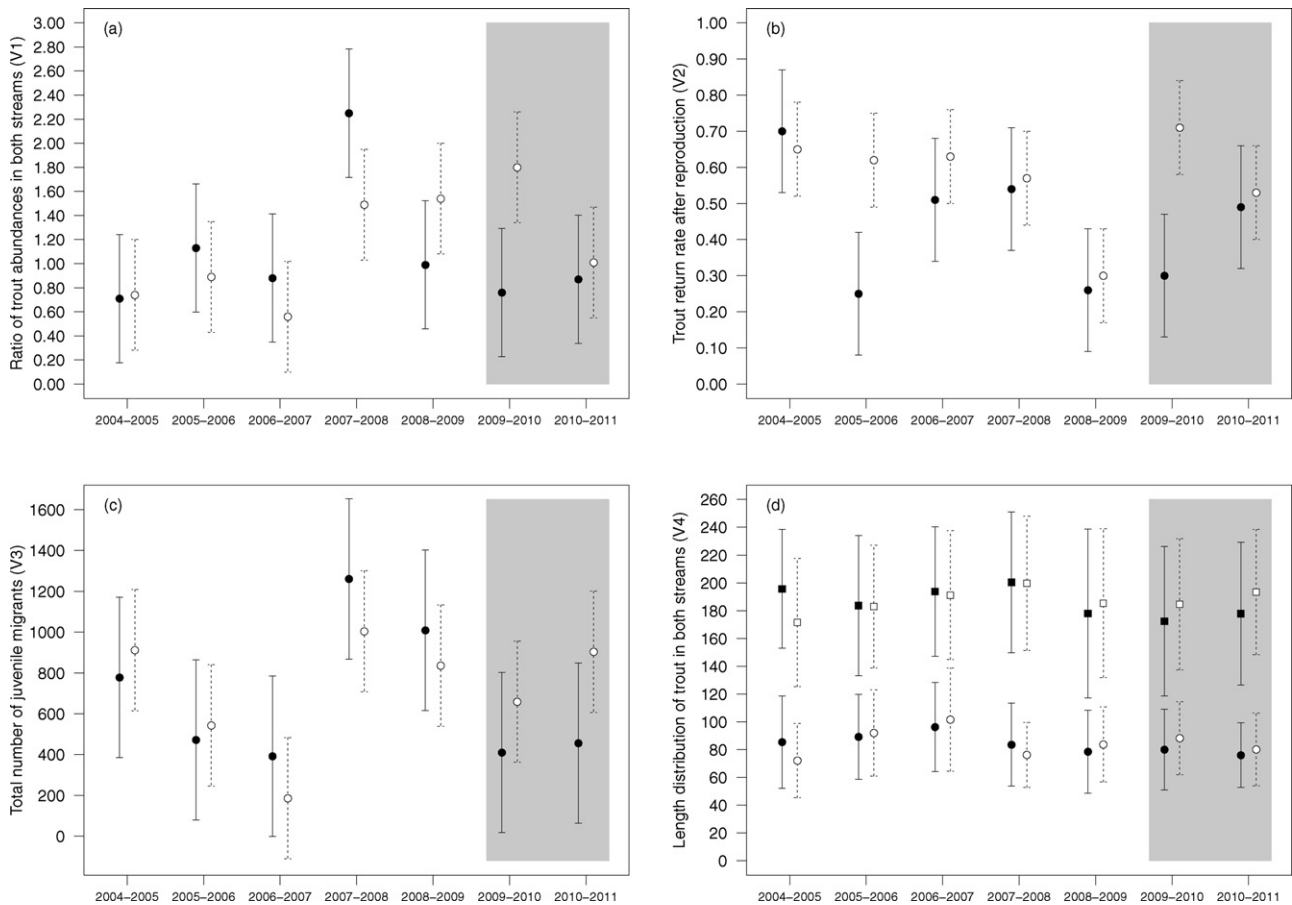


Fig. 4. Pattern-matching validation performed on the DemGenTrout individual-based model, with observed (solid circles) and simulated (open circles) patterns within one standard deviation range. Four patterns were considered: (a) ratio of trout abundances in both streams, (b) trout return rate after reproduction, (c) total number of juvenile migrants, (d) trout length distributions in stream C (circles) and stream L (squares). The last 2 years of each pattern are independent data (i.e., not previously used during model parameterization and optimization).

the year 2010–2011 contributed the most to the SSSE of the pattern (36%). For V4 (Fig. 4(d)), the fit between observed and simulated values was excellent over the years 2005–2011 with all contributions to respective SSSE values <16%, but rather poor in 2004–2005 (>26%).

3.2. Sensitivity analysis

3.2.1. Screening of non-influential and influential parameters

Among all parameters of the DemGenTrout model, survival rate of age-0 trout in stream C (*streamC-age0-survival*) was the one that influenced the most the trout abundance of this stream (Fig. 5). Abundance in stream L seemed to be only slightly impacted. Considering the three genetic outputs, survival rates were also among parameters that showed the strongest influences. In particular, the F_{IS} of trout in stream C was mainly impacted by the survival rates of age-0 and age-1 trout in stream C. The F_{IS} of trout in stream L was influenced by fry survival in both streams, but also by the *streamC-age2-survival* parameter. The F_{ST} between trout of both streams was mostly impacted by *streamC-age0-survival*, and in a lesser extent by *streamC-age1-survival* and *streamC-age2-survival*. Moreover, the *spawn-mean-cond* parameter appeared to have a strong impact on both F_{IS} indicators, while *streamL-parK* mainly influenced the F_{ST} and F_{IS}^C .

The model was insensitive to the growth parameters linked to the length–weight relationship for trout in both streams (*streamX-parA* and *streamX-parB* parameters), and to the variables of the logistic function for the probability of moving for trout of age 1

(*move-age1-varA* and *move-age1-varB* parameters). The heritability of length at age for fry (*length-heritability* parameter) also appeared to have a small impact on the five indicators.

3.2.2. Prioritization of parameters

The six parameters of DemGenTrout identified as the most influential by the Morris method were analysed using the Sobolj method (total number of runs = $500 \times (6 + 1) = 3500$). Each parameter was varied over 11 levels, with a range specified as follows: from 0 up to 1, by increments of 0.1 for the *streamC-age0-survival*, *streamC-age1-survival*, *streamC-age2-survival* and *streamL-age0-survival* parameters; from 0 up to 0.02, by increments of 0.002 for *streamL-parK*; and from 0.5 up to 1.5, by increments of 0.1 for *spawn-mean-cond*.

For trout abundance in stream C, the *spawn-mean-cond* and *streamC-age0-survival* parameters contributed almost equally to the output variance in an amount of 55% and 41%, respectively (Fig. 6(a)). In the case of abundance in stream L, *spawn-mean-cond* explained 89% of the output variance (Fig. 6(b)). For the three genetic outputs, *streamC-age0-survival* was clearly the parameter that could reduce the most the variance when fixed to its true value (Fig. 6(c–e)). Indeed, it explained 60, 87 and 65% of the variance observed in the F_{IS}^C , F_{IS}^L and F_{ST} outputs, respectively. The *spawn-mean-cond* parameter also contributed to the variance reduction of the F_{IS}^C output (27%) and of the F_{ST} output (16%). For this latter output, *streamL-parK* also explained 18% of the variance.

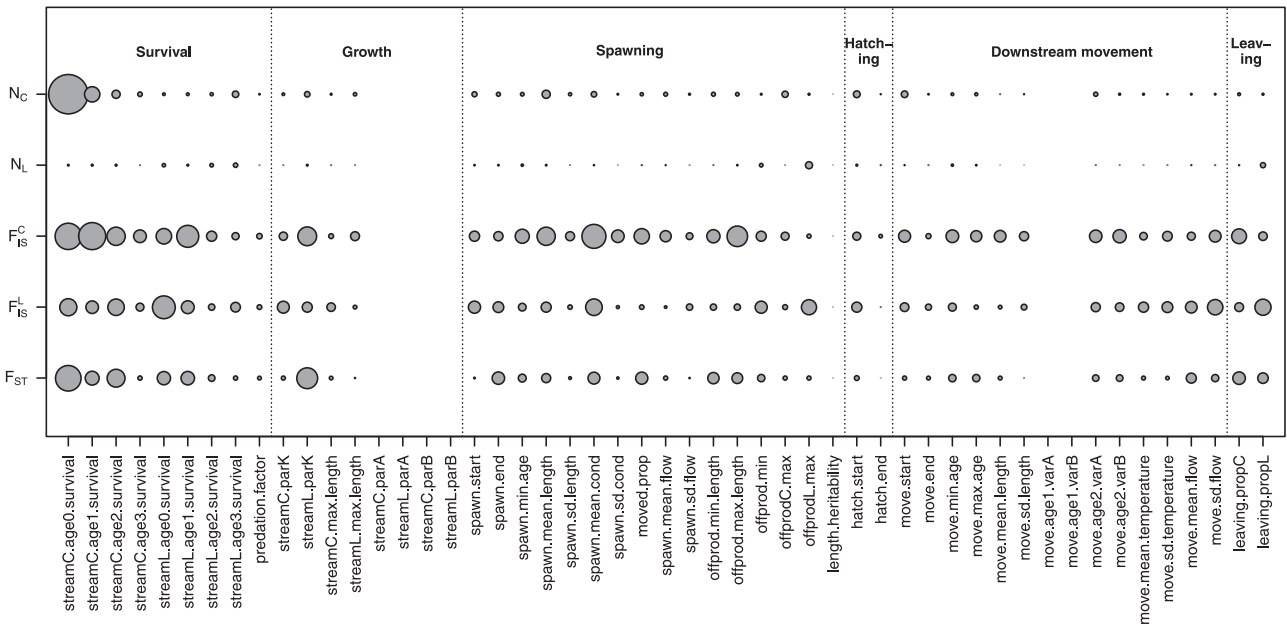


Fig. 5. Results of the sensitivity analysis conducted on the DemGenTrout individual-based model (Morris method). All 51 parameters were varied over five levels and 50 trajectories or elementary effects were randomly selected. Parameters were grouped according to the survival, growth, spawning, hatching and leaving stream L forever processes. For each parameter, the estimate of the mean of the distribution of the absolute values of the elementary effects (μ^*) was computed for the five following demogenetic indicators: trout abundance (N) and inbreeding coefficients (F_{IS}) in both streams, as well as the fixation index (F_{ST}) between trout of both streams (C: Chicheron Brook, L: Lesse River). The size of the bubbles is proportional to the μ^* values.

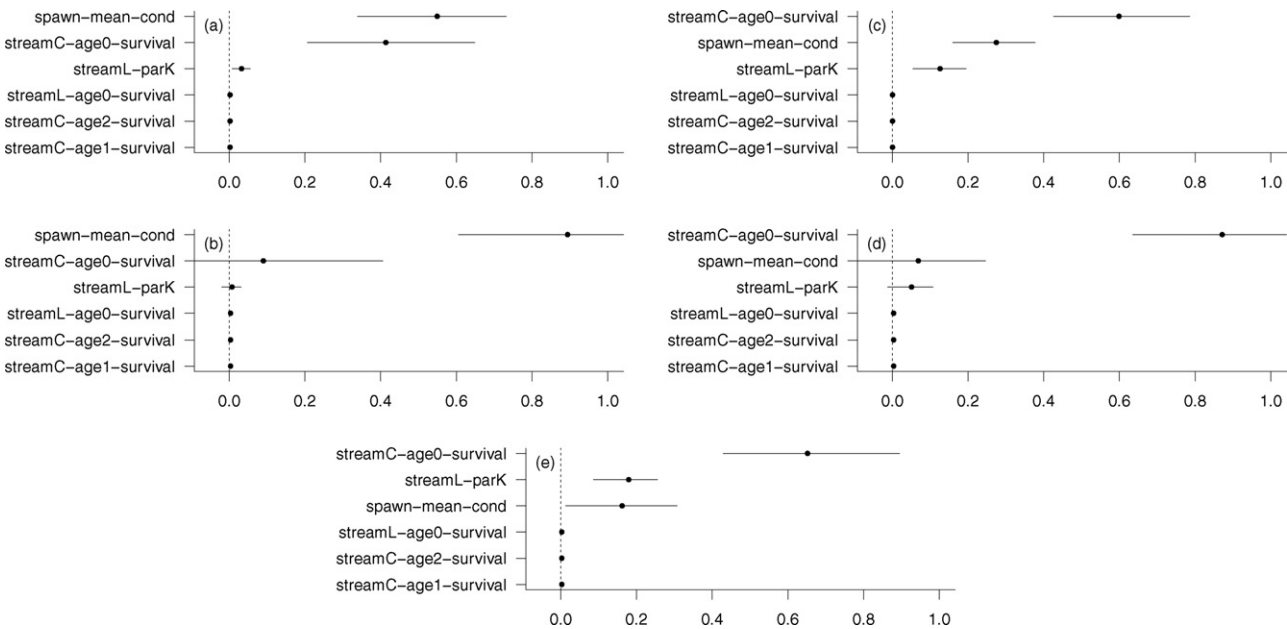


Fig. 6. Sobol first-order indices of sensitivity for the six parameters of the DemGenTrout individual-based model identified as the most influential by the Morris method. Each index was computed for the five following demogenetic outputs: (a) trout abundance in stream C, (b) trout abundance in stream L, (c) trout inbreeding coefficient in stream C, (d) trout inbreeding coefficient in stream L, and (e) fixation index between trout of both streams (C: Chicheron Brook, L: Lesse River). Parameters were ordered for each output according to their mean estimates of Sobol indices, and the corresponding 95% confidence intervals are represented by horizontal lines.

3.3. Scenarios comparison

3.3.1. Evolution of trout abundance in both streams

The trout population size in the river/nursery brook system stabilized around 5500 individuals in the baseline scenario (i.e., with no disturbances). On average, we observed 3432 individuals in the Chicheron Brook and 2077 in the Lesse River the last 5 years of simulation (Table 5). In the scenario with migration barrier, trout abundance in both streams has drastically decreased (Fig. 7(a)). Trout in stream C went extinct after 13 years, while

only 2 individuals remained in stream L at year 35. In the three versions of the stocking scenario (i.e., with a coefficient of 50, 70 and 90%, respectively), abundance of wild trout stayed more or less identical over the 35 simulated years, with a mean close to 3400 individuals in stream C and around 2050 in stream L the last 5 years (Table 5).

Proportions of wild trout, hybrids and stocked trout in both streams were compared in the case of the stocking scenario. Observations among the three versions did not vary much, and we observed proportions of about 99.9% wild trout, 0.01% hybrids and

Table 5

Comparison of the scenarios simulated with the DemGenTrout individual-based model. Values of the five following demogenetic outputs at the beginning and averaged over the last 5 years of simulation are given: trout abundance in stream C (N_C) and in stream L (N_L), trout inbreeding coefficients in stream C (F_{IS}^C) and in stream L (F_{IS}^L), and fixation index between trout of both streams (F_{ST}) (C, Chicheron Brook; L, Lesse River; W, wild trout; H, hybrids; S, stocked trout).

Scenario	N_C	N_L	F_{IS}^C	F_{IS}^L	F_{ST}
Beginning of simulation (year 1)					
All situations	3285	1215	0.026	0.046	0.010
End of simulation (years 30–35 averaged)					
Baseline situation	3432	2077	−0.014	−0.013	0.001
Migration barrier	0	2	NA	NA	NA
50% stocking	W: 3418, H: 1, S: 0	W: 2072, H: 1, S: 0	−0.014	−0.007	0.001
70% stocking	W: 3414, H: 2, S: 0	W: 2056, H: 2, S: 0	−0.012	−0.011	0.002
90% stocking	W: 3392, H: 3, S: 0	W: 2068, H: 2, S: 0	−0.014	−0.010	0.002

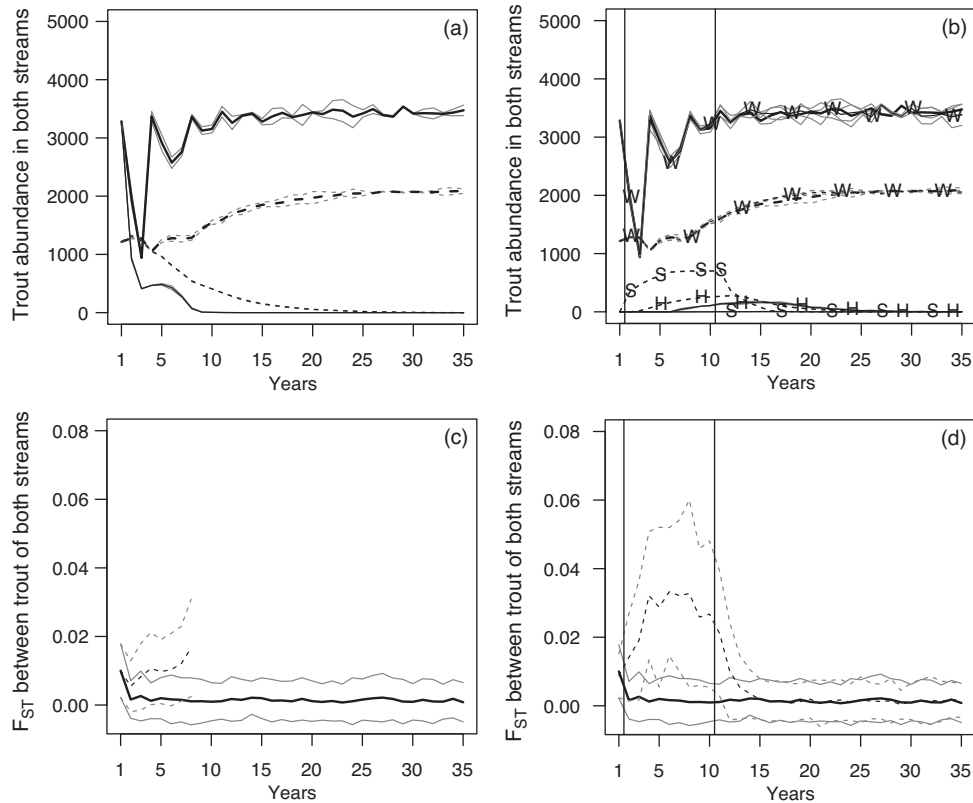


Fig. 7. Comparison of two scenarios simulating anthropogenic disturbances for brown trout over 35 years. Impacts of (a) migration barrier and (b) stocking with a coefficient of 90% on the abundance of trout in stream C (solid lines) and abundance in stream L (dashed lines). Impacts of (c) migration barrier and (d) stocking with a coefficient of 90% on the fixation index F_{ST} between trout of both streams (dashed lines). In each graphic, heavy black lines indicate the baseline situation, and grey lines represent upper and lower 95% confidence limits. In (b), wild trout, hybrids and stocked trout abundances are directly identified by letters W, H and S, respectively; in (b) and (d), vertical lines represent the 10-year stocking period.

0% stocked trout in both streams the last 5 years of simulation. In the case of the scenario with a 90% stocking coefficient, hybrids did not appear in stream C until year 7. Then, their number increased to reach a peak of 167 individuals at year 15, for finally decreasing until almost complete disappearance at year 35 (Fig. 7(b)). For the 50 and 70% stocking coefficients, peaks of 104 and 132 hybrids were reached at years 16 and 15, respectively (data not shown). In any case, stocked trout appeared in the brook between years 9–11 and 18–20, in a very low abundance (i.e., no more than 4 individuals). In stream L, the number of hybrids steadily increased from year 1 until reaching a peak at year 12 of 161, 220 and 277 individuals, respectively. Then, it steadily decreased until almost complete disappearance the last 5 years of simulation (Table 5). For each scenario version, the number of stocked trout in stream L never exceeded half the number of wild trout, although maxima of 386, 548 and 704 individuals were observed at year 11. Abundance of hatchery-reared trout rapidly decreased afterwards, until complete disappearance around year 22 (Fig. 7(b)).

3.3.2. Evolution of the inbreeding coefficients and the fixation index

In the baseline situation, trout inbreeding coefficients in each stream (F_{IS}) were positive and near zero at the beginning of the simulation. The last 5 years, values became negative although still being around zero (Table 5). The population thus switched from heterozygote deficiency (inbreeding) to heterozygote excess (outbreeding) compared with Hardy–Weinberg equilibrium expectations. In the case of the scenario simulating a barrier to migration, F_{IS} values were only valid until year 8 for stream C and until year 20 for stream L. After these years, the number of individuals was insufficient to compute the F -statistics. In stream C, the last computed F_{IS} value was equal to -0.043 . In comparison, the value in the baseline scenario that same year was -0.008 . In stream L, the value did not vary much from the baseline situation (-0.022 vs -0.014). For the three versions of the stocking scenario, F_{IS} values were comprised between -0.015 and 0.050 in both streams (data not shown). A slight inbreeding situation was however observed in

stream L from years 2 to 5, with values comprised between 0.090 and 0.115.

In the barrier scenario, the fixation index F_{ST} between trout of both streams steadily increased until reaching a value of 0.017 at year 8 (Fig. 7(c)). In comparison, the F_{ST} was equal to 0.001 that same year in the baseline situation. In the stocking scenario with a coefficient of 90%, F_{ST} values >0.020 were observed between years 4 and 11 (Fig. 7(d)). In the simulations with coefficients of 50% and 70%, the time periods were shorter (i.e., between years 6–8 and 4–8, respectively). After this period, the values showed little variation. In all situations, including the baseline, F_{ST} values were between 0.001 and 0.002 the last 5 simulated years (Table 5).

4. Discussion

4.1. Innovations and model structure

The DemGenTrout model was designed to provide accurate predictions of changes in the demogenetic structure of a brown trout population facing medium-term anthropogenic disturbances. To our knowledge, this is the first attempt of an individual-based demogenetic model developed for a stream-dwelling brown trout population at the local scale, through the combined use of NetLogo and R. Indeed, existing individual-based models for salmonids integrated either the demographic and spatial dimensions (e.g., inSTREAM), or the demographic and genetic dimensions (e.g., VORTEX) (Frank et al., 2011). Since we could not find any fish individual-based models integrating population dynamics, population genetics and the spatial dimension, we decided to build a completely new model. The inSTREAM software has been a very inspirational source during the development of the DemGenTrout model.

There is confusion in the naming of models including a genetic dimension, linked to the existence of two specific fields: population genetics and quantitative genetics. On the one hand, population genetics models aim to understand and to predict the genetic structure of populations (i.e., their allele and genotype frequency distributions) taking into account ecological and evolutionary factors such as population size, patterns of mating, gene flow, genetic drift, mutation and natural selection (Hartl and Clark, 1989; Allendorf and Luikart, 2007). On the other hand, quantitative genetics models aim to study the distributions of fitness-related phenotypic characters such as growth rate, age and size at maturity, and the temporal change of the means and variances of these distributions (Coulson et al., 2010). We therefore propose to reserve the term “eco-genetic” to models related to quantitative genetics, and the naming “demogenetic” to models related to population genetics. In our opinion, the IBASAM model recently developed by Piou and Prévost (2012) is thus an eco-genetic individual-based model.

The DemGenTrout model was parameterized for a specific Belgian watershed. Its extrapolation to completely new conditions would therefore require further developments. For instance, if another fish species is considered, spawning and hatching periods should be adapted accordingly. Furthermore, several simplifications were made in the structure of the model. First, we considered that the brown trout population was living in autonomy in a closed system, characterized by a homogeneous habitat. DemGenTrout was thus not spatially explicit except for the consideration of two compartments, a section of a main stream, the Lesse River, and its tributary, the Chicheron Brook. Second, the egg stage was skipped so that fry were directly produced. In accordance with timing observed in real trout, a ten week-delay was introduced between the spawning and hatching processes. Third, sources of mortality were not explicitly taken into account as they were integrated into survival rates. An exception was however made for predation by herons on spawners during their stay in the brook. There is thus

room for further improvements of the model. For instance, feeding and habitat could be explicitly modelled, and the egg stage could be integrated. However, these improvements would undoubtedly lead to an increase of the model complexity and consequently of the computation time needed for its optimization.

4.2. Model optimization and validation

To ensure its structural realism, the DemGenTrout model was optimized by means of submodel selection and calibration to reproduce eight patterns, which were based on observations made on the real system over the years 2004–2009. The model was then validated against four patterns that were partially dependent with the previously used patterns, excepted for the last two years (2009–2011).

During submodel selection, two alternative models were compared according to three genetic patterns to test the influence of the mating mode on the genetic structure of the brown trout population. The model including polygamy was selected over the one with monogamy. In comparison, eggs are produced from monogamous matings in inSTREAM, while polygamous matings are considered in IBASAM.

The calibration was based on five demographic patterns, and we found that those linked to trout population size in the Chicheron Brook and to the number of age-1 migrants caught at the downstream trap were the less well reproduced by the model. Variables of the two functions describing the downstream movement of age-1 and age-2 trout were included into the calibration step. During the parameterization, the fitting of generalized linear models on capture–recapture data suggested a linear and an exponential relation in each respective case. However, the process was modelled by a logistic function to allow for the consideration of all three relations during the calibration. Both relations were indeed transformed, into a logistic and a linear forms, respectively. The trends remained identical: the probability of moving downstream for age-1 trout increased with density, while an inverse relationship was observed for age-2 trout.

The DemGenTrout model was validated against four demographic patterns. The highest discrepancies between observed and predicted values were found at year 2004–2005 for the pattern of trout length distributions in both streams, and at years 2009–2010 and 2010–2011 for the three other patterns (i.e., ratio of trout abundance in both streams, return rate of spawners to the Lesse River after reproduction and total number of juvenile migrants). The two last years, which were considered as independent data, contributed for about 49% of these discrepancies. For the pattern of trout abundance ratio, discrepancies observed for years 2007–2008 and 2008–2009 were explained by the fact that twice as many individuals migrating downstream were observed these two years, in comparison with the other years. The model was thus less successful in adapting to exceptional events. The discrepancy observed in 2005–2006 for the spawner return rate pattern was explained by the performance of model calibration. Indeed, the discrepancy for this year was the highest for the calibration pattern linked to the number of upswimming spawners, with 61 simulated individuals instead of 145.

4.3. Model applications

The sensitivity of the validated DemGenTrout model to its parameters was analysed. Two simulation scenarios were then compared (i.e., migration barriers and stocking with hatchery trout) to study the subsequent changes such human disturbances can cause on the demogenetic structure of a brown trout population. For both applications, two demographic (i.e., trout abundance in the Chicheron Brook and in the Lesse River) and three genetic outputs

(i.e., inbreeding coefficient F_{IS} in each stream, and fixation index F_{ST} between trout of both streams) were monitored.

4.3.1. Sensitivity analysis

The DemGenTrout model was not sensitive to the four parameters describing the trout length–weight relationship, and to the parameter of length heritability. These parameters do not influence the chosen demogenetic outputs for the following reasons. In the first case, they intervene in the growth process to determine the fish new weight, which is never used in the model as a physical criterion for the selection of trout for moving or spawning. In the second case, length heritability was varied from 0 to 1 during the sensitivity analysis. With these extremes values, either the environmental deviance or the genetic deviance is null, and their respective contribution to the offspring length is smaller (<35%) than the one of the parental population mean. Furthermore, two years will elapse before trout length intervenes as a criterion, and during that time interval, other parameters such as those of the von Bertalanffy growth equation will act on length values. The variables of the logistic function for the probability of moving for age-1 trout also have no impact on the five demogenetic indicators. This result was quite surprising since this parameter directly regulates trout abundance in the brook. This effect was masked by the high quantity of age-0 trout (40–80% of the total population) present in the brook during the migration period in comparison with the number of age-1 migrants (1–20%). For the goal currently achieved by the DemGenTrout model, its structure could be simplified by (i) removing the length–weight relationship in the growth process and replacing the criterion in the selection of spawners by their length instead of their condition factor, (ii) omitting the phenotypic deviance term in the equation of Kempthorne (1957).

Four survival rates (for age-0, age-1, age-2 trout in the Chicheron Brook, and age-0 trout in the Lesse River) were identified to have a strong influence on trout abundance in the brook and on the genetic outputs. These latter were also highly influenced by two other parameters, the von Bertalanffy growth coefficient for trout in the main stream, and the mean of the condition factor distribution of spawners. After the analysis of these six parameters with the variance decomposition method of Sobol, we found that survival of fry in the brook was the parameter that, once fixed to its true value, would reduce the most the variance of all demogenetic outputs. The second more important parameter was the mean of the spawner condition factor distribution, which contributed mainly to the reduction of both trout abundance variances. The parameter linked to the von Bertalanffy growth coefficient was involved in a lesser extent in genetic outputs variance reduction.

Trout survival rates and von Bertalanffy growth equation parameters were estimated by fitting Bayesian hierarchical models to capture–recapture data. These estimates are probably the most accurate value currently achievable, given that quite extensive and precise data were available for the studied hydrological system. The mean of the spawner condition factor distribution was derived from length and weight measurements obtained during capture–recapture experiments. Almost three quarters of the model parameters were directly or indirectly quantified from field observations (i.e., 66 parameters out of 91). Availability of data can therefore be an issue and can compromise the applicability of the DemGenTrout model to less informative systems.

Parameter values could almost always be derived from literature, but this can be problematic for parameters linked to survival and growth because of their highly variable nature. Survival in stream-dwelling salmonids may be influenced by several factors. Among them, hydrological variability, food availability, and biological interactions between individuals have been demonstrated

to be of major importance (Nehring and Anderson, 1993; Jowett, 1995; Cattaneo et al., 2002). Growth variation is mainly regulated by food availability and water temperature (Lobon-Cervia and Rincon, 1998; Vollestad et al., 2002; Dineen et al., 2007). To illustrate this point, we compared von Bertalanffy growth curves based on values found in Büttiker and Labous (2002) and Arslan et al. (2007) and obtained with the Lesse River parameters. Lengths of age-2 trout predicted by literature were comprised between 89 and 238 mm, while we found a value equal to 206 mm in the case of the Lesse River.

4.3.2. Impact of anthropogenic disturbances on brown trout

Both scenarios simulating anthropogenic disturbances were assumed to have a strong impact on the demogenetic structure of brown trout. First, it was expected that the number of wild trout in the Chicheron Brook would decrease over the 35 years of simulation. This was only the case in the migration barrier scenario, for which a drastic decrease was observed. In the three versions of the stocking scenario, abundance of wild trout were in range with value of the baseline scenario (i.e., without any disturbances). Second, an increase of the trout inbreeding coefficient in the brook was expected. This effect was very significant when a barrier preventing the migration of spawners was simulated, but was absent in the case of the stocking scenarios. Third, the evolution of genetic differentiation among trout of both streams showed a similar trend as the one observed for the F_{IS} . For the barrier scenario, the F_{ST} has increased as expected, but not for the stocking scenarios.

Results from the migration barrier scenario revealed a severe reduction in trout abundance in the brook, until its complete extinction after 13 years. This was obviously caused by its isolation from the main river, which prevented spawners to move upstream and to contribute to offspring production. The negative relation between abundance and downstream movement of age-2 trout noted in observed data and after calibration was responsible in great part for this phenomenon. Indeed, when we reiterated the simulation by setting the variables of this function identical to those used for age-1 migrants, we found that the extinction in the stream did not occur. We observed a mean abundance of only 263 individuals the last 5 years of the simulation, and this confirmed the importance of the negative relation. The disconnection also limited the gene flow between both streams and resulted in the significant increase of the F_{IS} value computed at year 8, which was five times higher than the one found in a situation without disturbances. A negligible genetic differentiation was observed within the trout population, since F_{ST} values stayed below 0.020 during all the simulation period, although it was 17 times higher at the end of the simulation than at the beginning.

Our results confirm that a barrier to migration can have a strong impact on the demogenetic structure of a local brown trout population, as previously shown in other studies. It not only increases the extinction risk (Morita and Yamamoto, 2002; Letcher et al., 2007), but it can also lead to an accelerated loss of genetic diversity in above-barrier populations as well as an increase of genetic differentiation among populations (Carlsson and Nilsson, 1999; Meldgaard et al., 2003; Neville et al., 2006).

The analysis of the 10-year stocking scenario with different intensities showed that abundance of wild trout in the brook stayed in range with the baseline situation. The increases of inbreeding coefficient and genetic differentiation were not significant, since values averaged over the last 5 years of simulation were close to the ones obtained in the baseline scenario. F_{IS} values were around -0.013 , while F_{ST} values were comprised between 0.001 and 0.002 with maxima around 0.018–0.033 between years 6 and 8. Demogenetic impacts of stocking were thus relatively weak after 35 years.

These unexpected results might be either due to the low probability of spawning hypothesized for stocked trout, or to their low survival during their first year in the main river. Consequently, we reiterated the simulation by implementing (i) a spawning probability equal to 1 for all breeds, (ii) a survival rate for freshly stocked trout similar to wild trout, (iii) the two previous modifications. In all situations, a medium short-term genetic differentiation was observed among wild trout of both streams when a significant number of stocked fish survived in the wild. If in addition stocked trout had a spawning probability similar to wild trout, serious ecological and genetic issues occurred at both time frames: (i) an inbreeding situation and a medium genetic differentiation at short term, and (ii) a drastic reduction in abundance of wild trout at long term.

5. Conclusions

The overall purpose of the DemGenTrout individual-based model was to contribute to the management of wild brown trout populations by simulating the demogenetic structure of a population at the scale of a river/nursery brook hydrological system.

The extensive collection of demographic, genetic, and environmental data available for the studied system allowed us to design a model with a fairly complex structure (i.e., 9 submodels and 91 parameters). As the model was optimized and validated within the pattern-oriented modelling framework, using a total of 12 patterns observed in the field, its complexity seems to not compromise its reliability to represent the general behaviour of brown trout individuals between a main river and its headwater tributary.

From the sensitivity analysis of the DemGenTrout model, we found that modifications in survival and spawning parameters could lead to important changes in the demogenetic structure of the brown trout population. This was verified by the results obtained from the comparison of the two scenarios simulating anthropogenic activities during 35 years. First, the overall impacts caused by a barrier to spawning migration on the demogenetic structure of the population were responsible for the extinction of the brook population after only 13 years. Second, stocking with hatchery fish, an activity that modifies both trout survival and reproductive potential, showed a relatively weak impact on the structure of the population provided that hatchery trout had lower survival and spawning probabilities than wild trout. This impact nevertheless resulted in an irreversible loss of genetic variability within the population.

In the future, we hope that the DemGenTrout model will be used and extended by others. For instance, the watershed scale could be considered so that interactions among several brown trout populations could be integrated. To this end, the model was uploaded to the NetLogo User Community Models public Web space.

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Appendix A. Supplementary Data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2012.09.017>.

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