Brown trout demogenetics in the Belgian Ardennes: An individual-based modelling approach

Béatrice Frank

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Jury members

Pr. Jacques Mahillon (Chairman)	Université catholique de Louvain
Pr. Philippe Baret (Supervisor)	Université catholique de Louvain
Pr. Pierre Defourny	Université catholique de Louvain
Dr. Justin Travis	University of Aberdeen (UK)
Pr. Filip Volckaert	Katholieke Universiteit Leuven

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Summary

The brown trout (*Salmo trutta* L.) is one of the vertebrate species presenting the highest degree of intraspecific biological diversity. 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, by providing (i) a descriptive tool to study the functioning of a brown trout population at the stream scale, (ii) a predictive tool to evaluate the medium-term impacts of anthropogenic disturbances on native populations.

The DemGenTrout model was first parameterized with demographic, genetic, and environmental data collected over 5 years on the Lesse River drainage (Belgium). A methodology for attributing a birth year to tagged trout of this hydrological system was developed. This information was used to determine the values of several parameters of the main four processes of the model (i.e., survival, growth, reproduction, movement). Second, the model was optimized and validated using the Pattern-oriented modelling strategy, which consists of systematically testing how well the model reproduces multiple patterns observed in the field. Third, the sensitivity of the model to its parameters was analysed.

Two scenarios mimicking anthropogenic disturbances were simulated over 35 years: (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, whereas 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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A	Number of alleles per locus
CB or stream C	Chicheron Brook
CJS	Cormack-Jolly-Seber (model)
CR	Capture-recapture
DNA	Deoxyribonucleic acid
E_A	Effective number of alleles
FCA	Factorial correspondence analysis
F_{IS}	Wright's F_{IS}, or Wright's F statistics among Individuals relative to the Subpopulation
F_{ST}	Wright's F_{ST}, or Wright's F statistics among Subpopulations relative to the Total population
GIS	Geographic information system
H_E	Expected heterozygosity (allelic frequency)
H_{NB}	Unbiased expected heterozygosity (allelic frequency)
H_O	Observed heterozygosity (allelic frequency)
IBM	Individual-based model
IFIM	Instream flow incremental methodology
IPM	Integral projection model
JS	Jolly-Seber (model)
LR or stream L	Lesse River
LWR	Length-weight relationship
MCMC	Markov Chain Monte Carlo
MSCR	Multistate capture-recapture
ODD	Overview, Design concepts, Details
OOP	Object-oriented programming
POM	Pattern-oriented modelling
PIT	Passive integrated transponder
PVA	Population viability analysis
QG	Quantitative genetics

SD	Spatial dynamics
TF	Trapping facility
VBE	von Bertalanffy equation
WUA	Weighted usable area
YOY	Young-of-the-year

Related publications

- **Frank B.M.**, Baret P.V. and Piccolo J.J. (2011). A review of ecological models for brown trout: towards a new demogenetic model. *Ecology of Freshwater Fish* 20 (2): 167–198.
- **Frank B.M.**, Gimenez O. and Baret P.V. (2012). Assessing brown trout (*Salmo trutta*) spawning movements with multistate capture-recapture models: a case study in a fully controlled Belgian brook. *Canadian Journal of Fisheries and Aquatic Sciences* 69 (6): 1091–1104.
- **Frank B.M.** and Baret P.V. (in press). Simulating brown trout demogenetics in a river / nursery brook system: the individual-based model DemGenTrout. *Ecological Modelling*.

Introduction and objectives

> *"What distinguishes a mathematical model from, say, a poem, a song, a portrait or any other kind of model, is that the mathematical model is an image or picture of reality painted with logical symbols instead of with words, sounds or watercolors."* – John Casti, 1997, Reality Rules: Picturing the World in Mathematics, Vol. 1.

In the present thesis, we focus on the impacts caused on wild brown trout (*Salmo trutta* L.) populations by impassable obstacles and stocking from hatcheries. Anthropogenic threats can induce demographic and genetic (i.e., demogenetic) deleterious effects on populations.

The study conducted by Huet and Timmermans (1979) on a small stream network of the Lesse River, in the Belgian Ardennes, was used as a starting point. They investigated movements of brown trout between a main river and one of its headwater tributaries. Such movements are frequent since the species uses main stems to grow and mature (Baglinière *et al.*, 1987; Jonsson and Jonsson, 1993; Forseth *et al.*, 1999) and first-order streams as spawning and nursery areas (Elliott, 1994; Crisp, 1996; Armstrong *et al.*, 2003). Experiments like those of Huet and Timmermans are one way to explore this question. Owing to advances in capture and marking, as well as in computer science, modelling approaches can nowadays be used to study individual responses to migration[1].

Studying the functioning of a brown trout population and evaluating how it is impacted by anthropogenic activities require understanding the demographic and genetic characteristics of this population. Modelling

[1] In ecology literature, the term "migration" refers to movement of individuals in a periodically and geographically predictable way, whether it occurs just once or many times (Sugden and Pennisi, 2006). In population genetics literature, migration refers to genetic exchange among breeding groups, or gene flow (Allendorf and Luikart, 2007). To avoid confusion in this thesis, we will use the meaning adopted in ecology.

approaches have the advantage of considering the different temporal scales needed to deal with both aspects: short scales (i.e., every year) for demographic studies, and longer scales (i.e., 10 years) for evolutionary studies.

After an ecological background on the brown trout species in the first section, the study area and the techniques used to capture and mark the individuals are presented in Section B. In Section C, we demonstrate how the progressive use of individual-based simulation techniques has led to the emergence of the demogenetics field and its associated models. In Section D, we first describe the modelling cycle we followed to develop an individual-based model able to simulate the demogenetic structure of a brown trout population at the local scale. Then, field data available for the studied hydrological system are presented, and their specific use in the model is explained. Eventually, the main characteristics of the model are given, and its design choices are justified. The last Section E presents the objectives and the outline of the thesis.

A The brown trout species

A.1 Distribution and ecology

The brown trout (*Salmo trutta* L.) is a fish species that was originally distributed in Europe and in North Africa. During the 20^{th} century, the species was introduced worldwide, in more than twenty countries (Fig. 1). Factors determining the success of these introductions were the great adaptability of this species to diverse ecological conditions and its high tolerance to habitat changes (Baglinière and Maisse, 2002; Klemetsen *et al.*, 2003).

Within the species, two life-history strategies and three ecological forms are distinguished: the migratory type, which is either marine (*Salmo trutta trutta*) or lacustrine (*Salmo trutta lacustris*), and the resident type living in rivers (*Salmo trutta fario*) (Baglinière and Maisse, 1991). Studies based on trout mitochondrial DNA revealed the presence of five major evolutionary lineages (Bernatchez, 2001): Atlantic, Mediterranean, Adriatic, Danubian and *marmoratus*. In Belgium, wild brown trout populations are mainly present in the upper basin of the Meuse River and are associated with the Atlantic lineage.

Life expectancy of a brown trout is 5 to 6 years, and its adult length varies between 20 and 50 cm, for a weight between 0.1 and 1.2 kg (DGRNE, 2004). On average, 2 500 eggs per kilogram of female are

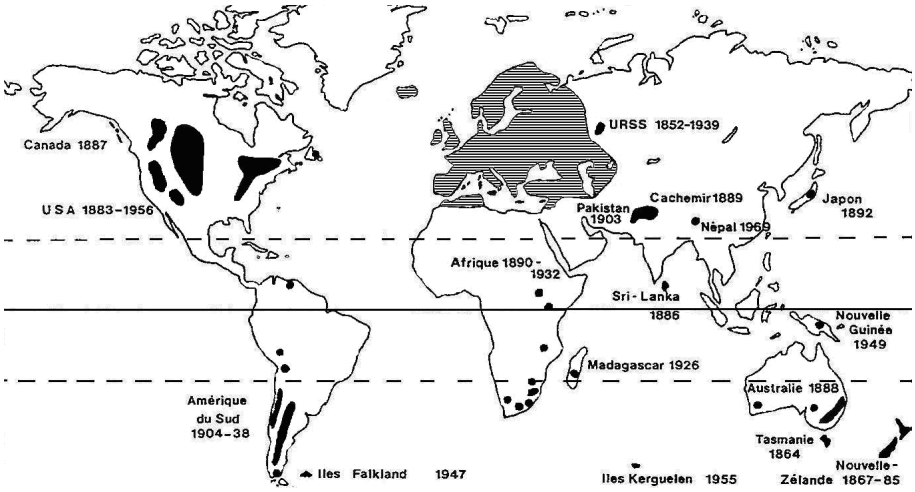

Figure 1: Natural area of distribution (hatched) and areas of introduction (solid black) of brown trout (*Salmo trutta* L.). Modified from Baglinière (1999).

laid in gravel from November to January, and the eggs hatch in early spring (Milner *et al.*, 2003; DGRNE, 2004). Then, alevins (i.e., larvae of 15 to 25 mm) remain in the gravel for a short period (4-6 weeks), feeding on their yolk sacs. They emerge as fry and begin their feeding on drifting invertebrates (Milner *et al.*, 2003). Fry are located mainly in streams and basin heads, and begin to colonize the main river when they grow older.

A.2 Threats to genetic diversity

The wide geographical distribution and the high polymorphism of *Salmo trutta* have contributed preventing its classification as an endangered species in the IUCN Red List[2]. However, the trout is one of the vertebrate species presenting the highest degree of intraspecific biological diversity, including strong genetic and phenotypic variation among populations. Management activities have induced a loss in brown trout genetic diversity, and many wild populations are now faced with a medium-term risk of extinction (Laikre, 1999; Dudgeon *et al.*, 2006; Caudron *et al.*, 2011).

Indeed, fish are managed directly through the commercial and sport harvest of individuals, and indirectly by land use activities (e.g., agricul-

[2] International Union for Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species, `http://www.iucnredlist.org`. Version 2011.2. Web site consulted on 3 January 2012.

ture, urbanisation, hydroelectric development) that change the physical environment of fish (Young, 2004). This management incorporates conservation, environmental, social and economic considerations. Conservation is sometimes considered as the collection of actions necessitated by prior mismanagement (Young, 2004), and includes methods such as designation of nature reserves, regulation of exploitation, and captive breeding programmes for stock enhancement (Collares-Pereira and Cowx, 2004). In Europe, the main anthropogenic threats to the brown trout species are (i) environmental degradation (pollution, altered flow, habitat fragmentation), (ii) stocking from hatcheries, (iii) overexploitation (Laikre, 1999).

B The Lesse River / Chicheron Brook hydrological system

B.1 Study area

The stream network of the Lesse River, a tributary to the Meuse River, occupies an area of 1343 km^2 and is located in southern Belgium (Fig. 2). The study area consists of a 1.1 km-long section of a main stream (Lesse River) with one 1.2 km-long tributary (Chicheron Brook). The Lesse River is located at the boundary between the trout and the grayling fish assemblage zones; the stream has a 0.8% slope, is 13 to 27 m wide, has an average depth of 0.5 m, and has a 4 $m^3.s^{-1}$ average discharge rate. The studied section of the river flows through a wide forested area and offers excellent water quality. 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.

B.2 Capture and marking of brown trout

Over the years, different devices, either static (trapping facilities) or mobile (electrofishing), were used to capture brown trout of the Lesse River / Chicheron Brook hydrological system. Three periods of observations are distinguished: from 1957 to 1987, from 1996 to 2002, and from 2003 to today. The second one is a transition period used to define and improve the capture procedures, and results obtained during this period are therefore not considered in this thesis.

In 1957, a trap was built 20 m upstream from the confluence of the Chicheron Brook into the Lesse River. The trap was monitored for 30

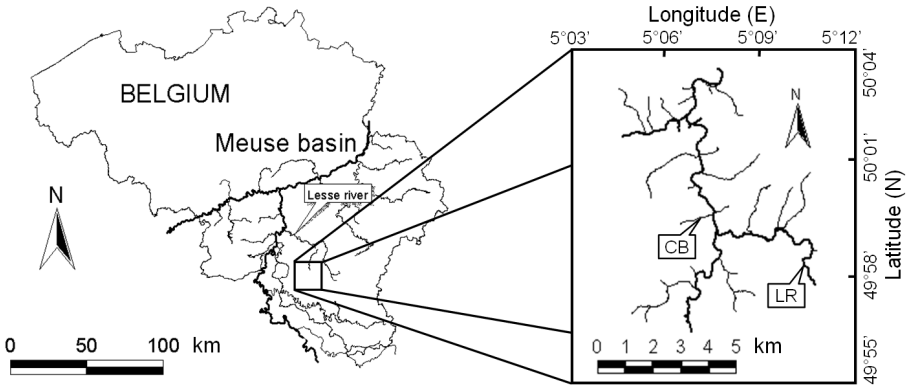

Figure 2: Situation plan of the Lesse River (LR) in the Meuse basin, and position of the Chicheron Brook (CB) in the Lesse basin.

years by M. Huet and J.A. Timmermans (Station de Recherches des Eaux et Forêts, Groenendaal-Hoeilaart), and its catch efficiency was around 70% due to its malfunction during spate events (E. Dupont, Earth and Life Institute, Université catholique de Louvain, Croix du Sud 2 Box L7.05.14, 1348 Louvain-la-Neuve, Belgium, personal communication, 2011). Trout were marked by fin removal, a different fin being cut each year. The following movements were identified (Huet and Timmermans, 1979): (i) an upstream migration of mature adults from the river to the brook for spawning in autumn and winter, (ii) the return of these adults to the river after spawning, (iii) a downstream migration of fry and juveniles from the brook to the river in spring and summer of that same year or the next years. Thus, three main types of movements are observed during one given year between the Chicheron Brook and the main stream (Fig. 3).

The trap was abandoned from 1987 until 1996. It was then restored under the supervision of E. Dupont (Centre de Recherche de la Nature, des Forêts et du Bois, Marloie). An auto-powered and self-cleaning trapping facility was built in 2003 with the purpose of getting more precise results about the migration pattern of brown trout. The new trapping system is able to cope with flooding and can be considered as exhaustive (i.e., all individuals entering or leaving the tributary are captured in the upstream and downstream traps), making the Lesse River / Chicheron Brook system fully controlled. The migration pattern observed by Huet and Timmermans was confirmed (Dupont, 2009); each winter, 100 to 500 spawners are observed to migrate from the Lesse River to the Chicheron Brook to spawn, and 300 to 900 young trout swim down to the main river during the successive spring and summer (see also Chapter 2).

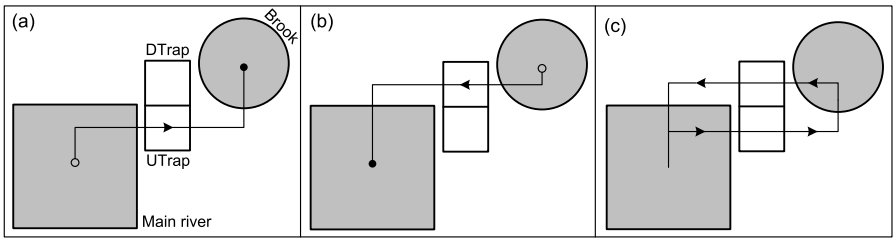

Figure 3: Brown trout can perform three types of movement between the Lesse River and the Chicheron Brook, during which they are caught in the upstream (UTrap) and/or downstream (DTrap) traps. During the reproduction period, trout immigrate to then emigrate from the brook. For some of the spawners, the immigration will be permanent because they may die or decide to stay (and die) in the tributary (a); the others will return to the main river after the spawning (c). In spring and summer, some fry and juveniles born in the tributary swim downstream to the main stem (b).

This exhaustive trapping was supplemented by electrofishing operations in both streams. Individuals were captured once a year from 2001 in the Lesse River in autumn (before the spawning migration of mature adults) and twice a year from 2004 in the Chicheron Brook in autumn and in spring (before and after the stay of the adults, respectively). From the year 2003, all trout caught either by trapping or electrofishing and with a body length > 7.5 cm (6 cm since 2007) were marked with passive integrated transponder (PIT; Réseaumatique, Bernay, France) tags following anaesthesia with clove oil. In addition to the marking operation, the adipose fin of each newly tagged fish was removed and stored in a -80 °C refrigerator for subsequent genetic analyses. All captured fish were measured for total length (mm), and most of them were weighed (g).

C Ecological models for brown trout: state of the art

Considerable advances have been achieved in the development of ecological models for brown trout over the past 30 years (see Chapter 1). Population dynamics and population genetics models evolved mostly in separate ways until recently, when attempts including either more genetic realism into population dynamics models or more biological realism into population genetics models begin to appear. Indeed, several studies showed that ecological and life history characteristics such as population size, dispersal pattern[3] and mating system could influence fish popula-

[3] The term "dispersal" encompasses all movements of individuals with potential consequences for gene flow across space (Ronce, 2007).

tion genetic divergence through their effects on genetic drift and gene flow (Turner and Trexler, 1998; Dawson *et al.*, 2002; Whiteley *et al.*, 2004).

A new field called demogenetics has begun to emerge. This discipline integrates 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 (Crawford, 1984; Waples, 2006).

The use of individual-based simulation techniques has greatly facilitated the development of the demogenetics field and its associated 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). To our knowledge, only a few individual-based demogenetic models have been specifically developed for or applied to salmonids. We identified four nonspatial models: one population dynamics model, VORTEX (Lacy, 2000b; Lacy *et al.*, 2005), and three quantitative genetics models (Dunlop *et al.*, 2009; Wang and Hook, 2009; Piou and Prévost, 2012). VORTEX is used for population viability analysis, which predicts the likelihood of the persistence of an endangered species for a given time (DeSalle and Amato, 2004). Quantitative genetics models, also called eco-genetic models, 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).

One step further in the development of ecological models for brown trout would be the integration of the spatially explicit methodology into demogenetic models, to better address the important issue of ecological scale. The interplay between environmental processes and demogenetic characteristics is indeed crucial. For instance, at the stream scale, an environmental perturbation can represent a radical and rapid change in the demographic and genetic structure of a population, producing local catastrophes and reductions in suitable areas where fish can thrive (Pertoldi and Topping, 2004). At a larger scale, the structure and complexity of the riverscape can affect the demogenetics of fish populations by influencing the occurrence of their dispersal strategies, and by interacting with the micro-evolutionary processes.

Individual-based simulation techniques would be a valuable tool to include different levels of spatial details, as they were designed to ex-

plore how the properties of higher level ecological entities, like populations, emerge from interactions of individuals with each other and their environment (Grimm and Railsback, 2005). Five major types of individual variation can be explicitly included into individual-based models (DeAngelis and Mooij, 2005): spatial (local interactions and movement), ontogenetic (life cycle and development), phenotypic (plasticity and behaviour), cognitive (experience and learning), and genetic (evolution). Although a few individual-based models combining these three dimensions already exist (e.g., KERNELPOP; Strand and Niehaus, 2007), no comprehensive, spatially explicit, demogenetic model was ever proposed for brown trout populations. In the literature, we identified only two spatially explicit bioenergetic individual-based models, the one developed by R.C. Addley during his M. Sc. thesis in 1993, and the inSTREAM software of Railsback *et al.* (2009). Bioenergetic models integrate both demographic and spatial dimensions, and therefore not the genetic one. They evaluate fish 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).

D A model to simulate the demogenetic structure of brown trout

A model called DemGenTrout was developed to simulate the demogenetic structure of the brown trout population living in the Lesse River / Chicheron Brook hydrological system (see Section B). We used individual-based simulation techniques to explicitly include three types of individual variability in the DemGenTrout model: demographic (life cycle), spatial (movement between the two streams), and genetic (natural selection).

For the development of the model, we followed a modelling cycle comprising four phases, i.e., conceptualisation, specification, implementation, and analysis (Section D.1). During this cycle, different types of field data collected on the hydrological system were used. They are presented in Section D.2. The main characteristics of the model are then given in Section D.3.

D.1 Modelling cycle

The modelling cycle comprised four phases (Grimm and Railsback, 2005). In the conceptualisation phase, the purpose and the main structure of the model are described in words but also by a conceptual diagram. During the specification phase, the design of the model is defined, and a detailed description of the included processes and input data is provided. In the third phase, the model is translated into a programme, which is thoroughly documented. The initial values of all variables and parameters are also specified. In the last phase, the model is analysed in order to improve its performances and to be validated.

Throughout this modelling process, two protocols were used. The first one is called ODD, for "Overview, Design concepts, Details" (Grimm *et al.*, 2006, 2010), and is explained in detail in Section D.1.1. The conceptualisation and specification phases of a model are gathered through this protocol. The second protocol is the Pattern-oriented modelling (POM; Grimm *et al.*, 1996; Wiegand *et al.*, 2003; Grimm *et al.*, 2005) strategy, which is formally defined as "the multi-criteria design, selection, and calibration of models of complex systems" (Grimm and Railsback, 2012). The POM protocol is used during the implementation and analysis phases of a model, and is presented in Section D.1.2. The model was coded in NetLogo (Wilensky, 1999), a free platform that offers a programmable modelling environment for individual-based simulations (Section D.1.3).

D.1.1 Model conceptualisation and specification following the "Overview, Design concepts, Details" protocol

The "Overview, Design concepts, Details" (ODD) protocol consists of three categories, comprising in total seven elements (Fig. 4). A template document for writing the ODD description of models is provided as supplementary material in Grimm *et al.* (2010). This template can be used as a check list and includes questions and explanations for each element of the protocol. The purpose of this protocol is to ease the communication and replication of individual-based models. Indeed, ODD promotes rigorous model formulation, facilitates reviews and comparisons of models, and may also encourage the use of more holistic modelling approaches (Grimm *et al.*, 2010).

Using the ODD protocol is thus a means of producing a transparent and comprehensive model description, which allows to make individual-based models less subject to criticism for being irreproducible (Grimm

et al., 2010; Schmolke *et al.*, 2010). Frequently raised critiques are that the protocol is redundant, is overdone for simple models, and separates properties (state variables) and methods (processes), which form one unit in object-oriented programming (Grimm *et al.*, 2010). Another weakness of ODD is that it is designed to describe a definite model version, whereas the modelling cycle is an iterative process that requires frequent back and forth between the phases (Grimm and Railsback, 2005; Grimm *et al.*, 2010). To overcome this issue, a general framework for "transparent and comprehensive ecological modelling documentation", TRACE, has been proposed (Schmolke *et al.*, 2010). This framework includes not only the model description but also elements of its development and analysis. An ODD protocol would thus be part of a TRACE documentation.

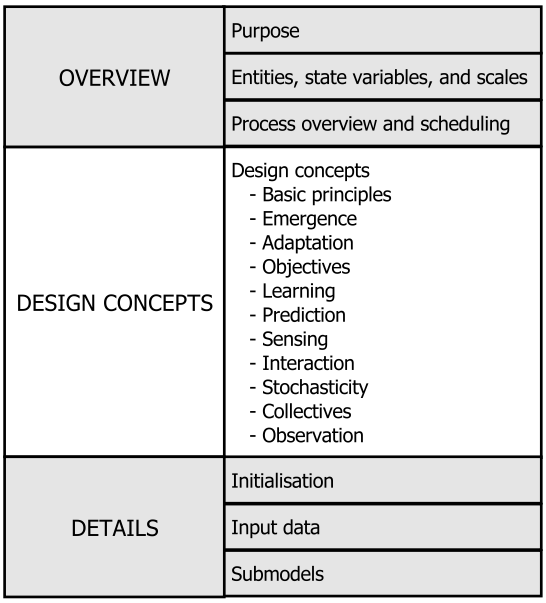

Figure 4: The seven elements of the ODD protocol, grouped in three categories ("Overview, Design concepts, Details"). Figure redrawn from Grimm *et al.* (2010).

The first three elements provide an overview of the model, by stating (i) the question addressed, (ii) its structure in terms of entities (agents), state variables, temporal and spatial scales, (iii) its dynamics, i.e., the order in which the processes (submodels) of the model are executed.

In the fourth element, the model design is depicted through 11 key concepts. The first one, named basic principles, is very general and al-

lows modellers to describe theories, hypotheses, and general approaches motivating their models. The 10 other design concepts are borrowed from the field of complex adaptive systems, which focuses on how the properties of individual aggregations can be determined by their characteristics and behaviour (Railsback, 2001). In this theory, a *trait* is a set of rules describing actions of individuals at particular time or in response to specific situations in a model. A *behaviour* corresponds to the action actually performed by an individual or a system during a simulation. It is an outcome, whereas a trait is a set of model rules that individuals use to select their behaviours. An *adaptive trait* is a trait that includes some kind of active choice among alternative behaviours, with the decisions depending on environmental or internal conditions. A *state* is a measure of the status of some model part that can be described by a single number, and a *submodel* is a part of a model formulation that represents one trait or process. The meaning of each design concept is summarized hereafter:

- Emergence, a system property or behaviour not directly specified by individual traits;
- Adaptation, a choice actively made by the individuals among alternative behaviours;
- Objectives, the measure of the success of an individual at meeting some objectives such as fitness;
- Learning, the change over time of adaptive traits by individuals as a consequence of their experience;
- Prediction, the way individuals foresee the future outcomes of their decisions;
- Sensing, the way individuals obtain information about their environment and neighbouring individuals;
- Interaction, the communication of individuals with each other or their effect on each other;
- Stochasticity, the representation of a submodel by pseudo-random numbers;
- Collectives, aggregations of individuals that have their own characteristics and behaviour;
- Observation, the process of collecting data and information.

The remaining three elements of the ODD protocol complete the model description. They provide further details about model initialisation, input data, and submodels.

D.1.2 Model implementation and analysis within the pattern-oriented modelling framework

The pattern-oriented modelling (POM) framework proposes guidelines to develop models reproducing multiple patterns observed in the field and to systematically evaluate the agreement between these patterns and those predicted by the model (Piou *et al.*, 2009; Grimm and Railsback, 2012). A *pattern* is a defined characteristic of a system, a clearly identifiable structure in nature itself or in the data extracted from nature (Wiegand *et al.*, 2003). Examples of patterns are time series data of population counts, self-thinning relationship in a population, or the maximum distance moved by individuals.

The objective of the POM strategy is to make ecological models more structurally realistic and predictive (Grimm and Railsback, 2012). This allows to increase the reliability of individual-based models, which have suffered critics about their internal complexity and the high specificity of their results. In POM studies, traditional methods of goodness of fit (e.g., sum of squares evaluation) or ad hoc comparisons of fitting errors and variations are recommended as a baseline approach (Piou *et al.*, 2009; Grimm and Railsback, 2012). These methods are possibly followed by more rigorous approaches based on information theory (Piou *et al.*, 2009), on approximate Bayesian computing (Csilléry *et al.*, 2010; Beaumont, 2010), or likelihood-based (Hartig *et al.*, 2011; Martinez *et al.*, 2011).

The POM strategy is used throughout the modelling cycle, and follows four steps (Grimm and Railsback, 2012). In the first step, the purpose is to help improving the structure of the model. The key processes are first identified. Often, they correspond to the adaptive traits present in the model. A set of observed patterns (ideally 3 or 4) against which the model will be tested is then defined, along with criteria for pattern-matching (i.e., outputs used to evaluate whether the model reproduces each pattern). The structure of the model is finally revised so that the chosen patterns can be reproduced.

The second step of POM is linked to model parameterization and calibration. Parameter values are first determined directly (i.e., from literature, expert knowledge, sampling, experiments, etc.) in order to reduce the parameter space (Duboz *et al.*, 2010). A calibration of the model is then conducted to estimate the remaining unknown parameters, either manually or using automated approaches such as genetic algorithms. Calibration patterns as well as acceptance criteria are de-

fined, and simulations are undertaken for each parameter combination to test.

The third step of POM is the selection of the most appropriate submodels for the previously identified key processes. Different hypotheses are formulated for these processes, which are implemented in alternative models. The latter are then tested against the selected patterns. The procedure is repeated until a model implementation reproducing all the patterns is found (Grimm and Railsback, 2012).

Model validation corresponds to the fourth step of the POM strategy. It is the same method as the one presented for submodel selection, except that it is applied to the whole model. Furthermore, observed patterns must come from an independent data set, i.e., not used during parameterization or calibration (van Waveren *et al.*, 1999; Grimm and Schmolke, 2011).

D.1.3 The NetLogo platform

We chose the NetLogo platform, a multiagent programmable modelling environment, to implement the model. Originally authored by Uri Wilensky in 1999, NetLogo is now developed at the Center for Connected Learning and Computer-Based Modeling (Northwestern University, Evanston, IL).

Two other programming platforms were considered, Swarm (Minar *et al.*, 1996) and CAPSIS (de Coligny *et al.*, 2010), but the three following arguments finally promoted the use of NetLogo. First, the language used in NetLogo is simple and the modelling environment is easy to understand. Second, the software comes with a large collection of prewritten simulations that can be used and modified. Finally, extensive documentation and tutorials are available, and training workshops are regularly organised in Europe.

The individual-based approach lends to the use of *object-oriented programming* methods. In such methods, elements of the program are 'objects' which pass, receive, and respond to 'messages', and there is a direct correspondence between individuals in the model and objects in the program (Kimmerer *et al.*, 2001). An *agent* or entity is an object that behaves as a unit and may interact with other objects or be affected by external environmental factors. Its current state is characterised by its *state variables* or attributes. *Processes* or submodels are equations and rules that describe the dynamic behaviour of the model entities and that cause changes of the state variables. *Parameters* are constants that

quantify the relationships among state variables: they quantify when, how much, and how fast the variables change.

In NetLogo, a simple language structure, the Logo dialect, is used to give instructions to agents[4] operating independently in the model. These instructions are of two types: commands and reporters. A *command* is an action carried out by agents; a *reporter* computes a result and report it. A large vocabulary of built-in language commands and reporters (called *primitives*) is available and users have the possibility to write their own commands and reporter (called *procedures*). The example below illustrates how age of trout agents was updated at each time step in DemGenTrout.

■ ***Example.*** Let be assumed 10 agents with age as a state variable. State variables can be either already built into NetLogo or defined by the user, as in our example. User-defined state variables have to be declared at the beginning of the program, using the `turtles-own` keyword. Each turtle (agent) has its own variable value, and values can be changed with commands, either built into NetLogo (primitive) or user-defined (procedure). The keywords `to` and `end` mark the beginning and the end of a procedure. Once defined, a procedure can be used anywhere in the code.

In the following program, there are four primitives (i.e., `clear-all`, `create-turtles`, `tick`, `ask`) and three procedures (i.e., `setup`, `go`, `update-age`). Some of the primitives take an input, and use it to carry out the instruction. For instance, the `create-turtles` primitive in the `setup` procedure will produce, once executed, 10 turtles. The other primitive in the `setup` procedure is `clear-all`, which resets all global variables to zero as well as time, patches, drawings, plots, and kill all turtles. In the `go` procedure, the time counter is first advanced by one with the help of the `tick` primitive. Then, turtles are asked to run the `update-age` procedure, which simply increments the age of all agents by one.

```
turtles-own [ age ]

to setup
  clear-all
  create-turtles 10
end

to go
  tick
  ask turtles [ update-age ]
end

to update-age
  set age age + 1
end
```

■

[4] In NetLogo, agents are called “turtles” for historical reasons.

D.2 Field data used in the model

Three types of field data (i.e., demographic, genetic, and environmental) were available for the Lesse River / Chicheron Brook hydrological system (Section B) and were used for the development, optimization, and analysis of the DemGenTrout model (Table 1).

We followed the ODD protocol to describe the model (see Section 2.2 of Chapter 6, page 173). This latter was initialised with observations made in autumn 2004 at the system, and parameterized with demographic and environmental data available for the years 2001-2009 (see Chapter 5). Then, using demographic and genetic data, it was optimized by means of calibration and submodel selection, and validated within the POM framework (see Section 2.3.1 of Chapter 6, page 190). Eventually, two scenarios of anthropogenic disturbances were simulated, and one of them required demographic and genetic data from hatcheries (see Section 2.5 of Chapter 6, page 194).

Demographic data contain capture-recapture observations for trout of the studied system: place and method of capture, date, total length and for some of them weight (75%) and sex (10%). In total, more than 12 000 fish were caught and tagged, either when they were electrofished in both streams, or when they moved through the trapping facility. Trout length and weight measurements from electrofishing in autumn 2004 in both streams were used for model initialisation. Both electrofishing and trapping data were used to parameterize the survival, growth, spawning and movement processes of the model. These data were also involved during the calibration and submodel selection steps, and their analysis provided results that were used for model validation. Demographic data from the Ochamps hatchery were also used to simulate the stocking scenario, as 477 trout were measured for total length.

The genotypes of 288 trout were determined. Among them, 240 were electrofished in both streams and were used for the initialisation and optimization of the DemGenTrout model (96 trout from the Lesse River, 144 from the Chicheron Brook). The remaining 48 individuals were sampled from the Mirwart hatchery and were used for the simulation of the stocking scenario. The DNA extracted from their adipose fin was analysed with 12 microsatellite markers (see Section 2.2, Chapter 3).

Environmental data consist of time series of water temperature, flow rate and water height in both streams, and were used in model initialisation, and parameterization of the spawning and downstream movement processes. They also served as input data to represent how hydrological conditions in each stream change over time in the model. Water

Table 1: Available field data for the Lesse River / Chicheron Brook hydrological system used throughout the development of the DemGenTrout individual-based model. Data are of demographic, genetic, or environmental nature. The modelling steps during which each data type are used, and the time periods and sources for each of them are specified.

Type	**Modelling step**	**Data**	**Years**	**Sources**
Demographic	Parameterization, calibration, validation	Capture-recapture histories for wild trout	LR: 2001-2011 CB: 2004-2011	Electrofishing[a]
	Initialisation, parameterization, validation	Length and weight measurements of wild trout	LR: 2003-2011 CB: 2004-2011	Electrofishing
	Parameterization, calibration, validation	Length and weight measurements of wild trout, time periods of migration	2002-2011	Trapping facility[a]
	Simulation	Length measurements of hatchery trout	2008	Ochamps hatchery, Libin
Genetic	Initialisation, submodel selection	Genotypes of wild trout	LR: 2004, 2008 CB: 2003-2004, 2008	ISV/UCL[b]
	Simulation	Genotypes of hatchery trout	2008	Mirwart hatchery, Saint-Hubert
Environmental	Initialisation, input data, parameterization	Hourly water temperature in both streams	2004-2009	Data loggers[a]
	Initialisation, input data, parameterization	LR: daily flow rates	2004-2009	Station 8341, Wacondah network[c]
	Initialisation, input data, parameterization	CB: daily water heights	2004-2009	Trapping facility

CB, Chicheron Brook; LR, Lesse River.

[a] Direction Générale de l'Agriculture, des Ressources Naturelles et de l'Environnement, Service public de Wallonie.

[b] Institut des Sciences de la Vie, Université catholique de Louvain.

[c] Direction Générale de la Mobilité et des Voies Hydrauliques, Service public de Wallonie.

temperature in both streams was recorded every hour with automatic loggers. Daily flow rates for the Lesse River were available from a nearby permanent gauging station located in Daverdisse, and for the Chicheron Brook, water heights were recorded on days when the trapping facility was checked.

D.3 Characteristics of the model

Among the factors that may affect the demogenetic structure of brown trout, only those identified as crucial for fulfilling the final modelling objective (i.e., predicting the impacts of anthropogenic activities) were integrated into the DemGenTrout model (Fig. 5). During the development of the model, the emphasis was placed on the temporal dimension and the individual variability. We considered an unique population of brown trout living in autonomy in a closed system, characterized by an homogeneous habitat. DemGenTrout is thus not spatially explicit except for the consideration of two compartments, the Chicheron Brook and a section of the Lesse River.

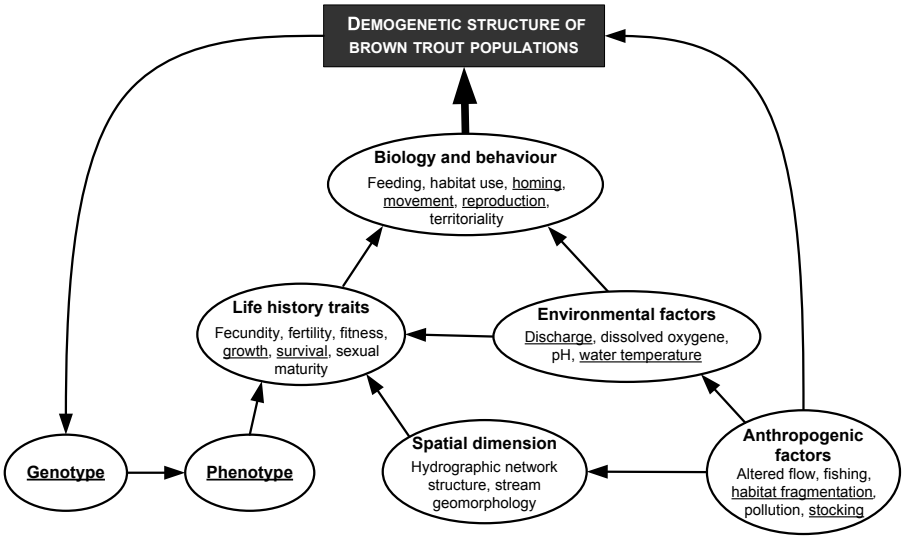

Figure 5: Factors influencing the demogenetic structure of brown trout populations. Underlined factors are considered in the DemGenTrout individual-based model.

Two types of entities were comprised in the model: two streams, representing the studied hydrological system, and trout agents. The following processes were considered: the update of hydrological conditions

for each stream agent; mortality, growth, ageing, spawning, and movement for each trout agent.

Data of different nature were used to parameterize the DemGenTrout model (i.e., demographic, genetic, and environmental; see Section D.2). Demographic and environmental data were extensive and precise for the studied hydrological system, allowing us to thoroughly model the trout life cycle. We decided to keep this part as simple as possible, and we provided only enough detail to meet the modelling purpose. For instance, we did not include stream physical characteristics and their influence on trout survival and growth as we were not interested in predicting how changes in habitat affect the demogenetics of the brown trout population.

Genotypes of individuals were derived from 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, for instance with F-statistics (Wright, 1969) (see Section 3.1.2 of Chapter 1, page 43).

The DemGenTrout model is compared hereafter with the most recent nonspatial and spatially explicit individual-based models for stream fish, IBASAM and inSTREAM (Table 2). This comparison served two purposes: (i) to explain why a new individual-based model was built from scratch, (ii) to highlight the limitations of the DemGenTrout model to address other questions than the one it was designed to, by identifying the differences among the models.

Neither IBASAM nor inSTREAM could have been used to meet our modelling objective of simulating the impacts of anthropogenic disturbances on a brown trout population, even after substantial adaptations. The first model, IBASAM, is an eco-genetic model designed by Piou and Prévost (2012) to study the impacts of environmental conditions on the life history strategies of Atlantic salmon. It explicitly includes environmental influence and the genetic transmission of traits, two characteristics that were not useful to consider in our case. The second model, inSTREAM, was developed by Railsback *et al.* (2009) to understand how salmonid populations would respond to habitat alteration. The model fully integrates the spatial dimension but no genetic aspects. If we were to use this model, supplementary field data such as turbidity regimes and stream morphology as well as important coding effort to integrate the genetic dimension into the software would have been required.

Table 2: Comparison of the DemGenTrout model with two other stream fish individual-based models, IBASAM (Individual Based Atlantic SAlmon Model) and inSTREAM (individual-based Stream Trout Research and Assessment Model).

Characteristic	**DemGenTrout**	**IBASAM**	**inSTREAM**
Modelling topic	Anthropogenic disturbances (migration barrier, stocking)	Environmental fluctuations (temperature, flow, marine conditions)	Habitat alteration (temperature, flow, turbidity, channel morphology)
Model organism	Brown trout (*Salmo trutta* L.)	Atlantic salmon (*Salmo salar* L.)	Salmonids
Model type	Demogenetic	Quantitative genetics	Bioenergetic
Agents	Fish, stream or compartment	Fish, redds, compartment	Fish, redds, reach, cell
Spatial extent	Two streams or compartments	Two compartments, a river and an ocean	Multiple linked reaches
Spatial resolution	Each stream is about 1 km-long	The river covers an area of about 40 000 m^2	The minimum size of one rectangular cell is 1 m^2
Time step	Weekly	Daily	Daily
Software	NetLogo/R	C++/R	Swarm

The four main processes of the DemGenTrout model (i.e., survival, growth, reproduction, movement) were simplified to some extent. Hereafter, we compare our implementation of each of these processes with the ones made in IBASAM and inSTREAM:

- Mortality sources are not explicitly modelled in the survival process. Comparatively, in the other two models, fish survival is function of habitat conditions: inSTREAM includes mortality sources such as high velocity and poor condition, while in IBASAM, eggs survival depends on flow and water temperature. Predation by terrestrial animals and by other fish are also directly accounted for in the survival submodel of inSTREAM.
- The DemGenTrout growth submodel does not explicitly include the feeding process of trout, and does not consider the influence of environmental conditions. IBSASAM does not consider feeding either, but juvenile growth is function of water temperature, flow and density. In inSTREAM, feeding strategies such as drift-food intake and active search for food are implemented, and standard bioenergetic approaches are used to calculate net energy intake for each feeding strategy. Water velocity, turbidity and temperature intervene in this process.

- Reproduction is simplified in our model as we do not consider the egg stage, and the maturation process of individuals is not explicitly modelled. In inSTREAM, production of eggs is modelled, and fish length, age, and condition are used to identify individuals ready to spawn, as we do in DemGenTrout. In IBASAM, the egg stage is included and maturing salmons can accumulate fat reserves.
- Two types of trout movement are considered in DemGenTrout: (i) migration of spawners to the brook and their return to the Lesse River after reproduction, (ii) movement of juveniles born in the brook to the Lesse River, modelled as a density-dependent process. These movements are simulated by a change of state variable of the concerned individuals. In IBASAM, the two migration phases of Atlantic salmon are simulated the same way. inSTREAM includes explicit movement of individuals among cells.

E Objectives and presentation of the thesis

The general objective of the present thesis is to contribute to the conservation of the brown trout species, by providing (i) a descriptive tool to study the functioning of a brown trout population at the stream scale, (ii) a predictive tool to evaluate the impacts of anthropogenic disturbances on native populations.

The studies conducted by Huet and Timmermans in 1957-1969 and by Dupont in 1996-2009 to better understand movements of brown trout between the Lesse River and one of its tributaries, the Chicheron Brook, were used as a starting point to design an individual-based demogenetic model. Some of the observations obtained earlier by Huet, Timmermans and Dupont were precisely quantified and supplemented with new findings. The final aim of this model, called DemGenTrout, is to predict medium-term impacts of human activities on the demogenetic structure of a brown trout population at the stream scale.

The thesis is structured in six chapters (Fig. 6). Two supplementary methodological boxes, located before the chapter to which they are linked, present the main modelling techniques used throughout this work: capture-recapture modelling (Box I, pages 63–66) and finite mixture distribution modelling (Box II, pages 109–110).

The **first Chapter** is a comprehensive review and synthesis of the brown trout ecological modelling literature. First, a bibliometric analysis revealed the existence of two main categories of models: population ecology (including population dynamics and population genetics models) and population distribution (including habitat-hydraulic and spatial

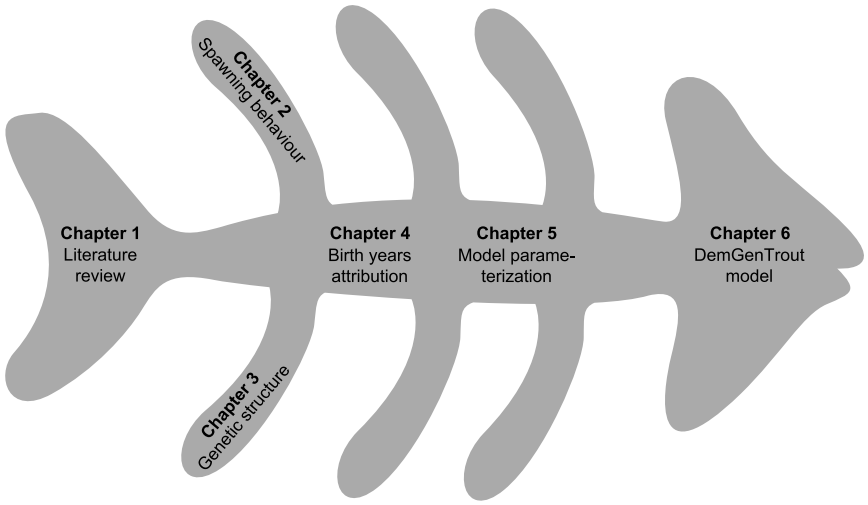

Figure 6: Thesis outline. After identifying the best suitable model type through a literature review (Chapter 1), a demogenetic individual-based model was developed for brown trout. Spawning behaviour and genetic structure of trout of the studied hydrological system were first investigated (Chapters 2-3). Discrimination of individuals by age (Chapter 4) was prior information required to parameterize the DemGenTrout model (Chapter 5). The model was then optimized and validated, and was finally used to simulate two scenarios of anthropogenic disturbances (Chapter 6).

distribution models). We then demonstrated how some of these models have already begun to be combined, and how they might be used to address questions relevant to the conservation and management of stream fish. We concluded the review by proposing a framework for a spatially explicit demogenetic model for brown trout populations that involved the use of individual-based simulation techniques. This framework was unfortunately not fully applied in this thesis. As explained in Section D.3, habitat was not explicitly modelled in the DemGenTrout model.

The next two chapters are independent studies conducted on the studied hydrological system. In **Chapter 2**, a multistate capture-recapture model (see Box I) was developed to infer brown trout spawning behaviour in the system. **Chapter 3** was an attempt to determine if significant genetic differentiation existed between migratory and sedentary trout born in the Chicheron Brook.

In **Chapter 4**, we present a methodology developed to assign birth years to trout through the decomposition of their length frequencies into age classes with finite mixture distribution models (see Box II). This in-

formation was required to parameterize the survival, growth, reproduction and movement processes of the model (**Chapter 5**). We used several statistical methods to determine the parameter values, from simple ones such as summary statistics or linear regressions, to more sophisticated ones such as Bayesian hierarchical modelling (see Box I).

The **last Chapter** gathers all the steps that led to the development of the DemGenTrout model. First, the model was described according to the ODD protocol, and simulation experiments conducted for its optimization and validation within the POM framework were presented. Then, results obtained from a sensitivity analysis were examined in order to identify influential parameters. Finally, two scenarios simulating anthropogenic disturbances were compared, and their respective impacts on the demogenetic structure of the brown trout population were evaluated.

Note: This thesis contains articles that were published in peer-reviewed scientific journals. When relevant, this information is specified by footnotes at the beginning of each chapter.

Chapter 1

A review of ecological models for brown trout: towards a new demogenetic model*

Ecological models for stream fish range in scale from individual fish to entire populations. They have been used to assess habitat quality and to predict the demographic and genetic responses to management or disturbance. In this paper, we conduct the first comprehensive review and synthesis of the vast body of modelling literature on the brown trout, *Salmo trutta* L., with the aim of developing the framework for a demogenetic model, i.e., a model integrating both population dynamics and genetics. We use a bibliometric literature review to identify two main categories of models: population ecology (including population dynamics and population genetics) and population distribution (including habitat-hydraulic and spatial distribution). We assess how these models have previously been applied to stream fish, particularly brown trout, and how recent models have begun to integrate them to address two key management and conservation questions: (i) How can we predict fish population responses to management intervention? and (ii) How is the genetic structure of fish populations influenced by landscape characteristics? Because salmonid populations tend to show watershed scale variation in both demographic and genetic traits, we propose that models combining demographic, genetic and spatial data are promising tools for improving their management and conservation. We conclude with a framework for an individual-based, spatially explicit demogenetic model that we will apply to stream-dwelling brown trout populations in the near future.

Key words: brown trout; demogenetics; ecological model; population dynamics; population genetics

* This chapter was published in Ecology of Freshwater Fish. Authors: Béatrice M. Frank, John J. Piccolo (Biology Department, Karlstad University, Sweden), Philippe V. Baret. An online version of Table 1.6 is available at `http://sites-final.uclouvain.be/gena-truites/EFF_Table6.html`.

1 Introduction

Over the past three decades, ecological models have increasingly been applied in the management and conservation of freshwater fish populations (e.g., Larkin, 1978; Barnard *et al.*, 1995; Whipple *et al.*, 2000; Filipe *et al.*, 2004; Einum *et al.*, 2008). These models have been used to predict abundance and population growth rate (Lebreton, 2006), population subdivision and gene flow (Pearse and Crandall, 2004), habitat quality (Anderson *et al.*, 2006) and large-scale distribution (Ahmadi Nedushan *et al.*, 2006). Thus, ecological models are increasingly being used to guide management decisions, especially for threatened and exploited species. Models for stream fish have ranged in scale from individuals to populations; early models focused on physical habitat (Bovee, 1982) and on population-level responses such as demographic (Elliott, 1994) and genetic variations (Wright, 1969). Later developments included functions to predict spatial patterns of either fish occurrence (e.g., Stanfield and Gibson, 2006) or genetic diversity (e.g., Dillane *et al.*, 2008). Most recently, individual-based simulation techniques have been developed to explicitly include individual variation, as well as demographic and environmental stochasticity, into ecological models (e.g., Strand and Niehaus, 2007; Landguth and Cushman, 2010; Schumaker, 2011).

The rapid expansion in ecological modelling parallels technological advances in field methods (i.e., individual tagging and tracking), computing, and genetic analyses. Stream ecologists are now poised to model and to better understand how the interaction of demographic and genetic factors influences the distribution and abundance of fish. This is a daunting task, however, because of the difficulty of assimilating the broad knowledge base that has developed, somewhat independently, in a number of subdisciplines (e.g., demography, genetics, physical habitat simulations, etc.). In this paper, we assemble and synthesise for the first time the vast body of ecological modelling literature on stream fish, focusing on the brown trout, *Salmo trutta* L. Our goal is to demonstrate how these previously independent models have begun to be integrated, and how further integration will allow ecologists to better address important questions for the management and conservation of freshwater fish.

The brown trout is a species particularly well-suited for serving as a model organism for both management and conservation. Its quantitative ecology, from individual habitat selection to population dynamics, is as well known as that of any stream fish (e.g., Elliott, 1994, but see numerous others). It is also one of the vertebrate species presenting the high-

est degree of intraspecific biological diversity including strong genetic and phenotypic variation among populations (Laikre, 1999; Bernatchez, 2001). This genetic variability among brown trout populations is attributable to several factors, including the effects of recent glaciations, the physical characteristics of the hydrographic systems and local differentiation without barriers owing to territorial behaviour and strong homing instinct (i.e., individuals return to spawn in the stream in which they were born) (Laikre, 1999; Antunes *et al.*, 2006). These factors result in limited gene flow among populations, producing partially isolated random mating units both within and among watersheds (Ferguson, 1989). This often leads to adaptation to local environmental conditions, changes in genetic structure and the development of unique demographic traits like morphology, feeding preferences and life history strategies (Laikre, 1999; Klemetsen *et al.*, 2003; Ferguson, 2006). The importance of this intraspecific diversity for fisheries management has long been recognised (e.g., Ricker, 1972; Spangler *et al.*, 1981; Taylor, 1991), and most recently Schindler *et al.* (2010) identified its crucial role in providing ecosystem services. Human activities, including environmental degradation (pollution, altered flow, fragmentation of habitat), fishing and fish stocking (Laikre, 1999; Cowx and Gerdeaux, 2004; Dudgeon *et al.*, 2006), have resulted in a loss of intraspecific diversity of brown trout, and many remaining native stocks are now faced with a medium-term risk of extinction (e.g., Laikre, 1999; Caudron *et al.*, 2011).

In recent years, considerable attention has been paid to the ecology of brown trout. Population dynamics of a number of populations were reviewed (e.g., Roussel and Bardonnet, 2002; Klemetsen *et al.*, 2003; Lobon-Cervia, 2005, 2007; Northcote and Lobon-Cervia, 2008), and molecular genetic techniques have contributed to improving the basic genetic information available on population structure, both at large (Bernatchez, 2001) and at small spatial scales (Hansen *et al.*, 2001b; Sonstebo *et al.*, 2007b). Recent advances in fish marking techniques, spatial analyses and molecular genetics have allowed the establishment of long-term data sets of demography and population genetic structure based on sampling of individual fish (e.g., Hansen *et al.*, 2002; Lobon-Cervia and Rincon, 2004; Fraser *et al.*, 2007; Haugen *et al.*, 2008). Although advances have been achieved in both population dynamics and population genetics models, comprehensive models that integrate these two characteristics of salmonid populations are still in their infancy (Palsboll *et al.*, 2007). Because brown trout tend to show both demographic variation and genetic diversity at the watershed scale, models that link population dynamics and genetics (i.e., demogenetics) across spatial scales hold

great promise in providing insights into their management and conservation.

In this review, we show how ecological models have previously been applied to stream fish populations, particularly brown trout, and how the most advanced models might be integrated to develop a new demogenetic model. First, we conduct a bibliometric review of the literature on ecological models for brown trout, and we identify and summarise two categories and four types of models that have been developed over the past 30 years. Then, we demonstrate how some of these models have already begun to be integrated, and how they might be used to address two key questions relevant to the conservation and management of stream fish: (i) How can we predict fish population responses to management intervention? and (ii) How is the genetic structure of fish populations influenced by landscape characteristics? We conclude with a framework for a new demogenetic model for brown trout populations that will further integrate existing theory through the use of an individual-based, spatially explicit platform.

2 Methods

We developed a bibliometric approach to identify the main topics addressed by scientific publications of ecological models for brown trout. We followed two steps: the selection of publications, and the construction of the corresponding directed network of citations.

In the first step, we used the ISI Web of Knowledge^{SM} search engine to identify key publications, the references they cited and those that cited them (Table 1.1). We selected 68 publications (from 2003 to 2008), among which 59 articles, seven proceedings papers, one editorial material and one review, and their 2964 citations (from 1980 to 2009).

In the second step, a directed network was built. First, an adjacency matrix was created. This latter consists of a symmetric matrix whose row and column elements reflect vertices (nodes), and each cell contains the value of an edge (interaction). In our case, the vertices are the 68 publications and their 2964 references, while the edges are constituted with ones and zeros, each 'one' representing a link between two vertices (here, 3567 links). Then, the 3032 $\times$ 3032 adjacency matrix was converted into an edge list matrix, using the 'Network' R package (Butts *et al.*, 2008). It is a rectangular matrix with two columns. We chose a directed network and, in this case, each row element represents an edge and contains two vertices that are linked by this edge: the first one is

Table 1.1: Search criteria for the selection of publications devoting to the brown trout.

Feature	Search criterion
Publication database	Web of Science. Source: ISI Web of Knowledge CrossSearch, available on `http://www.isiknowledge.com/WOS`. Accessed January 20, 2009
Key words	Topic=(salmo* AND trutta AND model* AND (river* OR stream* OR basin* OR freshwater*) NOT sea* NOT lake* NOT (salmonel* OR chemi* OR tox* OR ion* OR metal*))
Time span	From 2003 to 2008
Citation database	Science Citation Index Expanded (SCI-EXPANDED), from 1980 to 2009

taken to be the tail vertex of the edge and the second one is the edge's head vertex (Butts, 2008). Finally, importing the edge list matrix into the Cytoscape software (Shannon *et al.*, 2003) allowed us to visualise the network properly by using, for instance, the 'Organic layout'. To facilitate the analysis of this network, its size was reduced: vertices with four or less input edges were deleted.We obtained a network made of 59 vertices (44 publications plus 15 citations) and 104 directed edges (Fig. 1.1). This allowed us to identify the major categories of models, the types of models within them and links among these.

3 Results: literature review and synthesis

Two main references display the largest number of input edges in the directed network (Fig. 1.1): R766 and R355, with 19 and 12 inputs, respectively. The former reference, R766, is the well-known book 'Quantitative Ecology and the Brown Trout' (Elliott, 1994). This book covers various subjects such as the global success of the brown trout species, growth and energetics, population dynamics of adults and juveniles, ecology and genetics. The latter reference, R355, is the report 'A Guide to Stream Habitat Analysis Using the Instream Flow Incremental Methodology' (IFIM) (Bovee, 1982). This guide explains how to assess riverine habitats and impact of disturbances on these habitats and fish that live there.

From these two main references, three clusters are observed in the network. Cluster One, population ecology, is in the left of Fig. 1.1 (light-gray nodes), centred on Elliott (1994). It comprises 18 articles and six references, mostly addressing the ecology of brown trout populations

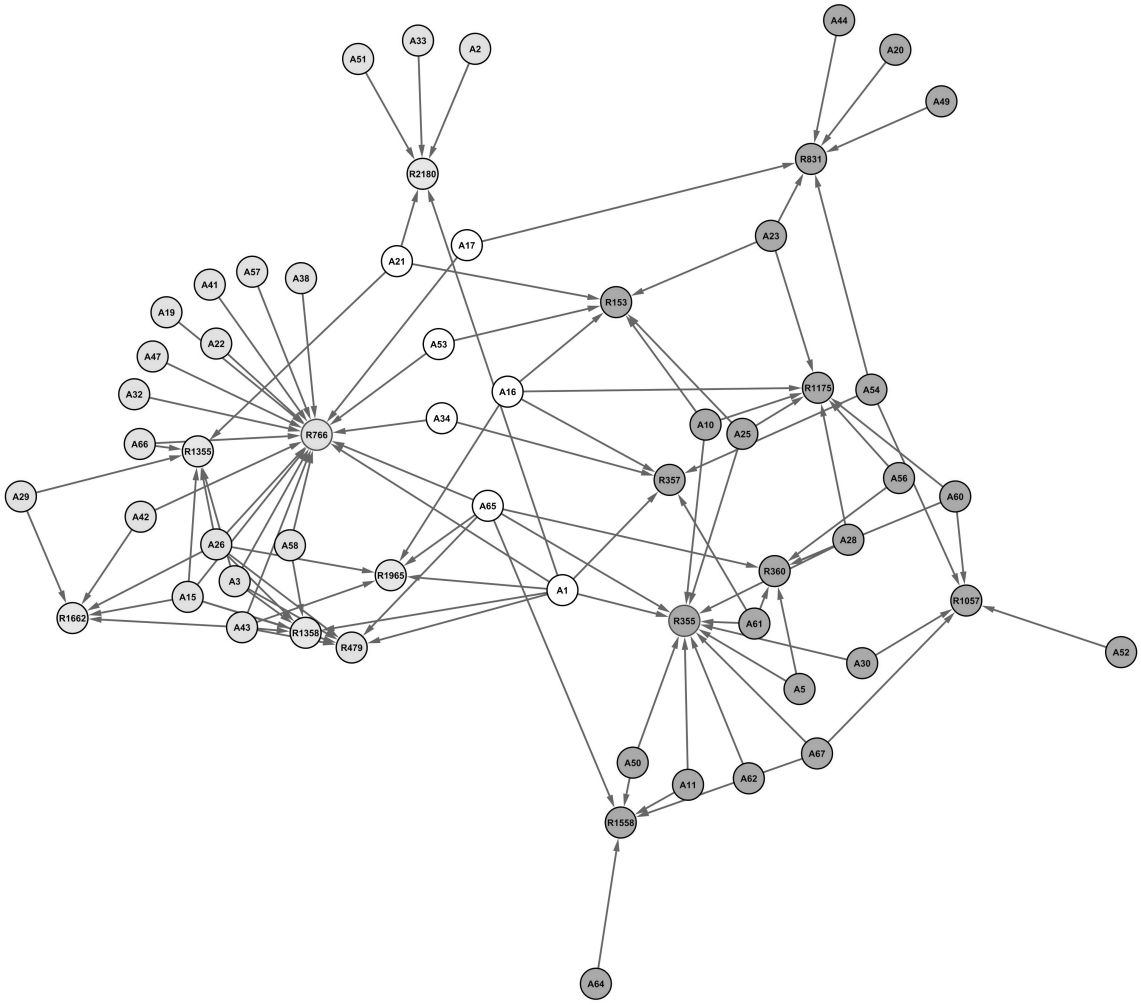

Figure 1.1: The reduced network used to categorise ecological models of stream-living brown trout populations. This network, made of 59 vertices (44 articles, labelled A, plus 15 references, labelled R) and 104 directed edges, was visualised with the Cytoscape software using an 'Organic layout'. Three clusters were identified, corresponding to the following categories: brown trout population ecology (Cluster One, light-gray nodes), population distribution (Cluster Two, dark-gray nodes), and a combination of the two previous categories (Cluster Three, white nodes).

(Table 1.2). Cluster Two, population distribution, is in the right of Fig. 1.1 (dark-gray nodes), centred on Bovee (1982). It comprises 19 articles and seven references that address either trout local habitat preferences or their distribution at the catchment scale (Table 1.3). Cluster Three (white nodes in Fig. 1.1) comprises seven articles linking Clusters One and Two. In this cluster, a number of publications represent

recent attempts to link population ecology and population distribution (Table 1.4).

Table 1.2: Vertices belonging to the 'Population ecology' cluster.

Vertices	First author (year)	Publication's title
R0479	Cattaneo (2002)	The influence of hydrological and biotic processes on brown trout population dynamics
R1355	Jenkins (1999)	Effects of population density on individual growth of brown trout in streams
R1358	Jensen (1999)	The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon and brown trout
R1662	Lobon-Cervia (2004)	Environmental determinants of recruitment and their influence on the population dynamics of stream-living brown trout *Salmo trutta*
R1965	Nehring (1993)	Determination of population-limiting critical salmonid habitats in Colorado streams using the physical habitat simulation system
R2180	Poff (1997)	The natural flow regime: a paradigm for river conservation and restoration
A02	Dauwalter (2008)	Distribution modelling to guide stream fish conservation: an example using the mountain sucker in the Black Hills National Forest, USA
A03	Budy (2008)	Exploring the relative influence of biotic interactions and environmental conditions on the abundance and distribution of exotic brown trout in a high mountain stream
A15	Vincenzi (2008a)	The role of density-dependent individual growth in the persistence of freshwater salmonid populations
A19	Kristensen (2008)	Variation in growth and aggression of juvenile brown trout from upstream and downstream reaches of the same river
A22	Matulla (2007)	Assessing the impact of a downscaled climate change simulation on the fish fauna in an Inner-Alpine River
A26	Zorn (2007)	Influences on brown trout and brook trout population dynamics in a Michigan River
A29	Vincenzi (2007)	Density-dependent individual growth of marble trout in the Soca and Idrijca river basins, Slovenia
A32	Schager (2007)	Status of young-of-the-year brown trout in Swiss streams: factors influencing YOY trout recruitment
A33	Weber (2007)	Spatio-temporal analysis of fish and their habitat: a case study on a highly degraded Swiss river system prior to extensive rehabilitation
A38	Leprieur (2006)	Hydrological disturbance benefits a native fish at the expense of an exotic fish
A41	Gregersen (2006)	Egg size differentiation among sympatric demes of brown trout: possible effects of density-dependent interactions among fry
A42	Lobon-Cervia (2006)	Instability of stream salmonid population dynamics under strong environmental limitations-a reply
A43	Daufresne (2006)	Population fluctuations, regulation and limitation in stream-living brown trout

Table 1.2: Vertices belonging to the 'Population ecology' cluster (continued).

Vertices	First author (year)	Publication's title
A47	Johansen (2005)	Relationships between juvenile salmon and invertebrate densities in the River Tana, Norway
A51	McRae (2005)	Factors influencing density of age-0 brown trout and brook trout in the Au Sable River, Michigan
A57	Yamamoto (2004)	Genetic differentiation of white-spotted charr populations after habitat fragmentation: Spatial-temporal changes in gene frequencies
A58	Koizumi (2004)	Metapopulation structure of stream-dwelling Dolly Varden charr inferred from patterns of occurrence in the Sorachi River basin, Hokkaido, Japan
A66	Brannas (2003)	Influence of food abundance on individual behaviour strategy and growth rate in juvenile brown trout

Table 1.3: Vertices belonging to the 'Population distribution' cluster.

Vertices	First author (year)	Publication's title
R0153	Armstrong (2003)	Habitat requirements of Atlantic salmon and brown trout in rivers and streams
R0357	Bovee (1986)	Development and evaluation of habitat suitability criteria for use in the instream flow incremental methodology
R0360	Bovee (1998)	Stream habitat analysis using the instream flow incremental methodology
R0831	Fausch (1981)	Competition between brook trout and brown trout for positions in a Michigan stream
R1057	Guay (2000)	Development and validation of numerical habitat models for juveniles of Atlantic salmon
R1175	Heggenes (1996)	Habitat selection by brown trout and young Atlantic salmon in streams: Static and dynamic hydraulic modelling
R1558	Lamouroux (1999)	Fish habitat preferences in large streams of southern France
A05	Clark (2008)	Spatial distribution and geomorphic condition of fish habitat in streams: An analysis using hydraulic modelling and geostatistics
A10	Mouton (2008)	Optimisation of a fuzzy physical habitat model for spawning European grayling in the Aare river (Thun, Switzerland)
A11	Ovidio (2008)	Regulated discharge produces substantial demographic changes on four typical fish species of a small salmonid stream
A20	Cucherousset (2007)	Stable isotope evidence of trophic interactions between introduced brook trout and native brown trout in a mountain stream of south-west France
A23	Dolinsek (2007)	Assessing the effect of visual isolation on the population density of Atlantic Salmon using GIS
A25	Mouton (2007)	Concept and application of the usable volume for modelling the physical habitat of riverine organisms
A28	Jowett (2007)	A comparison of composite habitat suitability indices and generalized additive models of invertebrate abundance and fish presence-habitat availability

Table 1.3: Vertices belonging to the 'Population distribution' cluster (continued).

Vertices	First author (year)	Publication's title
A30	Enders (2007)	Comparison between PIT and radio telemetry to evaluate winter habitat use and activity patterns of juvenile Atlantic salmon and brown trout
A44	Thurow (2006)	Utility and validation of day and night snorkel counts for estimating bull trout abundance in first- to third-order streams
A49	Franco (2005)	Effects of biotic and abiotic factors on the distribution of trout and salmon along a longitudinal stream gradient
A50	Pont (2005)	Modelling habitat requirement of European fishes: do species have similar responses to local and regional environmental constraints?
A52	Imre (2005)	Moon phase and nocturnal density of Atlantic salmon parr in the Sainte-Marguerite River, Quebec
A54	Jones (2004)	Resource selection functions for age-0 Arctic grayling and their application to stream habitat compensation
A56	Vilizzi (2004)	Assessing variation in suitability curves and selectivity profiles in temporal studies of fish habitat use
A60	Nykanen (2004)	Transferability of habitat preference criteria for larval European grayling
A61	Booker (2004)	Application of physical habitat simulation (PHABSIM) modelling to modified urban river channels
A62	Lopes (2004)	Hydrodynamics and water quality modelling in a regulated river segment: application on the instream flow definition
A64	Statzner (2003)	Contribution of benthic fish to the patch dynamics of gravel and sand transport in streams
A67	Mengin (2002)	ProCURVE: software to calculate habitat preferences of aquatic organisms

GIS, geographic information systems; PIT, passive integrated transponder.

Clusters One and Two are linked to two broad categories of ecological models for brown trout: population ecology models and population distribution models (Table 1.5). Each category is further divided into two subcategories; population ecology models include population dynamics and population genetics models, and population distribution models include habitat-hydraulic and spatial distribution models. Initially, these population ecology and population distribution models were developed largely independently, but more recently there have been efforts to integrate them. Spatial dynamics models and landscape genetics models are promising approaches that link either population dynamics models or population genetics models across spatial scales; spatial dynamics models emphasise the importance of temporal changes in population size and age structure, and spatial variability in stream habitats; landscape genetics models allow for studying the effects of environmental features on the genetic processes regulating a population. Below, we first review

Table 1.4: Vertices connecting the 'Population ecology' and the 'Population distribution' clusters.

Vertices	First author (year)	Publication's title
A01	Gouraud (2008)	Long-term simulations of the dynamics of trout populations on river reaches bypassed by hydroelectric installations - Analysis of the impact of different hydrological scenarios
A16	Louhi (2008)	Spawning habitat of Atlantic salmon and brown trout: General criteria and intragravel factors
A17	Ohlund (2008)	Life history and large-scale habitat use of brown trout and brook trout - Implications for species replacement patterns
A21	Vincenzi (2008b)	Potential factors controlling the population viability of newly introduced endangered marble trout populations
A34	Hauer (2007)	The importance of morphodynamic processes at riffles used as spawning grounds during the incubation time of nase
A53	Nislow (2004)	Testing predictions of the critical period for survival concept using experiments with stocked Atlantic salmon
A65	Capra (2003)	A population dynamics model and habitat simulation as a tool to predict brown trout demography in natural and bypassed stream reaches

population ecology models and population distribution models. Then, we review the two additional model types: spatial dynamics and landscape genetics models. We also introduce individual-based simulation techniques, which have become an integral component of these latter models.

Through this synthesis of the literature, we identify the study goals and estimated parameters associated with each of the six model types we describe (Table 1.5). We focus on models and methods that have been developed for stream-dwelling brown trout and use examples from other taxa in cases where models for brown trout are lacking. We do not consider models designed for multiple species. A comprehensive list of models and corresponding methods can be found in Table 1.6. For each model type, we provide one example of a research question that might be answered by using the model.

Table 1.5: The six types of ecological models for stream fish that we identify based on our literature review. The study goals and parameters estimated are described for each of them.

	Population dynamics models	**Population genetics models**
Study goal	Short- and long-term changes in the size and age structure of a population	Population-level effects of genetic phenomena such as segregation, recombination, transposition and mutation
Estimated parameters	Abundance, population growth rate	Degree of population differentiation, population of origin, number of populations, past and current gene flow, effective population size
	Habitat-hydraulic models	**Spatial distribution models**
Study goal	Habitat characteristics and preferences of stream fish populations	Relationship between organisms occurrence and catchment characteristics
Estimated parameters	Habitat suitability index in relation with stream discharge	Habitat suitability maps
	Spatial dynamics models	**Landscape genetics models**
Study goal	Limitation of population density by demographic processes, influences of flow on demographic rates	Interactions between landscape features and micro-evolutionary processes
Estimated parameters	Abundance, population growth rate, habitat selection and suitability	Locations of genetic discontinuities, genetic distance and connectivity

Table 1.6: Types of ecological models, software in which they are implemented, and examples of applications for brown trout (*Salmo trutta*) or other salmonid species.

Model types / Methods	Software	Applications examples
Population dynamics models		
e.g., 'What is the size of a fish population and how does it vary over time?'		
Stock-recruitment models	Equations resolving	Elliott (1994); Bell *et al.* (2000); Lobon-Cervia and Rincon (2004)
Matrix projection models	MATHEMATICA[1]	Sabaton *et al.* (1997); Charles *et al.* (1998); Gouraud *et al.* (2001); Daufresne and Renault (2006)
Integral projection models	R[2]	No *S. trutta* application found, but see Fukuwaka and Morita (2008)
Bayesian belief networks	NETICA[3]	Lee and Rieman (1997); Rieman *et al.* (2001)
	ANALYTICA[4]	Borsuk *et al.* (2006); Burkhardt-Holm (2008)
State-space models	WinBUGS (Lunn *et al.*, 2000)	No *S. trutta* application found, but see Rivot *et al.* (2004)
Population genetics models*		
e.g., 'How many genetically distinct fish populations are present in a system and what are the interactions among them?'		
F-statistics	ARLEQUIN (Excoffier *et al.*, 2005; Excoffier and Lischer, 2010)	Carlsson and Nilsson (2000); Ostergaard *et al.* (2003); Apostolidis *et al.* (2008)
	FSTAT (Goudet, 1995)	Carlsson and Nilsson (2000); Jensen *et al.* (2005b); Antunes *et al.* (2006); Hansen *et al.* (2007); Sonstebo *et al.* (2007a,b); Susnik *et al.* (2007); Heggenes *et al.* (2009); Vilas *et al.* (2010)
	GENEPOP (Raymond and Rousset, 1995; Rousset, 2008)	Estoup *et al.* (1998); Lehtonen *et al.* (2009)
	GENETIX (Belkhir *et al.*, 2004)	Aurelle and Berrebi (1998); Campos *et al.* (2006)

[1] Wolfram Research Inc., Champaign, Illinois, USA. `http://www.wolfram.com/mathematica`

[2] R Foundation for Statistical Computing, Vienna, Austria. `http://www.r-project.org`

[3] Norsys Software Corp., Vancouver, Canada. `http://www.norsys.com/netica`

[4] Lumina Decision Systems, Denver, Colorado, USA. `http://www.lumina.com/why-analytica`

* Multivariate methods such as those implemented in the adegenet R package (Jombart *et al.*, 2010) can also be used. See Stelkens *et al.* (2012) for an example of application for *S. trutta*.

Table 1.6: Types of ecological models, software in which they are implemented, and examples of applications (continued).

Model types / Methods	Software	Applications examples
	NEGST (Chakraborty *et al.*, 1982)	Bouza *et al.* (1999, 2001); Corujo *et al.* (2004)
Classification and clustering methods	GENECLASS (Cornuet *et al.*, 1999; Piry *et al.*, 2004)	Estoup *et al.* (1998); Ostergaard *et al.* (2003); Corujo *et al.* (2004); Heggenes and Roed (2006); Sonstebo *et al.* (2007b); Wollebaek *et al.* (2010)
	STRUCTURE (Pritchard *et al.*, 2000)	Ayllon *et al.* (2006); Sonstebo *et al.* (2007a); Massa-Gallucci *et al.* (2010); Wollebaek *et al.* (2010)
Parentage analysis	COLONY (Wang, 2004; Jones and Wang, 2010a)	Carlsson (2007); Serbezov *et al.* (2010a)
	PAPA (Duchesne *et al.*, 2002)	Duchesne *et al.* (2008)
	PARENTE (Cercueil *et al.*, 2002)	No *S. trutta* application found, but see Vandeputte *et al.* (2006)
	PEDAGREE (Coombs *et al.*, 2010)	No *S. trutta* application found, but see Hudy *et al.* (2010)
Ne - Heterozygote excess method	Luikart & England (Luikart and England, 1999)	Luikart and England (1999)
Ne - Linkage disequilibrium methods	LDNe (Waples and Do, 2008)	Massa-Gallucci *et al.* (2010)
	ONeSAMP (Tallmon *et al.*, 2008)	Wollebaek *et al.* (2010)
Ne - Temporal methods	MLNE (Wang, 2001; Wang and Whitlock, 2003)	Ostergaard *et al.* (2003); Jensen *et al.* (2005b); Campos *et al.* (2007); Fraser *et al.* (2007); Hansen *et al.* (2007)
	TempoFs (Jorde and Ryman, 2007)	Heggenes *et al.* (2009)
	TM3 (Berthier *et al.*, 2002)	Hansen *et al.* (2002); Campos *et al.* (2007)
Migration and gene flow estimators	BAYESASS (Wilson and Rannala, 2003)	Hansen *et al.* (2006, 2007); Apostolidis *et al.* (2008); Wollebaek *et al.* (2010)
	IM/IMa (Hey, 2004; Hey and Nielsen, 2007)	No *S. trutta* application found, but see Nikolic *et al.* (2009); Pavey *et al.* (2010)
	LAMARC (Kuhner, 2006)	Carlsson (2007); Susnik *et al.* (2007)
	MIGRATE (Beerli and Felsenstein, 2001; Beerli, 2006)	Campos *et al.* (2006); Fraser *et al.* (2007); Hansen *et al.* (2007)

Table 1.6: Types of ecological models, software in which they are implemented, and examples of applications (continued).

Model types / Methods	**Software**	**Applications examples**
Forward-time simulation models	EasyPOP (Balloux, 2001)	No *S. trutta* application found, but see Castric *et al.* (2002); Gomez-Uchida *et al.* (2008); Whiteley *et al.* (2010)
	FPG (Hey, 2004)	No salmonid application found
	SFS-CODE (Hernandez, 2008)	No salmonid application found
Coalescent simulation models	MS (Hudson, 2002)	No salmonid application found
	SEQ-GEN (Rambaut and Grassly, 1997)	Cortey *et al.* (2009)
	SIMCOAL (Excoffier *et al.*, 2000; Laval and Excoffier, 2004)	No salmonid application found
	DIY ABC (Cornuet *et al.*, 2008)	No *S. trutta* application found, but see Nikolic *et al.* (2009)
Quantitative genetics: animal model	MCMCglmm R package (Hadfield, 2010)	Serbezov *et al.* (2010b)
	VCE (Groeneveld, 1994)	No *S. trutta* application found, but see Martyniuk *et al.* (2003); Wilson and Rannala (2003); Norris (2004); Perry *et al.* (2004, 2005)
	DFREML (replaced by WOMBAT) (Meyer, 1988, 2007)	No *S. trutta* application found, but see Hard *et al.* (1999); Rogers *et al.* (2002); Garant *et al.* (2003); Araneda *et al.* (2005); Paez *et al.* (2010)
Hydraulic models		
e.g., 'How can we predict water depth and velocity throughout a stream reach?'		
One-dimensional models	ISIS Flow[5]	Lopes *et al.* (2004)
	HEC-RAS[6]	Borg and Roy (2006); Shieh *et al.* (2007)
Two- and three-dimensional models	River2D (Steffler *et al.*, 2006)	Alfredsen *et al.* (2004); Hayes *et al.* (2007); Clark *et al.* (2008)
	SSIIM (Olsen, 2010)	Halleraker *et al.* (2003); Alfredsen *et al.* (2004); Booker *et al.* (2004)

[5] MWH Soft Ltd., Wallingford, Oxfordshire, UK. `http://www.mwhsoft.com`

[6] U.S. Army Corps of Engineers, Hydrologic Engineering Center, Davis, California, USA. `http://www.hec.usace.army.mil/software/hec-ras`

Table 1.6: Types of ecological models, software in which they are implemented, and examples of applications (continued).

Model types / Methods	Software	Applications examples
Habitat suitability models		
e.g., 'What is the habitat suitability index of a fish population?'		
Empirical preference curves	Bovee's model (Bovee, 1982)	Belaud *et al.* (1989); Souchon *et al.* (1989); Lamouroux and Capra (2002); Lamouroux and Jowett (2005); Ovidio *et al.* (2008)
	Raleigh's model (Raleigh *et al.*, 1986)	Wesche *et al.* (1987)
Preference functions	VVF (Ortigosa *et al.*, 2000)	No salmonid application found
	HABSCORE (Milner *et al.*, 1993)	Barnard *et al.* (1995)
Habitat-hydraulic models		
e.g., 'What are the habitat preferences of a fish population in relation to stream discharge?'		
Suite of numerical models	PHABSIM (Waddle, 2001)	Harris and Hubert (1992); Nehring and Anderson (1993); Sabaton *et al.* (1997); Van Winkle *et al.* (1998); Gibbins and Acornley (2000); Spence and Hickley (2000); Ayllon *et al.* (2010)
Models derived from PHABSIM	RHABSIM (Payne, 2005)	Lopes *et al.* (2004)
	RHYHABSIM (Jowett, 2002; Clausen *et al.*, 2004)	Thorn and Conallin (2006)
	MesoHABSIM (Parasiewicz, 2001, 2007)	No salmonid application found
	EVHA (Ginot, 1995; Pouilly *et al.*, 1995)	Maridet and Souchon (1995); Lamouroux and Capra (2002); Roussel and Bardonnet (2002); Capra *et al.* (2003); Ovidio *et al.* (2008)
Fuzzy logic models	CASiMiR-Fish (Jorde *et al.*, 2000; Schneider and Jorde, 2003)	Jorde *et al.* (2001); Schneider *et al.* (2002)
Spatial distribution models		
e.g., 'How are fish distributed across a watershed and what is the relationship between their occurrence and the environmental characteristics?'		
Linear regression	SPSS[7]	McRae and Diana (2005); Schager *et al.* (2007); Weber *et al.* (2007)

[7] SPSS Inc., Chicago, Illinois, USA. `http://www.spss.com`

Table 1.6: Types of ecological models, software in which they are implemented, and examples of applications (continued).

Model types / Methods	**Software**	**Applications examples**
	STATISTICA[8]	Almodovar *et al.* (2006); Stanfield and Gibson (2006)
Multiple regression	MINITAB[9]	Lehane *et al.* (2004)
	JMP[10]	Jones *et al.* (2006)
	S-PLUS[11]	Gevrey *et al.* (2003); Pont *et al.* (2005)
	Software not mentioned	Baran *et al.* (1995); Jowett (1995); Baran *et al.* (1996); Creque *et al.* (2005); Zorn and Nuhfer (2007)
Discriminant analysis	STATISTICA[8]	Teixeira and Cortes (2007)
	Software not mentioned	Eklov *et al.* (1999); Zorn and Nuhfer (2007)
Classification and regression trees	CART[12]	Steen (2008)
	STATISTICA[8]	Stoneman and Jones (2000); Stanfield and Gibson (2006); Teixeira and Cortes (2007)
Artificial neural networks	MATLAB[13]	Lek *et al.* (1996); Reyjol *et al.* (2001); Leprieur *et al.* (2006)
	Software not mentioned	Baran *et al.* (1996); Lek and Baran (1997); Gevrey *et al.* (2003)
Mantel tests	ECODIST (Goslee and Urban, 2007)	Cattaneo *et al.* (2003); Hitt and Angermeier (2008)
Canonical correspondence analysis	CANOCO (ter Braak and Smilauer, 2002)	Weigel and Sorensen (2001); Teixeira *et al.* (2006)
Spatial dynamics models		
e.g., 'How can we predict fish population responses to management intervention or environmental modifications?'		
Bioenergetic models	Fish Bioenergetics (Hanson *et al.*, 1997)	Dieterman *et al.* (2004)

[8] StatSoft Inc., Tulsa, Oklahoma, USA. `http://www.statsoft.com`
[9] Minitab Inc., State College, Pennsylvania, USA. `http://www.minitab.com`
[10] SAS Institute Inc., Cary, North Carolina, USA. `http://www.jmp.com`
[11] TIBCO Software Inc., Palo Alto, California, USA. `http://spotfire.tibco.com/products/s-plus/statistical-analysis-software.aspx`
[12] Salford Systems Inc., San Diego, California, USA. `http://salford-systems.com/cart.php`
[13] MathWorks Inc., Natick, Massachusetts, USA. `http://www.mathworks.com/matlab`

Table 1.6: Types of ecological models, software in which they are implemented, and examples of applications (continued).

Model types / Methods	Software	Applications examples
	Hayes' model (Hayes *et al.*, 2000)	Booker *et al.* (2004)
	Hughes' model (Hughes and Dill, 1990; Hughes, 1992)	Hughes (1998); Hughes *et al.* (2003); Hayes *et al.* (2007)
	Elliott & Hurley's model (Elliott and Hurley, 1999, 2000)	Vik *et al.* (2001); Jensen *et al.* (2006); Johnson *et al.* (2006); Dineen *et al.* (2007)
Habitat suitability models and matrix models	MODYPOP (Sabaton *et al.*, 1997; Gouraud *et al.*, 2001)	Capra *et al.* (2003)
	Charles' model (Charles *et al.*, 1998)	Charles *et al.* (2000)
	SALMOD (Williamson *et al.*, 1993; Bartholow, 1996)	Hickey and Diaz (1999)
Spatially explicit stock-recruitment models	STELLA[14]	Jessup (1998)
Spatially explicit matrix projection models	MATLAB[13], R[2]	No *S. trutta* application found, but see Letcher *et al.* (2007)
Spatially explicit integral projection models	MATLAB[13], R[2]	No salmonid application found
Landscape genetics models*		
e.g., 'How is the genetic structure of fish populations influenced by landscape characteristics?'		
Mantel tests	GENEPOP (Raymond and Rousset, 1995; Rousset, 2008)	Estoup *et al.* (1998); Carlsson and Nilsson (2000); Campos *et al.* (2006); Hansen *et al.* (2007)
	GENALEX (Peakall and Smouse, 2006)	Sonstebo *et al.* (2007a); Lehtonen *et al.* (2009)
	NTSYSpc[15]	Bouza *et al.* (1999, 2001); Sonstebo *et al.* (2007b)
	FSTAT (Goudet, 1995)	Heggenes and Roed (2006)
	IBDWS (Jensen *et al.*, 2005a)	Vilas *et al.* (2010)
Regression analysis	GENEPOP (Raymond and Rousset, 1995; Rousset, 2008)	Estoup *et al.* (1998)

[14] isee systems Inc., Lebanon, New Hampshire, USA. `http://www.iseesystems.com/softwares/Education/StellaSoftware.aspx`

* Multivariate methods such as those implemented in the adegenet R package (Jombart *et al.*, 2008) can also be used. No example of salmonid application was found.

[15] Exeter Publishing Ltd., Setauket, New York, USA. `http://www.exetersoftware.com/cat/ntsyspc/ntsyspc.html`

Table 1.6: Types of ecological models, software in which they are implemented, and examples of applications (continued).

Model types / Methods	**Software**	**Applications examples**
Evolutionary trees	STREAM TREES (Kalinowski *et al.*, 2008)	No *S. trutta* application found, but see Kalinowski *et al.* (2008); Meeuwig *et al.* (2010)
Monmonier algorithm	BARRIER (Manni *et al.*, 2004)	No *S. trutta* application found, but see Dillane *et al.* (2008)
Canonical correspondence analysis	CANOCO (ter Braak and Smilauer, 2002)	No *S. trutta* application found, but see Angers *et al.* (1999); Costello *et al.* (2003)
Principal component analysis	PCA-GEN (Goudet, 1999)	Lehtonen *et al.* (2009)
Multidimensional scaling	ViSta (Young *et al.*, 2006)	Hansen *et al.* (2002, 2007)
Landscape metrics	FRAGSTATS (McGarigal *et al.*, 2002)	No *S. trutta* application found, but see Le Pichon *et al.* (2006)
Spatial clustering	BAPS (Corander and Marttinen, 2006)	Sonstebo *et al.* (2007b); Vilas *et al.* (2010)
	GENELAND (Guillot *et al.*, 2005)	No *S. trutta* application found, but see Dionne *et al.* (2008)
	TESS (François *et al.*, 2006)	No salmonid application found
	SPAGeDi (Hardy and Vekemans, 2002)	No salmonid application found
Coalescent population genetics models	SPLATCHE (Currat *et al.*, 2004; Ray *et al.*, 2010)	No salmonid application found
	AQUASPLATCHE (Neuenschwander, 2006)	No salmonid application found
	ABCtoolbox (Wegmann *et al.*, 2010)	No salmonid application found
Nonspatial individual-based models		
e.g., 'How can we simulate the evolution of a fish population in terms of demography, genetics, or both?'		
Population dynamics models	VORTEX (Lacy, 2000b; Lacy *et al.*, 2005)	No *S. trutta* application found, but see Sato and Harada (2008)
Forward-time population genetics models	simuPOP (Peng and Kimmel, 2005)	No salmonid application found
	NEMO (Guillaume and Rougemont, 2006)	No salmonid application found
Quantitative genetics models	Dunlop's ecogenetic model (Dunlop *et al.*, 2009)	No *S. trutta* application found, but see Thériault *et al.* (2008)
	Wang's model (Wang and Hook, 2009)	No *S. trutta* application found, but see Wang and Hook (2009)

Table 1.6: Types of ecological models, software in which they are implemented, and examples of applications (continued).

Model types / Methods	Software	Applications examples
Demogenetic models	METASIM (Strand, 2002)	No salmonid application found
Spatially explicit individual-based models		
e.g., 'How can we predict the response of a fish population to future changes in the environment?'		
Bioenergetic models	Addley's model (Addley, 1993)	Guensch *et al.* (2001); Addley (2006)
	inSTREAM (Railsback *et al.*, 2009)	Van Winkle *et al.* (1998); Railsback and Harvey (2002); Railsback *et al.* (2003)
Spatial dynamics models	HexSim (Schumaker, 2011)	No salmonid application found
Quantitative genetics models	quantiNEMO (Neuenschwander *et al.*, 2008a)	No salmonid application found
Landscape genetics models	CDPOP (Landguth and Cushman, 2010)	No salmonid application found
Demogenetic models	KernelPOP (Strand and Niehaus, 2007)	No salmonid application found

ABC, approximate Bayesian computation.

3.1 Population ecology models

We subdivide population ecology models into two types: population dynamics models and population genetics models. Population dynamics models address short- and long-term changes in the size and age structure of a population; typical outputs from these models are predictions of abundance and population growth rate (e.g., Lebreton, 2006). 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 (e.g., Hartl and Clark, 1989; Allendorf and Luikart, 2007).

Population ecology models are thus a means to explain changes occurring in the demographic or genetic structure of a population, caused either by dynamic processes (i.e., births, deaths and dispersal) or by micro-evolutionary processes (i.e., natural selection, genetic drift, gene flow and mutation). Population dynamics and population genetics mod-

els can be integrated with two other types of models, habitat-hydraulic and spatial distribution models, to obtain spatial dynamics models and landscape genetics models, respectively. These latter model types are both reviewed in the second section of this literature synthesis, and in the last section, we demonstrate how they can address two questions relevant to the management and conservation of freshwater fish.

Linking evolutionary and demographic processes in ecological models (i.e., demogenetic models) and applying these to understand the patterns of genetic variation in freshwater fish populations should provide new insights to address questions about their management and conservation. For instance, levels of fecundity, mortality, immigration and emigration may alter the degrees of genetic exchange among populations, and these are capable of feeding back into one another (Kool, 2009). As suggested at the end of this literature review and synthesis, the use of individual-based simulation techniques should greatly facilitate the development of the demogenetics field and its associated demogenetic models.

3.1.1 Population dynamics models

Population dynamics models can be subclassified into either mathematical or statistical models. Mathematical population models are dynamic and deterministic, because they describe how a population changes over time, and they have no random component (Ellner and Rees, 2006). Exponential (Malthus, 1798) and logistic (Verhulst, 1838) models of population growth are the simplest mathematical population models describing changes in a population's size. They differ on their assumptions about the availability of resources and are rarely used today. Another class of mathematical population models are the stock-recruitment models (e.g., Ricker, 1954; Beverton and Holt, 1957), which give the number of fish expected to survive (the recruits) at a later time, as a function of the number of spawners (the stock) at a previous time. For instance, Elliott (1994) used a Ricker model to describe the number of recruits at the different stages of the life cycle of brown trout, given the number of eggs at the beginning of each year. The last class of mathematical population models we describe here is the matrix projection models (see Caswell, 2001). Age-structured models developed by Leslie (1945) are the deterministic matrix models most commonly used in the literature, and several were developed for brown trout populations (e.g., MODYPOP: Sabaton *et al.*, 1997; Gouraud *et al.*, 2001, see also Table 1.6). The approach of Leslie was upgraded by classifying individuals into stages of development (Lefkovitch, 1965) or size classes (Usher, 1966) and was

eventually generalised to consider any structuring factor (Caswell, 2001). Recently, integral projection models, or IPMs, have been developed as a practical alternative to deterministic matrix models for structured populations with continuous trait variation. The IPM theory (Easterling *et al.*, 2000; Ellner and Rees, 2006) is used to understand how complex demographic processes, and the associated individual variation, affect population growth and the evolution of life history strategies (Jongejans *et al.*, 2008). Until now, such models have been mostly applied to plant and mammalian populations (e.g., Ramula *et al.*, 2009; Ozgul *et al.*, 2010).

Most statistical population models are static and stochastic (Sanz and Bravo de la Parra, 2007). They are divided into two classes: birth-death models and population growth models. On the one hand, birth-death models are a special case of continuous time Markov models and describe changes in a population through births and deaths, assuming that only one event happens at a time (Otto and Day, 2007). On the other hand, population growth models consider two sources of stochasticity simultaneously: demographic and environmental (Sanz *et al.*, 2003; Otto and Day, 2007). In small populations, the effects of demographic stochasticity may be crucial, sometimes even causing total population extinction (Sanz *et al.*, 2003; Sanz and Bravo de la Parra, 2007).

A link between mathematical and statistical population models has been made recently using a state-space framework. Two processes are considered in state-space population models: one for state and one for observation (Fig. 1.2). The first process describes the state of a population at successive time steps, through demographic processes such as birth, survival and movement. The observation process links the unknown states to data on the population, recorded during surveys or experiments, and gives the probability of obtaining a particular observation depending on the population's state (Thomas *et al.*, 2005; Buckland *et al.*, 2007; Patterson *et al.*, 2008) (for a mathematical description of state-space models, see Buckland *et al.*, 2004). To our knowledge, no state-space models have been applied to brown trout, although they have been successfully applied to Atlantic salmon (*Salmo salar*) by Rivot *et al.* (2004).

3.1.2 Population genetics models

Classical population genetics models rely on the Wright-Fisher assumption of an idealised population, in which the entire population reproduces simultaneously and no selection occurs (Otto and Day, 2007)

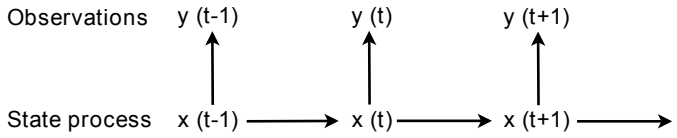

Figure 1.2: General structure of a state-space model. The y_t are data observed given the true, but unobserved, state x_t. Horizontal arrows depict the state process estimation of the true state of the population through time t, while vertical arrows depict the observation process. State-space models are a way to link mathematical and statistical population dynamics models.

(e.g., the infinite alleles and the stepwise mutation models of Kimura and Crow, 1964 and Ohta and Kimura, 1973, respectively; the island and the stepping-stone dispersal models of Wright, 1943 and Kimura and Weiss, 1964, respectively). The coalescent model (Kingman, 1982, reviewed by Hudson, 1990; Nordborg, 2001) is a natural extension of classical (forward-time) population genetics models, and it investigates the shared genealogical history of genes (Rosenberg and Nordborg, 2002; DeSalle and Amato, 2004). Forward-time simulation programs (e.g., EasyPOP: Balloux, 2001; SFS-CODE: Hernandez, 2008) and coalescent, or backward-time, simulation programs (e.g., SEQGEN: Rambaut and Grassly, 1997; MS: Hudson, 2002) provide a means to explore the effects of micro-evolutionary processes on populations of constant size. The forward-time approach is more appropriate for studying how the long-term behaviour of evolutionary systems depends on initial conditions (Rosenberg and Nordborg, 2002). The coalescent approach can be used as a simulation tool for (i) studying the effects of past evolutionary forces on current genetic variation, and thus to estimate parameters like migration rates and effective population sizes, and (ii) hypothesis testing and exploratory data analyses (Rosenberg and Nordborg, 2002; Kuhner, 2009).

The effects of the micro-evolutionary forces on populations can be studied through multiple analyses involving population genetics models (e.g., studies of Gomez-Uchida et al., 2008 on the Arctic charr (*Salvelinus alpinus*), and Whiteley et al., 2010 on the cutthroat trout (*Oncorhynchus clarkii*), both using the simulator EasyPOP). Here, we consider three main analyses. First, the genetic structure of a fish population can be investigated by using F-statistics (Wright, 1969) to analyse historical patterns of population subdivision (Hartl and Clark, 1989). Among the three inbreeding coefficients corresponding to the F-statistics, the F_{ST} coefficient detects changes in differentiation among populations and,

hence, quantifies the degree to which populations are subdivided (Allendorf and Luikart, 2007). Several studies on brown trout found moderate-to-strong genetic differentiation among Atlantic populations (global multilocus F_{ST} values from 0.03 to 0.60), both at the scale of river systems (Carlsson *et al.*, 1999; Hansen *et al.*, 2002; Lehtonen *et al.*, 2009) and at the scale of basins (Estoup *et al.*, 1998; Campos *et al.*, 2006; Vilas *et al.*, 2010), and strong differentiation among Mediterranean populations (F_{ST} values around 0.60; Krieg and Guyomard, 1983; Apostolidis et al., 1996; 2008).

Second, F_{ST} can also be used as a basis for estimating past gene flow, i.e., the number of migrants exchanged among populations per generation (Holderegger *et al.*, 2006), because gene flow is naturally related to population subdivision. Indeed, a lack of genetic exchange among populations is expected to result in genetic differentiation (Allendorf and Luikart, 2007). Classification methods (also called assignment tests) address the following question: 'Which population does a particular individual originate from?' (see the review of Manel et al., 2005), while clustering methods allow to determine how many distinct genetic populations are present in a system (Pearse and Crandall, 2004). Methods that permit both classification and clustering of individuals are the most frequently used (e.g., STRUCTURE: Pritchard et al., 2000; see Sonstebo et al., 2007a for an example of application to brown trout populations). Less sophisticated methods like multilocus contingency tests (as implemented in GENEPOP: Raymond and Rousset, 1995; Rousset, 2008) are a good alternative to clustering methods (Waples, 2006). In addition to assigning individuals to their population of origin, classification methods can also be used to infer first-generation migrants (e.g., BAYESASS: Wilson and Rannala, 2003). An alternative approach for studying current gene flow is the parentage analysis (reviewed by Wilson and Ferguson, 2002; Jones et al., 2010; Jones and Wang, 2010a). Using sibship and parentage analysis software (e.g., COLONY: Jones and Wang, 2010b; Wang, 2004), Hudy *et al.* (2010) were able to describe the spatial distribution of brook trout (*Salvelinus fontinalis*) spawning sites, and the dispersal from these sites after fry emergence (see Serbezov et al., 2010a for an example of application to brown trout). Broquet and Petit (2009) have recently reviewed the use of molecular genetic markers to estimate dispersal parameters.

Third, changes in genetic diversity and thus in population size can be inferred via the estimation of the effective population size, or Ne (Fisher, 1930; Wright, 1931). This is the size of an 'ideal population' that would have the same rate of genetic change owing to drift as does

the population under consideration (Schwartz *et al.*, 2007; Luikart *et al.*, 2010). More roughly, Ne is an approximation of the number of breeding individuals producing offspring that live to reproductive age, and it enables direct tests for changes in population size by quantifying it (Schwartz *et al.*, 2007). We focus on genetic methods that can be used to estimate contemporary or current Ne. Methods to estimate historical Ne have recently been reviewed in Charlesworth (2009). Recent coalescent programs are presented in Kuhner (2009); they estimate the product of effective population size times mutation rate (i.e., the effective number of migrants per generation) (e.g., MIGRATE: Beerli and Felsenstein, 2001; Beerli, 2006; LAMARC: Kuhner, 2006). Quantification methods of contemporary Ne can be divided according to the number of samples they require; the lower the intensity of sampling, the higher the number of assumptions (Broquet and Petit, 2009; Luikart *et al.*, 2010). Examples of methods requiring a single sample from the same population are the heterozygote excess in progeny method (e.g., Pudovkin *et al.*, 1996; Luikart and England, 1999), and the linkage disequilibrium method (e.g., LDNe: Waples and Do, 2008; ONeSAMP: Tallmon et al., 2008). They are less reliable compared to the temporal method, which is based on samples from the same population from at least two time periods (Schwartz *et al.*, 2007). Several approaches of the temporal method have been proposed, based on moment (e.g., TempoFs: Jorde and Ryman, 2007), likelihood (e.g., MLNE: Wang, 2001; Wang and Whitlock, 2003) or coalescent Bayesian (e.g., TM3: Berthier et al., 2002) estimators (Leberg, 2005; Luikart *et al.*, 2010). For instance, Ostergaard *et al.* (2003) as well as Jensen *et al.* (2005b) used a likelihood-based implementation of the temporal method on brown trout populations in Denmark (see also Table 1.6). All Ne quantification methods presented so far assume that samples come from a single isolated population, and thus concern related individuals, except for the MLNE program that was designed to jointly estimate Ne and migration rate using multiple samples from multiple generations of two or more populations (Vitalis and Couvet, 2001; Skalski, 2007).

Many fitness-related phenotypic characters (growth rate, age and size at maturity, etc.) are complex and quantitative in nature. They vary continuously and are coded by many interacting genes, which are in turn influenced in their expression by the environment (Naish and Hard, 2008). Population genetics methods presented earlier are no longer suitable for this kind of traits, so complementary genetic methods have been developed. In quantitative genetics, the aim is to understand distributions of quantitative characters, and the temporal change of the means and

variances of these distributions (Coulson *et al.*, 2010). The infinitesimal model (Falconer and Mackay, 1996; Lynch and Walsh, 1998) describes the genetic basis variation of quantitative traits within populations and assumes that phenotypic differences observed among individuals are related to differences in a large number of genes, each of them having a minor effect (Wilson *et al.*, 2010). Application of the infinitesimal model in natural populations is addressed by linear mixed effect models, and more specifically by the so-called animal model. This model is used to decompose the phenotypic variance of a trait into genetic and environmental sources of variance, to estimate parameters such as the heritability of this trait and genetic correlation with other traits (Wilson *et al.*, 2010). We refer the reader to Kruuk (2004) and Wilson *et al.* (2010) for a general introduction to the animal model, and to Serbezov *et al.* (2010b) for an example of application of this model to brown trout populations. In the field of management and conservation of fish populations, the role of quantitative genetic methods has been discussed by Naish and Hard (2008), considering evolutionary effects of both fishing and adaptation to climate change issues. Quantitative genetics has also allowed the integration of ecology and genetics. For instance, the approach described in Coulson *et al.* (2010) is based on integral projection models (IPMs, see the previous section on Population dynamics models) and is aimed to explain within and between species patterns in quantitative characters, life history and population dynamics.

3.2 Population distribution models

The second modelling category corresponds to population distribution models. Most of them are descriptive (or phenomenological); they concentrate on observed patterns in the data and give a quantitative summary of the observed relationship among a set of measured variables (Ellner and Rees, 2006; Bolker, 2008). At the stream scale, habitat characteristics (e.g., water depth and velocity, substrate size) and preferences of stream fish are evaluated using habitat-hydraulic models (e.g., Ahmadi Nedushan *et al.*, 2006; Anderson *et al.*, 2006). At a larger scale, the relationship between fish occurrence and catchment characteristics (e.g., rainfall, elevation, vegetative cover) is addressed by spatial distribution models (e.g., Olden and Jackson, 2002; Ahmadi Nedushan *et al.*, 2006).

Population distribution models are thus a means to explain fish habitat preferences and distribution. But they can also be used to address questions relevant to the management and conservation, when integrated

with population dynamics or population genetics models. That is the subject of the last section of this literature synthesis, which addresses spatial dynamics models and landscape genetics models and demonstrates how these can be used to predict the effects of anthropogenic impacts such as habitat alteration or barriers to gene flow on stream fish populations.

3.2.1 Habitat-hydraulic models

Habitat-hydraulic models are a combination of hydraulic models and habitat suitability models (Harby *et al.*, 2004; Mouton *et al.*, 2007b). Hydraulic models are intended to calculate water levels from characteristics such as water velocity, channel depth and channel width and can be one-, two- or three-dimensional (Harby *et al.*, 2004; Clark *et al.*, 2008). Habitat suitability models are used to evaluate the potential availability of fish habitat (Mouton *et al.*, 2007b).

The evaluation of fish habitat suitability comprises three steps. First, the frequencies with which animals use various habitat types and the availability of these habitat types are observed (Railsback *et al.*, 2003). Then, the ratio of habitat use to habitat availability is transformed into a measurement of habitat selection, the habitat suitability index. This index is based on curves representing the degree of preference displayed by fish over the complete range of different habitat variables found in a river, such as velocity, water depth and substrate size (Guay *et al.*, 2000). Preference indices range from 0 (poor habitat) to 1 (best habitat), for each of the considered physical parameters. The fish preference curves of Bovee (1982) are the most used, but modified versions can be developed to adapt them to the stream under study. Finally, the aquatic space available to a fish species for a river at a given flow is quantified by the weighted usable area or WUA, an aggregate measurement expressed in square metres of habitat per 1000 m of river. The WUA is simply the sum of the products of the habitat suitability index by the wet section areas (Booker and Dunbar, 2004; Clark *et al.*, 2008). For instance, Ovidio *et al.* (2008) calculated the WUA for adult brown trout living in a Belgian tributary. Other examples are listed in Table 1.6.

Hydraulic and habitat suitability models were linked by Bovee (1982), through his IFIM. This concept is a means to describe habitat by including discharge variability, i.e., the change of stream flow in magnitude, frequency or duration at some point in time and space (Petts and Kennedy, 2005). The methodology was first implemented in a suite of numerical models, called Physical HABitat SIMulation or PHABSIM

(Waddle, 2001). For example, such models were used by Nehring and Anderson (1993) to investigate the effect of flow related to habitat changes on wild rainbow trout (*Oncorhynchus mykiss*) and brown trout populations. Several other models based on PHABSIM were developed later, such as EVHA (Ginot, 1995; Pouilly *et al.*, 1995), and a new approach based on fuzzy set theory appeared recently (Ahmadi Nedushan *et al.*, 2006) (see Table 1.6 for examples of application of these methods). The IFIM approach linking instream hydraulics to fish distribution is now being applied worldwide by environmental managers as part of environmental assessments and decision-making (Tharme, 2003; Mouton *et al.*, 2007b; Clark *et al.*, 2008).

3.2.2 Spatial distribution models

The development of models aimed to predict the spatial distribution of organisms had two historic steps (Olden and Jackson, 2002; Joy and Death, 2004). Initially, only comparative studies were made describing linear and nonlinear relationships between environmental variables and the occurrence of populations or species. The next step was to predict their spatial distribution from these environmental factors by incorporating geographic information systems (GIS).

At the start, linear relationships between environmental variables (e.g., water depth) and fish occurrence (e.g., presence/absence data) were assumed. Traditional linear approaches include linear regression, multiple regression and discriminant analysis (see Table 1.6 for application examples). Because patterns of fish occurrence often exhibit complex (i.e., nonlinear) relationships to habitat heterogeneity and biotic interactions, alternative approaches were developed in the late 1990s. In such nonlinear models, occurrence is recorded for all sites or a random subset of sites in the study area (Buckland and Elston, 1993). Classification and regression trees and artificial neural networks are typical examples of nonlinear techniques. The capacity of predictive models using GIS to fill in the gaps between sample sites permits to enhance the accuracy of spatial maps of the probability of fish occurrence (Joy and Death, 2004; Dauwalter and Rahel, 2008).

Spatial distribution models are widely used in the field of management and conservation of fish populations (Guisan and Zimmermann, 2000; Olden and Jackson, 2002). For instance, a general linear model was used by Schager *et al.* (2007) to analyse the influence of selected abiotic and biotic parameters on the density of brown trout populations (see Table 1.6 for other examples). A large number of competing

approaches are available today. Therefore, comprehensive studies that compare the performance of these approaches (e.g., Manel *et al.*, 1999; Olden and Jackson, 2002) should be taken into consideration when using this kind of model.

3.3 Integration of population ecology and population distribution models - Addressing key questions for stream fish management and conservation

Here, we review two recently developed types of ecological models: spatial dynamics models and landscape genetics models. These models are attempts to integrate either population dynamics models or population genetics models across spatial scales; indeed, they combine population dynamics with stream scale habitat characteristics, and population genetics with landscape ecology, respectively. These two spatially explicit approaches make intensive use of individual-based simulation methods, for instance to incorporate demographic stochasticity (Marjoram and Tavaré, 2006; Epperson *et al.*, 2010; Segelbacher *et al.*, 2010), so we first introduce individual-based simulation models. We review spatial dynamics models and landscape genetics models in the two next sections, with the intent to show how these models can address two key questions relevant to the management and conservation of freshwater fish, with a focus on the brown trout (Fig. 1.3). For each question, we give examples of individual-based simulation models that have been or could be applied to brown trout, and we present the data they require. In the final section, we address the developing field of demogenetics that employs individual-based simulation models.

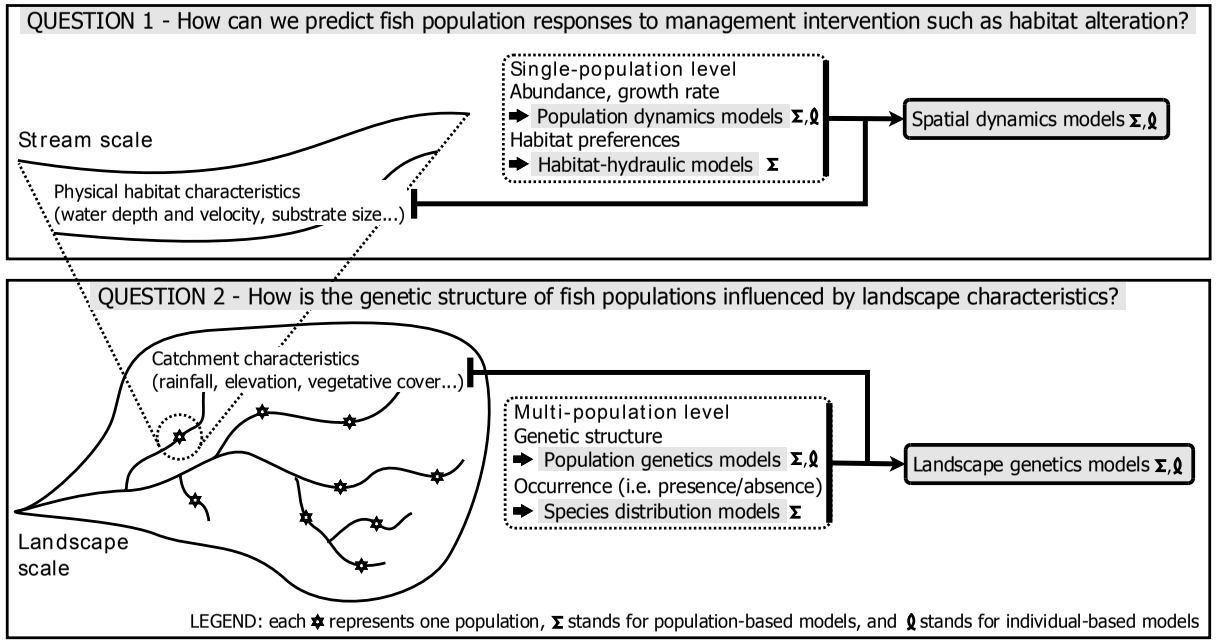

Figure 1.3: Current combinations of ecological models to answer two key questions about the management and conservation of freshwater fish. At the stream scale, population dynamics models and habitat-hydraulic models are integrated to obtain spatial dynamics models. At the landscape scale, population genetics models and spatial distribution models are integrated to obtain landscape genetics models.

3.3.1 Individual-based simulation models

Occasionally used in ecology since the 1960s, individual-based models (IBMs) made a breakthrough in the late 1980s when object-oriented programming (OOP) became available (Grimm, 1999; DeAngelis and Mooij, 2005; Breckling *et al.*, 2006). Since then, a number of applications have arisen in ecology: reproduction, dispersal, formation of patterns among individuals, foraging and bioenergetics, species interactions, local competition and community dynamics, population management strategies (Breckling *et al.*, 2005; DeAngelis and Mooij, 2005). Individual-based modelling techniques can be viewed as complex computer simulations, which the goal is to mimic a real-world empirical system by creating a 'computer world' to represent the system's biological processes (Peck, 2004). The approach lends itself directly to the use of OOP methods: elements of the program are 'objects' which pass, receive and respond to 'messages' (Kimmerer *et al.*, 2001). Thus, OOP is a natural way for implementing IBMs and is designed to be independent of software platforms.

Individual-based simulation techniques treat individuals as unique and autonomous discrete entities, and these models can be used to explore how the properties of higher level ecological entities, like populations, emerge from interactions of individuals with each other and their environment (Grimm and Railsback, 2005). The great potential of IBMs comes at a cost. First, demographic stochasticity is an intrinsic property of any IBM (DeAngelis and Mooij, 2005), and it is thus not possible to study the effects of its absence on a population. Second, data requirements can be a serious limitation. Indeed, IBMs require much data to be calibrated and validated (Jorgensen, 2008), with more complex models requiring more parameters to specify the processes (Grimm and Railsback, 2005; Breckling *et al.*, 2006). This structural complexity can make IBMs harder to implement, analyse and communicate than are equation-based models such as population dynamics models and F-statistics. Furthermore, the high number of parameters requires detailed biological knowledge (Breckling *et al.*, 2006), e.g., behavioural data that can be difficult to obtain for some species. Thus, limits in biological knowledge might restrict the application of this model type (Breckling, 2002).

The respective limitations and strengths of both equation-based and individual-based models should be considered when choosing the appropriate approach for an investigation (Breckling *et al.*, 2006). Individual-based models should be used when a modeller wants to consider one or

more of the following individual-level characteristics to explain system-level behaviour: heterogeneity among individuals, local interactions and adaptive behaviour which is based on decision-making (Thiele and Grimm, 2010).

Individual-based simulation models should not be confused with ecological models dealing in some way with individuals. For instance, in population genetics, classification and clustering methods are implemented in individual-centred programs, i.e., for which the main focus of the analysis is on individuals (Excoffier and Heckel, 2006).

3.3.2 Spatial dynamics models – How can we predict fish population responses to management intervention?

Stream fish populations are subject to natural control processes that continually affect their structure and abundance, as well as their life cycles, in response to a wide range of factors (Milner *et al.*, 2003). The knowledge of how fish populations are naturally regulated is thus necessary to determine how they might respond to a management intervention, for instance a modification of the stream flow resulting in an alteration of their habitat. The first step is to model the dynamics of the studied population. Then, we need to add habitat heterogeneity in the model and, therefore, consider small spatial scales. By modifying variables in the model, we can finally predict the outcome of the management intervention. The use of population dynamics models in a spatially explicit framework (i.e., spatial dynamics models) is one of the possible answers to address the first key question: 'How can we predict fish population responses to management intervention?' This question is management-oriented and focuses on a single population at a small spatial scale (i.e., the stream reach).

Our review of habitat-hydraulic models demonstrates that understanding the spatial variability of stream habitat and the complex interactions between habitat and fish is a major issue in stream ecology. Brown trout show strong preferences for habitat features such as spawning substratum, temperature, flow and water quality (see Elliott, 1994). The inclusion of stream scale habitat characteristics into population dynamics models has lead to the development of spatial dynamics models, which can theoretically be linked to the ecohydraulics field. Ecohydraulics is an interdisciplinary approach that tends to understand the demographic processes that limit population density, to determine which life stages are important and to determine whether, and how, demographic rates are affected by flow (Lancaster and Downes, 2010).

The first attempts to link habitat-hydraulic models with biological mechanisms were made using the bioenergetic approach (Hayes *et al.*, 2000; Guensch *et al.*, 2001). Bioenergetic models explain individual growth and 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). They have been used for drift-feeding salmonids to predict habitat selection (e.g., Hughes, 1998; Elliott and Hurley, 1999), habitat suitability (e.g., Braaten *et al.*, 1997) and long-term population growth (e.g., Railsback *et al.*, 1999; Hayes *et al.*, 2000). More sophisticated attempts have been made through the development of physically-based (e.g., Booker *et al.*, 2004; Hayes *et al.*, 2007) and individual-based bioenergetic models. For example, the individual-based model of Van Winkle *et al.* (1998), developed to evaluate behavioural responses of brown trout populations to physical habitat changes, has been substantially revised and implemented in the inSTREAM's software (Railsback *et al.*, 2009).

Another way to include biological characteristics into habitat-hydraulic models is to combine models dedicated to the evaluation of the physical habitat of fish, such as habitat suitability models and habitat-hydraulic models, with population dynamics models. First, matrix projection models were enhanced to include environmental stochasticity (Tuljapurkar, 1990). For instance, the fish survival rates in a Leslie matrix (see the section on Population dynamics models) can be reduced according to fluctuation in the habitat using WUA time series (see Capra *et al.*, 2003, for an example with brown trout). Most recently, Letcher *et al.* (2007) studied the importance of dispersal and fragmentation on the dynamics of a brook trout population, using a spatially explicit stage-based matrix model. Second, the development of integral projection model formulations for stochastic environments is another promising approach (see Rees and Ellner, 2009). Two examples applied to aquatic insects that illustrate the integration between ecology and hydraulics are described in Lancaster and Downes (2010). Third, spatial dynamics models implemented with individual-based simulation techniques permit the integration of not only habitat heterogeneity but also the complex interactions between individuals and their habitat (DeAngelis and Mooij, 2005). For instance, the software HexSim (Schumaker, 2011) enables the simulation of terrestrial populations' complex life history under multiple spatial themes representing habitat, disturbance regimes or even landscape barriers.

As a result of the merging of population dynamics and habitat-hydraulic models, spatial dynamics models need three types of data: demographic, hydraulic and habitat suitability. First, demographic and reproductive data on stream fish are gathered by observations, trapping and electrofishing. When fish are marked in some way (e.g., fin clipping), statistical methods known as 'capture-recapture methods' can be used for estimating the size of the studied population as well as fish survival rates. Reproductive observations such as number of eggs, number of nests and nest success are estimated by monitoring gravid females and nests counting. Second, hydraulic data are based on transect sampling of water depths and flow velocities and on visual estimation of substrate classes (Mouton *et al.*, 2007b). Third, preference curves needed to evaluate habitat suitability of fish (see the section on Habitat-hydraulic models) are produced from observational studies of habitat utilisation, literature surveys and expert opinion (Heggenes *et al.*, 2002).

3.3.3 Landscape genetics models – How is the genetic structure of fish populations influenced by landscape characteristics?

To manage natural fish populations living in a river basin, it is vital to identify both the number of populations to manage and the interactions that exist among them. These two points allow information to be gathered on the genetic structure of populations, which is a prerequisite to study the effects of landscape features on the genetic processes regulating those populations. The first step is to infer the current and historical genetic structure of a population to determine the number of genetically distinct fish populations present in a system and the interactions among them. Then, we need to integrate the riverscape (i.e., the riverine landscape, see Wiens, 2002) in the model. The use of population genetics models in a spatially explicit framework (i.e., landscape genetics models) is one answer to address the second key question: 'How is the genetic structure of fish populations influenced by landscape characteristics?' This question is conservation-oriented and considers several fish populations at a larger spatial scale.

In the field of population genetics, coalescent simulation programs have been extended to incorporate the influence of environmental parameters on migration (e.g., SPLATCHE: Currat et al., 2004). On the side of quantitative genetics, quantiNEMO (Neuenschwander *et al.*, 2008a) is an individual-based program that investigates the effects of mutation, selection, recombination and drift on quantitative traits in populations

connected by migration and located in a heterogeneous habitat. The inclusion of spatial details into genetics models allowed the development of landscape genetics models, theoretically linked to the discipline of the same name. Landscape genetics aims to study the interactions between landscape features and micro-evolutionary processes (i.e., within species) that generate genetic structure across space (Manel *et al.*, 2003), and it has been identified as a field that integrates population genetics, landscape ecology and spatial statistics (Storfer *et al.*, 2007).

The key steps of landscape genetics are twofold (Manel *et al.*, 2003; Pearse and Crandall, 2004). First, the spatial detection and location of genetic discontinuities among populations allow the determination of spatial genetic patterns (Manel *et al.*, 2003). Common patterns described in the salmonid literature are isolation by distance (i.e., genetic differentiation among populations that increases with their geographical distance, see Poissant *et al.*, 2005; Dionne *et al.*, 2008), barriers to gene flow (e.g., impassable waterfalls or dams, see Dillane *et al.*, 2008), mosaic structure of evolutionary lineages (see Sanz Ball-Ilosera *et al.*, 2002; McKeown *et al.*, 2010) and coexistence of anadromous and resident migration morphs (i.e., sympatric populations, see Ferguson, 2004; Narum *et al.*, 2008). The second key step is the correlation of spatial genetic patterns with environmental features, such as elevation, rainfall and upstream distance, using statistical methods similar to those presented in the section on Spatial distribution models. Geographic information systems are then used to produce statistical and visual materials on landscape characteristics and patterns (Johnson and Gage, 1997).

Statistical approaches and software used in landscape genetics have been reviewed (Excoffier and Heckel, 2006; Storfer *et al.*, 2007; Guillot *et al.*, 2009), and comparisons of different approaches have been made (Hauser *et al.*, 2006; Latch *et al.*, 2006; Chen *et al.*, 2007; Balkenhol *et al.*, 2009b). Research on landscape genetics initially focused on the terrestrial landscape (e.g., Bruggeman *et al.*, 2010), but the field has expanded to include marine and aquatic systems (Sork and Waits, 2010). In seascape genetics, a framework integrating biological-physical oceanographic and genetic models has been recently described by Galindo *et al.* (2010). In riverscape genetics, computer programs implementing statistical methods more adapted to freshwater fish have been developed. They assume that individuals can only disperse through stream corridors and no longer through a two-dimensional landscape (e.g., BARRIER: Manni et al., 2004; STREAM TREES: Kalinowski et al., 2008). Another example is the extension of the spatially explicit coalescent simulation program SPLATCHE to linear habitats (AQUASPLATCHE: Neuenschwan-

der, 2006), which was used to study the colonisation history of the Swiss Rhine basin by bullhead (*Cottus gobio*) (Neuenschwander *et al.*, 2008b). Other riverscape genetics studies investigated the influence of the spatial structure of river networks on population connectivity (e.g., Labonne *et al.*, 2008; Morrissey and de Kerckhove, 2009), and identified barriers to gene flow for fish (see Storfer *et al.*, 2010). Several partial attempts that have been made to apply the theory of landscape genetics to brown trout populations are presented in Table 1.6.

The flexibility of individual-based simulation models has progressively increased the incorporation of spatial and ecological details and processes into landscape genetics models (Balkenhol *et al.*, 2009a; Epperson *et al.*, 2010). For instance, an individual-based spatially explicit landscape genetics model, CDPOP, has recently been developed by Landguth and Cushman (2010) to simulate dispersal, mating and genetic exchange as probabilistic functions of cost distance among individuals (Segelbacher *et al.*, 2010). An alternative approach proposed by Epperson *et al.* (2010) is to combine individual-based programs from ecology and genetics like HexSim and simuPOP (Peng and Kimmel, 2005; Peng and Amos, 2008), but this has not been tested yet. The scope of the landscape genetics field is expanding and will tend to be more interdisciplinary as it merges with geography, ecology, evolution and phylogeography (Epperson *et al.*, 2010; Sork and Waits, 2010).

In landscape genetics models, genetic data are combined with spatial data. First, genetic data, i.e., individual multi-locus genotypes and allele frequencies of fish samples, are provided by DNA markers (e.g., microsatellites, see Carvalho and Hauser, 1998). DNA is extracted from fin or muscle biopsies, which are collected from fish captured either by trapping or by electrofishing. Second, spatial data are generally presented in the form of digital maps from GIS (Jager *et al.*, 2005). For stream fish, such data usually provide information about watershed characteristics. Guidance on sampling and analysis of landscape genetics data can be found in Anderson *et al.* (2010).

3.3.4 The developing field of individual-based demogenetics

The population dynamics and population genetics models reviewed earlier show that considerable advances have been achieved in both fields, mostly in separate ways. However, ecological and life history characteristics such as population size, dispersal pattern and mating system have been shown to influence fish population genetic divergence through their effects on genetic drift and gene flow (Turner and Trexler, 1998; Dawson

et al., 2002; Whiteley *et al.* 2004). Individual-based simulation techniques enable the joint generation and analysis of demographic and genetic data (Palsboll *et al.*, 2007) and have thus allowed the development of attempts including either more genetic realism into population dynamics models or more biological realism into population genetics models. Table 1.7 lists the software associated with these attempts, which are described below, and the software mentioned earlier in the section on Population ecology models. This table shows (i) the great flexibility of coalescent simulation techniques, which is somewhat limited by their difficulties in integrating natural selection in the simulations, and (ii) the progressive use of individual-based simulation techniques.

Table 1.7: List of software from population dynamics and population genetics relevant to individual-based demogenetic models. Features implemented in each program are specified. *In the new version of the MS program (released October 14, 2007), the user can specify if the population has been growing or shrinking exponentially.

Software (Reference)	**Field**	**IBM**	**VarPop**	**Sel**	**Rec**	**Migr**	**Mut**
MODYPOP (Sabaton *et al.*, 1997; Gouraud *et al.*, 2001)	PD	No	Yes	No	No	Yes	No
EasyPOP (Balloux, 2001)	PG-F	No	No	No	Yes	Yes	Yes
SFS-CODE (Hernandez, 2008)	PG-F	No	No	Yes	Yes	Yes	Yes
SEQ-GEN (Rambaut and Grassly, 1997)	PG-C	No	No	No	No	No	Yes
MS (Hudson, 2002)	PG-C	No	No*	No	Yes	Yes	No
MIGRATE (Beerli and Felsenstein, 2001; Beerli, 2006)	PG-C	No	Yes	No	No	Yes	No
LAMARC (Kuhner, 2006)	PG-C	No	Yes	No	Yes	Yes	No
METASIM (Strand, 2002)	PD + PG	Yes	Yes	Yes	No	Yes	Yes
VORTEX (Lacy, 2000a)	PD + PG	Yes	Yes	No	Yes	Yes	Yes
simuPOP (Peng and Kimmel, 2005; Peng and Amos, 2008)	PG-F	Yes	Yes	Yes	Yes	Yes	Yes
NEMO (Guillaume and Rougemont, 2006)	PG-F	Yes	Yes	Yes	Yes	Yes	Yes
Eco-genetic model (e.g., Wang, 2009)	QG	Yes	Yes	Yes	No	No	No

IBM, individual-based model; VarPop, variable population size; Sel, natural selection; Rec, recombination; Migr, migration or dispersal; Mut, mutation; PD, population dynamics; PG, population genetics, with forward-time (F) or coalescent (C) simulation programs; QG, quantitative genetics.

In the field of population dynamics, the individual-based model METASIM (Strand, 2002) provides a flexible environment, based on matrix projection theory, to simulate population genetics of complex popula-

tion dynamics. Population dynamics models are also frequently used for population viability analysis or PVA, which aims to predict the likelihood of the persistence of an endangered species for a given time in the future (DeSalle and Amato, 2004). PVA programs such as VORTEX (Lacy, 2000a) aim to study the effects of deterministic forces and stochastic events on the dynamics of populations, including changes in genetic variation.

In population genetics, earlier coalescent simulation programs assumed a constant population size, because the original formulation of the coalescent approach was made under the assumption of a Wright-Fisher model. More realistic versions of this approach have been developed to take into account factors such as genetic recombination, gene conversion, population subdivision, population growth and demography (Marjoram and Tavaré, 2006; Kuhner, 2009). A method named approximate Bayesian computation (Beaumont et al., 2002; reviewed by Bertorelle *et al.*, 2010; Csilléry *et al.*, 2010) proposed a more flexible framework to address complex scenarios (Segelbacher *et al.*, 2010). In addition, forward-time simulation programs such as simuPOP and NEMO (Guillaume and Rougemont, 2006) explicitly model the properties of individuals and specify arbitrary patterns of population size changes. In the field of quantitative genetics, the recent development of individual-based eco-genetic models allowed evaluating the relative importance of genetic and ecological effects on fish life-history traits and stock productivity by taking into account quantitative genetic traits inheritance (e.g., Dunlop *et al.*, 2009; Wang and Hook, 2009).

In all of these attempts to develop models that integrate demography and population genetic structure, the expected level of population genetic divergence is still estimated under specific population size change and dispersal rate patterns (Palsboll *et al.*, 2007). A further understanding of how demography influences the genetic structure of stream fish populations is an important next step in developing comprehensive individual-based demogenetic models.

4 Discussion and summary: towards a spatially explicit demogenetic model for brown trout

Our review demonstrates the historic development of ecological models for brown trout over the past 30 years, and the extent to which modelling currently plays a role in the management and conservation of freshwater fish. To our knowledge, this is the most comprehensive effort to date to

review and synthesise this broad topic. We found that initially the development of ecological models followed four separate trajectories: population dynamics, population genetics, habitat preferences and spatial distribution. Our review highlights efforts that have been made to integrate ecological models across spatial scales and shows the increasing use of individual-based simulation techniques. First, we addressed models integrating stream scale habitat characteristics into population dynamics (i.e., spatial dynamics models), or landscape ecology into population genetics (i.e., landscape genetics models). Table 1.8 lists the programs associated with these models and mentioned earlier. Second, there have been efforts to integrate population dynamics and population genetics models, and we reviewed individual-based demogenetic models that have appeared recently (second half of Table 1.7). Comprehensive and flexible individual-based demogenetic models however are in the early stages of development. Furthermore, we believe there is a need to integrate spatially explicit methodology into demogenetic models, to better address the important issue of ecological scale (e.g., Wiens, 1989; Peterson and Parker, 1998; Schneider, 2001; Lischke *et al.*, 2007).

Future model development efforts should include spatially explicit demogenetic models that integrate demographic, genetic and spatial data. The interplay between environmental processes and demogenetic characteristics is crucial. For instance, at the stream scale, an environmental perturbation can represent a radical and rapid change in the demographic and genetic structure of a population, producing local catastrophes and reductions in suitable areas where fish can thrive (Pertoldi and Topping, 2004). At a larger scale, the structure and complexity of the riverscape can affect the demogenetics of fish populations by influencing the occurrence of their dispersal strategies, and by interacting with the micro-evolutionary processes. Individual-based, spatially explicit demogenetic models may be particularly useful for fish and wildlife management and conservation questions. They can serve as a tool for understanding specific questions like the influence of barriers on the dispersal of a species, or as a simulation tool for testing hypotheses concerning the response of a population to future changes in the environment, either natural or anthropogenic.

To our knowledge, only one spatially explicit individual-based demogenetic model has been developed. KERNELPOP (Strand and Niehaus, 2007) provides a population genetics simulation environment with both demographic and spatial realism. According to the authors, this model allows the implementation of almost any arbitrary population demographic and genetic model in a spatially explicit context (Table 1.8).

Although R (R Development Core Team, 2010) was used as an interface for this model, the simulation engine was implemented in C++. Therefore, the ease with which new features can be added to the model may be limited, because the user has to learn the complex details of a standard programming language (i.e., C++ in this case). A flexible yet simple method to realistically link demography and population genetics at various spatial scales is needed.

Table 1.8: List of software from spatial dynamics and landscape genetics relevant to individual-based, spatially explicit demogenetic models. Features implemented in each program are specified. *In the new version of the program, SPLATCHE 2 (Ray et al., 2010), a recombination model has been implemented.

Software (Reference)	Field	IBM	VarPop	Sel	Rec	Migr	Mut
SPLATCHE (Currat *et al.*, 2004)	PG-C	No	Yes	No	No*	Yes	Yes
BARRIER (Manni *et al.*, 2004)	LG	No	No	Yes	No	Yes	No
STREAM TREES (Kalinowski *et al.*, 2008)	LG	No	No	No	No	Yes	Yes
AQUASPLATCHE (Neuenschwander, 2006)	PG-C	No	Yes	No	No	Yes	Yes
inSTREAM (Railsback *et al.*, 2009)	SD	Yes	Yes	No	No	Yes	No
HexSim (Schumaker, 2011)	SD	Yes	Yes	No	No	Yes	No
quantiNEMO (Neuenschwander *et al.*, 2008a)	QG	Yes	Yes	Yes	Yes	Yes	Yes
CDPOP (Landguth and Cushman, 2010)	LG	Yes	Yes	No	Yes	Yes	Yes
KERNELPOP (Strand and Niehaus, 2007)	SD + LG	Yes	Yes	Yes	No	Yes	Yes

IBM, individual-based model; VarPop, variable population size; Sel, natural selection; Rec, recombination; Migr, migration or dispersal; Mut, mutation; PG, population genetics, with forward-time (F) or coalescent (C) simulation programs; QG, quantitative genetics; SD, spatial dynamics; LG, landscape genetics.

NetLogo (Wilensky, 1999) provides a simplified programming language, a graphical interface and an automated simulation experiment manager that allows the user to build, observe and run IBMs. Furthermore, it is now possible to call R from NetLogo (Thiele and Grimm, 2010). We believe that the combination of these powerful tools may provide a simple and flexible framework to implement individual-based, spatially explicit demogenetic models, which can in turn become a major tool in management and conservation of freshwater fish populations.

In summary, the ecological models applied to brown trout have become increasingly complex, and they have been used to predict an expanding range of responses at various spatial and temporal scales. Most

recently, efforts have focused on linking the models across these scales and disciplines, but much remains to be done. Although a few models combining both demographic and genetic characteristics of populations have appeared recently, no comprehensive, spatially explicit, demogenetic model has been proposed. We have described the framework for such a model, advocating the use of individual-based simulation techniques to include individuals' variability and different levels of spatial details. This framework, which involves both NetLogo (for model programming) and R (for model development, testing and understanding), will be tested and applied to stream-dwelling brown trout populations to describe the variations in their demogenetic structure at both stream and watershed scales. We anticipate that the application of such spatially explicit, individual-based demogenetic models to fish and wildlife populations will further improve their management and conservation, by generating testable hypotheses as to how populations might respond to natural or anthropogenic disturbances.

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Box I: Capture-recapture modelling

Most of the time and certainly for freshwater fishes, a complete census of the studied population turns out to be impossible. Techniques to collect a sample from a population and indirect measurements are therefore used (Townsend *et al.*, 2000). The most common statistical methods used to analyse fish demographic data – gathered for instance by trapping or electrofishing – are those called capture-recapture (CR) methods (Amstrup *et al.*, 2005). These methods are based on the following common principle: individuals belonging to the studied population are caught, marked in some way and then released, this operation being repeated several times. Afterwards, a capture history is available for each marked animal, which consists in a vector of zeros (not seen) and ones (seen) giving the capture status of the individual at each occasion. A probabilistic model is then developed to describe the matrix of capture histories of all individuals. This model is used to derive estimators of the demographic quantities of interest (i.e., parameters), which differ according to the CR method used (Nichols *et al.*, 1992).

Capture-recapture methods were developed in the early 1930s to estimate the size of closed populations, in which no animal can enter or leave (Pollock, 1991; Lebreton, 2006). The most basic model is the Lincoln-Petersen index (Seber, 1973), from which all formulas and models for closed populations were derived. From the mid-19th century, CR models evolved to infer survival rates as well as to permit additions (births and immigrations) and deletions (deaths and emigrations) in the populations – therefore called 'open' (Lebreton *et al.*, 1992; Cooch and White, 2006). The first open CR model was developed independently by Jolly and by Seber in 1965. In the Jolly-Seber (JS) model, the assumption is made that marked and unmarked animals undergo the same sampling process, so population size and survival rates can be estimated together (Baillargeon and Rivest, 2007). To allow for the relaxation of this rule of equal capturability, a particular case of the Jolly-Seber model was developed: the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965). The CJS model thus applies when the released individuals are not a random sample of the population at a given capture occasion, and in this case, the analysis focuses on the estimation of survival rates of the animals that were released (Baillargeon and Rivest, 2007). The example below, derived from Cooch and White (2006), illustrates this concept for a CR experiment with three encounter occasions conducted on four individuals in order to estimate their survival and capture probabilities (CJS model).

■ ***Example.*** Let it be assumed that $n = 4$ individuals are involved in a capture-recapture experiment with $T = 3$ encounter occasions. The first animal, for which a capture history '1 0 1' was observed, was caught and marked during the first occasion T_1, alive but not encountered during the second occasion T_2, and caught alive during the third occasion T_3. The second individual with capture history '1 0 0' was captured and marked at T_1 and either (i) dead at T_2, (jj) alive but not encountered at T_2 and alive but not encountered at T_3, (iii) alive but not encountered at T_2 and dead at T_3. The third animal with capture history '1 1 0' was caught and marked at T_1, alive and encountered at T_2, and either (i) dead at T_3, (ii) alive but not encountered at T_3. The last individual with capture history '1 1 1' was caught and marked at T_1, alive and encountered at T_2 and T_3.

Let it be considered that the following four parameters are to be estimated (Fig. I.1):

- ϕ_1, the probability for an individual to survive between occasions T_1 and T_2
- p_2, the probability to capture an individual at occasion T_2
- ϕ_2, the probability for an individual to survive between occasions T_2 and T_3
- p_3, the probability to capture an individual at occasion T_3

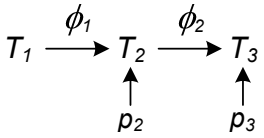

Figure I.1: Capture-recapture experiment with three encounter occasions. Four parameters are estimated: the survival probabilities ϕ_1 and ϕ_2, and the capture probabilities p_2 and p_3. The capture probability at first occasion, p_1, cannot be estimated since none of the individuals captured at that occasion has been previously marked.

A probability is associated with each marked animal. For instance, for the first individual with capture history '1 0 1', its probability to survive between the first and second occasions is given by ϕ_1, its probability of not being encountered, but to be alive on the second occasion is given by the complement of p_2 multiplied by the probability ϕ_2, and its probability of being captured at occasion T_3 is given by p_3. The probability of observing this particular capture history is then obtained by the product of the probabilities: $\phi_1 \times (1-p_2) \times \phi_2 \times p_3$. The associated probabilities for the other animals are:

- $(1 - \phi_1) + \phi_1 \times (1 - p_2) \times (1 - \phi_2) + \phi_1 \times (1 - p_2) \times \phi_2 \times (1 - p_3) = 1 - \phi_1 \times p_2 - \phi_1(1 - p_2) \times \phi_2 \times p_3$ (individual with capture history '1 0 0')
- $\phi_1 \times p_2 \times (\phi_2 \times (1 - p_3) + (1 - \phi_2)) = \phi_1 \times p_2 \times (1 - \phi_2 \times p_3)$ (individual with capture history '1 1 0')
- $\phi_1 \times p_2 \times \phi_2 \times p_3$ (individual with capture history '1 1 1')

Let it be noted N_{101}, N_{100}, N_{110} and N_{111} the number of animals presenting each of these four capture histories. Observed frequencies are used to estimate

p_2, p_3, ϕ_1, and ϕ_2, which are the most likely parameter values that maximize the chance of producing these frequencies, i.e., the value of the natural logarithm of the *Likelihood* function. This latter is given by the product of the probabilities of possible capture histories among those actually observed. In our example:

$$\begin{aligned} \textit{Likelihood} \;=\; & (\phi_1 \times (1-p_2) \times \phi_2 \times p_3)^{N^{101}} \\ & \times (1 - \phi_1 \times p_2 - \phi_1 \times (1-p_2) \times \phi_2 \times p_3)^{N^{100}} \\ & \times (\phi_1 \times p_2 \times (1 - \phi_2 \times p_3))^{N^{110}} \\ & \times (\phi_1 \times p_2 \times \phi_2 \times p_3)^{N^{111}} \end{aligned}$$

■

Most programs written over the years for CR data analysis imply the use of frequentist methods. For example, in the software MARK (White and Burnham, 1999), the estimates of model parameters are computed using numerical maximum likelihood techniques. Bayesian methods are also suitable, WinBUGS (Lunn *et al.*, 2000) being the most common software used. Frequentist and Bayesian approaches differ by their definition of probabilities. In the frequentist case, the probability of an event is defined as the limiting proportion of times it would occur given many repetitions (Seefeld and Linder, 2007). In the Bayesian case, subjective knowledge is incorporated and the probability of a proposition is the quantification of its plausibility given some contextual prior information.

The principle of the Bayesian approach is as follows: first, information contained in the data are translated into a *Likelihood* function, which expresses the degree of credibility of the data conditional on the parameters. Then, the information provided by the subjective knowledge of the investigator is represented as a *Prior* probability distribution. Following the theorem of Bayes (1764), the combination of the *Prior* and the *Likelihood* yields to a probability distribution called *Posterior*:

$$\textit{Joint posterior} \;\propto\; \textit{Likelihood} \;\times\; \textit{Joint prior}$$

Parameters are considered as random variables, and the plausibility of their values is quantified by their posterior probability distributions. Each posterior distribution is calculated conditional on the observed data, and a random sample with each posterior as distribution is generated.

When direct sampling of such a posterior is difficult, generic sampler algorithms are used. For instance, in WinBUGS, the joint posterior distribution of the parameters is sampled using the Metropolis-within-Gibbs algorithm, which belongs to the Markov Chain Monte Carlo (MCMC) methods.

In any MCMC method, a critical issue is whether the simulated chain has converged to its target distribution (Rivot and Prévost, 2002). To check this convergence, a diagnostic value noted $\hat{R}$ and based on a comparison of the within and between chain variance for each variable is computed[1]. $\hat{R}$ is equal to 1 at convergence and can be seen as a factor by which posterior intervals are expected to shrink if simulation continued, i.e., the potential scale reduction factor (Calvert *et al.*, 2009). In practice, two or more parallel MCMC chains (each with different initial values) are run for each model. The number of iterations until which $\hat{R}$ is close to the value of 1 is considered as a burn-in period and is thus not used to estimate the parameters.

In the example below, we consider a Cormack-Jolly-Seber model as in the previous section, applied to a generalized capture-recapture experiment.

■ ***Example.*** Let it be assumed that n individuals are involved in a capture-recapture experiment with T encounter occasions. Let $A_{i,t}$ and $X_{i,t}$ be two binary random variables, the former taking values 1 if individual i is alive at time t and 0 if it is dead at time t, the latter taking values 1 if individual i is encountered at time t and 0 otherwise. Let e_i be the occasion where individual i is encountered for the first time (at $t = 1$).

The parameters involved in the Cormack-Jolly-Seber model are $\varphi_{i,t}$, the probability that an animal i survives to time $t + 1$ given that it is alive at time t, and $p_{i,t}$, the probability of detecting individual i at time t ($t = 2, ..., T$).

If individual i is alive at time t ($A_{i,t} = 1$), then it has probability $p_{i,t}$ of being encountered and probability $1-p_{i,t}$ otherwise. Now if individual i is dead at time t ($A_{i,t} = 0$), then it cannot be encountered (Gimenez *et al.*, 2007; Schofield *et al.*, 2009).

Putting together these two pieces of reasoning, the distribution of the variable $X_{i,t}$ conditional on the variable $A_{i,t}$ is given by:

$$X_{i,t}|A_{i,t} \sim Bernoulli(A_{i,t}\ p_{i,t}) \text{ for } t \geq e_i, \text{ with } p_{i,e_i} = 1$$

The distribution of the variable $A_{i,t+1}$ conditional on the variable $A_{i,t}$ is given by:

$$A_{i,t+1}|A_{i,t} \sim Bernoulli(A_{i,t}\ \varphi_{i,t}) \text{ for } t \geq e_i, \text{ with } p_{i,e_i} = 1$$

■

[1] In this thesis, we used the Gelman and Rubin (1992) diagnostic $\hat{R}$ as modified by Brooks and Gelman (1998).

Chapter 2

Assessing brown trout spawning movements with multistate capture-recapture models: a case study in a fully controlled Belgian brook*

A multistate capture-recapture model was developed to estimate movements of brown trout (*Salmo trutta*) between a main stem and its headwater tributary, and their survival and recapture probabilities in each stream. As all individuals entering or leaving the tributary were captured by trapping, the studied ecological system was fully controlled. The performance of multistate models combining two sources of data (trapping and electrofishing) available for 6 years was first evaluated. Realistic estimates were obtained to infer the average spawning behaviour of trout: (i) 58% returned to their original site after spawning, (ii) 9% returned to their natal site for reproduction, (iii) 55% of the ascending individuals performed natal homing. Because less informative systems are pervading, we eventually assessed the sensitivity of multistate models to the level of trapping data integration. A lack of such data led to an underestimation of movement probabilities, and we found that this effect could be compensated by electrofishing samplings.

Key words: capture-recapture; multistate models; natal homing; post-spawning homing; *Salmo trutta*

* This chapter was published in Canadian Journal of Fisheries and Aquatic Sciences. Authors: Béatrice M. Frank, Olivier Gimenez (Centre d'Ecologie Fonctionelle et Evolutive, CNRS, France), Philippe V. Baret. Supplementary data are available in Appendix 1, page 229.

1 Introduction

Migration is a demographic process with a strong impact on population dynamics (Lebreton, 1996; Dingle, 1996). Indeed, immigration and emigration are two of four factors responsible for changes in the size and the structure of populations through time and space (Townsend *et al.*, 2000), the two other factors being birth and death processes. Movements can also affect genetic differentiation, local adaptation, and evolutionary persistence of populations (Clobert *et al.*, 2001). Substantial movement in populations of stream-dwelling fish species such as the brown trout (*Salmo trutta*) may occur (Gowan *et al.*, 1994; Gowan and Fausch, 1996), although several studies also suggest a high degree of local site fidelity (Bachman, 1984; Hesthagen, 1988; Carlsson *et al.*, 1999). Between-stream movements are frequent, as brown trout inhabiting complex systems use main streams to grow and mature (Baglinière *et al.*, 1987; Jonsson and Jonsson, 1993; Forseth *et al.*, 1999) and first-order streams as spawning grounds and nursery areas (Elliott, 1994; Crisp, 1996; Armstrong *et al.*, 2003).

To our knowledge, multistate capture-recapture (MSCR) models have never been used to study trout movements between spawning tributaries and the main river and have even rarely been used for other fish species (e.g., Massicotte *et al.*, 2008). Obstacles to the use of MSCR models for fish include the necessity to discriminate between mortality and emigration and to account for temporary emigration. Indeed, emigration cannot be directly estimated in most population studies, and this is accounted for in the estimate of survival, which is consequently underestimated and called "apparent survival" (Olsen and Vollestad, 2001; Fletcher *et al.*, 2002). Furthermore, emigration can be permanent or temporary (see Fujiwara and Caswell, 2002), and temporary emigration is often Markovian; the probability of being temporarily absent depends on whether or not an individual was absent during the previous occasion (Schaub *et al.*, 2004). To overcome these difficulties, electrofishing samplings in both streams supplemented by a comprehensive trapping of fish entering or leaving the tributary would be the ideal sampling design. When complete capture of migrants is not possible, extensions of MSCR models have nonetheless been developed to estimate emigration rates (Fujiwara and Caswell, 2002; Kendall and Nichols, 2002; Schaub *et al.*, 2004). For instance, the model proposed by Horton *et al.* (2011) separates true survival from permanent emigration using a combination of continuous data from a multiple-antenna array with instantaneous electrofishing live capture-recapture (CR) data.

In the present work, we investigated post-spawning homing and natal homing behaviours of brown trout. Post-spawning homing is the return of the trout to its original territory once reproduction is complete, while natal homing or natal site fidelity is the propensity of a trout to return to spawn in the stream of its birth (Stuart, 1957). We used trapping and electrofishing data from a 6-year CR study of brown trout spawning movements between a headwater tributary and the main river in southern Belgium. This ecological system is fully controlled (i.e., all individuals entering or leaving the tributary are captured in the upstream and downstream traps). Because less informative systems are more common than fully-controlled ones, analyses based on different levels of data integration were compared. Performance of MSCR models was evaluated from these comparisons in order to provide guidance for their future use in fish migration studies.

Radiotelemetry and CR are two complementary methods for studying trout spawning movements. Observations of radio-tagged fish provide fine-resolution estimates of the timing and distance of movements (e.g., Ovidio, 1999; Arnekleiv and Ronning, 2004; Rustadbakken *et al.*, 2004), while CR methods (see reviews by Schwarz and Seber (1999) and Seber and Schwarz (2002)) allow the study of fish movements at larger spatial and temporal scales (Gresswell and Hendricks, 2007). Single-state CR models enable estimating survival and detection (capture) probabilities among individuals while in MSCR models (Arnason, 1972, 1973; Hestbeck *et al.*, 1991), individuals can move between states (e.g., geographical sites, reproductive status, size classes, etc.) and thus have state-specific survival and detection probabilities (see Lebreton et al., 2009 for a review).

In this paper, two approaches were used in order to evaluate performance of MSCR models and to infer trout spawning behaviour. On the one hand, a simple analysis of trout movements at the trapping facility was used with two data sets: one including all observations at the traps (full data set), the other including only the half of these observations (reduced data set). On the other hand, MSCR modelling was applied on four individual CR histories: one constructed with all available data for the studied system (total capture histories), i.e., data from the traps and from electrofishing samplings, the others with all electrofishing data and a variable random sample of trapping data (partial capture histories). First, performance of MSCR models and their sensitivity to the level of data integration were evaluated through three questions: (i) Were MSCR estimates consistent with true movement observations obtained from the simple analysis? (ii) How were they affected by the quantity of trapping

data? (iii) To what extent can results from a half-efficient trapping facility be improved by an additional source of data (i.e., electrofishing)? Second, trout return rates to their original site after spawning and to their natal site for spawning were computed from results drawn from the simple analysis and MSCR modelling applied to the full data set and to total capture histories, respectively. Then, post-spawning and natal homing behaviours were inferred.

2 Materials and methods

2.1 Study area and data

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 km^2 and is located in southern Belgium (Fig. 2). The study area consisted of a 1.1 km-long section of a main stem (Lesse River, LR, fourth-order) with one 1.2 km-long first-order tributary (Chicheron Brook, CB). LR is located at the boundary between the trout and the grayling fish assemblage zones; the stream has a 0.8% slope, is 13 to 27 m wide, has an average depth of 0.5 m, and has a 4 $m^3.s^{-1}$ average discharge rate. The river flows through a wide forested area and offers excellent water quality. CB 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. This brook is a well-known area for its spawning grounds and nurseries and is exclusively populated with wild brown trout.

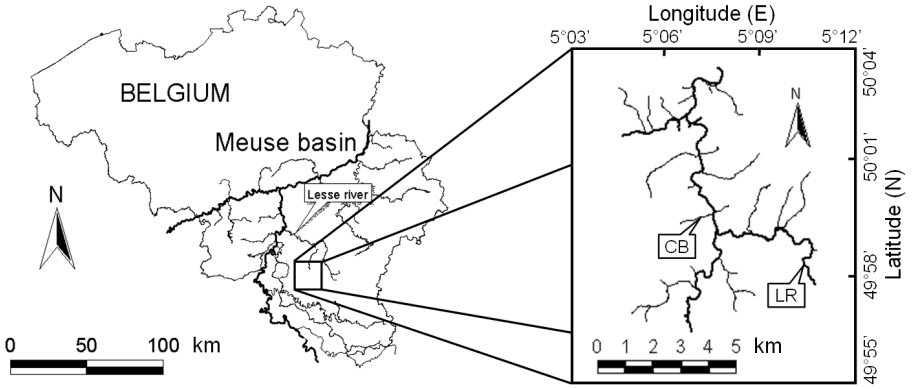

Figure 2.1: Situation plan of the Lesse River (LR) in the Meuse basin, and position of the Chicheron Brook (CB) in the Lesse basin.

The LR/CB local system was studied for 20 years by Huet and Timmermans (1979) and monitored afterwards for another 30 years. Three types of trout movements were observed between the main stream and the tributary: (i) an upstream migration of mature adults from LR to CB for spawning in autumn and winter, (ii) the return of these adults to LR after spawning, (iii) a downstream migration of fry and juveniles from CB to LR in spring and summer of that same year or the next years. The migration pattern seems to be always the same (Dupont, 2009); each winter, 100 to 500 spawners are observed to migrate from LR to CB to spawn, and 300 to 900 young trout swim down to LR during the successive spring and summer. A radiotelemetry study conducted between 2000 and 2004 on 21 spawners of the LR/CB system demonstrated that (i) trout always return to their original territory once the reproduction is complete (post-spawning homing), (ii) trout do not always frequent the same spawning ground and thus can have different reproductive behaviours during their lifetime (Dupont, 2004). Earlier, Huet and Timmermans (1979) suggested that the downstream movement of spawners could be determined not only by a tendency to return to the river of departure, but also by a density factor in the brook, which was already inhabited by a resident trout population. Moreover, they found no evidence of natal homing behaviour in the studied system.

More generally, five types of trout movements between a first-order tributary and the main stream are observed (Fig. 2.2; movement types I to V). At the temporal scale, all movement types occur during one given year. They are explained hereafter using brook as a reference. Types I and III involve spawners of the tributary, which in theory immigrate to then emigrate from the brook during the reproduction period. For some of the spawners, the immigration will be permanent because they may die or decide to stay (and die) in the brook (type I); the others will return to the main river after the spawning (post-spawning homing hypothesis – verified by radio-tracking) (type III). Movement type II involves fry and juveniles born in the tributary. Some of the young trout swimming downstream from the tributary to the main stem will leave the tributary forever, but some of them will come back during the reproduction period, once mature (natal homing hypothesis). Types IV and V refer to no movement at all; trout stay either in the brook or in the main stream, respectively.

In 2003, an auto-powered and self-cleaning trapping facility was built 20 m upstream from the confluence of the tributary to monitor trout movements. Upstream and downstream traps were checked daily. Furthermore, fish were sampled in the two streams on one or two occasions

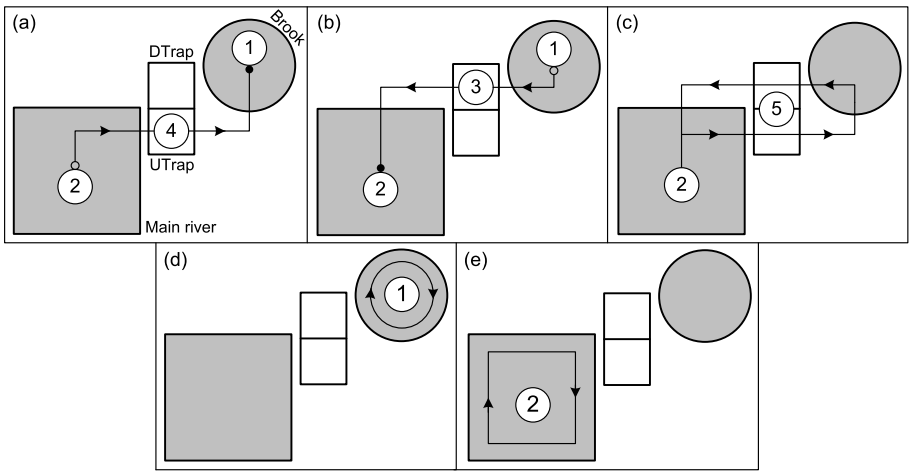

Figure 2.2: Trout can perform five types of movement: they can move between the main stream and the nursery brook (movement types I (a), II (b) and III (c)), or stay in each stream (types IV (d) and V (e)). Consequently, trout can be observed at five different locations: in the brook (1), in the main stream (2), at the downstream trap exclusively (3), at the upstream trap exclusively (4) or both at the upstream trap and the downstream trap (5).

in each year of the study (time period of 6 years, from 6 October 2004 to 9 July 2010). They were captured using standard electrofishing techniques (HERON, 350-450V DC in LR; DEKA, 250-600V DC in CB) once a year in LR in autumn (before the spawning migration of mature adults) and twice a year in CB in autumn and in spring (before and after the stay of the adults, respectively). Over the course of the study, 18 sampling occasions were recorded, and each period required 2-3 days to complete. Untagged electrofished trout > 7.5 cm (6 cm since 2007) were marked with passive integrated transponder (PIT; Réseaumatique, Bernay, France) tags following anaesthesia with clove oil. Tag loss was estimated by removing the adipose fin of all tagged trout. Fish captured in the traps undergo the same procedures as those that were electrofished. Trapping efficiency was estimated from inconsistencies in trout capture histories.

For the simple analysis of trout movements, we used observations of 4790 tagged individuals caught at the trapping facility for the full data set (noted FDS) and observations of 2587 individuals for the reduced data set (RDS). This latter number was obtained by taking a random sample of half the size of each set of observations made at the upstream and downstream traps. For the analysis involving MSCR modelling, four individual capture histories were constructed: total capture

histories (TCH) that comprise 10 289 trout, including 4028 individuals caught in LR, 3945 individuals caught in CB, and 4790 individuals caught at the trapping facility; partial capture histories (PCH1, PCH2 and PCH3), including the same number of individuals caught in LR and in CB as in TCH, but three-quarters, one-half, and one-quarter of the individuals caught at the trapping facility, respectively. Recaptured fish that died during the capture or marking process were included in the analyses (i.e., 55 individuals out of 10 289).

2.2 Simple analysis of trout movements at the trapping facility

After a classification of trout caught at the trapping facility according to their upstream and downstream movements, proportions of trout performing movement types I to III (Fig. 2.2) were determined for FDS and RDS. Then, trout return rates to their original site after spawning and to their natal site for spawning were computed.

Return rate of spawners to their original location under the post-spawning homing hypothesis was computed as the ratio of the number of individuals caught consecutively in the upstream and downstream traps (i.e., movement type III) to the total number of individuals caught in the upstream trap (i.e., types I and III). Some individuals strictly migrating out of the brook (movement type II) will come back, once mature, to the tributary for reproduction. These trout were observed first at the downstream trap and at least several months later at the upstream trap and thus performed movement types II then I or III. It was only possible to determine their total number over the 6 years of the study because both movement types did not occur at the same time. This number of homing individuals was used to compute the global return rate of trout to their natal site for reproduction under the natal homing hypothesis. It is equal to the ratio of the number of homing individuals to the number of individuals observed at the downstream trap exclusively (i.e., movement type II). Furthermore, spawning periods and frequencies for trout assigned to movement types I and III were analysed. We also investigated periods of descent for individuals assigned to movement type II as well as time elapsed between the descent and the first reproduction for homing individuals.

2.3 Multistate capture-recapture modelling

2.3.1 Model structure and parameters of interest

A general MSCR model incorporating the biological processes of interest was developed. We considered six states in the model. Five of them are underlying the movement types observed between the headwater spawning tributary CB and the main river LR (Fig. 2.2): spawners moving from LR to CB (movement type I, state SP1 for 'spawner 1') or moving from LR to LR (type III, state SP2 for 'spawner 2'), young trout moving from CB to LR (type II, state YT for 'young trout'), non-spawners staying in CB (type IV, state NS1 for 'non-spawner 1') or staying in LR (type V, state NS2 for 'non-spawner 2'). The last state corresponds to dead individuals (state D for 'dead').

We considered 12 occasions of capture, two for each year of the study, in order to separate observations made by electrofishing and by trapping (Fig. 2.3). At odd occasions (referred to as 'A' hereafter), individuals were always captured in state NS1 or NS2 (according to the stream sampled), as electrofishing took place before or after spawning migration of mature adults to CB and the movement of young trout from CB to LR. At even occasions (referred to as 'B'), only states YT, SP1, and SP2 are possible for the individuals caught in the trapping facility.

States are related to observations through recapture probabilities. We matched the events of capture histories with the states NS1, NS2, YT, SP1, and SP2 as follows, the notation being 0 when the individual was not captured: (1) NS1 caught by electrofishing in CB but not in the downstream trap, (2) NS2 caught by electrofishing in LR, (3) YT caught exclusively in the downstream trap, (4) SP1 caught exclusively in the upstream trap, (5) SP2 caught consecutively in the upstream and downstream traps. Because electrofishing in CB in the spring overlaps the downstream migration of young trout, a certain number of trout were captured at both events 1 and 3. We assigned these individuals to event 3 (551 trout out of 10 289 for TCH, 428 out of 9 726 for PCH1, 293 trout out of 9 134 for PCH2, 143 out of 8 499 for PCH3). Capture histories were also sorted into two groups, the first one including trout born in CB (i.e., trout captured in state YT) and the second one including trout of unknown origin (i.e., trout never captured in state YT). Examples of capture histories for the two groups are given in Table 2.1.

In addition to trout recapture probabilities in both streams (R_{CB} and R_{LR}) and in the trapping facility (R_{TF}), we also estimated trout survival probabilities in both streams (S_{CB} and S_{LR}) and the following

Table 2.1: Examples of multistate capture histories for the group of trout born in the Chicheron Brook (group 1) and the group of trout of unknown origin (group 2).

Group	History	Events
1	1013	Individual first caught as non-spawner by electrofishing in CB, not caught at the next trapping occasion, recaught as non-spawner by electrofishing in CB, and then recaught as juvenile in the downstream trap
	0324	Individual first caught as juvenile in the downstream trap, caught as non-spawner by electrofishing in LR, and then recaught as spawner in the upstream trap
	1305	Individual first caught as non-spawner by electrofishing in CB, caught as juvenile in the downstream trap, not caught at the next trapping occasion, and then recaught as spawner in both upstream and downstream traps
2	0525	Individual first caught as spawner in both upstream and downstream traps, recaught as non-spawner by electrofishing in LR, and then recaught as spawner in both upstream and downstream traps
	2410	Individual first caught by electrofishing in LR, recaught as spawner in the upstream trap, recaught as non-spawner by electrofishing in CB, and then not recaught at the last trapping occasion
	2504	Individual first caught by electrofishing in LR, recaught as spawner in both upstream and downstream traps, not caught at the next electrofishing occasion, and then recaught as spawner in the upstream trap

CB, Chicheron Brook; LR, Lesse River.

movement probabilities (Fig. 2.3): (i) $M_{CB\ to\ LR}$, the probability for a non-spawner of CB to emigrate to LR (i.e., transition from state NS1 to YT), (ii) $M_{LR\ to\ CB}$, the probability for a non-spawner of LR to spawn in CB and to not come back (i.e., transition from state NS2 to SP1), (iii) $M_{LR\ to\ LR}$, the probability for a non-spawner of LR to spawn in CB and to come back (i.e., transition from state NS2 to SP2). From (i) we derived M_{CB}, the complementary probability for a non-spawner of CB to stay in CB (i.e., remain in state NS1). From (ii) and (iii) we derived M_{LR}, the complementary probability for a non-spawner of LR to stay in LR (i.e., remain in state NS2). More details about the structure of the general MSCR model are given in Supplemental Appendix S1[1].

[1] Supplementary data are available with the article through the journal Web site at `http://nrcresearchpress.com/doi/suppl/10.1139/f2012-041`.

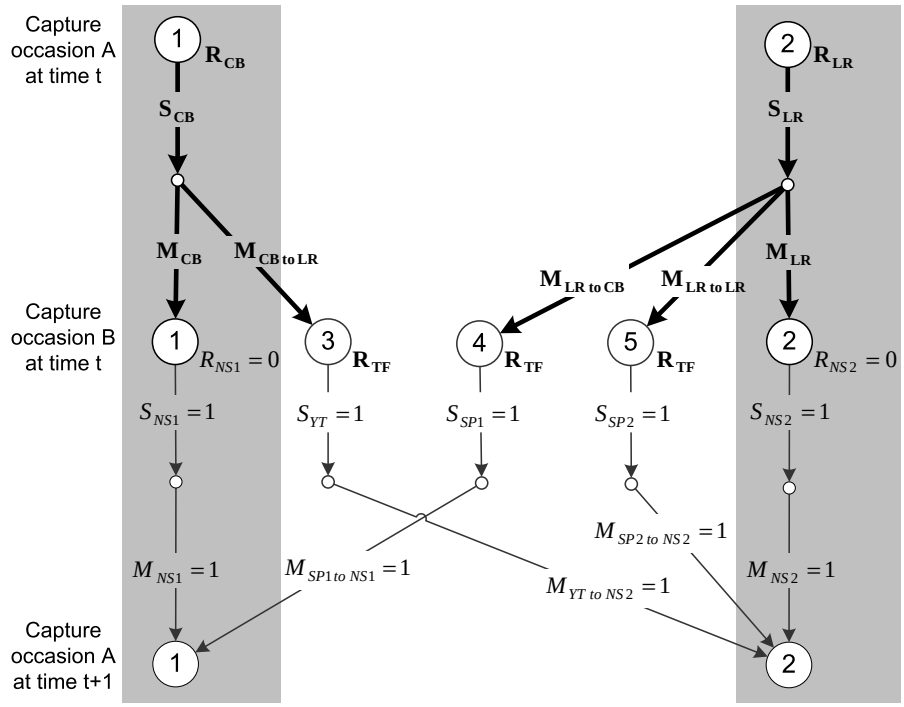

Figure 2.3: Conceptual representation of the general multistate capture-recapture model used to infer brown trout spawning behaviour between a headwater tributary (Chicheron Brook, CB, left grey part in the figure) and the main river (Lesse River, LR, right grey part in the figure) in southern Belgium. Trout movements between both streams were monitored by a trapping facility (TF, middle part in the figure). For each year of the study, two capture occasions were considered: individuals were captured by electrofishing in CB or LR at occasions A or caught in TF at occasions B. States and capture events correspond as follows: (1) non-spawners staying in CB (state NS1, movement type IV), (2) non-spawners staying in LR (state NS2, type V), (3) young trout moving from CB to LR (state YT, type II), (4) spawners moving from LR to CB (state SP1, type I), (5) spawners moving from LR to LR (state SP2, type III). Recapture (R), survival (S) and movement (M) probabilities estimated by the model are shown in bold. Recapture probabilities of trout at occasions B in states NS1 and NS2 were set equal to zero, and all survival and movement probabilities between occasions B and A were set equal to one (in italics).

2.3.2 Goodness-of-fit test, model selection and inferences

The fit of the general MSCR model was assessed using goodness-of-fit procedures (Pradel *et al.*, 2005) implemented in U-CARE (Choquet *et al.*, 2009a). We used modified versions of TCH and PCH in which each occasion A was pooled with the subsequent occasion B (event 3 was then converted to event 1 and events 4 and 5 were converted to event 2) and in which individuals from the two groups were treated separately. A global

test was obtained by adding the individual X^2 values and their respective degrees of freedom. The variance inflation factor ($\hat{c}$) was then calculated as the ratio of the global X^2 value to the total number of degrees of freedom, and applied in model selection to correct for overdispersion (see Supplemental Appendix S2 for more details about goodness-of-fit tests). Program E-SURGE (Choquet *et al.*, 2009b) was used to perform the MSCR analyses.

We constructed a set of 16 models (Table 2.2), each representing a different combination of four effects (i.e., constant, time, group, time × group) on each of the three parameters (recapture, survival, movement). The group effect allows discrimination of trout born in CB from trout of unknown origin. These models fitted on TCH were compared with the modified version of the Akaike information criterion ($QAIC_c$; Burnham and Anderson, 2002). Four of the models were used to evaluate performance of MSCR models and to infer trout spawning behaviour: (i) two models considering all trout of the LR/CB system (i.e., no group effect) and all parameters varying with time or held constant (models 9 and 16 in Table 2.2), (ii) two models including time-dependent and time-independent effects in interaction with a group effect for recapture, survival, and movement parameters (models 1 and 8). Time-dependent models allowed us to obtain estimates for each separated year while time-independent models gave estimates over all years 2004-2010 (models 1 and 9 *vs* models 8 and 16). Results for the year 2009-2010 were not considered because of parameter redundancy, i.e., the last survival probability and the last recapture probability cannot be separately estimated (Gimenez *et al.*, 2003). We used the following notation: considering TCH, estimates obtained from models 9 and 16 were affixed with a prime symbol ($'$) to be distinguished from models 1 and 8 estimates (no prime symbol); for PCH1, PCH2, and PCH3, estimates obtained from models 9 and 16 were affixed with superscripts 1, 2, and 3, respectively.

Parameter estimates derived from models 9 and 16 applied to TCH and PCH and results obtained from the simple analyses performed on FDS and RDS were used to evaluate performance of MSCR models. As a prerequisite, MSCR estimates derived from TCH and PCH2 were used to calculate proportions of individuals performing movement types I to III: ratio of $M'_{LR\ to\ CB}$ to the sum of $M'_{CB\ to\ LR}$, $M'_{LR\ to\ CB}$, and $M'_{LR\ to\ LR}$ for type I; ratio of $M'_{CB\ to\ LR}$ to the sum of $M'_{CB\ to\ LR}$, $M'_{LR\ to\ CB}$, and $M'_{LR\ to\ LR}$ for type II; and ratio of $M'_{LR\ to\ LR}$ to the sum of $M'_{CB\ to\ LR}$, $M'_{LR\ to\ CB}$, and $M'_{LR\ to\ LR}$ for type III. Then, three comparisons were performed: (C1) individual movement proportions from the FDS analysis were compared with those obtained from MSCR estimates derived

Table 2.2: Selection results for the 16 multistate capture-recapture models fitted on total capture histories. Effects considered on recapture, survival and movement probabilities are shown in the three first columns (group corresponds to trout natal origin). For each model, the number of estimable parameters (Np), the model deviance (Deviance), the modified version of the Akaike information criterion (QAICc), and the difference in QAICc between the model and the most highly ranked model (Δ_i) are given.

Model	Recapture	Survival	Movement	Np	Deviance	QAICc	Δ_i
1	Time × Group	Time × Group	Time × Group	81	55 640	40 423	0
2	Group	Time × Group	Time × Group	60	55 742	40 455	32
3	Time × Group	Group	Time × Group	67	55 786	40 501	78
4	Group	Group	Time × Group	45	55 896	40 536	113
5	Time × Group	Time × Group	Group	58	56 041	40 667	244
6	Group	Time × Group	Group	36	56 188	40 729	306
7	Time × Group	Group	Group	41	56 199	40 747	324
8	Group	Group	Group	17	56 497	40 914	491
9	Time	Time	Time	43	60 910	44 160	3737
10	Constant	Time	Time	32	61 094	44 271	3848
11	Time	Constant	Time	35	61 087	44 272	3849
12	Constant	Constant	Time	24	61 223	44 349	3926
13	Time	Time	Constant	30	61 462	44 533	4110
14	Constant	Time	Constant	19	61 606	44 616	4192
15	Time	Constant	Constant	21	61 627	44 634	4211
16	Constant	Constant	Constant	9	61 886	44 798	4375

from TCH in order to determine if they were consistent, (C2) TCH estimates were compared with those derived from PCH1, PCH2, and PCH3 to assess the sensitivity of MSCR models to the efficiency of the trapping facility, (C3) movement proportions from the FDS analysis were compared with those obtained from (i) the RDS analysis and (ii) estimates derived from PCH2 to determine if considering an additional source of data could be a solution when only limited trapping data are available.

Models 1, 8, 9, and 16 applied to TCH were used to infer trout spawning behaviour. Trout return rates to their original site after spawning were calculated from models 9 and 16 estimates by the ratio of $M'_{LR\ to\ LR}$ to the sum of $M'_{LR\ to\ CB}$ and $M'_{LR\ to\ LR}$. Trout return rates to their natal site were obtained from models 1 and 8 estimates as the sum of $M_{LR\ to\ CB}$ and $M_{LR\ to\ LR}$. In contrast with models 9 and 16, models 1 and 8 include a group effect, and only estimates obtained for the group of trout born in CB were needed to compute natal site return rates.

3 Results

3.1 Tag loss and trapping facility efficiency

PIT tag loss was estimated to be 2% in TCH (225 individuals out of 10 289), and half of the loss was observed on trout captured at the trapping facility. These fish were retagged before being released.

The efficiency of the trapping facility was equal to 98.14% on average. It was estimated from inconsistencies observed in TCH: 57 individuals were electrofished at least once in both streams but were never caught by trapping, 20 individuals were caught in CB then directly in the upstream trap, and 12 individuals were caught in the upstream trap then directly in LR. The catch efficiency was computed as the ratio of the number of trout that had left or entered the brook out of control (89 individuals) to the total number of individuals caught at the trapping facility over all years 2004-2010 (4790 individuals). All these leaks took place during the year 2005-2006, as fish moving downstream were "jumping" over the traps. Wooden screens were placed to prevent this problem.

3.2 Simple analysis of trout movements at the trapping facility

Proportions of trout performing movement types I to III and the annual return rates of adults to their location of origin after the reproduction

period were computed from observations at the trapping facility. Results obtained from FDS reflect true movements of trout owing to the high capture efficiency in the traps (Table 2.3). The same analysis was performed on RDS; results are presented in Supplemental Appendix S3.

Over the years 2004-2010, 561 spawners were observed in the upstream trap, and 329 were caught consecutively in the upstream and downstream traps. Thus, 59% of the spawners survived the reproduction period and returned to the main stream. We obtained a similar result over the years 2004-2008 (i.e., 60%; data not shown). Fluctuations were observed among years with the highest return rate during 2004-2005 (70%) and with the lowest return rate during 2005-2006, 2008-2009,and 2009-2010 (25%, 26%, and 30%, respectively). Rates during 2006-2007 and 2007-2008 were similar to the observed global rate (51% and 54%, respectively). We observed 311 homing individuals (i.e., performing movement types II then I or III) over the 6 years of the study. We calculated that 7% of these trout returned to spawn in the brook in which they were born.

The spawning period occurs mainly from November to January (97%) and more rarely in February and early March (3%). For trout assigned to movement types I and III, spawning frequencies were observed as follows: 85% of the trout (478 individuals) spawned only once, 14% (78) twice, and 1% (5) three times. Emigration of young trout to the main stream occurs mainly from March to September (89%) and more rarely from November to February (11%). Among the 311 individuals showing a homing behaviour, half (159 trout, 51%) waited until the following year to spawn in the brook, and one-third waited 1 more year (96 trout, 31%). In 15% of the cases (47 trout), spawning occurred the same year of the descent of the individual to the main stream. Trout waiting more than 2 years before reproducing were rare (9 trout, 3%).

Table 2.3: Number (and associated percentage) of tagged individuals performing various movement types during the 6 years of the study (full data set). Movement types are as follows: I, strict immigration; II, strict emigration; III, immigration then emigration; III / (I+III), return rate of spawners to their original site after reproduction. The last column presents results over the years 2004-2010.

Type	**2004-2005**	**2005-2006**	**2006-2007**	**2007-2008**	**2008-2009**	**2009-2010**	**2004-2010**
I	50 (7)	109 (18)	105 (15)	102 (7)	92 (8)	99 (21)	232 (5)
II	591 (78)	460 (76)	498 (70)	1167 (84)	1012 (89)	326 (70)	4229 (88)
III	117 (15)	36 (6)	111 (15)	120 (9)	32 (3)	43 (9)	329 (7)
III / (I+III)	- (70)	- (25)	- (51)	- (54)	- (26)	- (30)	- (59)

3.3 Goodness-of-fit and multistate model selection

The general MSCR model applied separately to trout born in CB and trout from unknown origin was rejected for all capture histories (TCH: $X^2 = 74.629$, df = 54, p = 0.033; PCH1: $X^2 = 96.416$, df = 69, p = 0.016; PCH2: $X^2 = 109.271$, df = 68, p = 0.001; PCH3: $X^2 = 119.919$, df = 72, p = 0.000). Two out of five test components, the trap-dependence (M.ITEC) and transience (3G.SR) tests, were significant for TCH and contributed the most to the JMV model rejection (see Supplemental Appendix S2). This means that the fact that a trout has already been caught could have an influence on its behaviour and that all individuals do not have the same probability of subsequent recapture. To improve the fitting of data, we used the calculated values of the variance inflation factor $\hat{c}$ in the analyses (1.382 for TCH; 1.397 for PCH1; 1.607 for PCH2; 1.666 for PCH3).

The 16 models fitted on TCH were compared according to QAICc (Table 2.2). The best supported model was the time-dependent model with a group effect (model 1; $\Delta_i = 0$); all parameters differed according to trout natal origin and varied over time. A huge discrepancy was found at the boundary between models considering a group effect at least on one parameter (models 1 to 8) and models without a group effect (models 9 to 16) (Δ_i between models 8 and 9 = 3245). Models 10 and 11 showed a Δ_i <1, meaning that considering both survival and movement time-dependent or both recapture and movement time-dependent was equivalent. Considering recapture or survival time-independent was best supported by the data than considering both recapture and survival time-independent, the worst of all being to not consider a time effect for movement.

3.4 Trout spawning behaviour

Estimates derived from four MSCR models were used to infer trout spawning behaviour: (i) two time-independent and time-dependent models considering all trout of the LR/CB system, (ii) two time-independent and time-dependent models considering only the group of trout born in CB. Survival, recapture, and movement probabilities estimated by the four models applied to TCH were analysed, and results are presented in Tables 2.4 and 2.5 (see also Supplemental Appendix S4). Trout return rates to their original site after spawning and to their natal site for spawning were computed from estimates derived from models 9 and 16 and from models 1 and 8, respectively. Results obtained from models

applied to PCH were not discussed here given the degradation of information they contain, but the raw estimates are available in Supplemental Appendix S4.

Trout survival probabilities in both streams (S'_{CB} and S'_{LR}) over all years 2004-2010 were estimated equal to 0.51 and 0.56, respectively (Table 2.4). Small variations occurred over years, and we observed a survival higher in CB than in LR during 2004-2006, but the reverse during 2006-2009. On average, recapture probabilities of trout in CB (R'_{CB} = 0.49) were slightly greater than those estimated for trout in LR (R'_{LR} = 0.30). Small variations occurred over years but the trend stays identical. Recapture probabilities of SP1, SP2, and YT in the traps (R'_{TF}) were all estimated nearly equal to unity by the time-independent model. Estimates for separated years given by the time-dependent model were all equal to or higher than 0.95. The probability for a trout in LR to move upstream for spawning can be computed by the sum of the probability for a non-spawner of LR to spawn in CB and to not come back ($M'_{LR\ to\ CB}$) and the probability that it does come back ($M'_{LR\ to\ LR}$); over all years, 12% of the trout moved upstream for spawning.$M'_{LR\ to\ CB}$ and $M'_{LR\ to\ LR}$ are associated with trout movement types I and III, respectively (Fig. 2.2). The probability that the trout returns to its place of origin was observed to be lower during 2005-2006 and 2008-2009 while being higher during 2006-2008. The probability that a young trout migrates from CB to LR was equal to 0.44 when considering over all years ($M'_{CB\ to\ LR}$; movement type II in Fig. 2.2), and small variations occurred for each separated year. Spawner return rate to their original site after reproduction was found to equal 0.58 on average. Fluctuations occurred over years, with higher values during 2004-2005, 2006-2007, and 2007-2008 (0.96, 0.69, and 0.69, respectively) and lower values during 2005-2006 and 2008-2009 (0.27 and 0.25, respectively).

A trout of LR born in CB has a probability to spawn in CB and to not come back ($M_{LR\ to\ CB}$) equal to 0.04, and the probability that it returns to its place of origin ($M_{LR\ to\ LR}$) was estimated equal to 0.05 over all years 2004-2010 (Table 2.5). This latter probability was observed to be lower for years 2005-2006 and 2008-2009 but higher during 2006-2008. In LR, the recapture probability of a trout born in CB (R_{LR}) was estimated equal to 0.22 on average. Comparatively, recapture probability for this group of trout in CB was greater (R_{CB} = 0.33). Recapture probabilities of trout at the trapping facility (R_{TF}) were estimated equal to unity by both time-independent and time-dependent models. It was expected because only trout captured in state YT at the downstream trap were considered. For the same reason, survival probabilities in CB (S_{CB}) were

all estimated nearly equal to unity, the probability that a trout born in CB emigrates to LR was estimated very high ($M_{CB\ to\ LR}$), and values for parameters M_{CB} and M_{LR} were estimated very low and very high, respectively. These two latter movement probabilities are linked to trout movement types IV and V (Fig. 2.2), i.e., they correspond to the probability for a trout born in CB to stay in CB and in LR, respectively. Trout return rate to their natal site for spawning was found to equal 0.09 over all years 2004-2010. Considering separated years, values did not fluctuate much (2005-2006: 0.07; 2006-2007: 0.14; 2007-2008: 0.17; 2008-2009: 0.06). The value for the year 2004-2005 was not computed, as the estimates were obviously incorrect.

Table 2.4: Survival (S'), recapture (R'), and movement (M') estimates with 95% confidence intervals, derived from the time-dependent model (separated years, model 9 in Table 2.2) and the time-independent model (years 2004-2010, model 16) applied to total capture histories and considering all trout of the Lesse River / Chicheron Brook system.

Probability	**2004-2005**	**2005-2006**	**2006-2007**	**2007-2008**	**2008-2009**	**2004-2010**
S'_{CB}	0.78 (0.70-0.84)	0.52 (0.46-0.57)	0.56 (0.50-0.62)	0.49 (0.45-0.54)	0.62 (0.50-0.72)	0.51 (0.49-0.53)
S'_{LR}	0.55 (0.50-0.60)	0.44 (0.39-0.48)	0.61 (0.55-0.66)	0.68 (0.61-0.75)	0.88 (0.68-0.97)	0.56 (0.54-0.58)
R'_{CB}	1.00 (1.00-1.00)	0.59 (0.50-0.68)	0.40 (0.33-0.48)	0.58 (0.50-0.66)	0.53 (0.45-0.60)	0.49 (0.45-0.52)
R'_{LR}	1.00 (1.00-1.00)	0.35 (0.32-0.39)	0.36 (0.33-0.40)	0.35 (0.32-0.38)	0.27 (0.24-0.29)	0.30 (0.29-0.32)
R'_{TF}	1.00 (1.00-1.00)	0.95 (0.90-0.97)	1.00 (1.00-1.00)	0.99 (0.94-1.00)	0.99 (0.88-1.00)	0.97 (0.94-0.98)
$M'_{LR\ to\ CB}$	0.04 (0.03-0.07)	0.11 (0.08-0.14)	0.05 (0.04-0.07)	0.05 (0.04-0.07)	0.03 (0.02-0.04)	0.05 (0.05-0.06)
$M'_{CB\ to\ LR}$	0.60 (0.53-0.67)	0.60 (0.53-0.66)	0.34 (0.29-0.41)	0.48 (0.43-0.53)	0.36 (0.29-0.44)	0.44 (0.42-0.47)
$M'_{LR\ to\ LR}$	0.96 (0.93-0.97)	0.04 (0.03-0.06)	0.11 (0.09-0.14)	0.11 (0.09-0.14)	0.01 (0.01-0.02)	0.07 (0.06-0.08)
M'_{CB}	0.40 (0.33-0.47)	0.40 (0.34-0.47)	0.66 (0.60-0.71)	0.52 (0.47-0.57)	0.64 (0.56-0.71)	0.56 (0.53-0.58)
M'_{LR}	0.00 (0.00-0.00)	0.85 (0.81-0.88)	0.84 (0.80-0.87)	0.84 (0.81-0.86)	0.96 (0.94-0.97)	0.88 (0.87-0.89)

CB, Chicheron Brook; LR, Lesse River; TF, trapping facility.

Table 2.5: Survival (S), recapture (R), and movement (M) estimates with 95% confidence intervals, derived from the time-dependent model (separated years, model 1 in Table 2.2) and the time-independent model (years 2004-2010, model 8) applied to total capture histories and considering only the group of trout born in the Chicheron Brook.

Probability	**2004-2005**	**2005-2006**	**2006-2007**	**2007-2008**	**2008-2009**	**2004-2010**
S_{CB}	1.00 (1.00-1.00)	1.00 (1.00-1.00)	0.92 (0.85-0.96)	0.98 (0.94-0.99)	0.91 (0.85-0.95)	0.95 (0.93-0.96)
S_{LR}	0.50 (0.50-0.50)	0.45 (0.36-0.53)	0.54 (0.45-0.62)	0.73 (0.61-0.82)	0.70 (0.57-0.81)	0.59 (0.55-0.62)
R_{CB}	1.00 (1.00-1.00)	1.00 (1.00-1.00)	0.18 (0.05-0.48)	0.62 (0.38-0.81)	0.39 (0.27-0.53)	0.33 (0.25-0.41)
R_{LR}	1.00 (1.00-1.00)	0.22 (0.18-0.26)	0.25 (0.21-0.29)	0.25 (0.21-0.29)	0.23 (0.20-0.25)	0.22 (0.21-0.24)
R_{TF}	1.00 (1.00-1.00)	1.00 (1.00-1.00)	1.00 (1.00-1.00)	1.00 (1.00-1.00)	1.00 (1.00-1.00)	1.00 (1.00-1.00)
$M_{LR\ to\ CB}$	0.33 (0.33-0.33)	0.06 (0.03-0.10)	0.03 (0.01-0.06)	0.05 (0.03-0.07)	0.04 (0.03-0.06)	0.04 (0.04-0.05)
$M_{CB\ to\ LR}$	0.97 (0.92-0.99)	0.99 (0.96-1.00)	0.91 (0.85-0.95)	0.89 (0.84-0.92)	0.91 (0.85-0.95)	0.91 (0.89-0.93)
$M_{LR\ to\ LR}$	0.33 (0.33-0.33)	0.01 (0.00-0.04)	0.11 (0.08-0.16)	0.12 (0.09-0.15)	0.02 (0.01-0.03)	0.05 (0.05-0.07)
M_{CB}	0.03 (0.01-0.08)	0.01 (0.00-0.04)	0.09 (0.05-0.15)	0.11 (0.08-0.16)	0.09 (0.05-0.15)	0.09 (0.07-0.11)
M_{LR}	0.33 (0.33-0.33)	0.93 (0.88-0.96)	0.86 (0.81-0.90)	0.84 (0.79-0.87)	0.94 (0.92-0.96)	0.90 (0.89-0.91)

CB, Chicheron Brook; LR, Lesse River; TF, trapping facility.

3.5 Performance of MSCR models

Proportions of individuals performing movement types I, II, and III (Fig. 2.2) computed from the simple analysis of FDS were first compared with those derived from MSCR models 9 and 16 (Table 2.2) applied to TCH (comparison C1). Then, differences between survival and movement parameter estimates derived from the same models applied to TCH, PCH1, PCH2, and PCH3 were examined (C2). Eventually, FDS results were compared with those obtained from RDS and PCH2 (C3).

Results of the C1 comparison were visualised (Fig. 2.4) and allowed us to determine if estimates from MSCR models were consistent with true movement observations. Indeed, results from the simple analysis of FDS reflected true movements of trout and not estimates, because the capture efficiency in the traps is almost 100%. Considering movement type I, differences between estimated and computed values were all below 6%. One value out of six was overestimated (years 2004-2010) by models applied to TCH, but two were consistent (years 2007-2008 and 2008-2009); other values were all underestimated. For values linked to movement type II, one out of six was overestimated (year 2005-2006) by models, but two were consistent (years 2006-2007 and 2008-2009); other values were all underestimated. Differences between estimated and computed values were all below 10%, excepted for the year 2004-2005 (40%). Two of the six values associated with movement type III were consistent (years 2005-2006 and 2008-2009), and other values were all overestimated by models. Differences between estimated and computed values were all below 9%, excepted for the year 2004-2005 (44%). Overall, six values were comparable for each proportion of individuals performing movement types I to III; two of them were consistent while the others were either underestimated or overestimated by MSCR models. If results obtained for the year 2004-2005 are discarded, discrepancies between estimated and computed values were all below 10%.

The sensitivity of MSCR models to the efficiency of the trapping facility was assessed by the C2 comparison, in which survival and movement probabilities derived from TCH were compared with those from PCH1, PCH2, and PCH3 (TCH and PCH2 comparison is shown in Fig. 2.5 as an example). The following effects were observed. First, trout survival probabilities were most of the time underestimated when considering PCH. The discrepancy between TCH and PCH estimates was, however, smaller for LR than for CB. Second, an overestimation was observed for trout probabilities to stay in CB (associated with movement type IV) when considering PCH. On the contrary, an underestimation

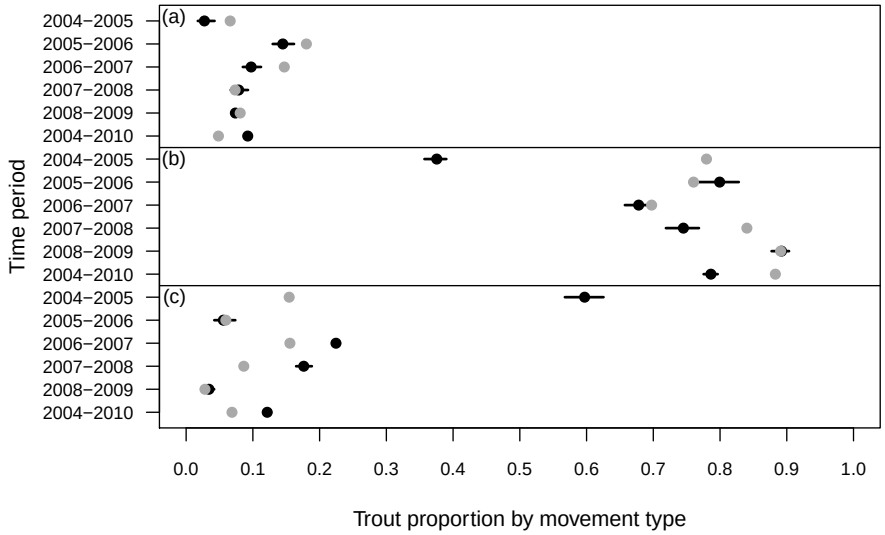

Figure 2.4: Proportions of individuals performing movement types I (a), II (b), and III (c) computed from the full data set of observations at the trapping facility (grey circles) compared with those derived from multistate capture-recapture models 9 and 16 applied to total capture histories (black circles). 95% confidence intervals are displayed for each estimate (no intervals were available for computed values).

was observed for probabilities to stay in LR (type V) when considering PCH. Discrepancies between TCH and PCH estimates over all years 2004-2010 were rather large. Third, young trout movement probabilities from CB to LR (type II) were underestimated, while movement probabilities for spawning in CB and coming back (type III) were overestimated when considering PCH. Surprisingly, TCH and PCH estimates of spawning movement probabilities to CB (type I) were all in accordance. In general, observed over- or under-estimations were better with PCH1 and worse with PCH3. Discrepancies between TCH and PCH survival estimates and those associated with movement types II and IV were weak (i.e., below 7% for PCH1; 15% for PCH2; 23% for PCH3) and even weaker for type I (i.e., below 6% for PCH1, PCH2, and PCH3). Large discrepancies were observed for probabilities linked to movement types III and V (i.e., around 88% for PCH1, PCH2, and PCH3). Furthermore, probabilities associated with types I, III, and V were not correlated with the quantity of trapping data.

Results of the C3 comparison allowed us to evaluate the effects of combining two sources of data when the efficiency of the trapping facility was reduced to 50% (RDS). The purpose was to determine if results were

improved or not by the presence of electrofishing data. When comparing results from the simple analysis applied on FDS and RDS, all differences were below 8.1% for all movement types. Yet, it appears that they were on average higher for movement types I and III. The comparison of FDS and PCH2 results showed that all differences were below 17% for types I and III (except for type III during year 2004-2005, for which it was 30%) and between 47% and 86% for type II. These differences were compared between them to quantify the expected improvement. For type I, we found no change over all years 2004-2010 (values between -2% and 7%), except for a small improvement for year 2005-2006 (14%). The same result was obtained for type III, with values between 1% and 7% when considering over all years and a small improvement for the year 2004-2005 (22%). Considering movement type II, high improvements were observed with values between 45% and 85% for separated years and 84% over all years 2004-2010.

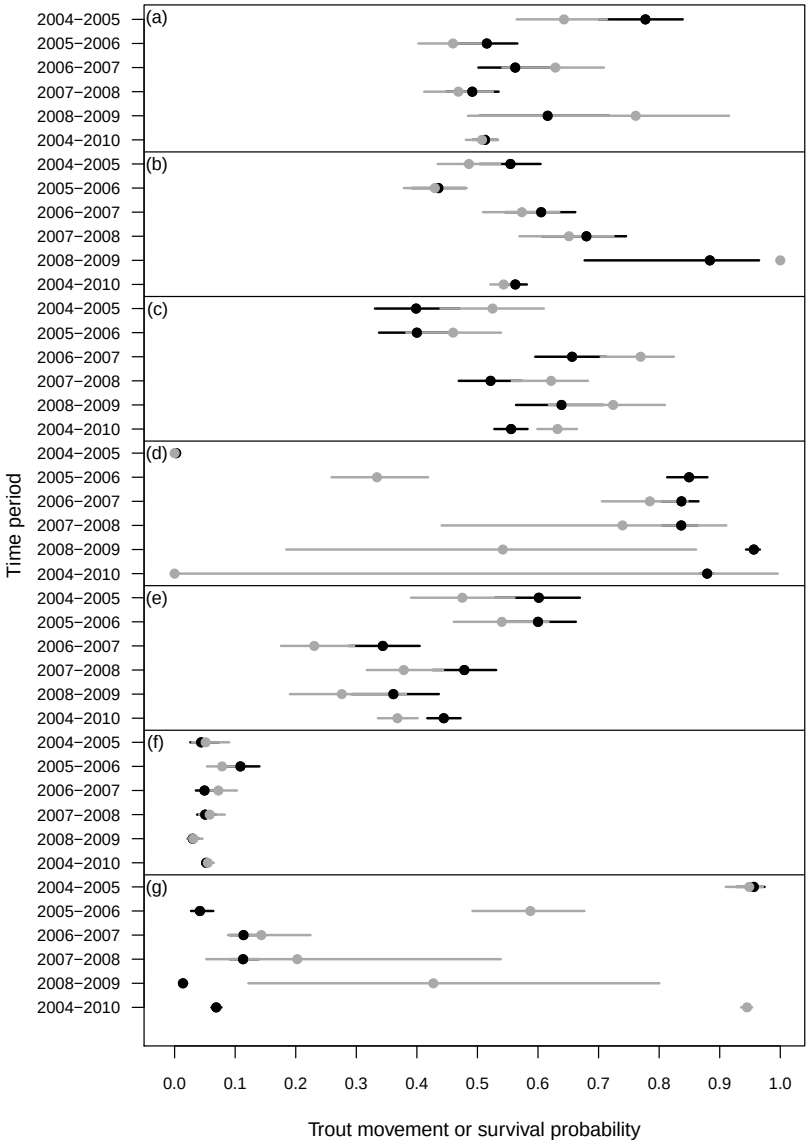

Figure 2.5: Comparison between trout survival and movement probabilities estimated by the time-dependent multistate capture-recapture model (separated years, model 9 in Table 2.2) and the time-independent model (years 2004-2010, model 16) applied to total capture histories (black circles) and to partial capture histories 2 (grey circles): (a) trout survival in the Chicheron Brook (CB), (b) survival in the Lesse River (LR), (c) stay in CB, (d) stay in LR, (e) movement from CB to LR, (f) movement from LR to CB and (g) movement from LR to LR. 95% confidence intervals are also displayed.

4 Discussion

In this paper, we first evaluated performance of MSCR models and their sensitivity to the level of data integration. On the one hand, MSCR estimates were consistent with true movement observations at the trapping facility, as we found only a low error (10%) when they were compared. Besides, their narrow confidence intervals gave evidence of their accuracy. We concluded that MSCR estimates can be safely used to infer trout spawning behaviour. On the other hand, we quantified the extent to which estimates of MSCR models were inaccurate or biased when they were applied to partial capture histories, constructed by varying the sample size of the trapping data. We also determined if considering an additional source of data could be a solution for ecological systems where only limited trapping data are available. Results showed that two trout movement probabilities were the most sensitive: (i) the probability for a trout to stay in LR, (ii) the probability for a trout to spawn in CB and to come back. These probabilities were underestimated by 88% because some trout that were captured exclusively at the downstream trap were not detected afterwards. We also found that results of young trout downstream movement probability were improved by 85% when electrofishing data were combined with data from a half-efficient trapping facility.

The second objective of the paper was to study the role of CB as spawning ground and nursery area for brown trout. We used results drawn from two different approaches to investigate their spawning behaviour: (i) a simple analysis of the full data set of movement observations at the trapping facility and (ii) MSCR modelling applied to total capture histories. Comparing results obtained for the same hydrological system over the years 1957-1969 by Huet and Timmermans (1979), mean numbers derived from the simple analysis are all in the same ranges. Indeed, on average and over the years 2004-2010, 169 adults migrated from LR to CB to spawn (respective extremes: 124 and 222), 77 adults returned to LR after spawning (extremes: 32 and 120) and 819 juveniles (i.e., 676 tagged plus 143 untagged fish; extremes: 328 and 1311) moved from CB to LR. In the study conducted by Huet and Timmermans (1979), these numbers were 242 upspawners (extremes: 83 and 530), 150 downspawners (extremes: 70 and 201), 464 juveniles (extremes: 286 and 1007), respectively. Likewise, current spawning and downstream migration periods are roughly identical to those observed 50 years ago.

The simple analysis also revealed that 85% of the adults spawn in the brook only once in their lifetime and that 59% of them returned to

the main stream after the reproduction period. The return rate computed from MSCR model estimates was equal to 58% and higher during 2006-2007 (70%) and 2007-2008 (69%). All these results are in accordance with those previously obtained by Huet and Timmermans (1979). Indeed, they found a return rate of spawners equal to 62% on average (extremes: 38% and 84%). Survival rate of trout in the brook (the probability of the fish surviving and remaining in the brook) was estimated equal to 51%. If we extrapolate this finding and consider that half of the upswimming spawners died during their stay in the brook, post-spawning homing behaviour appears exclusive, as originally hypothesised by Dupont (2004); if they had survived, all the spawners would have returned to their original territory. It seems likely that this high mortality is due to predation by herons (E. Dupont, Earth and Life Institute, Université catholique de Louvain, Croix du Sud 2 Box L7.05.14, 1348 Louvain-la-Neuve, Belgium, personal communication, 2011). Spawning movements between the main stream and the brook are influenced by the year period and appear limited by high flow and probably also water temperature (Huet and Timmermans, 1979). In fact, a recent study showed that the upstream migration of spawners to CB is mainly driven by environmental conditions such as water level (B.M. Frank, E. Dupont, P.V. Baret and B. Jonsson, unpublished data).

Estimates from MSCR models revealed that a young trout has a probability of 44% to migrate from the brook to the main stream, with fluctuations over years between 34% and 60%. Analysis of observations at the downstream trap showed that years 2007-2008 and 2008-2009 were exceptional, with twice as many individuals emigrating downstream compared with the other years. This movement could be explained by the rising of waters in the spring (Ovidio *et al.*, 1998), as well as by density-dependent mechanisms, such as territorial competition or limited food availability (Milner *et al.*, 2003). Besides, Huet and Timmermans (1979) suggested that juvenile downstream migration is mainly driven by water temperature. They observed that the movement usually begins when the temperature in the brook is above 10°C. Return rates of trout to their natal site for spawning were low (computed and estimated values were all below 18%). Comparatively, in France, Baglinière *et al.* (1987) reported that 22% of the spawners moving from the Scorff River to a nursery stream were young trout that had previously emigrated from this stream. This finding can be explained by the fact that this movement takes at least 2 years and trout have to survive until then. Indeed, 82% of the individuals were observed to return to their natal brook the second and third year after their downstream migration, sug-

gesting that they took advantage of this richer feeding area to grow and mature (Baglinière *et al.*, 1987; Jonsson and Jonsson, 1993). These results are in agreement with the hypothesis that this downstream movement can be voluntary and advantageous and is thus not entirely driven by density-dependent population regulation (Jonsson, 1985; Steingrimsson and Grant, 2003). Moreover, recent results support the assumption that the tendency for juveniles to emigrate from nursery brooks is both density- and climate-dependent (B.M. Frank, E. Dupont, P.V. Baret and B. Jonsson, unpublished data). Previous studies found that brown trout preferentially spawn in first-order streams because they seem to be more advantageous for reproduction and for juvenile growth (Baglinière and Maisse, 1990; Armstrong *et al.*, 2003). The strong homing instinct of the trout is also a factor to consider (Elliott, 1994; Laikre, 1999). Among the 561 spawners observed in the upstream trap over the years 2004-2010, 311 had already been captured as juveniles in the downstream trap (i.e., homing individuals). The percentage of ascending trout performing natal homing is thus equal to 55%, and this finding is in disagreement with the opinion expressed by Huet and Timmermans (1979).

Additional results about survival and recapture probabilities were found with MSCR modelling. On average, trout survival was equal to 54% in both streams, but we observed survival rates respectively 19 and 27% higher in the main river than in the brook in 2007-2008 and 2008-2009. These results are explained by the high emigration rate of trout to the main stream observed for both years. Also, a 2% rate of tag loss was observed, and this could lead to an underestimation of survival, as previously shown for Atlantic salmon (*Salmo salar*) (Sigourney *et al.*, 2005). Estimates of trout recapture probabilities in the tributary were always greater than in the main river, considering either over all years (49% *vs* 30%) or each separated year. As electrofishing sampling techniques are size-selective (Bohlin *et al.*, 1989; Dolan and Miranda, 2003), recapture efficiency should be higher in the main stream, which is mainly inhabited by adults. However, catchability is also dependent of the physical characteristics of the sampling site (e.g., stream width, depth, substrate, water velocity). Indeed, the electrofishing efficiency is known to decrease with increasing river width (Kennedy and Strange, 1981), and this could explain why trout were easier to catch in the small CB than in the larger LR. Another hypothesis is that the catchability difference could simply be due to the electrofishing equipment used, i.e., a mobile system for CB *vs* a stationary one for LR.

Advantages of MSCR modelling over the simple analysis of trout movements, or over the kind of study conducted by Huet and Tim-

mermans in the 1960s, are twofold. First, it has allowed uncertainty on parameters to be quantified via confidence intervals. The combination of data collected from multiple sources in capture-recapture models is a way to increase the precision of estimates, to control for bias in parameter estimations, and to produce additional estimates. Second, MSCR models have brought additional biological knowledge on the hydrological system. More particularly, trout survival and recapture probabilities were estimated for both streams. Furthermore, we demonstrated that post-spawning homing and natal homing were frequent behaviours for the trout of the studied system.

The approaches presented here can be adapted to other animal migration studies with similar sampling design (e.g., fish, amphibians). The MSCR model could be extended by including abiotic factors (i.e., covariates, see Pollock, 2002; Lebreton, 2006) such as temperature or water level to address additional questions about the interaction of migrating animals with their environment.

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Chapter 3

Genetic study of brown trout migratory behaviour in the Lesse River / Chicheron Brook hydrological system

Both environmental and genetic factors can explain why a fish decides to migrate, but the respective contribution of each of these factors is still unclear. The brown trout of the Lesse River / Chicheron Brook hydrological system show a partial migratory behaviour: individuals spawn in the brook, where the young either establish territories or migrate to the Lesse River. Different groups of trout were defined according to their place of birth and their behaviour, and 48 samples from each group were studied with twelve microsatellite markers. Three statistical methods were applied to the obtained genotypes to determine if genetic differences existed between migratory and resident trout born in the brook: factorial correspondence analysis, clustering and Student's t-tests. As no significant differentiation was found, we concluded that the genetic structure was mainly determined by the respective spawning events in which the trout were involved. A possible influence of the natal homing behaviour observed in trout of the studied system was discussed.

Key words: genetic structure; life-history polymorphism; microsatellites; population genetics; *Salmo trutta*

1 Introduction

Several species of salmonids exhibit variable life-history strategies (also referred to as 'life-history forms' or 'ecotypes'). Individuals can remain in freshwater throughout their life (resident), or can migrate from freshwater to sea and back (anadromous). In addition, partial migration can occur within these two life-history forms, i.e., some individuals migrate and others do not (Jonsson and Jonsson, 1993). To date, it remains unclear whether migration is governed by environment or genetics, and it is difficult to estimate or even prove their respective contribution.

Trout migratory behaviour is triggered by environmental (Arnekleiv and Kraabol, 1996; Ovidio *et al.*, 1998; Jonsson and Jonsson, 2002; Olsson and Greenberg, 2004) and/or genetic factors (Jonsson, 1982; Naslund, 1993). Indeed, environmental factors can influence the decision made by the fish to migrate. Density-dependence could also act to maintain these two life-history forms within the same population provided that there is reproductive isolation (Jonsson and Hindar, 1982; Adriansen and Dhont, 1990). However, it cannot be excluded that the differences observed between migratory and resident individuals are genetically programmed (Olsson and Greenberg, 2004). For instance, the heritability of the migratory behaviour could be explained by the transmission of some traits related to growth (e.g., physiological state, see Forseth *et al.* (1999)) or growth itself.

Existence of genetic differences between migratory and resident life-history forms of several salmonid species have been reported (e.g., Vuorinen and Berg, 1989; Klemetsen *et al.*, 2002; Narum *et al.*, 2004). In the brown trout, studies have led to conclusions ranging from a lack of genetic divergence (Hindar *et al.*, 1991; Pettersson *et al.*, 2001; Charles *et al.*, 2005) to some degree of differentiation (Jonsson, 1982; Naslund, 1993). In most of these investigations, the use of protein data has been privileged, and microsatellite markers have been scarcely used despite their higher potential to address questions related to ecotypes differentiation in trout (Charles *et al.*, 2005). Indeed, studies of fish populations based on loci that are neutral or nearly neutral to selection are necessary to reveal the underlying genetic structure of these populations (Ryman, 1983; Hindar *et al.*, 1991).

When there is a genetic divergence between the migratory and resident forms, its existence is difficult to interpret as it can be explained in different ways, such as geographical isolation due to the presence of obstacles (Jonsson, 1982; Knutsen *et al.*, 2001), delay in the process

of gonad maturation (Jonsson, 1985), existence of behavioural barriers that may prevent mating from occurring (Campbell, 1977), or differential stocking effects on each of the ecotypes (Krieg and Guyomard, 1985; Hansen *et al.*, 2000). Conversely, the absence of genetic divergence reflects a high level of gene flow between the two forms, and indicates frequent interbreeding (Charles *et al.*, 2006).

The brown trout of the Lesse River / Chicheron Brook hydrological system belong to the resident form, and show a partial migratory behaviour: individuals spawn in the brook, where the young either establish territories or migrate to the Lesse River. We analysed the genetic differentiation between the resident and migratory forms observed in this system with microsatellite markers. Trout were first divided into groups according to their place of birth and their behaviour. Then, statistical methods were used to test the following hypothesis: is the genetic structure of migratory and sedentary trout born in the Chicheron Brook significantly different? The alternative hypothesis is that this structure depends on the respective spawning events in which the trout are involved.

2 Materials and methods

2.1 Study area, individual assignment and sampling

The Lesse River / Chicheron Brook system has already been described in Section B of the Introduction and objectives, page 4, and in Section 2.1 of Chapter 2, page 70. Brown trout of this system can be caught either by electrofishing in autumn and spring (only in autumn for the Lesse River), or when they move through the trapping facility. Four capture locations are thus possible: electrofishing in the Chicheron Brook, electrofishing in the Lesse River, capture in the upstream trap, and capture in the downstream trap.

Three groups were defined: (i) trout belonging to group CR are those caught at least once in the Chicheron Brook but never found in the traps and never caught in the Lesse River, (ii) trout belonging to group CM are those captured at least once in the downstream trap, (iii) trout belonging to group EX are those caught at least once in the Lesse River, but never found in the traps and never caught in the Chicheron Brook. As we wanted also to take into account a possible time effect, the number of samples selected for the CR and EX groups were doubled (the ones collected the first time were named CRa and EXa, the others EXb and CRb). Samples a and b were spaced by 4 years, corresponding to one

generation interval for the trout of the studied system (732 observations on 264 individuals, averaged over 2002-2009). The letters used to defined the groups correspond as follows:

- A trout can be native to the Chicheron Brook (C), or to the Lesse River or another tributary of the Lesse River (E);
- A trout can remain all its life in the same river and thus be a resident (R), or can migrate to another river at a given time in its life cycle and be a migrant (M);
- A trout can have no available information on its behaviour (X).

For each of the five groups, 48 individuals were selected among the 11 643 marked during the years 2004-2010 (samples were considered representative). The selection of these 240 individuals to be analysed with microsatellite markers was based on their membership to groups CR (3395 individuals), CM (4256), and EX (3414), and three criteria of age, size and recaptures (Table 3.1). Criteria of tagging and birth years were used to select trout that received a PIT tag at the same time and age. The length criterion ensured that trout of the CR and CM groups are aged of maximum 1 year old and were therefore born in the Chicheron Brook. This criterion also allowed us to discriminate between resident and migratory trout from CR and EX groups, by identifying individuals that have had the opportunity to migrate several times to the Lesse River or the Chicheron Brook but never did. For all groups, information on recaptures permitted to be certain that the selected trout were alive and remained in the study area.

2.2 Microsatellite analysis

DNA was extracted from adipose fin tissue of the 240 selected trout 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 microsatellite), Ssa197 (tetranucleotide microsatellite) (OReilly *et al.*, 1996), Ssa408 (tetranucleotide microsatellite) (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

Table 3.1: Criteria used for the selection of brown trout to genotype, according to CRa, CRb, CMa, EXa and EXb groups (48 individuals per group). Trout were caught at four different locations: by electrofishing in the Chicheron Brook (C) and in the Lesse River (L), by capture in the upstream (U) and in the downstream (D) traps. For the CRb group, it was necessary to consider both electrofishing occasions in autumn (A) and spring (S) to obtain a sufficient number of individuals (n) after the application of all criteria.

Criterion	**CRa** n=51	**CRb** n=35(A)+17(S)	**CMa** n=99	**EXa** n=52	**EXb** n=61
Caught at least once	C	C	D	L	L
Never caught	L, U, D	L, U, D	-	C, U, D	C, U, D
Tagging year	2004	2008	2003	2004	2008
Birth year	2003	2007 or 2008	2002	2002	2006
Length (mm) at tagging	A: ≤ 113	A: ≤ 113; S: ≤ 86	≤ 100	≥ 150 and ≤ 195	≥ 150 and ≤ 180
Recapture year	≥ 2005	≥ 2009	-	≥ 2005	≥ 2009

of the capillary was transformed into electrophoregrams with GeneScan and GeneMapper programs.

2.3 Statistical analyses

GENETIX 4.05 (Belkhir *et al.*, 2004), GENEPOP 4.0.10 (Raymond and Rousset, 1995; Rousset, 2008) and Micro-Checker 2.2.3 (Van Oosterhout *et al.*, 2004) were used to (i) estimate the number of alleles per locus (A), the observed heterozygosity (H_O), the expected heterozygosity (H_E) and the unbiased expected heterozygosity (H_{NB}), (ii) test the assumption of Hardy-Weinberg equilibrium, (iii) identify null alleles and estimate their frequency. Then, we used three statistical methods to check if sedentary and migratory trout of the studied hydrological system were genetically distinct: a factorial correspondence analysis (FCA), a partitioning method, and Student's t-tests.

First, a FCA was conducted using GENETIX to describe the genetic relationships among individuals of the CRa, CRb, CMa, EXa and EXb groups. In this analysis, all individuals were seen as a cloud of points in a hyperspace that has as many dimensions as there are alleles of different loci. The algorithm aims at finding composite axes which are a combination of the variables and which optimise the differences among the analysed individuals (Jug *et al.*, 2005). The relationships among individuals were visualised in two dimensions. By convention, the first

axis has the largest contribution to the total inertia (i.e., the proportion of the total information explained by an axis, given in percent).

Second, a clustering analysis was performed using STRUCTURE (Pritchard *et al.*, 2000) in order to divide the samples into clusters of individuals, with or without a priori information on their membership to one of the five groups. Then, CLUMPP 1.1.2 (Jakobsson and Rosenberg, 2007) and DISTRUCT 1.1 (Rosenberg, 2004) were used for processing and visualising the results. The method implemented in STRUCTURE is based on a Bayesian Markov Chain Monte Carlo (MCMC) approach, in which the criteria for grouping individuals are to minimise Hardy-Weinberg disequilibrium and gametic phase disequilibrium between loci within groups. The number of clusters (K) represented by the 240 samples as well as individual admixture coefficients (i.e., the likelihood for each individual to belong to a cluster) were estimated.

Individuals were clustered in two different ways. On the one hand, they were characterised without a priori information, for a number of clusters equal to 2, 3 and 4, respectively. We used a burn-in period of 100 000 iterations followed by 200 000 MCMC replicates, and each experiment was repeated 10 times. The percentage of trout from each of the five groups present in each cluster was computed. On the other hand, we used the initial classification into five groups as a priori information to find the most likely number of clusters. We proceeded as follows. First, K was varied from 1 to 5 and each experiment was repeated 20 times (100 runs of 200 000 iterations each, with 50 000 burn-in iterations). The best K value was then inferred using three methods implemented in the CorrSieve R package (Campana *et al.*, 2011): a non-parametric method (Wilcoxon test), the ΔK (Evanno *et al.*, 2005) and the ΔF_{ST} statistics (Campana *et al.*, 2011). These latter statistics are based on the estimated values of the likelihood probability $L(K)$ and of the fixation index F_{ST}, respectively. Finally, we estimated the admixture coefficients of each individual for the most likely K, using 10 times repetitions of 100 000 burn-in iterations followed by 200 000 replicates.

Third, the adegenet (Jombart *et al.*, 2008) and pegas (Paradis, 2010) R packages were used to compute allele frequencies averaged over all loci for each of the five groups of individuals, as well as F_{ST} coefficients between groups. In addition, we estimated the inbreeding coefficient (F_{IS}) in each group with GENETIX. Comparisons of mean allele frequencies between groups were then performed using Student's t-tests (Table 3.5): T1 comparing sedentary trout (CR group) with migrants (CM) to test the null hypothesis; T2 comparing trout born in the Chicheron Brook (CR and CM) with individuals born elsewhere (EX) to test the alterna-

tive hypothesis; and T3 comparing a and b samples to test the temporal effect.

3 Results

3.1 Genetic statistics

Four individuals with missing data (for SsoSL85, Ssa171, Str85 and T3-13) were identified and removed from the data set containing the 240 genotyped individuals obtained by microsatellite analysis. The 236 remaining genotypes were analysed at each locus to measure the level of polymorphism and to assess deviations from Hardy-Weinberg expectations (Table 3.2). The observed heterozygosities are within the range of those usually reported for brown trout (e.g., Ryman, 1983; Ferguson, 1989). Six markers were found in Hardy-Weinberg disequilibrium. Among them, three were positively tested for the presence of null alleles: SsoSL85, Ssa171 and T3-13.

Table 3.2: Characteristics of the 12 microsatellite markers used to analyse the 236 samples. The total number of alleles (A), the P-values from Hardy-Weinberg equilibrium tests with their associated significance level (NS when P-value $>= 0.05$, * when < 0.05, ** when < 0.01, *** when < 0.001), as well as the observed (H_O), expected (H_E) and unbiased expected (H_{NB}) heterozygote rates per locus are given.

Locus	A	**P-value**	H_O	H_E	H_{NB}
SsoSL417	11	0.2986 (NS)	0.4534	0.4865	0.4876
SsoSL85	12	0.0000 (***)	0.4449	0.5405	0.5416
Ssa85	7	0.0572 (NS)	0.5805	0.5278	0.5289
Str15	7	0.0143 (*)	0.6695	0.6797	0.6811
Str60	2	0.7802 (NS)	0.4661	0.4560	0.4570
Str73	4	0.1535 (NS)	0.5254	0.5461	0.5449
Ssa171	19	0.0025 (**)	0.4364	0.5502	0.5514
Ssa197	8	0.4287 (NS)	0.5212	0.5311	0.5322
Ssa408	27	0.0164 (*)	0.8814	0.9262	0.9282
SsoSL438	7	0.3587 (NS)	0.7331	0.7441	0.7457
Str85	9	0.0021 (**)	0.6441	0.6421	0.6435
T3-13	21	0.0000 (***)	0.5466	0.6475	0.6489

The three markers identified as presenting null alleles were not considered in the FCA nor in the clustering analysis, but well when performing the Student's t-tests. Besides, individuals with missing data were not

included in FCA or when performing the t-tests, but well in the clustering analysis since STRUCTURE has a special function to deal with them. We ended up with the following number of genotypes for each analysis: 239 at nine markers for FCA (as data were missing for only one trout at the Str85 loci), 240 at nine markers for clustering, and 236 at 12 markers for the t-tests.

3.2 Factorial correspondence analysis

The relationships among the five groups of individuals CRa, CRb, CMa, EXa and EXb were visualised by FCA (Fig. 3.1). Three main clouds can be distinguished: three of them are clustered at the positive side of the first axis (left of the figure), while the remaining two are located at the negative side of this axis (right). The differentiation between CRa/CRb/CMa and EXa/EXb is the main observed structure explained by this first axis (42% inertia). EXa and EXb groups were discriminated regarding the second axis (24% inertia), as they are placed at its positive and negative side, respectively. This represents the second strong structure included in the data.

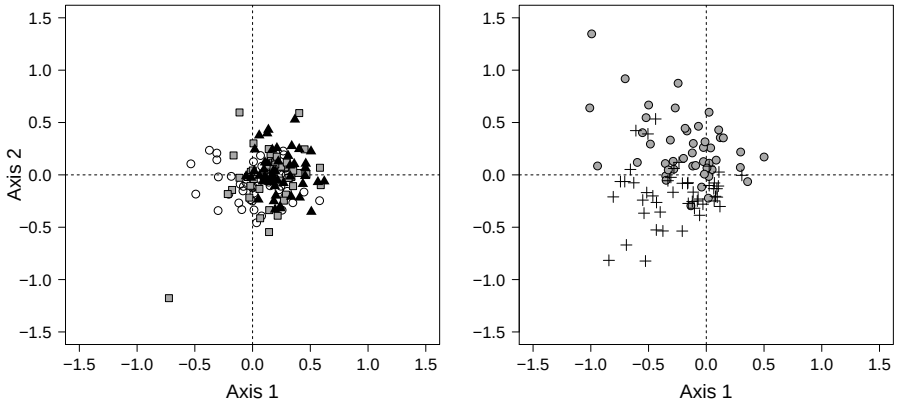

Figure 3.1: Genetic relationships among the five groups of trout, based on factorial correspondence analysis: CRa (open circles), CRb (grey solid squares), CMa (black solid triangles), EXa (grey solid circles) and EXb (positive signs).

3.3 Clustering analysis

Two approaches were performed for the clustering analysis, with or without a priori information on the membership of individuals to one of the five groups (CRa, CRb, CMa, EXa and EXb).

The first approach with a priori information revealed three clusters among the 240 brown trout individuals. Indeed, the likely number of clusters found with the Wilcoxon test and the ΔK statistic was 3, while it was equal to 2 or 3 with the ΔF_{ST} method. The corresponding estimated population structure is shown in Fig. 3.2: CRa forms one cluster, CMa/CRb the second one, and EXa/EXb the third one.

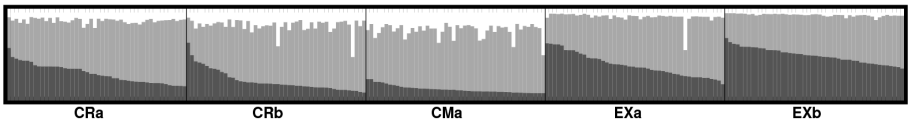

Figure 3.2: Estimated population structure among the five groups of trout, CRa, CRb, CMa, EXa and EXb, using the clustering approach with a priori information. Each individual is represented by a vertical line, which is partitioned into three segments that represent the individual estimated membership fractions in the three clusters.

For the clustering approach without a priori information, we computed the percentage of individuals from each of the five groups (CRa, CRb, CMa, EXa and EXb) present in each cluster (Table 3.3). For K = 2 or 3, we observed two clusters: individuals from the CRa/CRb/CMa groups in the first one, trout of EXa/EXb in the other. For K = 4, two clusters were also found: CRa/EXa/EXb and CRb/CMa.

Table 3.3: Percentage of trout belonging to each of the five groups, CRa, CRb, CMa, EXa and EXb (n=48 in each case), for the approach without a priori information considering a number of clusters (K) equal to 2, 3 and 4. Bolded numbers correspond to the highest percentages.

K	% CRa	% CRb	% CMa	% EXa	% EXb
1	**52**	**65**	**60**	48	31
2	48	35	40	**52**	**69**
1	**40**	**40**	**46**	42	23
2	35	35	25	**46**	**54**
3	25	25	29	13	23
1	**33**	29	10	**44**	**50**
2	31	**38**	**44**	33	19
3	29	23	40	13	23
4	6	10	6	10	8

3.4 Student's t-tests

Average allele frequencies computed over all loci for each of the five groups CRa, CRb, CMa, EXa and EXb, and inbreeding coefficient in each group are presented in Table 3.4. A decrease in the F_{IS} values was observed between EXa and EXb groups, while an increase was observed between CRa and CRb.

Table 3.4: Mean allele frequencies over all loci (M_A) for each group of trout, CRa, CRb, CMa, EXa and EXb, and effective number of alleles (E_A) and inbreeding coefficient (F_{IS}) in each group.

Group	M_A	E_A	F_{IS}
CRa (n=48)	0.0805	1.6624	0.0466
CRb (n=46)	0.0784	1.7250	0.1017
CMa (n=48)	0.0896	1.7651	0.0360
EXa (n=46)	0.0714	1.6157	0.0671
EXb (n=48)	0.0698	1.5689	0.0136

Student's t-tests were performed and F_{ST} coefficients were estimated (Table 3.5). For each test, we found that the mean allele frequencies for the compared groups were not significantly different (P-value > 0.05). These results lead to the reject of both null hypothesis (T1 test) and alternative hypothesis (T2 test); they also highlight the lack of temporal effect for the CR and EX groups (T3 tests). F_{ST} results do not show any proof of genetic structure between groups: less than 1% of the detected variation comes from differences between groups. However, the F_{ST} value associated with the T1 test is three times higher than the other values, indicating a possible genetic difference between trout of the CRa and CMa groups.

4 Discussion

PIT-tagged stream-dwelling brown trout of the Lesse River / Chicheron Brook system were gathered into five groups according to their place of birth, their resident or migratory behaviour, and their time of capture: residents born in the Chicheron Brook caught (i) in 2004 and (ii) in 2008, (iii) migrants born in the Chicheron Brook captured in 2003; trout native to the Lesse River or another tributary with unknown behaviour caught (iv) in 2004 and (v) in 2008. Then, 48 individuals per group were

Table 3.5: Results of the Student's t-tests and estimated F_{ST} coefficients for each comparison involving the CRa, CRb, CMa, EXa and EXb groups of trout. P-values are presented with their associated significance level (NS when P-value >= 0.05, * when < 0.05, ** when < 0.01, *** when < 0.001). T1 test compares sedentary trout (CR group) with migrants (CM); T2 test compares trout born in the Chicheron Brook (CM and CR) with individuals born elsewhere (EX); and T3 tests compare a and b samples of CR and EX groups.

Test name	**Compared groups**	**P-value**	F_{ST}
T1	CRa *vs* CMa	0.5365 (NS)	0.0068
T2	CRa/CMa *vs* EXa	0.2275 (NS)	0.0018
T3-1	CRa *vs* CRb	0.8748 (NS)	0.0019
T3-2	EXa *vs* EXb	0.8787 (NS)	0.0024

selected, and their DNA was analysed at nine microsatellite markers. Finally, we answered the question "Is the genetic structure of migratory trout significantly different from the one of sedentary individuals?" using three statistical methods.

First, the factorial correspondence analysis revealed two main groupings consisting of (i) sedentary and migratory individuals born in the Chicheron Brook (CRa/CRb/CMa groups), (ii) individuals born elsewhere (EXa/EXb groups). For this latter grouping, a moderate temporal effect was also found.

Second, the two approaches of clustering analysis (i.e., with and without a priori information) showed that the group of migrants (CMa) never formed a cluster on its own. This suggests the rejection of the null hypothesis, which considers that the genetic structure of sedentary and migratory trout is significantly different. The power of assignment tests depends on several factors, among which the number of loci, the degree of polymorphism, and the sample size (Hansen *et al.*, 2001a; Manel *et al.*, 2005). In the analysis without a priori information, we used 9 loci with 2-27 alleles per locus, on 240 individuals (48 per population). This seems to be sufficient as the recommendation is to use at least 8 loci and 30 individuals per population when the F_{ST} is very low (Cornuet *et al.*, 1999). Furthermore, the conclusion of both clustering analyses were identical, and this proves the accuracy of the assignment test performed without a priori information.

Third, Student's t-tests comparing mean allele frequencies between groups were performed, and F_{ST} as well as F_{IS} coefficients were estimated. All tests were not statistically significant, whereas F_{ST} results

indicated a possible genetic differentiation between residents and migrants (CRa *vs* CMa). F_{ST} values were very low (0.001-0.007) in comparison to other studies on brown trout, in which moderate values ranging from 0.03 to 0.06 were found (Carlsson *et al.*, 1999; Hansen *et al.*, 2002; Lehtonen *et al.*, 2009). F_{IS} values in any group of trout were positive and ranged from 0.01 to 0.11, demonstrating a slight inbreeding situation in each case (i.e., heterozygote deficiency in comparison with Hardy-Weinberg equilibrium expectations). Possible causes are the mixing of isolated and differentiated reproductive units (Wahlund effect; Wahlund, 1928), or the mating of close relatives (Wright, 1921). We noted that the F_{IS} in the CRb group was higher than in CRa. This could indicate that the genetic diversity of trout born in the Chicheron Brook has deteriorated between 2004 and 2008, but this result should be confirmed. We also observed an improvement of the genetic diversity of non-native trout of the Chicheron Brook from one generation to the next (between 2004 and 2008; EXa *vs* EXb), probably due to the input of new genotypes coming from other hydrological systems. Indeed, large populations typically have higher levels of genetic diversity than small populations, as they possess more genetically diverse individuals (Frankham *et al.*, 2002).

From these results, we decided to perform five supplementary t-tests (S1 to S5 tests; Table 3.6). All obtained P-values but one were < 0.05, indicating a significant difference between mean allele frequencies of each compared groups from tests S2 to S5. The reduction in the F_{IS} values observed between EXa and EXb groups explains why S1 test was not statistically significant while the S2 and S3 tests did. On the contrary, the increase in the F_{IS} values observed between CRa and CRb groups as well as the similar F_{IS} values for CRa and CMa explain the higher degree of significance obtained for the S5 test, in comparison with the S4 test.

Table 3.6: Supplementary Student's t-tests and estimated F_{ST} coefficients for each comparison involving the CRa, CRb, CMa, EXa and EXb groups of trout. P-values are presented with their associated significance level (NS when P-value $>= 0.05$, * when < 0.05, ** when < 0.01, *** when < 0.001).

Test name	**Compared groups**	**P-value**	F_{ST}
S1	CRa/CRb/CMa *vs* EXa/EXb	0.7322 (NS)	0.0024
S2	CRa/CRb/CMa *vs* EXa	0.0102 (*)	0.0012
S3	CRa/CRb/CMa *vs* EXb	0.0104 (*)	0.0025
S4	CRa *vs* CMa/CRb	0.0475 (*)	0.0018
S5	CRa/CRb *vs* CMa	0.0062 (**)	0.0053

All results obtained with the factorial correspondence analysis, the clustering analysis and the Student's t-tests converge towards the rejection of the null hypothesis. No significant genetic differentiation was found between the migratory and sedentary trout born in the Chicheron Brook. Some of the young trout that have migrated from the brook will come back during the reproduction period, once mature, and this facilitates the breeding between migratory and sedentary individuals. These results corroborated those obtained in other brown trout studies (e.g., Hindar *et al.*, 1991; Charles *et al.*, 2005).

In contrast, significant genetic differences were found between trout spawning in geographically separate areas. The alternative hypothesis is thus more likely: in the studied system, the genetic structure of trout appears determined by the respective spawning events in which the trout are involved. One possible explanation for this genetic divergence is the presence of natal homing, which was estimated equal to 55% for the trout of the studied system (see Chapter 2). This behaviour involves differences in life-history characteristics such as time and place of spawning, and predisposes for the development of genetically different populations in different spawning locations, even in the absence of physical barriers (Hindar *et al.*, 1991; Ferguson, 2004). Natal homing is also responsible for the slight decrease of F_{IS} values for trout born in the Chicheron Brook between 2004 and 2008. Individuals reproducing in the brook are mainly native ones, and this might contribute to the increase of inbreeding in this stream.

The fact that natal homing behaviour of brown trout may be under genetic control have important implications for the management of populations. Indeed, genetically different local populations are susceptible to the effect of stocking with hatchery fish, which can result in the loss of unique gene pools through competition between native and stocked fish and/or interbreeding (Taggart and Ferguson, 1986). Even a small number of stocked fish could produce hybrids with poor homing capabilities, and this could cause the breakdown of the reproductive isolation (Ferguson, 2004). It is thus crucial to identify reproducing units in brown trout populations to take appropriate conservation measures.

Although no genetic differences were found between migratory and sedentary trout born in the Chicheron Brook, genetics appears to play some role in this life-history polymorphism. Movement of young individuals leaving their natal stream for the Lesse River could also be explained either by environmental factors or by density-dependent mechanisms, such as territorial competition or limited food availability.

Box II: Finite mixture distribution modelling

A mixture distribution is a combination of statistical distributions, which arises when sampling from inhomogeneous populations (or mixed populations) with a different probability density function in each component (Du, 2002). Length-frequency distributions in fish populations with distinct age groups are an example of such mixed distributions. A finite mixture has a finite number of components, i.e., the number of age classes is predetermined.

The mixdist R package (Macdonald and Du, 2009) contains functions for fitting finite mixture distribution models to capture-recapture data by the method of maximum likelihood using a combination of a Newton-type algorithm and the expectation-maximisation algorithm. Two types of data can be used, grouped or conditional. Length-frequency are *grouped data*: observations of sampled fish (i.e., their length) are divided into groups and the occurrence frequency of individuals in each group is recorded. *Conditional data* are available subsamples which give the age class of some individuals. Such data bring additional information to the grouped data and thus usually improve the fitting of the mixture distribution (Du, 2002).

The procedure for fitting mixture distribution models to capture-recapture data comprises four steps: (i) Data preparation, (ii) Determination of interval between groups, number of components, starting values for parameters, and constraints, (iii) Estimation of mixture distribution parameters, (iv) Model evaluation. The example below illustrates this procedure, for a data set of 1086 trout caught by electrofishing in the Chicheron Brook in autumn 2008. The means and standard deviations of the corresponding age class Normal distributions estimated by the mixture distribution models may be subsequently used to determine length criteria that may in turn be used to assign an age class to each trout.

■ ***Example.***

Step 1 - Data preparation: Electrofishing observations are converted into a capture-recapture table containing a row for each trout and its length measurement observed in 2008 in one column.

Step 2 - Determination of interval between groups, number of components, starting values for parameters, and constraints: The interval of grouped data should not be too wide or too narrow, and should include at least five observations so that the validity of a constraint can be tested (Du, 2002). The number of components (i.e., age classes) and the starting values for the means μ_i of the distributions of each age class i are found by inspecting the length frequency histogram. Initial values for the standard deviations σ_i should

be chosen too small rather than too large, while starting values for the proportions π_i attributed to each distribution are less critical and can be left undefined (Du, 2002). Different constraints can be set on the means and standard deviations: (i) means free or fixed, all means equal, means equally spaced (assumption of linear growth), means forced to lie along a von Bertalanffy growth curve, (ii) standard deviations free or fixed, all standard deviations equal, coefficients of variation fixed or constant. Choosing the constraints mainly depends on some form of prior information about the parameters or the relations among them. For the data set in this example, we used a length interval between groups of 0.5 cm since it was the precision of the length measurement. After examination of the length frequency histogram, we decided to carry on the analysis with two age classes ($i = 0, 1$). The starting values for means were set to 6 cm for μ_0 and 10 cm for μ_1, respectively.

Step 3 - Estimation of mixture distribution parameters: Parameters of the finite mixture distributions are estimated using iterative algorithms implemented within the `mix` function of the mixdist package. For the example data set, the means and standard deviations estimated for the distributions of each age class were $\mu_0 \pm \sigma_0 = 5.90 \pm 0.74$ and $\mu_1 \pm \sigma_1 = 9.68 \pm 0.95$, with proportions π_i attributed to each distribution equal to 0.76 for age class 0 and 0.24 for class 1.

Step 4 - Model evaluation: The fitted distribution model is verified visually by plotting the histogram for the grouped data with the estimated values of parameters (Fig. II.1). A test of goodness-of-fit of the model is also performed, a P-value between 0.1 and 1 indicating that the estimated model is consistent with the data. For the example data set, we obtained a P-value of 0.20.

■

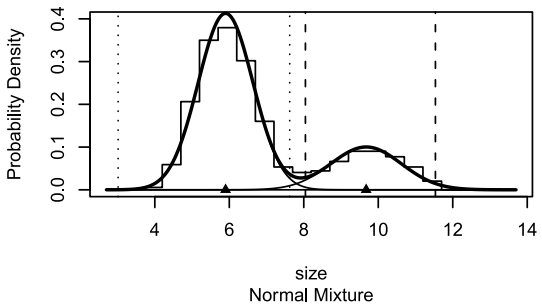

Figure II.1: Length frequency of brown trout of age class 0-1 electrofished in the Chicheron Brook in autumn 2008. Fitting curve of each age class normal distribution (thin lines with means represented by triangles), overall fitting curve (thick line) are represented. Length intervals were defined and used to assign an age class (0: dotted vertical lines; 1: dashed vertical lines) to trout.

Chapter 4

A systematic methodology to determine birth years of fish from length measurements*

A three-step methodology based on size-frequency data extrapolation was designed to automatically assign a birth year to fish through the determination of their age classes, which are themselves function of their length. The strategy was adapted and applied to tagged brown trout of the Lesse River / Chicheron Brook hydrological system. Length frequencies were decomposed with finite mixture distribution models, and length intervals were determined for several age classes. They were then used to directly derive the birth year of each trout by subtracting its age class from the year of capture. This information will be used in Chapter 5 to estimate several parameters of the survival, growth, spawning, and movement processes of the DemGenTrout model, in which individuals are processed by age class. A birth year was assigned to 70% of the captured and marked trout of the studied system. The age structure of individuals before and at migration was then studied. Most trout were aged from 1 to 3 years old in the Lesse River, and were of age 0 and 1 in the Chicheron Brook. No fish older than 2 years old were found in the downstream trap, and most spawners caught at the trapping facility were aged from 3 to 5 years old.

Key words: age class distribution; birth year determination; finite mixture distribution models; length frequency analysis; *Salmo trutta*

* Supplementary data are available in Appendix 2, page 253.

1 Introduction

In ecology, determination of age is important for obtaining information about mortality, growth, population age structure, and other factors linked to demographic and life history studies. In this thesis, this information will be used for the parameterization of the DemGenTrout model, since individuals are processed by age class in the survival, growth and movement submodels (see Chapter 5). Two main families of methods for age determination exist (Halliday and Verrell, 1988): the examination of hard anatomical parts, and the mark-recapture of individuals.

As for trees, for which an age may be determined by counting annual rings in a cross section of the trunk, anatomical structures such as scales, otoliths, fin rays, dorsal spines, or vertebrae show alternating structural marks caused by changes in growth rates. Validation of a regular periodicity in these marks permits assigning a time scale and determination of age (Penttila and Dery, 1988). For amphibians and reptiles, growth layers are clearly visible in phalanges, and age determination requires only the removal of a toe (Yilmaz *et al.*, 2005). In salmonids, scale reading is the most commonly used method for age determination, and practical manuals provide standardized criteria to interpret scales (Rifflart *et al.*, 2006). However, the accuracy can be low in some situations (e.g., Alvord, 1953; Burnet, 1969), and otoliths have proven to be a better alternative to scales although their use requires the sacrifice of the fish (Hoxmeier and Dieterman, 2011).

In capture-recapture methods, a cohort of animals are individually marked and later recaptured at regular time intervals (see also Box I, pages 63–66). Provided that the age of the individuals is known when they are first marked, this method yields precise data on life history of the species under study. However, in the majority of cases, individuals are of known size, not age, and extrapolation from size-frequency data has to be done. In these methods, the body sizes of a large number of individuals are measured to produce a size-frequency histogram. It is assumed that all size classes have an equal probability of being captured and that measurements are made at an instantaneous moment in time. The mean age of a group (i.e., age class) can then be assigned to the size-frequency distribution by examining it for discontinuities (Halliday and Verrell, 1988). Methods range from simple but subjective ones, such as the visual inspection of the histograms, to more sophisticated and objective ones, such as the statistical decomposition of measurement frequencies into separate normal distributions, using techniques of polymodal distribution analysis. Despite the early development of sev-

eral software programs such as MIX (Macdonald and Green, 1988) or MULTIFAN (Fournier *et al.*, 1990), the use of length-frequency data analysis is still secondary to ageing from calcified structures (Hoxmeier and Dieterman, 2011).

In this Chapter, we present a methodology to assign a birth year to fish based on size-frequency data extrapolation. Its application was illustrated for brown trout of the Lesse River / Chicheron Brook hydrological system. The purpose was to assign a birth year to as many tagged individuals as possible. Indeed, we assumed that the accuracy of parameter estimates linked to the survival, growth and movement processes of the DemGenTrout model should increase with the quantity of trout for which we are certain of their ages. The strategy was first to extract length frequency distributions from capture-recapture data, and to divide them into age classes. Length criteria were then defined for each age class, and used to assign a birth year to each trout on basis of its year of capture (e.g., if a trout caught in 2007 belongs to the age class 1, we know it was born in 2006). Eventually, we investigated the age structure of trout in the Lesse River and in the Chicheron Brook, and of individuals migrating between both streams.

2 Methods

The general methodology to assign birth years to fish comprised three steps. The first step consisted in the preparation of capture-recapture tables to obtain the initial data sets used throughout the analysis. The second step was the independent assignment of birth years to tagged individuals in each data set with the help of finite mixture distribution models (see Box II, pages 109–110 for theoretical background). In the last step, birth years of combined data sets were compared in order to identify errors and improve the assignment in each data set.

2.1 Data preparation

The goals of this first step were to (i) convert the field observations into capture-recapture tables, containing a row for each individual and the length measurements observed a particular year for this individual as columns, (ii) correct the obtained capture-recapture tables, if necessary.

Length measurements from each capture occasion are analysed together. As not all capture-recapture operations occur at a particular time, those that are more or less continuous should be aggregated over

appropriate time intervals (Fournier *et al.*, 1998). Furthermore, for long-term operations, fish lengths need to be considered by year in order to account for interannual variability in growth.

2.2 Finite mixture distribution modelling

In this second step, annual length measurements extracted from each data set were first plotted as frequency histograms. Then, we used the mixdist package (Macdonald and Du, 2009) in the software program R (R Development Core Team, 2011) to fit finite mixture distribution models to these length frequency distributions. Means and standard deviations of the fitted normal distributions for each age class were used to compute annual length criteria, that were in turn used to assign an age class to each individual, and thus deduce its birth year.

Length frequency distributions were divided into several components, corresponding to age classes. Proportions, means and standard deviations of the fitted normal distributions for each age class are the parameters estimated by mixdist. When the components in the length distributions are heavily overlapped, estimating these parameters is difficult, and two solutions can be applied (Du, 2002): constraints can be imposed on the parameters, or information can be brought from additional analyses (i.e., lengths from known-aged fish can be used as conditional data). We thus fitted two types of mixture models to the data sets: (i) an unconstrained model without conditional data when the components were clearly separated, (ii) a constrained model seeded with conditional data otherwise.

As explained in the example presented in Box II, page 109, four technical choices have to be made before fitting any mixture distribution models to data (i.e., interval between groups, number of components, starting values for each parameter, constraints). In each case, we tested a range of 0.3 to 1.3 cm by step of 0.1 cm for the length interval between groups, since the length measurement precision on the field was 0.5 cm. The number of components were determined visually by inspecting the length frequency histograms. In the case of the unconstrained models, the starting values for the means were also determined visually and no constraints on the parameters were imposed. For the constrained models with conditional data, the starting values for the means corresponded to those computed from conditional data, and we tested a combination of constraints on means μ and standard deviations σ corresponding to six different mixture models. The constraints were as follows: equally spaced μ and no constraint on σ (MES-NONE model), von Bertalanffy

growth curve for μ and no constraint on σ (MGC-NONE), no constraint on μ and constant coefficient of variation for σ (NONE-CCV), equally spaced μ and constant coefficient of variation for σ (MES-CCV), von Bertalanffy growth curve for μ and constant coefficient of variation for σ (MGC-CCV), no constraints on μ and σ (NONE-NONE).

Means and standard deviations estimated for each age class normal distributions in each data set were used to compute annual length criteria. These criteria were defined so that birth years were assigned with the highest certainty as possible. For instance, individuals for which the measured lengths were too close to the intersection of two age distributions were not considered. In the case of unconstrained models, the lower limit of the length interval for age class 0 was calculated as $\mu - 3.92\sigma$, and the upper limit of the interval for age class 1 as $\mu + 1.96\sigma$. The two other boundaries were determined using the intersection of the two distributions: for age class 0, the upper length limit was located at the intersection minus 0.25σ, and for age class 1, the lower length limit was located at the intersection plus 0.25σ. For the constrained models with conditional data, the intervals were only determined for the first four age classes, as we considered that the gained information would have been too uncertain for the other distributions due to their high overlapping. These length intervals were defined as follows: for age class 0 and 1, the lower and the upper limits were calculated as $\mu \pm \sigma$, for age class 2 and 3, we used $\mu \pm 0.5\sigma$ and $\mu \pm 0.4\sigma$, respectively. Eventually, birth years were assigned to fish meeting these annual length criteria, given their year of capture. For example, an individual caught in 2007 with a length comprised in the computed interval for age class 1 was born in 2006.

2.3 Combination of data sets

The completion of the two previous steps allowed us to assign a birth year to a certain number of fish. Each data set thus contained individuals with both unassigned and assigned birth years. The next and last step of the methodology was to combine the data sets two by two, identify individuals that were in common (i.e., fish with the same PIT tag) and compare their birth years. Indeed, a same individual can be observed in two different data sets since it can be caught in different locations at different times.

The comparison of birth years between two data sets led to two operations. First, errors of assignment were identified. When an individual with two different birth years was found, these latter were considered as uncertain and removed. Second, the assignment of birth years was

completed in each data set. When a fish with an assigned birth year was found in a data set but not in the other, this new information was added.

3 Results

The methodology was followed to assign a birth year to tagged brown trout of the Lesse River / Chicheron Brook hydrological system. Two types of field observations were used: electrofishing operations conducted in both streams, and observations at the trapping facility. These data were converted into capture-recapture tables in Section 3.1, corresponding to the first step of the methodology. The second and last steps were adapted to this specific case study (Sections 3.2 to 3.5). Final results were used to investigate the population dynamics of trout living in this system (Section 3.6).

A preliminary analysis of the available field data revealed several features that had to be accounted for in the application of the methodology. First, we observed that the youngest trout of the system were caught either in the Chicheron Brook, or during their descent to the Lesse River. Consequently, the corresponding field data contained few age classes with very distinct length groups, allowing for the fitting of unconstrained mixture distribution models. However, two main difficulties were encountered when we tried to apply such models to trapping observations: (i) captures of trout in the downstream trap were continuous and extended over a long time period (i.e., from November to September), in comparison with a few days for the electrofishing samplings, (ii) the period of descent greatly varied from one year to another. After several inconclusive trials, we had to renounce and the length criteria were determined by visual inspection of the frequency histograms of length measurements aggregated by month.

Second, we found that both untagged and tagged trout needed to be considered, in particular when fitting the mixture distribution models to the electrofishing data of the Chicheron Brook. In that case, not including the untagged individuals could clearly bias the estimations for the first age class (e.g., Fig. 4.1).

Third, length distributions for trout electrofished in autumn in the Lesse River appeared heavily overlapped (Fig. 4.2). As we have seen in Section 2.2, this issue can only be overcome by using constrained mixture distribution models seeded with conditional data. Unfortunately, lengths from known-aged fish were not available in the case of the Lesse

River, since scale reading or any other technique for estimating age from anatomical parts of trout was never performed in the studied system. However, we took advantage of the fact that each trout were identified by an unique PIT tag. A same individual can be caught in different locations at different times, and conditional data were thus obtained by applying the third step of the methodology (i.e., combination of data sets).

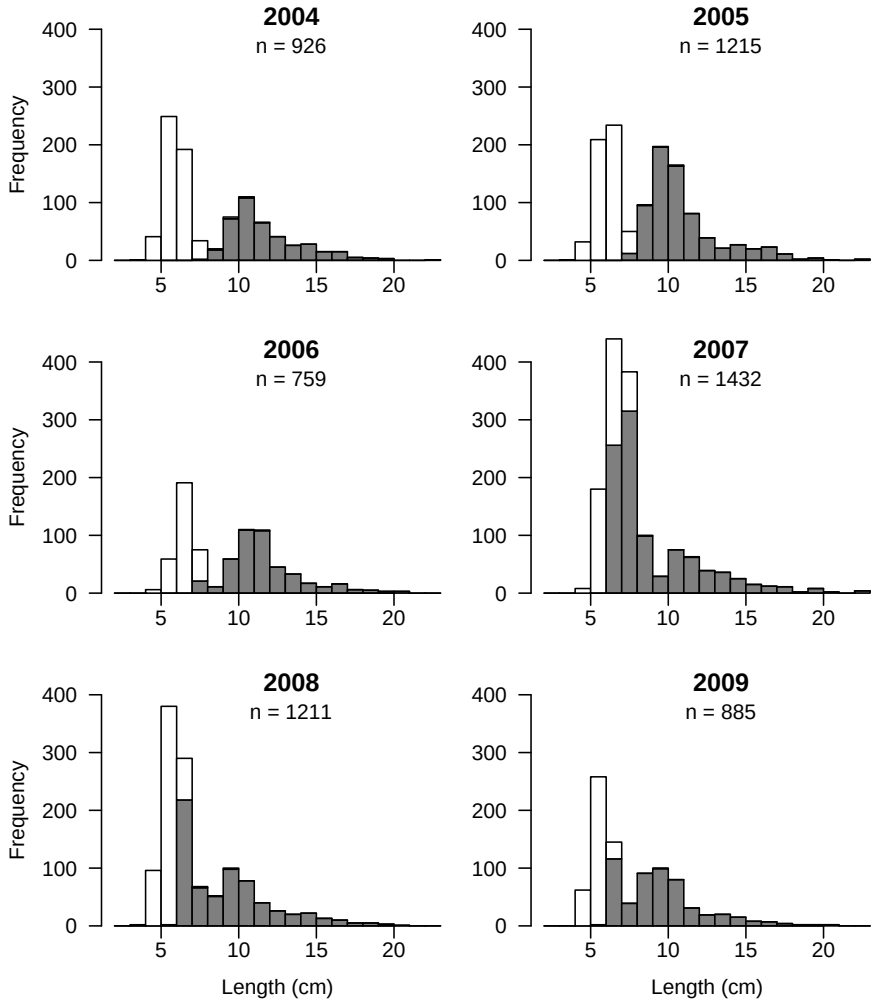

Figure 4.1: Length frequencies of brown trout electrofished in the Chicheron Brook in autumn 2004-2009 (Chicheron Autumn data set, 1-cm length classes). Both untagged trout (white) and tagged trout (grey) are represented, and the number of available length measurements (n) is given.

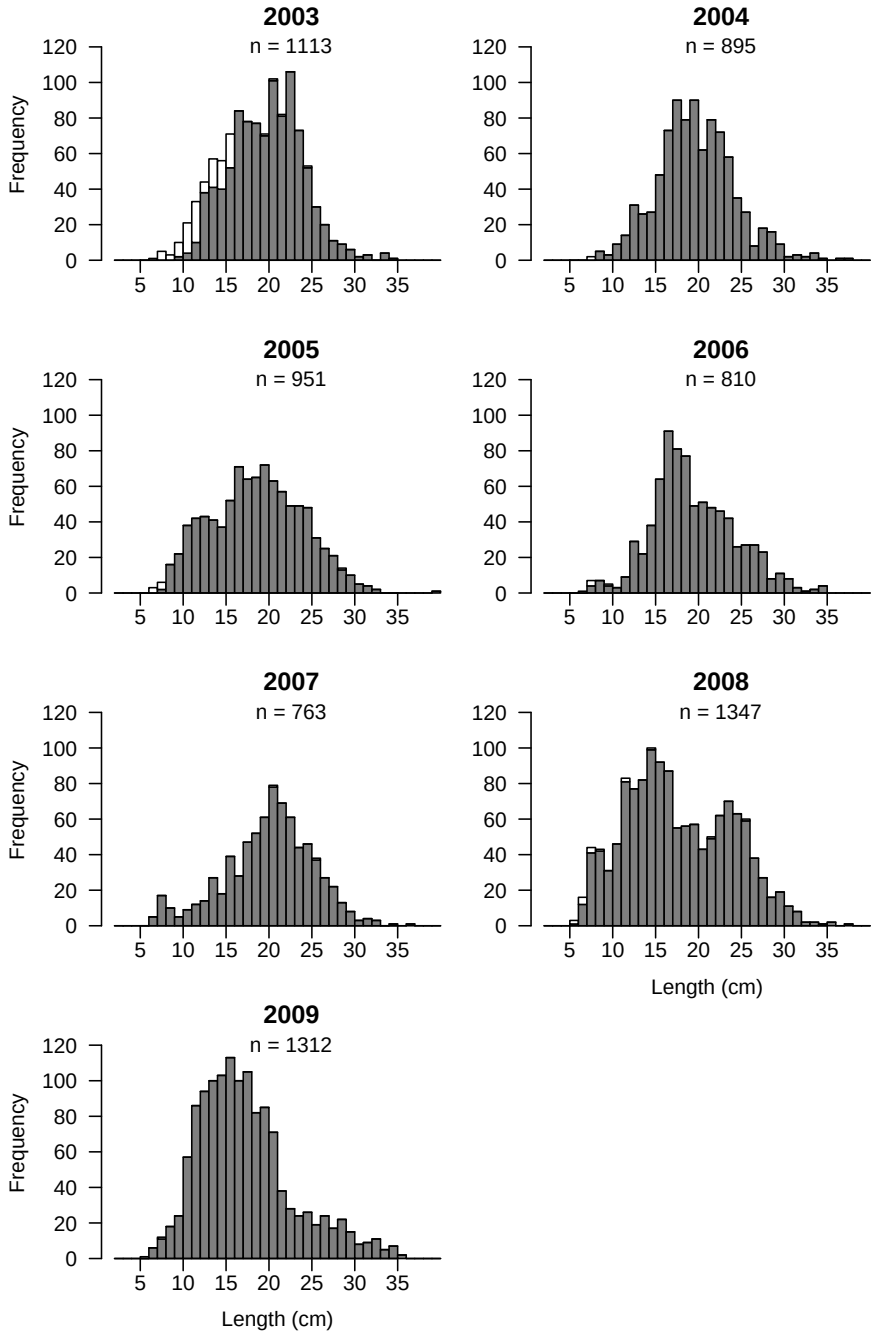

Figure 4.2: Length frequencies of brown trout electrofished in the Lesse River in autumn 2003-2009 (Lesse Autumn data set, 1-cm length classes). Both untagged trout (white) and tagged trout (grey) are represented, and the number of available length measurements (n) is given.

As a consequence of these adaptations, steps 2 and 3 were applied two times each. The adapted methodology followed to assign a birth years to tagged trout of the Lesse River / Chicheron Brook system thus comprises the following five steps (Fig. 4.3):

- STEP 1: Preparing capture-recapture tables to obtain the five data sets that will be analysed (Chicheron Autumn, Chicheron Spring, Lesse Autumn, Juveniles Trap, Spawners Trap);
- STEP 2: Fitting unconstrained finite mixture distribution models to the Chicheron Autumn and Spring data sets (and visually inspecting length histograms for trout of the Juveniles Trap data set);
- STEP 3: Merging all five data sets to (i) identify errors and improve birth year assignment in the Chicheron Autumn, Chicheron Spring, and Juveniles Trap data sets, (ii) assign birth years to trout of the Lesse Autumn and Spawners Trap data sets;
- STEP 2bis: Fitting constrained finite mixture distribution models to the Lesse Autumn data set, using conditional data obtained in the previous step;
- STEP 3bis: Merging all five data sets once more to account for the new birth years available in each data set.

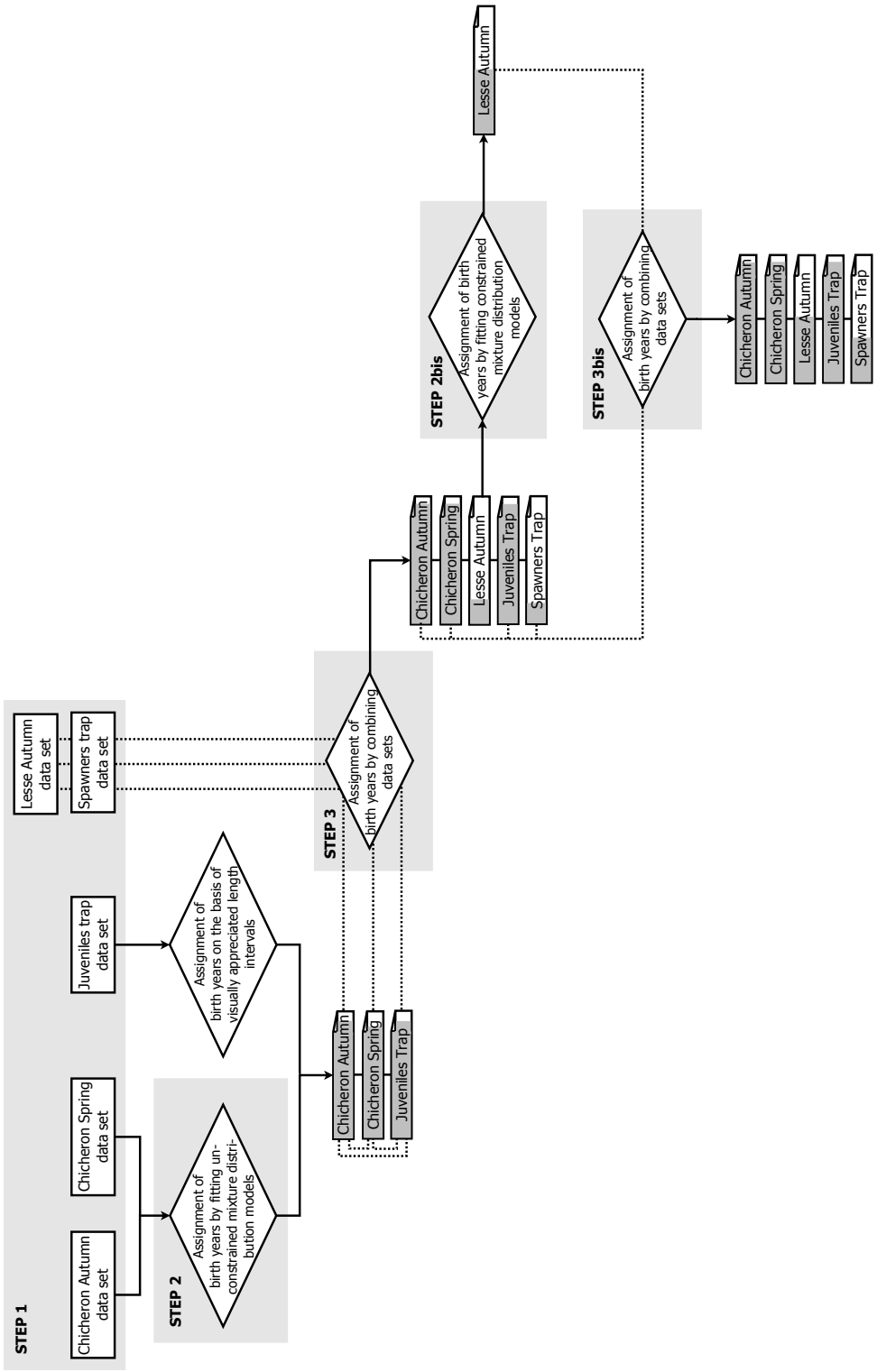

Figure 4.3: The adapted methodology followed to assign birth years to tagged brown trout of the Lesse River / Chicheron Brook hydrological system. Each data set is represented by a rectangular box, in which the shaded area corresponds to the proportion of trout with a known birth year.

3.1 Data preparation

Trapping observations were first divided as follows to consider adults moving to the brook for reproduction on the one hand, and young trout born in the brook and migrating from it on the other hand: (i) all individuals caught in the upstream trap were considered as spawners, (ii) individuals caught in the downstream trap with a length measurement strictly lower than 12 cm (i.e., the minimum length found for upswimming spawners) were considered as recruits (the remaining individuals being spawners).

Then, trapping and electrofishing observations were converted into capture-recapture tables (STEP 1 in Fig. 4.3). We ended up with five different data sets (Table 4.1): Chicheron Autumn, Chicheron Spring, Lesse Autumn, Juveniles Trap, and Spawners Trap. The first three data sets were corrected, and 4 length measurements from the Chicheron Autumn data set, 2 from the Chicheron Spring data set, and 29 from the Lesse Autumn data set were deleted, as they were not in ascending order year after year or implied a growth outside a plausible range (i.e., larger than the upper bound of the 95% confidence interval of the corresponding length distribution).

In each capture-recapture table, each row corresponds to an individual and the columns contain the length measurements observed a particular year for each individual. In order to account for interannual variability in trout growth, we divided each capture-recapture table by year (i.e., we considered the data by column).

Table 4.1: Number of tagged and untagged trout (number of length measurements) available in each data set at the end of the Data preparation step.

Data set	Years	Tagged trout	Untagged trout
Chicheron Autumn	2004-2009	3321 (3732)	2696 (2696)
Chicheron Spring	2005-2009	1614 (1752)	374 (374)
Lesse Autumn	2003-2009	5057 (7039)	152 (152)
Juveniles Trap	2003-2009	4196 (4201)	1302 (1302)
Spawners Trap	2002-2009	1693 (2638)	0 (0)

3.2 Assignment of birth years to trout electrofished in the Chicheron Brook or caught as juveniles at the trapping facility

Finite mixture distribution models were first fitted to length frequencies of trout of the Chicheron Autumn and Spring data sets (STEP 2 in Fig. 4.3). Estimated parameters of the normal distributions for each age class were used to compute annual length criteria. Then, length frequency histograms of the Juveniles Trap data set were examined, and length criteria were visually appreciated. Age classes were assigned to tagged trout of these three data sets with the help of the length criteria, and their birth year was determined.

3.2.1 Trout electrofished in the Chicheron Brook

The means and standard deviations of the age class normal distributions were estimated by fitting unconstrained mixture distribution models to each Chicheron data set, split by year of capture (i.e., from autumn 2004 to 2009, and from spring 2005 to 2009). Each annual data set contained length measurements for both untagged and tagged trout ranging from 600 to 1400 measurements in the case of the Chicheron Autumn data set, and from 200 to 600 measurements for the Chicheron Spring data set.

In each case, the number of considered components was two: age class 0 and 1 in autumn, and age class 1 and 2 in spring. Starting values for means of each age class are presented in Table 4.2. We computed the P-value of each unconstrained mixture model by varying three parameters by step of 0.1 cm (i.e., the length interval between groups, the left-hand boundary of the first group, and the right-hand boundary of the last group). Parameters for which the P-value of the considered model was maximal were chosen.

Trout length distributions obtained for each age class of the Chicheron data sets with the best identified model appear influenced by the capture year (Fig. 4.4). For age class 0 and 1 in autumn, and 1 and 2 in spring, median values of length over all years were found to equal 6.1, 10.3, 7.7 and 11.5 cm, respectively, while sums of squared errors were equal to 0.9, 3.1, 1.3 and 2.8, respectively. The interannual variability of trout length in the Chicheron Brook was thus particularly high for age class 1 in autumn and age class 2 in spring.

Length criteria determined for the Chicheron Autumn data set are presented in Fig. 4.5. Corresponding interval values are available for both

Table 4.2: Fitting unconstrained mixture distribution models to the length frequency histograms of trout electrofished in the Chicheron Brook in autumn 2004-2009 and spring 2005-2009, divided according to the season and year of capture. In each case, the starting values for the means (μ) of age class 0-1 (Chicheron Autumn data set) or 1-2 (Chicheron Spring data set), the best length interval between groups (BLI), and the P-value derived from the goodness-of-fit test of the model are given.

Season	Year	Range (cm)	μ (cm)	BLI (cm)	P-value
Autumn	2004	4.0 to 14.0	6.0; 11.0	1.3	0.2812
Autumn	2005	3.8 to 12.9	6.0; 10.0	1.3	0.1302
Autumn	2006	4.3 to 14.0	6.5; 11.0	1.1	0.1483
Autumn	2007	4.7 to 13.5	7.0; 11.0	0.9	0.1525
Autumn	2008	3.7 to 11.5	6.0; 10.0	0.5	0.1959
Autumn	2009	4.1 to 11.5	6.0; 9.50	1.3	0.5571
Spring	2005	5.5 to 13.0	7.5; 12.0	1.0	0.9995
Spring	2006	6.1 to 12.8	8.0; 11.5	0.6	0.9589
Spring	2007	5.5 to 12.9	8.0; 11.5	1.0	0.9830
Spring	2008	5.5 to 14.0	8.0; 13.0	0.9	0.8023
Spring	2009	5.2 to 11.8	7.0; 11.0	1.2	0.2489

data sets in Tables A2.1 and A2.2 of Appendix 2, page 254. The assignment of birth years to tagged trout meeting these length criteria was equal to 89% (2954 individuals out of 3321) for the Chicheron Autumn data set, and to 85% (1370 individuals out of 1614) for the Chicheron Spring data set.

3.2.2 Juveniles caught at the trapping facility

The Juveniles Trap data set was separated by year (i.e., from 2003 to 2009). Each annual data set contained between 400 and 1400 length measurements for both untagged and tagged trout. Length frequency histograms broken by month were examined in order to define length criteria for trout of age class 0, 1 and 2. Corresponding interval values are available in Table A2.3 of Appendix 2, page 255.

Using these visually determined criteria, we were able to assign a birth year to 87% of the tagged trout present in the Juveniles Trap data set (3655 individuals out of 4196).

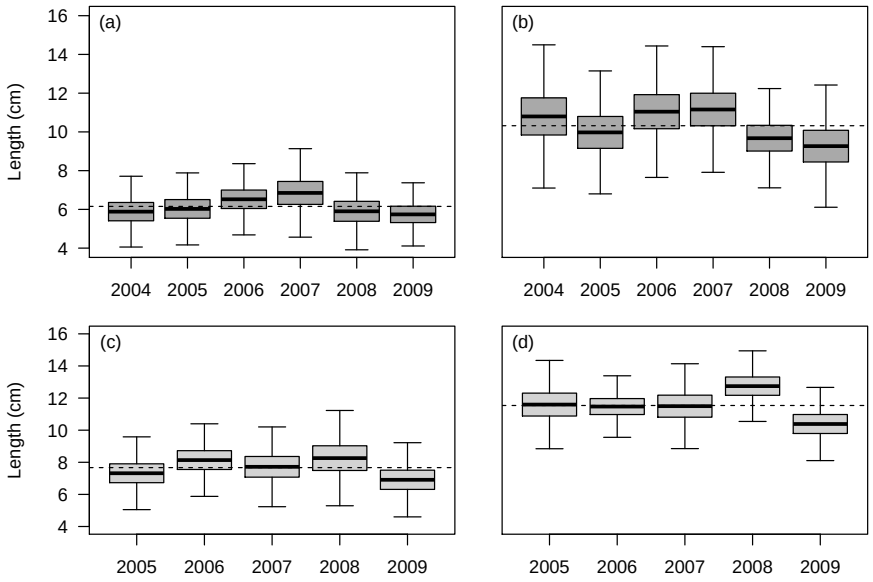

Figure 4.4: Length distribution of trout electrofished in the Chicheron Brook in autumn 2004-2009 (Chicheron Autumn data set; a-b: age class 0-1) and spring 2005-2009 (Chicheron Spring data set; c-d: age class 1-2). The 2.5 (lower bound of the 95% confidence interval), 25 (lower quartile), 50 (median), 75 (upper quartile), 97.5 (upper bound of the 95% confidence interval) percentiles are displayed. Median values over all years are indicated by dotted lines.

3.3 First combination of data sets

The Chicheron Autumn, Chicheron Spring, and Juveniles Trap data sets considered altogether now contain 90% of tagged trout with an assigned birth year (6564 individuals out of 7324). This latter information was used to (i) correct and complete the birth year assignments in these three data sets, (ii) assign a birth year to the tagged trout of the Lesse Autumn and Spawners Trap data sets.

In total, nine combinations of two data sets were considered (STEP 3 in Fig. 4.3). Table 4.3 shows the number of tagged trout that were in common for each combination.

First, 461 trout with an assigned birth year caught both in autumn and spring in the Chicheron Brook were identified (Table 4.3). Among them, 21 individuals had two different birth years, and the corresponding information were deleted in both data sets. We ended up with 88% (2933 individuals out of 3321) and 84% (1349 individuals out of 1614) of trout having an assigned birth year for the Chicheron Autumn and Chicheron Spring data sets, respectively.

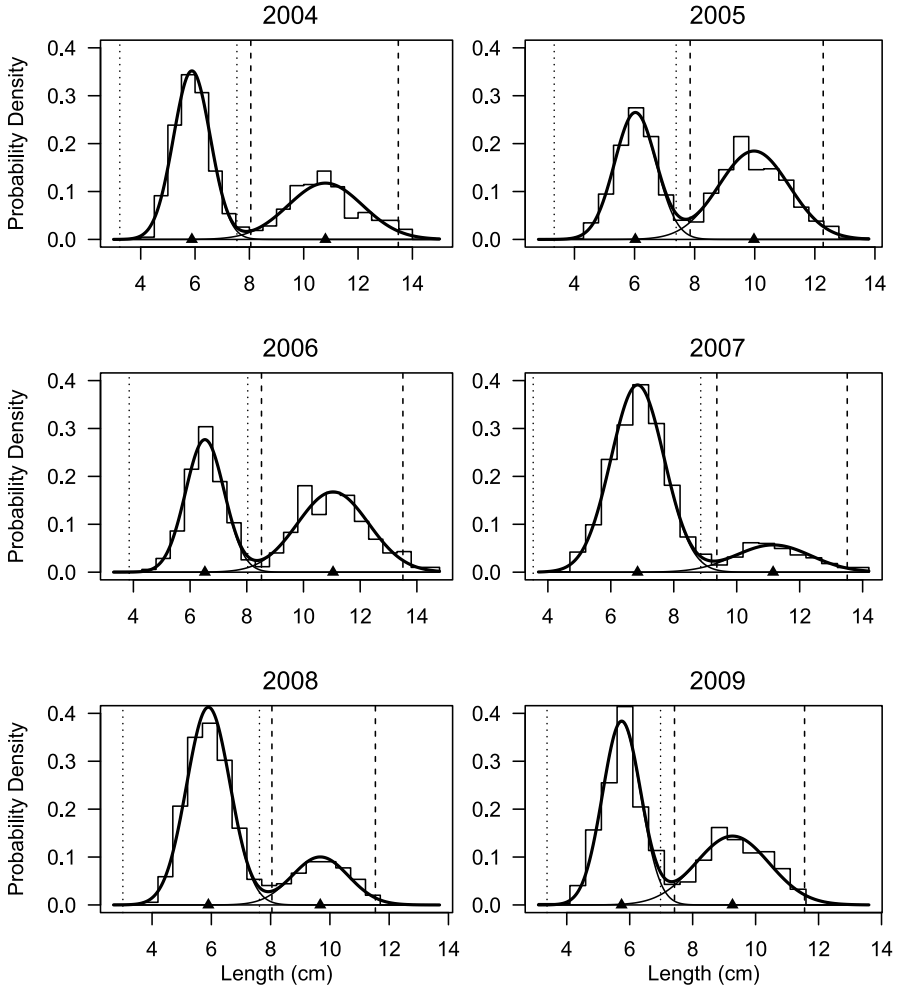

Figure 4.5: Length frequencies of age class 0-1 trout electrofished in the Chicheron Brook in autumn 2004-2009 (Chicheron Autumn data set). Fitting curve of each age class normal distribution (thin lines with means represented by triangles), overall fitting curve (thick line), length intervals for age class 0 (dotted vertical lines) and age class 1 (dashed vertical lines) are represented.

Second, the Juveniles Trap data set was successively merged with the Chicheron Autumn and Spring data sets, and we found that 640 and 368 tagged trout having a birth year were in common, respectively (Table 4.3). After the merging, 13 trout with different birth years were removed from the Juveniles Trap data set, but 105 trout with newly assigned birth years were added. For the Chicheron Autumn and Spring data sets, we removed 12 and 2 individuals and added a birth year for 57 and 122 trout, respectively. We eventually obtained an assignment

Table 4.3: Number of identical tagged trout having an assigned birth year considering each combination of two data sets.

Data set	Chicheron Spring	Juveniles Trap	Lesse Autumn	Spawners Trap
Chicheron Autumn	461	640	274	302
Chicheron Spring	-	368	123	78
Juveniles Trap	-	-	852	223

percentage equal to 90% (2990 trout out of 3321), 91% (1471 trout out of 1614) and 90% (3760 trout out of 4196) for the Chicheron Autumn, Chicheron Spring and Juveniles Trap data sets, respectively.

Third, the Lesse Autumn data set was successively merged with the Chicheron Autumn, Chicheron Spring and Juveniles Trap data sets (274, 123, and 852 trout were in common, respectively; see Table 4.3). Only 2 trout with different birth years were found and removed from this data set. Among the 5057 tagged trout initially present in the data set (Table 4.1), we were able to assign a birth year to 987 of them (20%).

Finally, we proceeded the same way for the Spawners Trap data set that shared 302, 78, and 223 common individuals with the Chicheron Autumn, Chicheron Spring and Juveniles Trap data sets, respectively (Table 4.3). No trout were removed, and we obtained a percentage of 17% for birth year assignment (296 individuals out of 1693).

3.4 Assignment of birth years to trout electrofished in the Lesse River

In order to improve the percentage of birth year assignment for trout of the Lesse River data set, constrained mixture models were fitted to this data set split by capture year (i.e., from autumn 2003 to 2009) (STEP 2bis in Fig. 4.3). Each annual data set contained 600 to 1100 length measurements for both untagged and tagged trout.

The length measurements of the 987 trout for which a birth year was previously assigned were first transformed into age classes (1433 in total) to be used as conditional data. Then, estimated means and standard deviations of the age class normal distributions were used to compute the length criteria.

Each distribution mixture comprised seven age classes (from 0 to 6), and the starting values for the means corresponded to those computed by age class. For each annual data set, we tested a set of six constrained

mixture distribution models (i.e., MES-NONE, MGC-NONE, NONE-CCV, MES-CCV, MGC-CCV, NONE-NONE; see Section 2.2).

Table 4.4: Fitting different mixture distribution models to the length frequency histograms of trout electrofished in the Lesse River in autumn 2003-2009 (Lesse Autumn data set). In each case, the range of the available length measurements, the starting values for the means (μ) of age classes 0-6, and the best model are given, along with the corresponding length interval between groups (BLI) and P-value derived from the goodness-of-fit test.

Year	Range (cm)	μ (cm)	Best model	BLI (cm)	P-value
2003	6.9 to 35.0	8.0, 11.6, 13.8, 20.5, 23.0, 24.3, 26.0	MES-CCV	0.9	0.9984
2004	7.1 to 37.1	8.0, 12.2, 16.6, 20.5, 23.0, 24.3, 26.0	MES-CCV	1.1	0.8308
2005	6.3 to 40.2	9.0, 11.5, 16.5, 20.5, 23.0, 24.3, 26.0	MES-NONE	0.9	0.5810
2006	6.7 to 34.9	8.0, 12.6, 16.3, 20.5, 22.0, 24.3, 26.0	MES-NONE	1.3	0.9933
2007	6.5 to 36.3	8.0, 12.5, 16.4, 20.0, 22.0, 24.3, 26.0	MES-NONE	1.1	0.3944
2008	5.7 to 37.4	8.0, 12.1, 16.4, 19.7, 22.8, 24.3, 26.0	NONE-NONE	0.8	0.7376
2009	5.1 to 35.6	8.0, 11.2, 17.0, 20.0, 22.9, 24.3, 26.0	NONE-CCV	0.9	0.5056

Trout length distributions obtained for each age class of the Lesse Autumn data set with the best identified model appear influenced by the capture year (Fig. 4.6). Median values of trout length over all years for age class from 0 to 3 were found to equal 8.1, 12.7, 16.8 and 20.9 cm, respectively, while sums of squared errors were equal to 1.2, 1.3, 3.3 and 8.6, respectively. The interannual variability of trout length in the Lesse River was thus particularly high for age class 3.

Length criteria determined for the first four age classes of the Lesse Autumn data set are presented in Fig. 4.7. Corresponding interval values are available in Table A2.4 of Appendix 2, page 256. When we assigned a birth year to the tagged trout meeting these length criteria, we found and removed 157 individuals that showed different birth years. Eventually, we were able to assign a birth year to 54% of the trout of the Less Autumn data set (2732 individuals out of 5057).

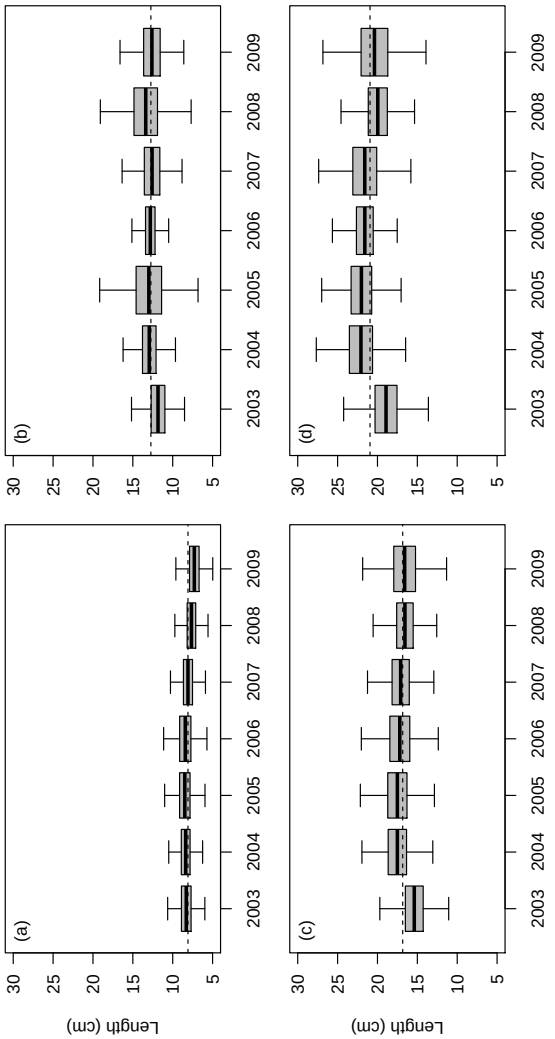

Figure 4.6: Length distribution of trout electrofished in the Lesse River in autumn 2003-2009 (Lesse Autumn data set; a-d: age class 0-3). The 2.5 (lower bound of the 95% confidence interval), 25 (lower quartile), 50 (median), 75 (upper quartile), 97.5 (upper bound of the 95% confidence interval) percentiles are displayed. Median values over all years are indicated by dotted lines.

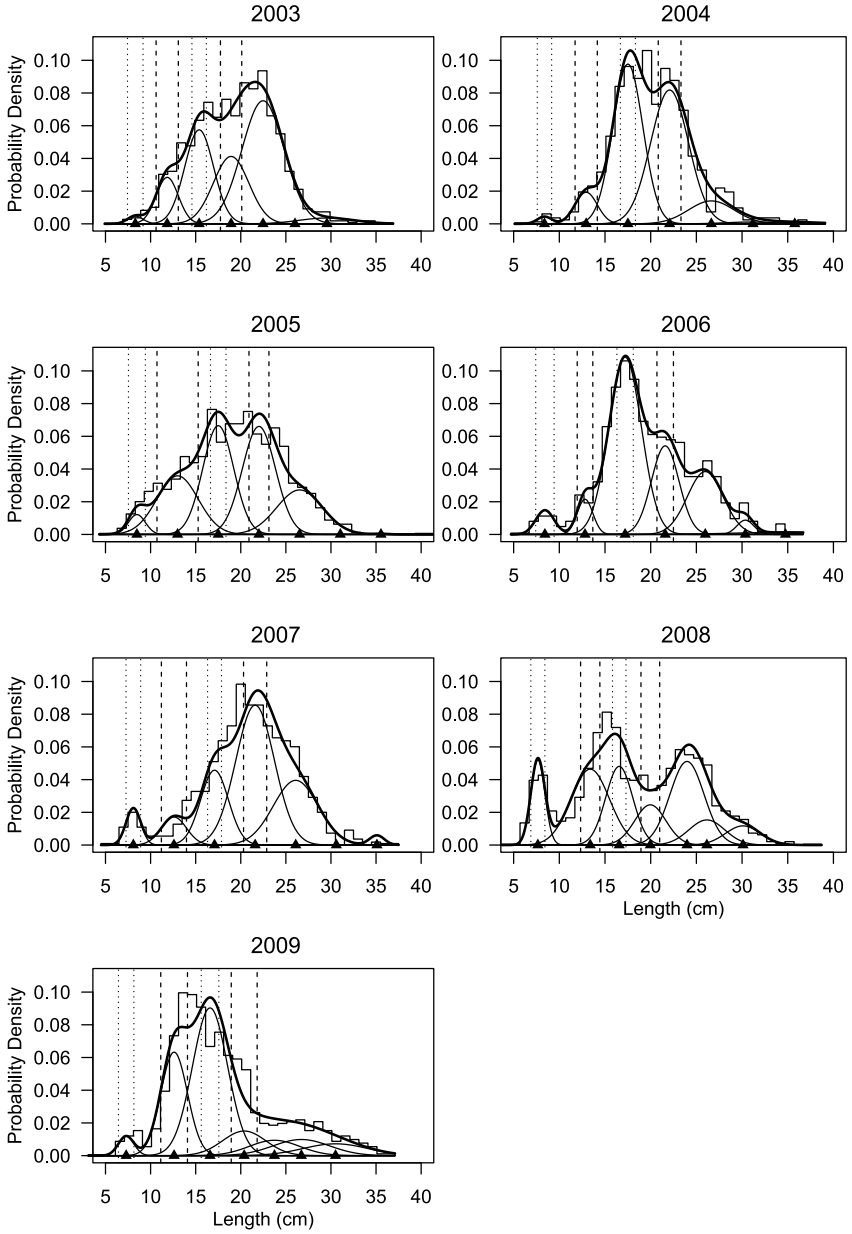

Figure 4.7: Length frequencies of age class 0-3 trout electrofished in the Lesse River in autumn 2003-2009 (Lesse Autumn data set). Fitting curve of each age class normal distribution (thin lines with means represented by triangles), overall fitting curve (thick line), length intervals for age class 0 to 3 are alternately represented by dotted and dashed vertical lines.

3.5 Second combination of data sets

The Lesse Autumn data set was successively merged with the Chicheron Autumn, Chicheron Spring, Juveniles Trap and Spawners Trap data sets (STEP 3bis in Fig. 4.3). This merging allowed us to update the five data sets, by accounting for the new birth years available.

In each case, no correction was done since we found no trout with two different birth years after the merging. Birth years were added for 7, 15, 0, 62 and 247 individuals in each data set, respectively.

In the end, we obtained the following percentages of birth year assignment to tagged trout:

- 90% for the Chicheron Autumn data set (2997 trout out of 3321);
- 92% for the Chicheron Spring data set (1486 trout out of 1614);
- 54% for the Lesse Autumn data set (2732 trout out of 5057);
- 91% for the Juveniles Trap data set (3822 trout out of 4196);
- 32% for the Spawners Trap data set (543 trout out of 1693).

3.6 Trout population dynamics

We investigated the dynamics of the brown trout population of the Lesse River / Chicheron Brook system, by combining information on trout birth years with electrofishing and trapping observations. We first compared the distributions of trout age classes in autumn in both streams. Then, the age structure of spawners and juveniles migrating between the two streams was studied.

In the first analysis, we considered observations on tagged trout derived from electrofishing operations conducted in both streams in autumn (i.e., Chicheron Autumn and Lesse Autumn data sets of Table 4.1). In the brook, individuals of age 0 and 1 were mainly found, with proportions equal to 32% and 58%, respectively (Fig. 4.8(a)). In the Lesse River, all age classes were represented, with a greater part of age ≥ 2 trout (70%) in comparison with the brook (Fig. 4.8(b)).

In the second analysis, we considered observations on tagged trout caught at the trapping facility located at the confluence of the Chicheron Brook in the Lesse River (i.e., Juveniles and Spawners Trap data sets of Table 4.1). Age of trout reproducing in the Chicheron Brook was comprised between 3 and 5 years old (83%), with a maximum at 3 (33%) (Fig. 4.8(c)). Trout migrated from the Chicheron Brook to the Lesse River mainly at the age of 1 (68% of the individuals), although some

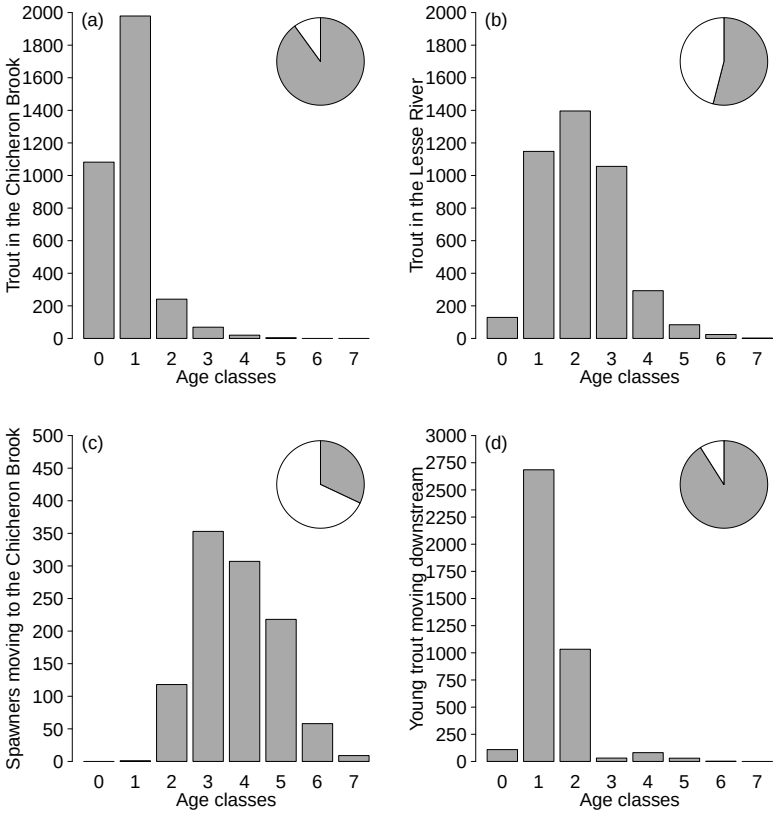

Figure 4.8: Age distribution of trout caught in (a) the Chicheron Brook in autumn (2004-2009), (b) the Lesse River in autumn (2003-2009), (c) the trapping facility as spawners (2002-2009) and (d) the trapping facility as juveniles (2002-2009). The respective percentages of birth year assignment to tagged trout are represented in the top right corner (grey: assigned, white: unassigned).

individuals left the brook at 2 years old (26%) (Fig. 4.8(d)). Emigration at age 0 was rather rare (3%). The remaining trout were of age 3 to 5 (3%).

4 Discussion

The three-step methodology presented in this Chapter was designed to automatically assign a birth year to fish through the determination of their age classes, which are themselves function of their length. The strategy was applied to the Lesse River / Chicheron Brook hydrological system, and had to be adapted by (i) developing an ad-hoc approach for trout caught as juveniles in the downstream trap, (ii) repeating the second and third steps of the methodology to deal with the heavy overlap of length distributions observed for trout electrofished in the Lesse River. At the end of the first repetition, a birth year was assigned to 54% of the trout (6552 individuals out of 12036). At the end of the whole procedure, the percentage of assignment increased up to 70% (8400 trout out of 12036), corresponding to a global improvement of 16%. Considering each data set, these percentages were improved by $\approx 1\%$ for those containing the trout electrofished in the Chicheron Brook or caught as juveniles, and by 34 and 15% for the data sets linked to the trout electrofished in the Lesse River and caught as spawners, respectively. These results illustrate the necessity of applying steps 2 and 3 a second time.

Other software using techniques of polymodal distribution analysis exist, such as Bhattacharya's and Hasselblad's NORMSEP methods implemented in FiSAT (FAO-ICLARM Stock Assessment Tool; Gayanilo *et al.*, 1995). They were not appropriate in our case for two reasons. First, the mixdist R package can deal with cases where components heavily overlapped by applying constraints on parameters to be estimated, and this was necessary to treat the length distributions of trout electrofished in the Lesse River. Second, working with R allowed us to keep a trace of the code we used by storing it in script files. This way, the chosen methodology is systematic as birth year assignments were not made "by hand", except for the visual determination of length criteria for juveniles caught at the trapping facility (i.e., 42% of all trout).

Several drawbacks are however associated with methods linked to size-frequency data extrapolation (Halliday and Verrell, 1988). First, they assume that age and size are statistically related, and this is a strong hypothesis. Second, it is often not clear what age class should be assigned to individuals with a size located near the intersection of two distributions. That is why we defined strict length criteria excluding these individuals. In the case of length measurements available for trout of the Lesse River, this precaution was not sufficient, and we had to remove the birth years for 157 individuals. These wrong assignments mainly concerned trout of age class 3 and 4 (65%). This can be explained

by the high interannual variability in length observed for trout of age class 3 (and probably higher) in the river (Fig. 4.6, page 128).

Another check was made to ensure that birth years were assigned with the highest certainty as possible. In several occasions, errors of assignment were identified by intersecting data sets two by two. When a trout with two different birth years was found, both of them were considered as uncertain and removed. For example, the birth years assigned to 21 individuals were removed when we merged the data sets containing length of trout electrofished in autumn and spring in the Chicheron Brook. These individuals were mainly assigned to the age classes for which a high interannual variability was found with percentages equal to 62 and 67%, respectively (i.e., age class 1 in autumn and age class 2 in spring; Fig. 4.4, page 124).

The comparison of trout age distributions in autumn in both streams highlighted the nursery role of the brook. We observed that distributions highly varied in the case of the Lesse River (i.e., age classes from 0 to 7) while individuals belonging to age class 0 and 1 were mainly found in the Chicheron Brook. It is noteworthy that these age distributions only accounted for tagged trout (i.e., individuals with a measured length $>$ 7.5 cm before 2006 and $>$ 6 cm afterwards). In the Chicheron Brook, a high number of electrofished trout are not tagged (Fig 4.1, page 117). This means that trout of age 0 are probably dominant in the brook. For the Lesse River, this issue does not exist (Fig 4.2, page 118), but another type of bias was introduced in the results since a birth year could only be assigned to half the trout of this stream.

From the analysis of the data set containing the individuals caught at the trapping facility, we found that most spawners were aged from 3 to 5 years old, and that most juveniles were of age 1 and 2. However, in the case of age distribution of spawners, the percentage of birth year assignment was around 30% and, consequently, these results are incomplete. In the case of the juvenile age distribution, the same issue as the one mentioned for trout electrofished in the brook occurs (i.e., numerous untagged trout). However, after examining each annual length histogram, we noticed that only few untagged individuals with a length between 3 and 5 cm were captured, while individuals with a length between 5 and 7 cm were more numerous, particularly in 2006-2007 and 2007-2008. This finding confirms that age 0 trout rarely leave the brook, while the number of migrating age 1 trout is probably higher than the value we found. The few trout of age 3-5 observed in Fig. 4.8(d) were probably spawners wrongly identified as juveniles during the separation of trapping observations into two data sets (see Section 3.1).

In this Chapter, the purpose was to assign a birth year to trout of the Lesse River / Chicheron Brook system in order to use this information to parameterize the survival, growth and movement processes of the DemGenTrout individual-based model (Chapter 5). We wanted to assign a birth year to as many tagged trout as possible, because we assumed that the accuracy and quality of the parameters would increase with the number of data that can be used to estimate them. This goal was fulfilled since a birth year was assigned to 70% of the trout.

Chapter 5

Parameterization of the DemGenTrout individual-based model with field data collected on the Lesse River drainage

Brown trout life cycle is influenced by the state of the individuals (e.g., age, size, physiology) and hydrological conditions (e.g., water temperature and flow). The survival, growth, spawning, movement processes of the DemGenTrout individual-based model were parameterized with field data collected over 5 years on the Lesse River / Chicheron Brook hydrological system. Individual characteristics such as age, length, weight and physiology must necessarily be known to model such processes, which may also be influenced by water temperature and flow. To estimate trout survival probabilities, Bayesian hierarchical models were applied to electrofishing capture-recapture data divided by age class, an information gained in Chapter 4. For the growth process, trout birth year information was also needed to fit Bayesian hierarchical models and to apply a log-log regression to electrofishing data. Determination of the parameter values of the spawning and downstream movement processes were based on trout observations at the trapping facility and on environmental data. The other parameters of DemGenTrout that were derived from literature, guestimated or calibrated are considered in Chapter 6.

Key words: Bayesian hierarchical models; finite mixture distribution models; parameterization; regression methods; *Salmo trutta*

1 Introduction

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). Water temperature and discharge are two of the environmental factors influencing survival. For brown trout, the upper lethal temperature in fresh water is at 24.7°C (Jonsson and Jonsson, 2009). Low water levels might decrease the availability of fish habitats (Lund *et al.*, 2003), while high discharges and subsequent high water velocities might prevent alevins to maintain their stream position or to find shelters (Cattaneo *et al.*, 2002). Density-dependence mortality in salmonids mostly occurs during the first few months of their life (Mortensen, 1977). With increasing fish density, competition for limited resources such as food and space also increases, and this results in lower survival (Hayes *et al.*, 1996; Cattaneo *et al.*, 2002). Other sources of mortality, underdocumented in literature, are cannibalism and bird predation. Trout frequently eat eggs or smaller conspecifics (Vik *et al.*, 2001; Aymes *et al.*, 2010), while birds such as herons have been observed to remove large numbers of individuals from small shallow streams (Larsson, 1985; Feunteun and Marion, 1994; Hodgens *et al.*, 2004).

The question of estimating survival probabilities was early addressed with life-table approaches (e.g., Deevey, 1947), then was incorporated into capture-recapture (CR) methods (see Box I, pages 63–66). CR models were first designed to estimate the size of a closed population (e.g., Lincoln-Petersen index), and then evolved to infer survival rates and to consider open populations (i.e., in which additions and deletions are allowed). The most well-known open CR models are the Jolly-Seber (JS) model (Jolly, 1965; Seber, 1965) and the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965), a particular case of the JS model. CR models are commonly used in the brown trout literature. For instance, CJS models were used in several studies to estimate survival probabilities (e.g., Olsen and Vollestad, 2001; Lund *et al.*, 2003; Budy *et al.*, 2008).

Growth variation in fish is mainly regulated by food availability and water temperature (Lobon-Cervia and Rincon, 1998; Vollestad *et al.*, 2002; Dineen *et al.*, 2007). Temperature can influence fish physiology both negatively or positively. Elliott (1994) observed higher growth rates in winter and negligible growth in summer for a British brown trout population, while Lobon-Cervia and Rincon (1998) found that trout experi-

enced faster growth at higher temperatures in Spain. Growth rate seems also influenced by fish density (Grant and Kramer, 1990; Klemetsen *et al.*, 2003; Milner *et al.*, 2003). Average growth declines with increasing density, and this phenomenon can be explained by two main factors, in potential interaction: (i) exploitative competition, i.e., the depletion of food by competitors (Keddy, 1989; Imre and Boisclair, 2005), (ii) spatial competition, i.e., individuals competing for foraging sites that vary spatially in quality (Ward *et al.*, 2007).

Most of the time, growth models are based on mathematical relationships. Two of them have been widely used for brown trout: the equation of von Bertalanffy (1957) that expresses the length of an individual over time (e.g., Cooper *et al.*, 1992; Büttiker and Labous, 2002; Arslan *et al.*, 2007), and the length-weight relationship of Ricker (1975) (e.g., Oscoz *et al.*, 2005; Railsback *et al.*, 2009). First, the parameters of the von Bertalanffy equation (VBE) are generally estimated by fitting nonlinear regression techniques to length-at-age data: the asymptotic size, the growth coefficient, and a time used to calculate size at age 0. Age determination of the studied individuals is thus a prerequisite to resolve the VBE. When length-at-age data are not available or scarce, the regression is impossible and Bayesian models using only length data were developed (Siegfried and Sanso, 2006). Second, the length-weight relationship (LWR) allows determining trout weight when only length measurements are available. Two parameters intervene in this relation. The first one is the condition factor, for which a standard value assuming that the weight of the fish is proportional to the cube of its length can be computed (Ricker, 1975). This standard condition factor, or Fulton's coefficient, is a practical index of the fish condition (Petrakis and Stergiou, 1995): its value 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. The second parameter describes the rate of change of weight with length (Morey *et al.*, 2003; Samat *et al.*, 2008). When its value is equal to 3, increase in weight is isometric, and when the value is different than 3, it is allometric (positive if > 3, negative if < 3).

Brown trout are iteroparous; spawning only occurs during the breeding season each year, but individuals can spawn several times during their life (Belica, 2007). Trout are capable of adapting their reproductive behaviour to external conditions and their own state (e.g., Nelson *et al.*, 1987; Nicola and Almodovar, 2002). The breeding begins in November and ends in late January, exceptionally late February (Huet and Timmermans, 1979; Baglinière and Maisse, 1991). The timing of spawning seems related to photoperiod and water temperature, and varies with

latitude and elevation across their range (Elliott, 1994). Brown trout individuals inhabiting large rivers usually move into first-order tributaries to spawn (Elliott, 1994; Armstrong *et al.*, 2003). Homing to natal rivers is particularly strong in salmonids (Belica, 2007). However, some individuals might decide to not reproduce in their home river, a behaviour called 'straying' (Rieman and Dunham, 2000; Castric and Bernatchez, 2004). Autumn low flows and drought conditions can influence the spawning timing, and trout may congregate at the mouths of tributaries awaiting flow increases to migrate upstream to spawning grounds (Bachman, 1991). Trout usually return to their original territory once reproduction is complete (i.e., post-spawning homing behaviour; Stuart, 1957).

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). Satellite males are smaller, subordinate males unable to defend their territory that may sneak in to spawn with a female, despite the presence of a larger male (Klemetsen *et al.*, 2003; Belica, 2007). Many factors can affect fecundity and egg size in brown trout. Female size, age, and condition are the main variables responsible for the observed variability. For instance, fecundity tends to increase with female size (Fleming, 1996; Belica, 2007). On average, 2 500 eggs per kilogram of female are laid in redds in gravel, and hatch in early spring after an incubation period of about 400 degrees days (2-4 months), depending on water temperature and other hydrological events (Milner *et al.*, 2003; DGRNE, 2004). Then, alevins (i.e., larvae of 15 to 25 mm) remain in the gravel for a short period (4-6 weeks). They emerge as fry, and begin to disperse from the redds (Milner *et al.*, 2003). This phase is characterised by aggressive, territorial behaviour and high mortality rates (Elliott, 1994; Milner *et al.*, 2003).

Between-stream movements are frequent in brown trout, as 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 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 state of the individuals (e.g., age, size, physiology) and hydrological criteria (e.g., water temperature and flow). The migratory behaviour of brown trout might also be under genetic control (Jonsson, 1982; Naslund, 1993). Downstream migration of juveniles occurs mostly in spring, and is sometimes extended until autumn (Huet and Timmermans, 1979; Baglinière *et al.*, 1989). Both water

temperature and flow may influence this timing (Ombredane *et al.*, 1998; Jonsson and Jonsson, 2002; Young *et al.*, 2010). Growth and body size have also been demonstrated to be key factors in the decision to migrate (Cucherousset *et al.*, 2006; Olsson *et al.*, 2006). Fish activity and their need for food increase with temperature, which acts as a stimulus for initiating feeding migrations (Forseth *et al.*, 1999; Jonsson and Jonsson, 2002). Landergren (2004) showed that for high initial fry density, fluctuating or decreasing water depth could initiate the descent of young trout. The migration of young trout to territories offering proper feeding opportunities 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).

The purpose of this Chapter is to explain how the values of the parameters involved in the four main processes of the DemGenTrout individual-based model were determined.

2 Materials and methods

We first give an overview of the equations and methods used to model the survival, growth, spawning and downstream movement processes of the DemGenTrout individual-based model, as well as the parameters linked to these processes (Section 2.1). Then, we present the field data collected on the Lesse River / Chicheron brook system that were used to determine the values of these parameters (Section 2.2). Finally, we explain how these values were estimated with each method (Sections 2.3 to 2.6).

2.1 Main processes of the DemGenTrout model

The survival, growth, spawning and downstream movement processes of the DemGenTrout model are modelled as follows (Table 5.1; see also Chapter 6 for details).

As trout agents challenge their survival, a random number between 0 and 1 is drawn for each individual. If this number is higher than the survival rate corresponding to the trout current age and stream location (*streamX-ageY-survival* parameters), then the individual dies.

If alive, trout first update their length with the VBE. If L_t represents the length of an individual at time t, its length at time $t+1$ is given by:

$L_{t+1} = L_t + k(L_\infty - L_t)$, where k is the growth coefficient (*streamX-parK*) 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 LWR (*streamX-parA* and *streamX-parB*): $W_h = a \times L_{t+1}^b$. Finally, the weight (W) of each trout is computed as its relative condition factor (K_r) multiplied by its healthy weight according to Le Cren's formula (1951): $W = K_r \times W_h$.

Trout then have the possibility to reproduce in each stream during a limited period (*spawn-start* and *spawn-end*). The spawning process includes three steps. First, candidate spawners are identified according to criteria linked to age (*spawn-min-age*), length (*spawn-mean-length* and *spawn-sd-length*), and condition factor (*spawn-mean-cond* and *spawn-sd-cond*). The second step is the movement of candidate spawners from the Lesse River to the Chicheron Brook when flow rates are suitable (*spawn-mean-flow* and *spawn-sd-flow*). The *moved-prop* parameter determines which proportion of individuals born in the brook and in the main river are selected to move upstream. The last step is the reproduction itself. The number of offspring produced by a female depends on its length and follows a linear function $Y = \alpha \times X + \beta$, where α and β are described by four parameters (*offprod-min-length*, *offprod-max-length*, *offprod-min* and *offprodX-max*).

Finally, trout living in the brook have the possibility to move downstream (i.e., to the Lesse River) during a limited period (*move-start* and *move-end*). Trout are candidates for migration if their age (*move-min-age* and *move-max-age*) and length (*move-mean-length* and *move-sd-length*) are adequate. When water temperature and flow rate in the Chicheron Brook are suitable (*move-mean-temperature*, *move-sd-temperature*, *move-mean-flow* and *move-sd-flow*), a random number between 0 and 1 is drawn for each candidate migrant. If this number is higher than the probability of moving downstream, then the individual does not move. The migration probability follows a logistic function described by two parameters (*move-ageZ-varA* and *move-ageZ-varB*): $Y = \exp(A \times X + B)/(1 + \exp(A \times X + B))$.

Table 5.1: The parameters, methods, and data used to model the survival, growth, spawning and downstream movement processes of the DemGenTrout individual-based model.

Process	Parameters (number)	Equation / model	Methods	Type of data
Survival	*streamX-ageY-survival* (7)	Cormack-Jolly-Seber model	Bayesian hierarchical modelling	Electrofishing
Growth	*streamX-parK*, *streamX-max-length* (4)	von Bertalanffy equation	Bayesian hierarchical modelling	Electrofishing
	streamX-parA, *streamX-parB* (4)	Length-weight relationship	Regression methods	Electrofishing
Spawning	*spawn-start*, *spawn-end*, *spawn-min-age*, *moved-prop*, *offprod-min-length*, *offprod-max-length* (6)	-	Direct estimation	Trapping
	offprod-min, *offprodX-max* (3)	Linear equation	Regression methods	Trapping
	spawn-mean-length, *spawn-sd-length*, *spawn-mean-cond*, *spawn-sd-cond*, *spawn-mean-flow*, *spawn-sd-flow* (6)	Statistical distribution	Finite mixture distribution modelling	Trapping, environmental
Movement	*move-start*, *move-end*, *move-min-age*, *move-max-age* (4)	-	Direct estimation	Trapping
	move-ageZ-varA, *move-ageZ-varB* (4)	Density-dependent logistic equation	Regression methods	Trapping, electrofishing
	move-mean-length, *move-sd-length*, *move-mean-temperature*, *move-sd-temperature*, *move-mean-flow*, *move-sd-flow* (6)	Statistical distribution	Finite mixture distribution modelling	Trapping, environmental

streamX = Chicheron Brook (C) or Lesse River (L); *ageY* = age class 0, 1, 2 or ≥ 3; *ageZ* = age class 1 or 2.

2.2 Field data

Different types of data collected on the Lesse River / Chicheron brook system were used to determine the values of the parameters of the DemGenTrout model (i.e., electrofishing, trapping, and environmental data; see also Section D.2 in the Introduction and objectives, page 15).

2.2.1 Electrofishing data

Electrofishing data come from capture-recapture operations conducted in the two streams. Fish were sampled once a year in the Lesse River (in autumn, before the spawning migration of mature adults) and twice a year in the Chicheron Brook (in autumn and in spring, before and after the stay of the adults, respectively). The following data were used to estimate survival, growth and movement parameters (Table 5.1): (i) nine electrofishing occasions in autumn in the Lesse River from 2001 to 2009, (ii) eleven electrofishing occasions in autumn and in spring in the Chicheron Brook from 2004 to 2009. We created different data sets according to birth year, an information obtained in Chapter 4, and length or weight measurements.

First, for estimating trout survival by age class, electrofishing data for both streams were subset by selecting only trout with an assigned birth year. We ended up with the two following data sets: 2364 individuals divided into eight cohorts and electrofished in the Lesse River at nine capture occasions (autumn 2001-2009), 2483 individuals belonging to five cohorts that were electrofished in the Chicheron Brook at six occasions (autumn 2004-2009). The number of individuals by cohort and capture event for each data set is presented in Table 5.2.

Second, for the estimation of the VBE parameter values, we restricted the data to trout for which at least two length measurements were available. We discarded individuals for which the length measurements were not in ascending order year after year. We also decided to remove measurements that implied an annual growth greater than 55 mm for trout of the Lesse River and 35 mm for trout of the Chicheron Brook. We ended up with the two following data sets: 1262 individuals electrofished in the Lesse River at seven occasions (autumn 2003-2009), 739 individuals electrofished in the Chicheron Brook at eleven occasions (autumn and spring 2004-2009). Birth years were used as a priori information in the von Bertalanffy growth models, and were available for 756 and 616 trout in these data sets, respectively.

Third, for the estimation of the LWR parameter values, we used only electrofishing data of trout for which both weight and length were measured at the same time. We ended up with the following two data sets: 4595 individuals electrofished in the Lesse River at five occasions (autumn 2004-2008), 1033 individuals electrofished in the Chicheron Brook at two occasions (autumn 2004-2005).

Table 5.2: Number of trout by cohort and by capture event (C) available in data sets derived from electrofishing data in the Lesse River and the Chicheron Brook. Bolded numbers indicate the capture occasions that were considered to estimate trout survival probabilities.

Data set	**Cohort**	C_1	C_2	C_3	C_4	C_5	C_6	C_7	C_8	C_9
Lesse	2001	2	7	**156**	**153**	**69**	**18**	**10**	1	0
River	2002	-	1	**54**	**169**	**125**	**35**	**14**	8	1
	2003	-	-	0	**68**	**164**	**84**	**42**	**18**	9
	2004	-	-	-	5	**118**	**214**	**169**	**81**	**22**
	2005	-	-	-	-	**19**	**38**	**103**	**108**	**36**
	2006	-	-	-	-	-	7	**53**	**192**	**142**
	2007	-	-	-	-	-	-	**19**	**324**	**277**
	2008	-	-	-	-	-	-	-	**56**	**342**
Chicheron	2004	3	**524**	**25**	**18**	3	0	-	-	-
Brook	2005	-	1	**304**	**58**	**19**	3	-	-	-
	2006	-	-	**31**	**206**	**37**	**11**	-	-	-
	2007	-	-	-	**648**	**247**	**33**	-	-	-
	2008	-	-	-	-	**278**	**303**	-	-	-

2.2.2 Trapping observations

Trapping observations correspond to the census of trout caught at the trapping facility during the years 2004-2009 (Table 5.3). Individuals passing through the upstream trap are all mature adults, swimming from the Lesse River to the Chicheron Brook for reproduction in winter. Individuals caught at the downstream trap (i.e., moving from the brook to the Lesse River) can be either spawners coming back from the brook or young trout migrating from it for the first time. These individuals were discriminated as described in Section 2.1 of Chapter 4. Furthermore, young trout were divided by age class, using information on birth years gained from Chapter 4.

Table 5.3: Annual number of tagged trout ascending or descending the Chicheron Brook (2004-2009).

Year	Upswimming spawners	Downswimming spawners	Downswimming age-1 trout	Downswimming age-2 trout
2004-2005	167	117	519	259
2005-2006	145	36	168	304
2006-2007	216	111	205	187
2007-2008	222	120	1044	217
2008-2009	124	32	813	196

2.2.3 Environmental data

The following time series of collected observations were available for the studied system: water temperatures (°C) in both streams, flow rates ($m^3.s^{-1}$) in the Lesse River, and water heights (m) in the brook. All data were subsequently restricted to the time period from 29 November 2004 to 31 December 2009, and each time series was transformed into a weekly time series using the xts R package (Ryan and Ulrich, 2010), as one time step of the DemGenTrout represents one week.

Water temperatures in both streams were automatically recorded every hour with loggers, from 17 December 2003 to 31 December 2010. Unfortunately, the loggers were stolen twice during this period. Missing data were supplemented with monthly measurements from a nearby station located in Halma (Aquaphyc network, Direction Générale de l'Agriculture, des Ressources Naturelles et de l'Environnement, Service public de Wallonie), and the remaining missing values were replaced by linear interpolation, using the zoo R package (Zeileis and Grothendieck, 2005).

Daily flow rates in the Lesse River were available from 1989 to 2009 from a nearby gauging station located in Daverdisse (Q_D) (Wacondah network, Direction Générale de la Mobilité et des Voies Hydrauliques, Service public de Wallonie). We used the following equation to compute flow rates at the study 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 in 2004-2009 at a rectangular weir located at the Chicheron Brook mouth (Fig. 5.1). 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 com-

munication, 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. As water heights were only recorded on days when the trapping facility was checked, the few missing values of flow rates were replaced by linear interpolation.

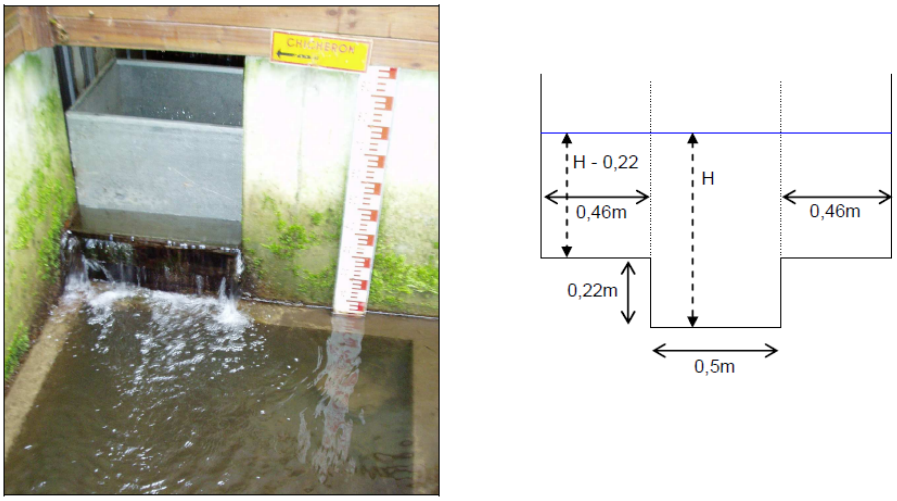

Figure 5.1: Rectangular weir at the Chicheron Brook mouth (left) and detailed section of the weir (right).

2.3 Direct estimation

The values of 10 parameters of the spawning and downstream movement submodels of DemGenTrout were directly determined from trapping observations (see Section 2.2.2).

First, it was assumed in the model that trout can only spawn or move on weeks within a period specified by the *spawn-start* and *spawn-end* parameters or by the *move-start* and *move-end* parameters. Time periods were determined from the study presented in Chapter 2. Value of *moved-prop*, the proportion of trout born in the Lesse River moving to the brook for spawning, was also obtained from this study.

Then, the analysis of age distributions of upswimming and downswimming individuals in Chapter 4 allowed us to find the values of the minimum age at which trout spawn (*spawn-min-age*), and of the minimum and maximum age at which trout move (*move-min-age* and *move-max-age*).

Eventually, we analysed the length distribution of the upswimming spawners, and chose the lower and upper bounds of the 95% confidence interval as values for the *offprod-min-length* and *offprod-max-length* parameters, the minimum and maximum length at which trout spawn. These parameters intervene in the linear equation linking the length of a female and the number of offspring it produces (see Section 2.5).

2.4 Bayesian hierarchical modelling

Theory on Bayesian hierarchical modelling has been presented in Box I, pages 63–66. This technique was applied to capture-recapture electrofishing data to estimate 11 parameters of the DemGenTrout model: (i) the survival rates of trout in both streams, corresponding to the seven *streamX-ageY-survival* parameters (Section 2.4.1), (ii) the values of the VBE parameters intervening in the growth process, corresponding to the four *streamX-parK* and *streamX-max-length* parameters (Section 2.4.2).

In each case, we used the R2WinBUGS R package (Sturtz *et al.*, 2005) to implement the Bayesian models and to check the convergence of the MCMC chains. Only trout with a birth year were used in the first case, while this information was used a priori in the growth models.

2.4.1 Survival

Two CJS models were fitted with Bayesian hierarchical methods to the two electrofishing data sets described in Section 2.2.1, in order to estimate the mean trout survival probabilities in both streams between two autumnal capture occasions. The basic version presented in Box I, page 66, was extended in two ways, the Multi-Group CJS model and an improved version including permanent emigration, described hereafter. We implemented these two extensions by adapting the WinBUGS code provided in Schofield *et al.* (2009).

First, for the Multi-Group CJS model, capture-recapture data were divided by birth year, so that trout survival probability could be estimated by cohort between each consecutive pair of capture occasions. Let $\pi_{i,j}$ be the probability that individual i belongs to the cohort j. A time-constant covariate g_i is included into the basic CJS model, and is modelled by a categorical distribution:

$$g_i \sim Cat(\pi_{i,j} \text{ with } j = 1, 2, ..., c$$

This model was used to estimate apparent survival probabilities for trout of the Lesse River and of the Chicheron Brook. In each case, we used a

burn-in period of 10 000 iterations followed by 10 000 MCMC replicates for posterior summarization, and we obtained a convergence diagnostic $\hat{R} < 1.10$ for all parameters.

Second, the probability of trout to migrate from the Chicheron Brook was integrated into the Multi-Group CJS model, taking advantage of the fact that the brook is fully controlled by the trapping facility. We considered that the trout caught once in the downstream trap but never again in the upstream trap left the brook forever. This information allowed us to estimate the real survival of trout instead of the apparent one. Indeed, the apparent survival φ is a function of mortality and permanent emigration, and is equal to $F_t \times S_t$, where F_t is the probability that an individual in the marked population has not migrated at occasions t and $t+1$, and S_t is the (real) survival probability between these two occasions. Three parameters are thus estimated in this version of the CJS model: $s_{i,t}$ (instead of $\varphi_{i,t}$), $p_{i,t}$ and $f_{i,t}$, the probability that an animal i is available for capture at time $t+1$ given that it was present in the study area at time t. The binary random variable $F_{i,t}$ is used, taking values 1 if individual i is available for capture at time t and 0 otherwise. The distribution of the variable $F_{i,t+1}$ conditional on the variable $F_{i,t}$ is given by the equation:

$$F_{i,t+1}|F_{i,t} \sim Bernoulli(A_{i,t}\ f_{i,t}) \text{ for } t \geq e_i, \text{ with } f_{i,e_i} = 1$$

The distribution of the variable $A_{i,t+1}$ conditional on the variable $A_{i,t}$ is given by:

$$A_{i,t+1}|A_{i,t} \sim Bernoulli(A_{i,t}\ s_{i,t}) \text{ for } t \geq e_i, \text{ with } p_{i,e_i} = 1$$

The distribution of the variable $X_{i,t}$ conditional on the variable $A_{i,t}$ is modified as:

$$X_{i,t}|A_{i,t} \sim Bernoulli(A_{i,t}\ f_{i,t}\ p_{i,t}) \text{ for } t \geq e_i, \text{ with } f_{i,e_i} = 1 \text{ and } p_{i,e_i} = 1$$

This model including permanent emigration was used to estimate real survival probabilities for trout of the Chicheron Brook. We used 10 000 burn-in iterations followed by 20 000 replicates for posterior summarization ($\hat{R} < 1.02$ for all parameters). Real survival estimates were then compared with the previously obtained apparent estimates in order to quantify the discrepancy between them, and we used this latter to correct the survival rates obtained for trout of the Lesse River.

2.4.2 Growth

In Bayesian hierarchical models, each individual is assumed to grow according to its own von Bertalanffy curve (Zhang *et al.*, 2009). Both k

(*streamX-parK*) and L_∞ (*streamX-max-length*) parameters are modelled to be of random effect, i.e., individual variation is incorporated in both parameters. The expected length of individual i at tagging is calculated as: $\hat{L}_{i,0} = L_{\infty,i}\ (1 - e^{-k_i A_i})$, where A_i is the relative age at tagging for individual i (i.e., the age at tagging for individual i, t_i, minus the theoretical age at which the trout length is zero, t_0). It is assumed that $L_{\infty,i}$, k_i and A_i are independent of each other. Hierarchical models are also based on the idea of exchangeability of parameters: it is mathematically equivalent to assume that they come at random from some population distribution (Zhang *et al.*, 2009). Here, $L_{\infty,i}$ and k_i are assumed to be exchangeable and to come from Normal distributions: $L_{\infty,i} \sim N(U_\infty, \sigma^2_\infty)$ and $k_i \sim N(U_k, \sigma^2_k)$, where the hyperparameters U_∞ and U_k are the population mean values for L_∞ and k, respectively. The associated variances, σ^2_∞ and σ^2_k, are the between-individual variances in L_∞ and k, respectively.

We assumed that the values of the VBE parameters were different for the two streams, and Bayesian models were thus applied to the two electrofishing data sets described in Section 2.2.1. For the Lesse River data set, we used a burn-in period of 15 000 iterations followed by 15 000 MCMC replicates for posterior summarization. For the Chicheron Brook data set, we set a burn-in period of 5 000 iterations, and estimations were based on the 5 000 subsequent MCMC replicates. In each case, $\hat{R}$ was $<$ 1.02 for all parameters. The relative age at tagging A_i of each individual for which a birth year was available was deduced from its date of first capture, with birth month and day arbitrarily set to January 1. Indeed, eggs laid by brown trout during autumn and winter (i.e., from November to January) hatch after an incubation period of about 2-3 months, i.e., from January to April. The expected length of individual i at the j^{th} recapture was then calculated as: $\hat{L}_{i,j} = L_{\infty,i}\ (1 - e^{-k_i(A_i+R_{i,j})})$, where $R_{i,j}$ is the time (in years) between tagging and the j^{th} recapture for individual i.

In order to draw the von Bertalanffy growth curves and compare them to literature results, we computed for each individual i the theoretical age at which its length was zero (parameter t_0) as the truncated age at tagging t_i minus the relative age as tagging A_i. Finally, the equation of the growth curve was given by: $L_i = L_{\infty,i}\ (1 - e^{-k_i t_0})$.

2.5 Regression methods

Regression methods were applied to parameterize the growth, spawning and downstream movement processes of the DemGenTrout model, using

either electrofishing or trapping data, or both. Eleven parameters were estimated: (i) the LWR parameters, *streamX-parA* and *streamX-parB*, by regression of trout weight *vs* length, (ii) the *offprod-min*, *offprodC-max* and *offprodL-max* parameters, by regression of the number of produced offspring *vs* female length, (iii) the *move-ageY-varA* and *move-ageY-varB* parameters, by regression of the probability for young trout of moving downstream *vs* abundance in the Chicheron Brook.

2.5.1 Growth

We proceeded in two steps to estimate parameters a and b of the LWR, corresponding to the *streamX-parA* and *streamX-parB* parameters of DemGenTrout. They were assumed to vary among streams, and we used the two electrofishing data sets described in Section 2.2.1.

In step 1, individuals in good condition were identified in the two data sets, using the method presented in the inSTREAM software (Railsback *et al.*, 2009). The Fulton's condition factor (corresponding to parameter a of the LWR) was computed for each trout, as 100 000 times the weight (g) divided by the length (mm) cubed, i.e., with b considered isometric. Trout in the top third of all values were selected and considered in good condition. This method forces the fish to maintain a standard relation between length and weight during periods of positive growth (Railsback *et al.*, 2009).

In step 2, weight (W) and length (L) measurements of the selected individuals were analysed. Values of a and b parameters were estimated for each stream by linear regression of the transformed equation:

$$\log(W) \quad = \log(a) + b \log(L)$$

We reiterated the regression for length measured in centimetres instead of millimetres, in order to compare them to results found in brown trout literature.

2.5.2 Spawning

In DemGenTrout, the number of offspring produced per female in each stream depends on its length and follows a linear function, with a slope α equal to $(F_2 - F_1)/(L_+ - L_-)$ and an intercept β given by $F_1 - \alpha \times L_-$. L_- and L_+ correspond to the *offprod-min-length* and *offprod-max-length* parameters, and their values were derived from direct observations at the trapping facility (see Section 2.3). Values of α and β were obtained by

linear regression of produced offspring *vs* female length, and were then used to derive the values of F_1 and F_2, the minimum and maximum number of produced offspring. F_1 was assumed identical for both streams (*offprod-min* parameter), while F_2 varied among streams (*offprodX-max* parameters).

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). Eggs were obtained by stripping, and the mean number of eggs by female was roughly estimated equal to 100, 220, 320, 400 for an average length of 165, 215, 255, and 290 mm, respectively. These numbers of eggs were translated into numbers of fry, by assuming that only 10% of the eggs survived to the next stage (Baglinière and Maisse, 1991; Elliott, 1994). The females were caught in the upstream trap and were thus on their way to reproduce in the Chicheron Brook. Consequently, the regression on these data allowed us to estimate *offprodC-max* only. The value of *offprodL-max* was set as *offprodC-max* / 4, as we assumed that fecundity of spawners in the Chicheron Brook was four times higher than in the Lesse River, as found in Huet and Timmermans (1979) (i.e., 24 eggs by m^2 in the brook *vs* 6 eggs by m^2 in the main river).

2.5.3 Downstream movement

Migration rates of juveniles between the Chicheron Brook and the Lesse River were computed each year as the ratio of descending fish of age 1 or 2 over the estimated abundance of trout in the brook during this period. Annual abundances were computed by summing (i) the number of downswimming individuals of age 1 and 2 observed in spring and summer, (ii) the estimated population size in the brook in autumn of the same year. (i) was derived from trapping data (Section 2.2.2), while (ii) was obtained by fitting JS models to electrofishing data of the Chicheron Brook (Section 2.2.1), using the POPAN formulation in program MARK (White and Burnham, 1999). A regression between the probability of moving downstream and trout abundance in the Chicheron Brook was then performed. A logistic function was fitted to the data, using the migration rate P as a response variable and the cohort size X as the explanatory variable: $P = \exp(A \times X + B)/(1 + \exp(A \times X + B))$, where A and B correspond to the two sets of parameters *move-age1-varA* and *move-age2-varA*, and *move-age1-varB* and *move-age2-varB*, respectively. The process was modelled by a logistic function to allow for the consideration of a linear or an exponential relation. Indeed, a logistic

function approximates a linear model when $A = 0$, and an exponential model when $B = 0$.

2.6 Finite mixture distribution modelling

In the DemGenTrout model, criteria used to identify trout born in the brook as candidates for spawning or migration and to restrict movements were described by statistical distributions. Finite mixture distribution modelling methods were used to fit normal and log-normal distributions to field data (see Box II, pages 109–110).

First, length distributions of spawners and migrants (*spawn-mean-length*, *spawn-sd-length*, *move-mean-length* and *move-sd-length*), and condition factor distribution of spawners (*spawn-mean-cond* and *spawn-sd-cond*) were derived from observations at the trapping facility. Second, water temperature distribution for movement (*move-mean-temperature* and *move-sd-temperature*), and flow distributions for spawning and movement (*spawn-mean-flow*, *spawn-sd-flow*, *move-mean-flow* and *move-sd-flow*) were determined by combining observations at the trapping facility and hydrological data.

3 Results

Estimated values of survival, growth, spawning and downstream movement parameters of the DemGenTrout model are synthesised in Table 5.4.

Table 5.4: Survival, movement, growth and spawning parameter values as used in the DemGenTrout individual-based model. Juveniles are trout of age 1 and 2.

Parameter name	Description	Value	Unit
Survival			
streamC-age0-survival	Survival rate for trout of age 0 in stream C	0.39	$year^{-1}$
streamC-age1-survival	Survival rate for trout of age 1 in stream C	0.37	$year^{-1}$
streamC-age2-survival	Survival rate for trout of age 2 in stream C	0.85	$year^{-1}$
streamL-age0-survival	Survival rate for trout of age 0 in stream L	0.38	$year^{-1}$
streamL-age1-survival	Survival rate for trout of age 1 in stream L	0.74	$year^{-1}$
streamL-age2-survival	Survival rate for trout of age 2 in stream L	0.87	$year^{-1}$
streamL-age3-survival	Survival rate for trout of ages 3 to 6 in L	0.69	$year^{-1}$
Growth			
streamC-parK	von Bertalanffy growth coefficient for trout in stream C	0.012	$week^{-1}$
streamL-parK	von Bertalanffy growth coefficient for trout in stream L	0.011	$week^{-1}$

Table 5.4: Survival, movement, growth and spawning parameter values as used in the DemGenTrout individual-based model (continued).

Parameter name	Description	Value	Unit
streamC-max-length	Asymptotic length for trout in stream C	179.80	mm
streamL-max-length	Asymptotic length for trout in stream L	267.00	mm
streamC-parA	Parameter a of the LWR for trout in C	14×10^{-6}	-
streamL-parA	Parameter a of the LWR for trout in L	13×10^{-6}	-
streamC-parB	Parameter b of the LWR for trout in C	2.95	-
streamL-parB	Parameter b of the LWR for trout in L	2.96	-
Spawning			
spawn-start	Start of the spawning period	6	week
spawn-end	End of the spawning period	17	week
spawn-min-age	Minimum age at which trout spawn	3	year
spawn-mean-length	Mean of the normal distribution for length of spawners	222.90	mm
spawn-sd-length	Std dev. of the normal distribution for length of spawners	33.82	mm
spawn-mean-cond	Mean of the normal distribution for condition factor of spawners	0.936	-
spawn-sd-cond	Std dev. of the normal distribution for condition factor of spawners	0.108	-
moved-prop	Proportion of trout born in stream L moving to stream C for spawning	0.45	-
spawn-mean-flow	Mean of the log-normal distribution for flow rate in stream L	6.85	$m^3.s^{-1}$
spawn-sd-flow	Std dev. of the log-normal distribution for flow rate in stream L	5.15	$m^3.s^{-1}$
offprod-min-length	Minimum length at which trout spawn in both streams	120.00	mm
offprod-max-length	Maximum length at which trout spawn in both streams	388.00	mm
offprod-min	Minimum number of offspring produced in both streams	0	-
offprodC-max	Maximum number of offspring produced in stream C	64	-
offprodL-max	Maximum number of offspring produced in stream L	16	-
Movement			
move-start	Start of the migration period for juveniles	23	week
move-end	End of the migration period for juveniles	48	week
move-min-age	Minimum age at which trout of stream C move downstream	1	year
move-max-age	Maximum age at which trout of stream C move downstream	2	year
move-mean-length	Mean of the normal distribution for length of juveniles	88.49	mm
move-sd-length	Std dev. of the normal distribution for length of juveniles	20.98	mm
move-age1-varA	Variable A of the logistic function for the probability of moving for age-1 juveniles	0.0005	-

Table 5.4: Survival, movement, growth and spawning parameter values as used in the DemGenTrout individual-based model (continued).

Parameter name	Description	Value	Unit
move-age1-varB	Variable B of the logistic function for the probability of moving for age-1 juveniles	-2.25	-
move-age2-varA	Variable A of the logistic function for the probability of moving for age-2 juveniles	-0.0010	-
move-age2-varB	Variable B of the logistic function for the probability of moving for age-2 juveniles	0.10	-
move-mean-temperature	Mean of the normal distribution for water temperature in stream C	9.72	°C
move-sd-temperature	Std dev. of the normal distribution for water temperature in stream C	3.72	°C
move-mean-flow	Mean of the log-normal distribution for flow rate in stream C	0.040	$m^3.s^{-1}$
move-sd-flow	Std dev. of the log-normal distribution for flow rate in stream C	0.038	$m^3.s^{-1}$

C, Chicheron Brook; L, Lesse River.

3.1 Survival parameters

Trout survival rates were estimated by age class with two modified versions of the CJS model by applying Bayesian hierarchical modelling methods. First, the Multi-Group CJS model was fitted to electrofishing data sets for the Lesse River and the Chicheron Brook to estimate apparent survival probabilities for trout in both streams. Then, the Multi-Group CJS model including permanent emigration was fitted to the Chicheron Brook data set alone in order to estimate real survival probabilities in the brook. These latter probabilities were compared with the apparent ones in order to quantify the discrepancy between them, and adjust the survival rates obtained for trout of the Lesse River.

As high standard deviations were found for some survival probabilities estimated by the models, we performed an analysis of variance. We found that the size of the 95% confidence intervals was related to the quantity of data used by the software, and more particularly to the number of recaptured trout (i.e., the lower the quantity, the higher the variability and the larger the confidence interval). We consequently decided to not consider the following results estimated with high standard deviations:

- Estimates between the two last capture occasions (i.e., $\varphi[\ ,8]$, $\varphi[\ ,5]$ or $S[\ ,5]$), because the last survival probability and the last recapture probability cannot be separately estimated[1];

[1] This is a particular property of the CJS model, which is parameter redundant, as explained in Gimenez *et al.* (2003).

- Estimates for which a lack of data was observed at the corresponding capture occasions (i.e., observations on less than 10 individuals; see Table 5.2 in Section 2.2.1).

Apparent survival probabilities estimated by the Multi-Group CJS model for trout of the Lesse River were averaged by age class (Fig. 5.2). With the Multi-Group CJS model including permanent emigration, we estimated that migration probabilities from the Chicheron Brook were around 0.50 for trout between the age of 1 and 2, and lower for older individuals (0.18) (data not shown). Real survival probabilities for trout of the brook found with this model were also averaged by age class (Fig. 5.3). As expected, real survival probabilities were on average 35% greater than the apparent ones (0.55 *vs* 0.37). Assuming an identical level of migration in both streams, we corrected the survival rates obtained for the trout of the Lesse River by multiplying each value by 1.35.

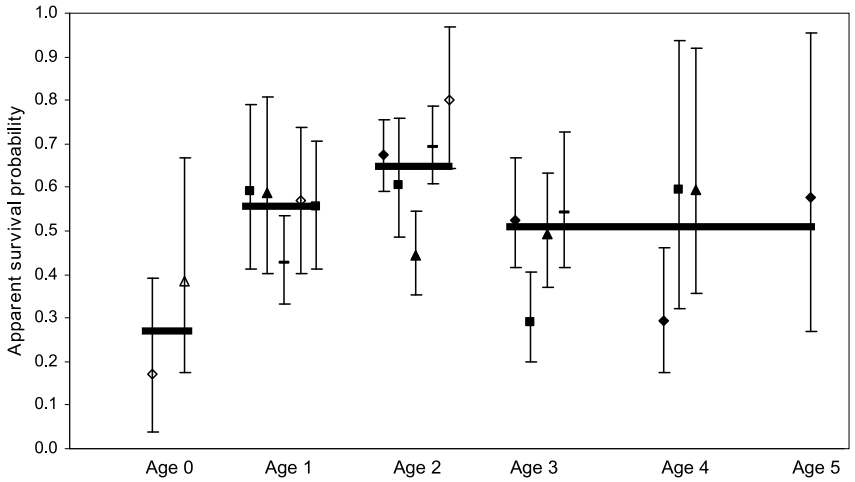

Figure 5.2: Trout apparent survival probabilities in the Lesse River, and their corresponding 95% confidence intervals by cohort (2001: solid diamond; 2002: solid square; 2003: solid triangle; 2004: negative sign; 2005: open diamond; 2006: open square; 2007: open triangle) and age, as estimated by the Multi-Group CJS model. Mean apparent survival rates represented by thick horizontal bars (age 0: 0.28, age 1: 0.55, age 2: 0.64, age $\geq$ 3: 0.51) were corrected (values were increased by 35%, see Table 5.4) and used as real survival rates in the DemGenTrout model.

Survival rates were used in the DemGenTrout model to draw annual probability density functions (Fig. 5.4). Three sources of mortality were integrated into the density functions: 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

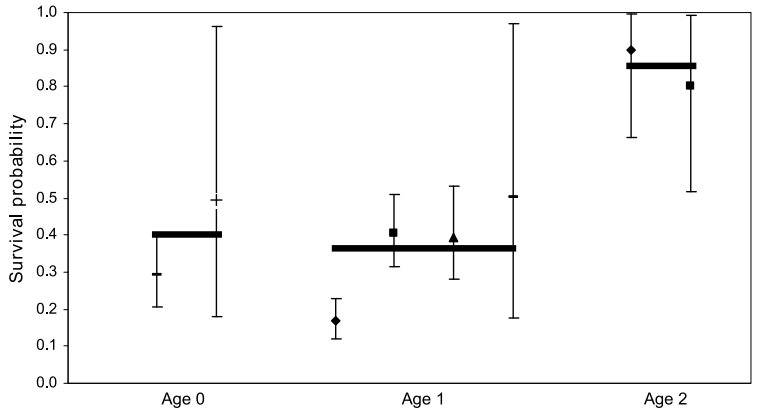

Figure 5.3: Trout survival probabilities in the Chicheron Brook, and their corresponding 95% confidence intervals by cohort (2004: solid diamond; 2005: solid square; 2006: solid triangle; 2007: negative sign; 2008: positive sign) and age, as estimated by the Multi-Group CJS model including permanent emigration. Mean survival rates used in the DemGenTrout individual-based model are represented by thick horizontal bars (see values in Table 5.4).

autumn for trout of age ≥ 2. Values of each probability density functions, corresponding to the *streamX-ageY-survival* parameters, were annual and were transformed into weekly values to account for the weekly time step in the model (i.e., survival rates exponent $1/52$).

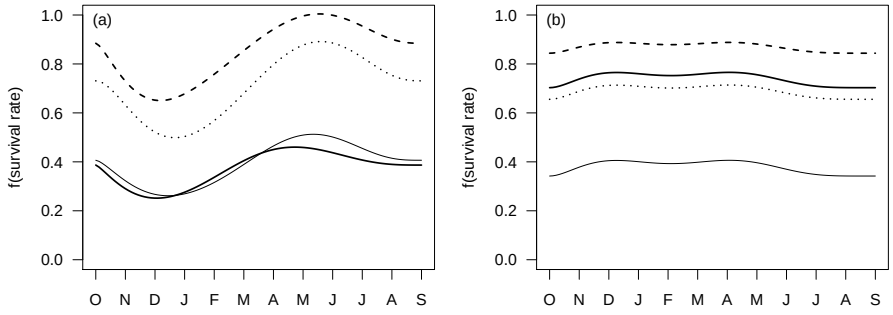

Figure 5.4: Annual probability density functions for trout survival rates (a: Chicheron Brook, b: Lesse River), from October (O) to September (S) and for trout of age 0 (thin solid line), age 1 (thick solid line), age 2 (dashed line), and age ≥ 3 (dotted line). Survival rates at a given week correspond to the *streamX-ageY-survival* parameters of the DemGenTrout individual-based model.

3.2 Growth parameters

The values of the VBE parameters for trout population of both streams were estimated with Bayesian hierarchical growth models. For the Lesse River, estimates were equal to 0.55 year^{-1} (95% CI: [0.53;0.57]) for k, the growth coefficient, and to 267.0 mm (95% CI: [262.1; 271.7]) for L_∞, the asymptotic length. For the Chicheron Brook, the values were 0.61 year^{-1} (95% CI: [0.58;0.65]) for k and 179.8 mm (95% CI: [172.8;185.7]) for L_∞. For parameter t_0, we found a mean of -0.70 years for all trout of the Lesse River, and -0.66 years in the case of the Chicheron Brook. The corresponding von Bertalanffy growth curves for trout of the two streams are shown in Fig. 5.5. The estimated parameters k and L_∞ correspond to the *streamX-parK* and *streamX-max-length* parameters of the DemGenTrout model, respectively. As the growth coefficients k were expressed in year^{-1}, each *streamX-parK* parameter was converted in week^{-1} to match the weekly time step in DemGenTrout.

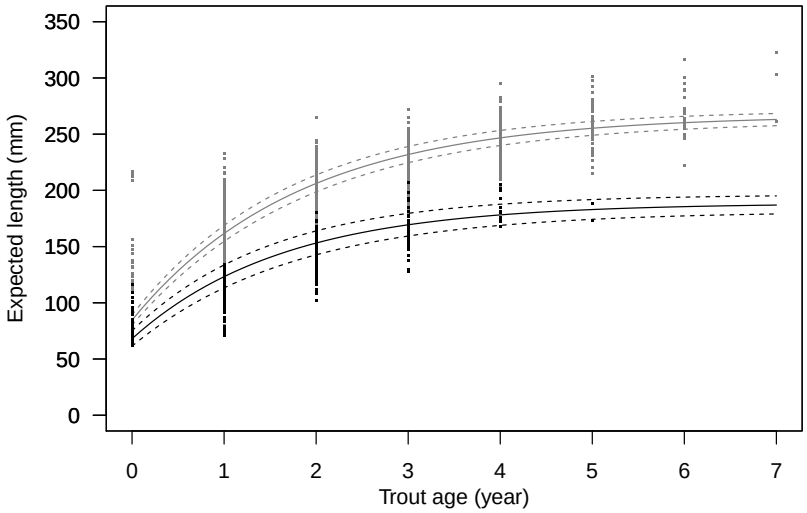

Figure 5.5: von Bertalanffy growth curves for trout of the Lesse River (grey) and the Chicheron Brook (black), and their corresponding 95% confidence intervals (dashed lines). The growth coefficient and the asymptotic length of the equation correspond to the *streamX-parK* and *streamX-max-length* parameters of the DemGenTrout individual-based model.

Parameters a and b of the LWR were estimated by a log-log regression of weight *vs* length for 1532 individuals in good condition in the Lesse River, and for 345 individuals in the Chicheron Brook (Fig. 5.6). In the case of the Lesse River, obtained values were 13.4×10^{-6} (95% CI: $[12.7\times10^{-6};14.1\times10^{-6}]$) for a and 2.96 (95% CI: [2.95;2.97]) for b. For

the Chicheron Brook, the values were 14.3×10^{-6} (95% CI: [12.1×10^{-6}; 16.8×10^{-6}]) and 2.95 (95% CI: [2.91;2.98]), respectively. When the log-log regression was performed with length expressed in centimeters, values of parameter a were found to equal 0.0122 for the Lesse River and 0.0127 for the Chicheron Brook. Values remained identical for parameter b. The estimated parameters a and b correspond to the *streamX-parA* and *streamX-parB* parameters of the DemGenTrout model, respectively.

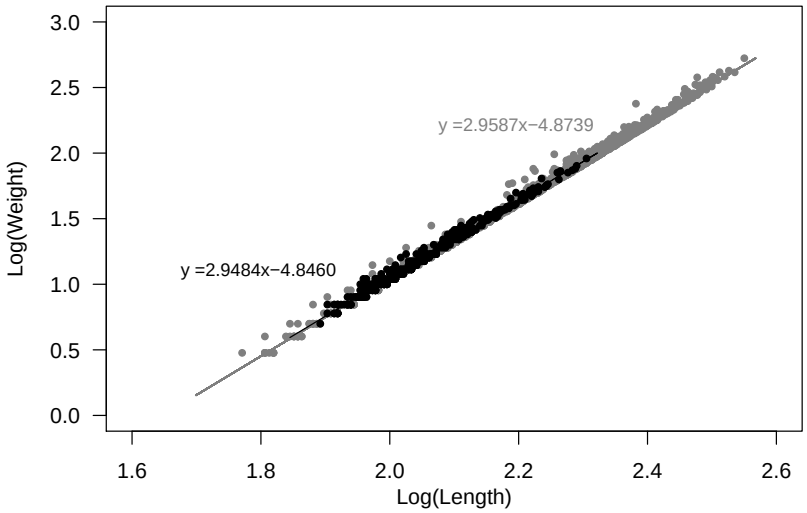

Figure 5.6: Log-log regression of weight *vs* length for the trout of the Chicheron Brook and the Lesse River performed to estimate the *streamX-parA* and *streamX-parB* parameters of the DemGenTrout individual-based model ($R^2 = 0.99$ for both regressions). 95% confidence intervals were too narrow to be displayed.

3.3 Spawning parameters

The spawning process of the DemGenTrout model was parameterized by applying three different methods: direct estimation, regression, and finite mixture distribution modelling.

From the analysis of trapping observations conducted in Chapter 2 (see Section 3.2, page 79), we set the values of the *spawn-start* and *spawn-end* parameters limiting the spawning period to week 6 (beginning of November) and week 17 (end of January), respectively. The study also highlighted that 55% of the ascending individuals performed natal homing (see Section 4 of Chapter 2, page 91), and the value of *moved-prop* parameter was set to 0.45 (i.e., 1 - 0.55). The age distribution analysis of Chapter 4 revealed that reproducing trout were at least 3

years old (*spawn-min-age* parameter) (see Section 3.6, page 130). From the length distribution of upswimming spawners (Fig 5.7), we found that the minimum and maximum length at which trout move to spawn was equal to 120 and 388 mm, respectively (*offprod-min-length* and *offprod-max-length* parameters).

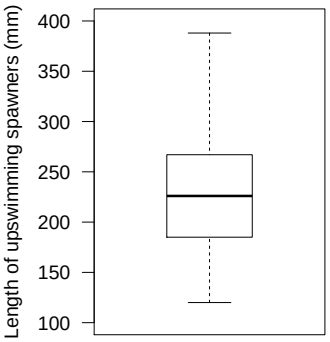

Figure 5.7: Length distribution of mature brown trout caught at the upstream trap when moving from the Lesse River to the Chicheron Brook for reproduction (2004-2009). The 2.5 (lower bound of the 95% confidence interval), 25 (lower quartile), 50 (median), 75 (upper quartile), 97.5 (upper bound of the 95% confidence interval) percentiles are displayed. Parameters *offprod-min-length* and *offprod-max-length* of the DemGenTrout individual-based model were set to the lower and upper bounds.

The slope α and the intercept β of the linear function describing the number of offspring produced per week by a female according to its length were estimated by regression on field data. Values of α and β were found to equal 0.24 and -29.75, respectively (Fig. 5.8). Parameters *offprod-min* and *offprodC-max* of DemGenTrout were computed as $\alpha \times L_- + \beta$ = -0.82 and $\alpha \times L_+ + \beta$ = 63.79, respectively (where L_+ and L_- correspond to parameters *offprod-min-length* and *offprod-max-length*). The two values were rounded to 0 and 64, respectively. Value of the *offprodL-max* parameter was set to 16 (i.e., four times lower than *offprodC-max*).

Parameters of the statistical distributions that identify trout as candidates for spawning, or restrict the upstream movement of spawners were estimated by finite mixture distribution modelling methods. The length of spawners was best described by a normal distribution (Fig. 5.9(a)), and parameters *spawn-mean-length* and *spawn-sd-length* were set to values found for the mean and standard deviation of this distribution (i.e., 222.90 and 33.82 mm, respectively). We proceeded the same way for the condition factor of spawners, which also followed a

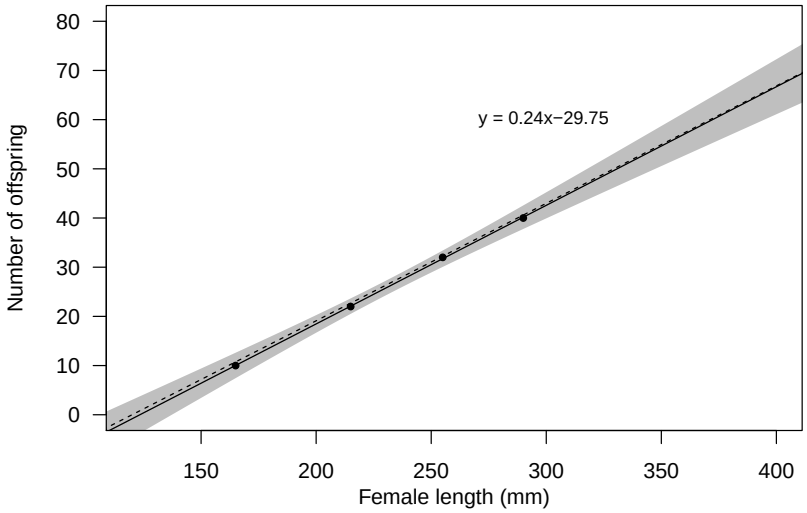

Figure 5.8: Linear regression of produced offspring *vs* female length in the Chicheron Brook, with 95% confidence intervals ($R^2 = 0.99$). The dashed regression line was obtained with parameter values of *offprod-min* and *offprodC-max* of the DemGenTrout individual-based model set to 0 and 64, respectively.

normal distribution (Fig. 5.9(b)), and the values of *spawn-mean-cond*, *spawn-sd-cond* were set to 0.936 and 0.108, respectively. The flow rates in the Lesse River at which spawning movements of trout can occur were specified by a log-normal distribution of mean and standard deviation equal to 6.85 and 5.15 $m^3.s^{-1}$, respectively (*spawn-mean-flow* and *spawn-sd-flow* parameters) (Fig. 5.9(c)).

3.4 Downstream movement parameters

The downstream movement process of the DemGenTrout model was parameterized by applying three different methods: direct estimation, regression, and finite mixture distribution modelling.

From the analysis of trapping observations conducted in Chapter 2 (see Section 3.2, page 79), we set the values of the *move-start* and *move-end* parameters limiting the migration period of young trout to week 23 (beginning of Mach) and week 48 (end of August), respectively. The age distribution analysis of Chapter 4 revealed that most of them migrated to the Lesse River when they were 1 or 2 years old (*move-min-age* and *move-max-age* parameters) (see Section 3.6, page 130).

Variables A and B of the function describing the downstream movement of juveniles were estimated by logistic regression on field data.

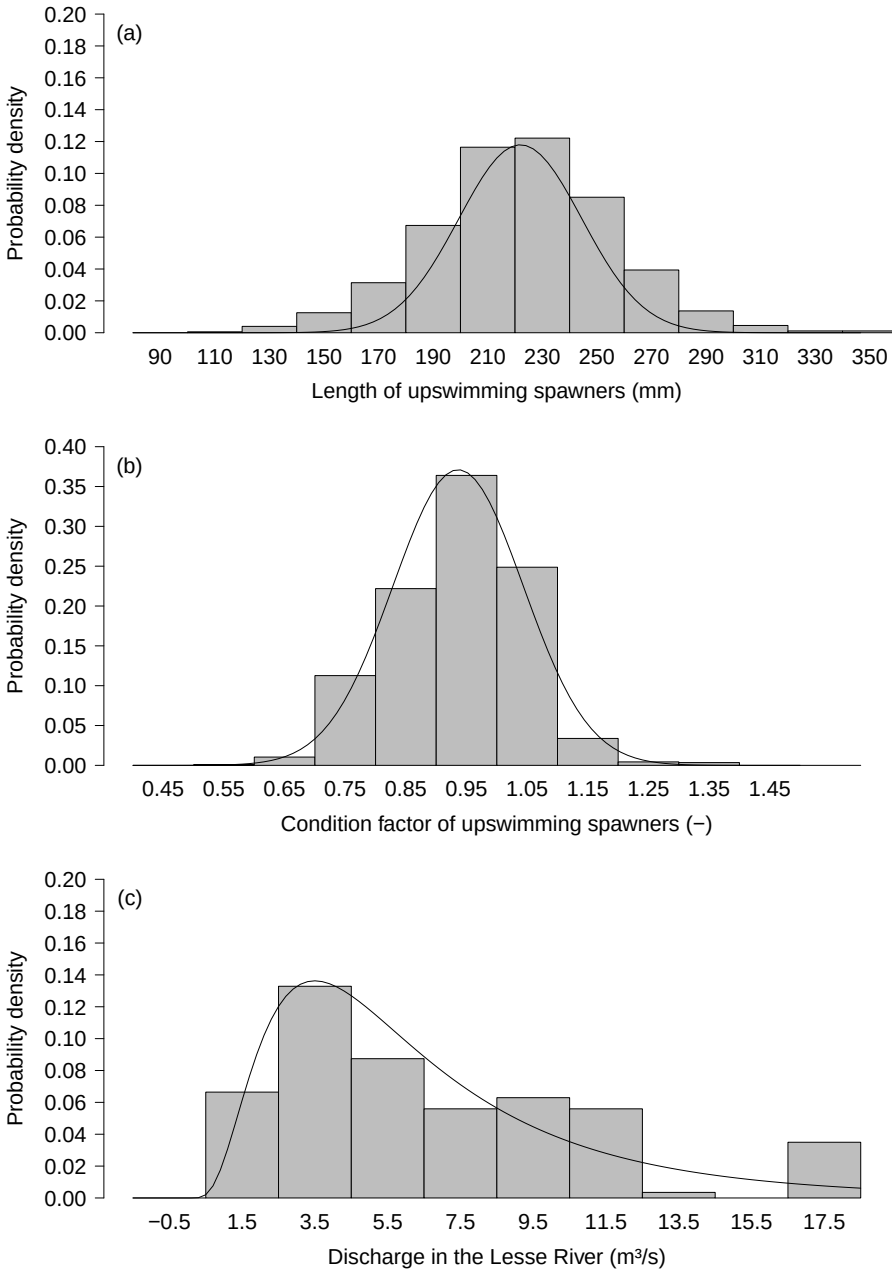

Figure 5.9: Normal distributions of (a) length and (b) condition factor for spawners, derived from trapping data (2004-2009), and log-normal distribution of (c) flow rate in the Lesse River, derived from trapping and environmental data (2004-2009). Parameters *spawn-mean-length*, *spawn-mean-cond*, *spawn-mean-flow* and *spawn-sd-length*, *spawn-sd-cond*, *spawn-sd-flow* of the DemGenTrout individual-based model were set to the corresponding means and standard deviations found for the fitted distributions.

These variables are age-specific and correspond to the *move-age1-varA*, *move-age1-varB*, *move-age2-varA*, and *move-age2-varB* parameters of the DemGenTrout model. Their values were found to equal 0.0005 and -2.25 for age-1 juveniles, and -0.0010 and 0.10 for age-2 juveniles, respectively (Fig. 5.10). The probability of moving downstream for age-1 trout increased with density, while an inverse relationship was observed for age-2 trout. The trend is almost linear in the first case (A close to 0) and exponential in the second case (B close to 0).

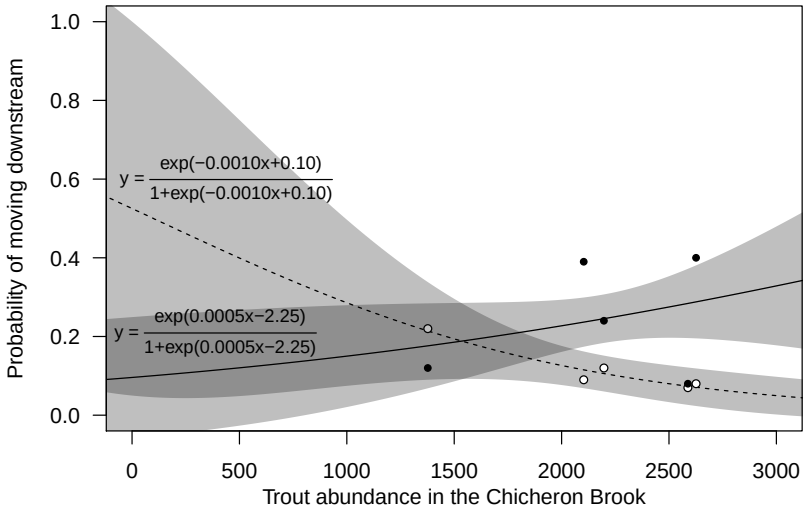

Figure 5.10: Logistic regression of the probability of moving downstream for trout of age 1 (solid line, solid circles) and age 2 (dashed line, open circles) *vs* trout abundance in the Chicheron Brook performed to estimate the *move-ageZ-varA* and *move-ageZ-varB* parameters of the DemGenTrout individual-based model. Corresponding 95% confidence intervals are also displayed.

Parameters of the statistical distributions that identify candidates for migration, or restrict movements of juveniles were estimated by finite mixture distribution modelling methods. The length of migrants was described by a normal distribution (Fig. 5.11(a)), and parameters *move-mean-length* and *move-sd-length* were set to values found for the mean and standard deviation of this distribution (i.e., 88.49 and 20.98 mm, respectively). The water temperature and flow ranges in the Chicheron Brook at which movements of juveniles can occur were specified by (i) a normal distribution of mean and standard deviation equal to 9.72 and 3.72°C, respectively (*move-mean-temperature* and *move-sd-temperature* parameters) (Fig. 5.11(b)), (ii) a log-normal distribution of mean and

standard deviation equal to 0.040 and 0.038 $m^3.s^{-1}$, respectively (*move-mean-flow* and *move-sd-flow* parameters) (Fig. 5.11(c)).

4 Discussion

Using data for brown trout of the Lesse River / Chicheron Brook hydrological system, different methods were applied to parameterize the survival, growth, spawning and downstream movement processes of the DemGenTrout individual-based model. As the objective of DemGenTrout did not justify a detailed representation of each of these processes, the modelling choices were as simple as possible to force the model to reproduce general behaviours observed for real trout. We used simple methods such as direct estimation or regression, as well as more sophisticated ones like Bayesian hierarchical and finite mixture distribution modelling, to determine parameter values. The common thread that links all the methods of this chapter is that they all involved somehow the use of R, and thus its power of making code reproducible. However, alternative methods were explored. For instance, length increments were used for estimating growth parameters of the VBE (see below).

Life expectancy of a brown trout is 5 to 6 years (DGRNE, 2004). On average, trout survival was found to be slightly higher in the main river than in the brook (0.67 *vs* 0.58). In the Chicheron Brook, we observed that survival rates for trout of age 0 and 1 (values around 0.40) were lower than the rate estimated for age-2 trout (0.85). This might be due to the cannibalism behaviour of spawners on fry and juveniles of age 1 during their stay in the brook (Vik *et al.*, 2001). In both streams, estimated survival rates for trout of age ≥ 2 are high with values ≥ 0.70. Variation between survival rates can be explained by differences in food availability, habitat quality, and other environmental factors, combined with probable bias due to sampling.

In the DemGenTrout model, growth of trout is modelled with the equation of von Bertalanffy (1957) and the length-weight relationship of Le Cren (1951). From Fig. 5.5, trout growth in the Lesse River seems higher than in the Chicheron Brook. This result is in agreement with the fact that brown trout use main stems to grow and mature (Baglinière *et al.*, 1987; Jonsson and Jonsson, 1993; Forseth *et al.*, 1999). The VBE parameters obtained for both streams of the Lesse River network are in a similar range as others studies (Fig. 5.12). In the curve obtained for the Chicheron Brook, L_∞ is approached faster than in any other curve, and this is probably due to the lack of available data for individuals of age

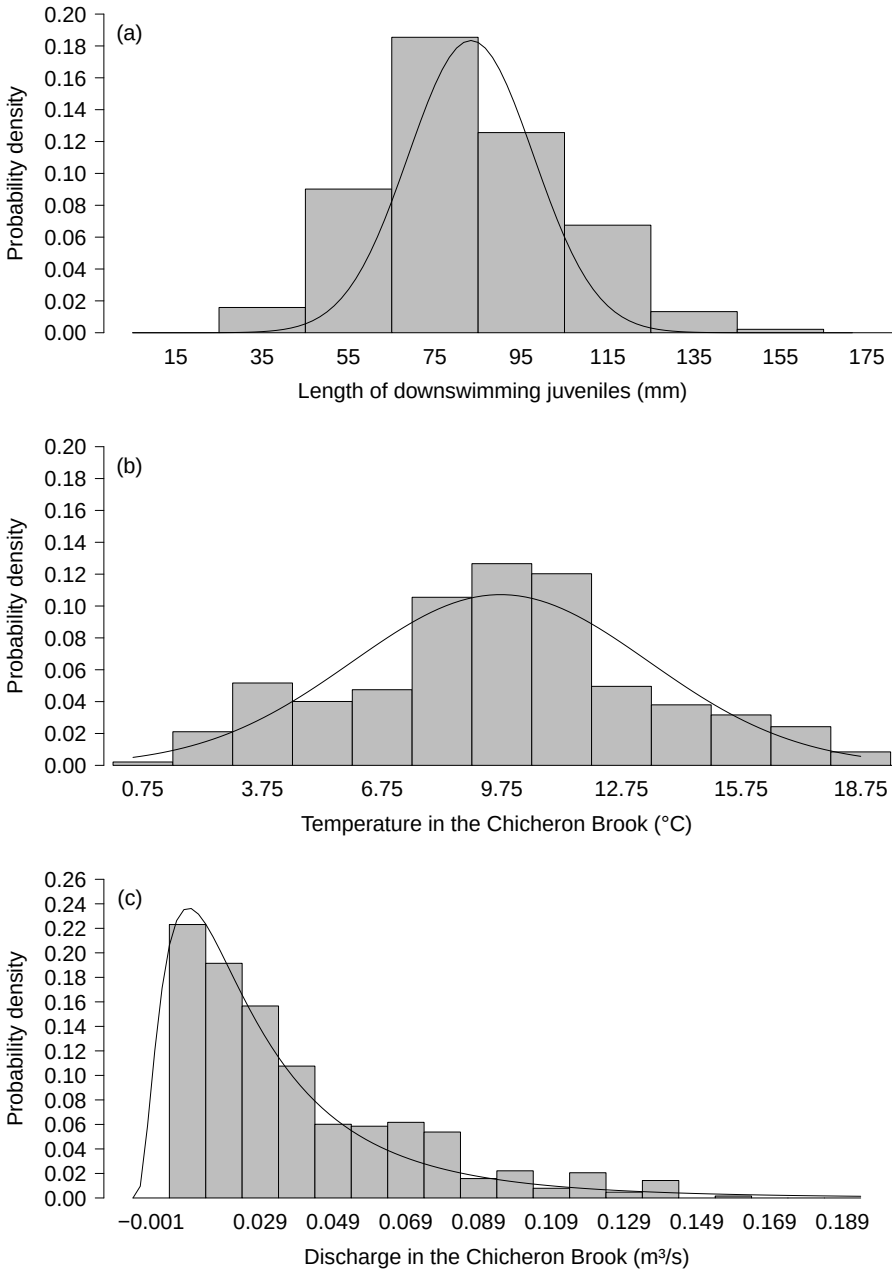

Figure 5.11: Normal distribution of (a) length for juveniles, derived from trapping data (2004-2009), and normal and log-normal distributions of (b) water temperature and (c) flow rate in the Chicheron Brook, derived from trapping and environmental data (2004-2009). Parameters *move-mean-length*, *move-mean-temp*, *move-mean-flow* and *move-sd-length*, *move-sd-temp*, *move-sd-flow* of the DemGenTrout individual-based model were set to the corresponding means and standard deviations found for the fitted distributions.

> 2. We used Bayesian hierarchical models to estimate the VBE parameters, but methods of Munro, Fabens and Appeldoorn implemented in FiSAT (FAO-ICLARM Stock Assessment Tool) (Gayanilo *et al.*, 1995) as well as an iterative approach of the Von Bertalanffy model involving a linear regression (VONBIT software; Stamatopoulos and Caddy, 2005) were also tested. Obtained results showed a high variation difficult to explain: k varied from 0.22 to 0.72 year^{-1}, and L_∞ from 251 to 371 mm for the Lesse River; k varied from 0.21 to 1.07 year^{-1}, and L_∞ from 142 to 206 mm for the Chicheron Brook.

From the results in Fig. 5.6, we see that the LWR parameters a and b do not vary much between both streams, and this is in contradiction with our initial assumption. We also observed that data are more dispersed in the case of the Lesse River. In each case, b is nearly equal to 3 (Lesse River: 2.96, Chicheron Brook: 2.95) and this reflects an isometric growth for brown trout of the studied hydrological system. Values of parameter b of the LWR as well as those obtained for parameter a for length measured in centimetres (Lesse River: 0.0122, Chicheron Brook: 0.0127) are within the range of those presented in the inSTREAM technical report: 0.0123 for a and 2.97 for b (Tule River, California). Oscoz *et al.* (2005) reported values of different European brown trout studies varying from 0.0055 to 0.0158 for a and from 2.91 to 3.16 for b.

Parameters linked to fish reproduction are in general not well defined in literature because this behaviour is very difficult to observe in the wild. In the case of the studied system, parameter values were mainly derived from trapping data. As the system is fully controlled (i.e., all individuals entering or leaving the tributary are captured at the trapping facility), these data can be considered as complete enough to derive the time period and the state of mature adults when they move from the Lesse River to the brook for reproduction. In the DemGenTrout model, we assumed that these criteria were also shared by individuals spawning in each stream. Besides, movements of spawners appear limited by high flow and are probably also influenced by water temperature (Huet and Timmermans, 1979).

Some spawning parameters of DemGenTrout are equivalent to those used in the inSTREAM software and their values were therefore compared. In inSTREAM, the spawning period was defined between October 1 and December 31, and minimum and maximum spawning temperatures were set to 4 and 10°C, as observed for trout of the Tule River (Van Winkle *et al.*, 1996). The period of spawning determined in Chapter 2 (i.e., from November to January), and the distribution of water temperature in the Lesse River (95% CI: [2.7;10.8]) were thus in accor-

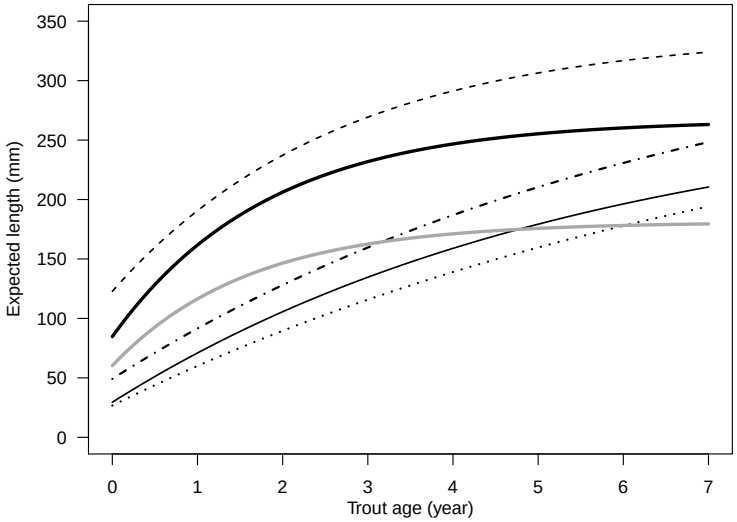

Figure 5.12: von Bertalanffy growth curves based on the parameters estimated for trout of the studied system and on values derived from the literature: Cooper *et al.* (1992) (thin solid line), Büttiker and Labous (2002) (dashed line), Arslan *et al.* (2007) (dotted line), Yildirim and Arslan (2007) (dotdashed line), present study - Lesse River (black bold line), present study - Chicheron Brook (grey bold line).

dance. The value of the minimum length at which trout spawn defined in inSTREAM was identical to the one we found (120 mm).

Trout generally mature as early as age-2 or age-3, although some individuals have been found to mature at younger ages (Bachman, 1991; Elliott, 1994). The minimum age at spawning determined from the study in Chapter 4 (3 years old) was thus plausible. According to the linear function parameterized for both streams, the number of offspring produced per season by a female spawner with an average size of 222.90 mm is equal to 25 in the brook and to 6 in the Lesse River. Huet and Timmermans (1979) estimated that around 240 000 eggs were produced by 200 spawners in the brook, against 60 000 eggs by 1000 spawners in the main river. If we apply the 10%-survival rule, these values correspond to 120 and 6 offspring per female, respectively. In other studies, fecundity of trout was estimated between 200 and 1500 eggs per female (Shepard *et al.*, 1997; Daufresne and Renault, 2006), corresponding to 20 to 150 offsprings.

Downstream movement of young trout occurred from March to August in the studied system, as determined from the study in Chapter 2, and this is in accordance with observations found in the literature (e.g.,

Huet and Timmermans, 1979; Baglinière *et al.*, 1989). The mean of the water temperature distribution in the Chicheron Brook was found to equal 9.7°C during the migration period. In comparison, Huet and Timmermans (1979) observed that the movement usually begins when the temperature in the brook is above 10°C. From Chapter 4, we found that trout caught in the downstream trap were mainly aged of 1 and 2 years old, and this is in accordance with results obtained with the Multi-Group CJS model including permanent emigration. Other studies conducted on brown trout also confirmed these observations (e.g., Baglinière and Maisse, 2002; Cucherousset *et al.*, 2006). Mean migration rate of trout from the brook estimated with the CJS model and computed over all age classes was found to equal 0.40. This value is close to the one estimated over the years 2004-2010 by multistate capture-recapture models (i.e., 0.44; see Table 2.4 of Chapter 2, page 85). In addition to age, individuals chosen for migration were restricted according to their size distribution (95% CI: [46.5;130.5]). Individuals moving from the Chicheron Brook appear smaller than migrants from the La Roche brook in Lower Normandy, where lengths ranging from 92 to 195 mm were observed (Ombredane *et al.*, 1998). The analysis of capture-recapture data including individuals caught in the downstream trap and electrofished in the brook indicated a density-dependent movement, positive for age-1 trout and negative for age-2 trout.

Chapter 6

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

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.

Keywords: agent-based model, pattern-oriented modelling, population dynamics, population genetics, *Salmo trutta*

* This chapter was accepted for publication in Ecological Modelling. Authors: Béatrice M. Frank, Philippe V. Baret. Supplementary data are available in Appendix 3, page 257.

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 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 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, 2000b) 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; Wiegand *et al.*, 2003; Grimm *et al.*, 2005), 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 Materials 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 km^2 and is located in southern Belgium (Fig. 6.1). The study area consisted of a 1.12 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 to 27 m wide, has an average depth of 0.5 m, and a mean flow of 3.5 $m^3.s^{-1}$. 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). 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.

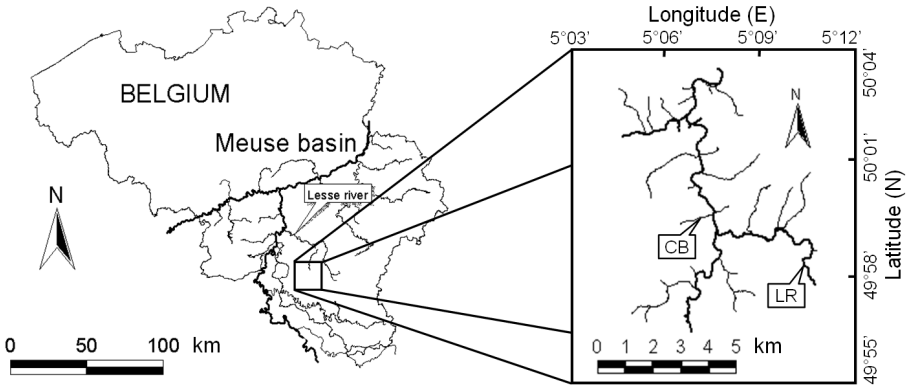

Figure 6.1: Situation plan of the Lesse River (LR) in the Meuse basin, and position of the Chicheron Brook (CB) in the Lesse basin.

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 $m^3.s^{-1}$ on average) and especially during autumn (0.008 $m^3.s^{-1}$ on average), which prevents large individuals from living in this narrow, shallow habitat. Water flow increases in late autumn (> 0.05 $m^3.s^{-1}$), 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 A3.1 of Appendix 3, page 258.

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 microsatellite), Ssa197 (tetranucleotide microsatellite) (OReilly *et al.*, 1996), Ssa408 (tetranucleotide microsatellite) (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 6.1). The spatial resolution and extent of the model are defined by the two possible locations for trout in the system (Fig. 6.1): 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. 6.2; see Section 2.2.3.3 for details): the update of hydrological conditions for each stream agent; survival, growth, reproduction, ageing, hatching, moving downstream, post-spawning homing, and leaving the system forever for each trout agent.

All actions occur in the same predetermined order (Fig. 6.3). 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

Table 6.1: 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	*stream*	Stream code	C, L
	temperature	Water temperature	Numeric (°C)
	flow	Flow rate	Numeric ($m^3.s^{-1}$)
Trout	*sex*[a]	Sex	F, M
	genotype[a]	Genotype	List of lists
	natal-stream[a]	Natal stream	C, L
	week-of-birth[a]	Week of birth	Numeric (-)
	current-stream	Current stream	C, L
	age	Age	0, 1, 2, 3, 4, 5, 6
	stage	Stage	Fry, juvenile, adult
	status	Status	Non-spawner, spawner, migrant
	body-length	Body length	Numeric (mm)
	body-weight	Body weight	Numeric (g)
	condition-factor	Body condition factor	Numeric (-)
	num-offspring	Number of offspring	Numeric (-)
	spawned?	Spawned this year	Boolean
	moved-to-spawn?	Moved to spawn this year	Boolean
	returned?	Returned to previous stream after spawning this year	Boolean

[a] fixed state variables.

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-

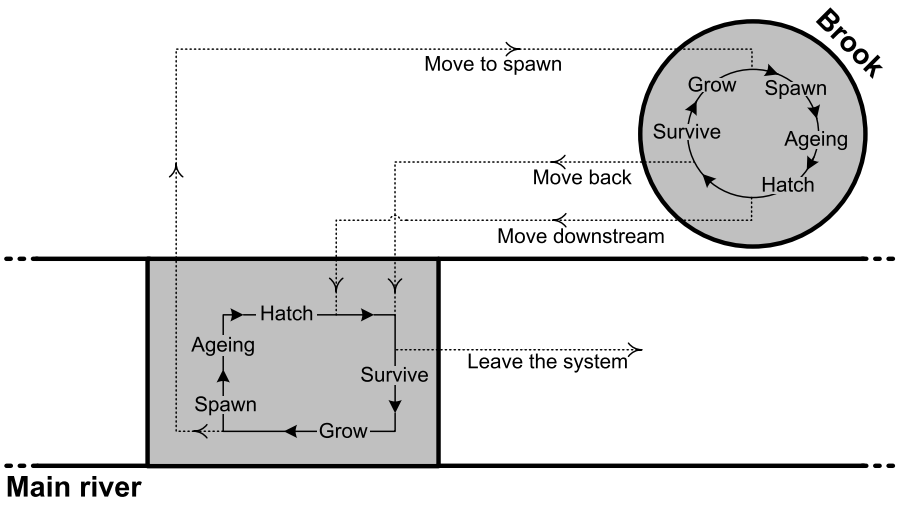

Figure 6.2: Conceptual diagram of the DemGenTrout individual-based model. Life cycle of brown trout, including movements of individuals between a main river section (stream L) and a brook (stream C), was implemented to mimic the behaviour of a population living in a Belgian hydrological system.

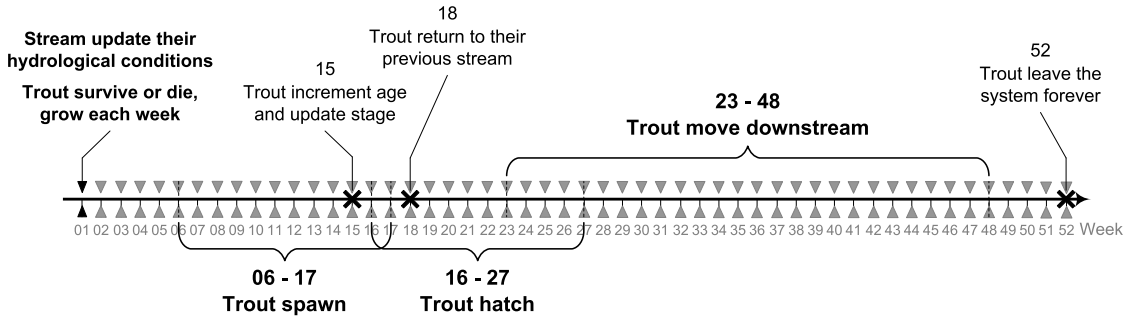

Figure 6.3: Fixed scheduling of the DemGenTrout individual-based model, as parameterized for the Lesse River / Chicheron Brook hydrological system. The update of stream conditions, trout survival and growth are actions executed once per time step. Spawning, hatching and downstream movement processes 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

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 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 hydrolog-

ical 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 6.2). 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 $\pm$ 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 A3.2 of Appendix 3, page 258).

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.

Table 6.2: Initial values for stream and trout variables of the DemGenTrout individual-based model, with their corresponding measure units (C, Chicheron Brook; L, Lesse River; std dev., standard deviation). Calibrated variables and values are noted with an asterisk (*).

Variable name	Description	Value	Unit
Stream			
streamC-temperature	Water temperature in stream C	9.8	°C
streamL-temperature	Water temperature in stream L	12.1	°C
streamC-discharge	Flow rate in stream C	0.004	$m^3.s^{-1}$
streamL-discharge	Flow rate in stream L	1.324	$m^3.s^{-1}$
Trout			
*init-N**	Trout abundance in both streams	4500*	indiv.
*prop-C**	Trout proportion in stream C	0.73*	-
prop-L	Trout proportion in stream L	0.27^a	-
*prop-age0-C**	Proportion of age-0 trout in stream C	0.76*	-
*prop-age1-C**	Proportion of age-1 trout in stream C	0.21*	-
*prop-age2-C**	Proportion of age-2 trout in stream C	0.02*	-
prop-age3-C	Proportion of trout of age 3 to 6 in stream C	0.01^b	-
*prop-age0-L**	Proportion of age-0 trout in stream L	0.10*	-

Table 6.2: Initial values for stream and trout variables of the DemGenTrout model (continued).

Variable name	Description	Value	Unit
*prop-age1-L**	Proportion of age-1 trout in stream L	0.22*	-
*prop-age2-L**	Proportion of age-2 trout in stream L	0.37*	-
prop-age3-L	Proportion of trout of age 3 to 6 in stream L	0.31[c]	-
*propC-inL**	Proportion of trout living in stream L that change their natal stream from L to C	0.67*	-
meanl-birth-C	Mean of the normal distribution for length of trout at birth in stream C	1.01	mm
meanl-age0-C	Mean of the normal distribution for length of age-0 trout in stream C	59.00	mm
meanl-age1-C	Mean of the normal distribution for length of age-1 trout in stream C	106.40	mm
meanl-age2-C	Mean of the normal distribution for length of age-2 trout in stream C	150.60	mm
meanl-age3-C	Mean of the normal distribution for length of trout of age 3 to 6 in stream C	191.70	mm
sdl-birth-C	Standard deviation of the normal distribution for length of trout at birth in stream C	0.85	mm
sdl-age0-C	Std dev. of the normal distribution for length of age-0 trout in stream C	6.48	mm
sdl-age1-C	Std dev. of the normal distribution for length of age-1 trout in stream C	12.90	mm
sdl-age2-C	Std dev. of the normal distribution for length of age-2 trout in stream C	13.49	mm
sdl-age3-C	Std dev. of the normal distribution for length of trout of age 3 to 6 in stream C	22.53	mm
meanl-birth-L	Mean of the normal distribution for length of trout at birth in stream L	1.04	mm
meanl-age0-L	Mean of the normal distribution for length of age-0 trout in stream L	82.28	mm
meanl-age1-L	Mean of the normal distribution for length of age-1 trout in stream L	132.42	mm
meanl-age2-L	Mean of the normal distribution for length of age-2 trout in stream L	178.27	mm
meanl-age3-L	Mean of the normal distribution for length of trout of age 3 to 6 in stream L	220.20	mm
sdl-birth-L	Standard deviation of the normal distribution for length of trout at birth in stream L	0.87	mm
sdl-age0-L	Std dev. of the normal distribution for length of age-0 trout in stream L	6.36	mm
sdl-age1-L	Std dev. of the normal distribution for length of age-1 trout in stream L	17.12	mm
sdl-age2-L	Std dev. of the normal distribution for length of age-2 trout in stream L	15.55	mm
sdl-age3-L	Std dev. of the normal distribution for length of trout of age 3 to 6 in stream L	16.73	mm
mean-bcf-C	Mean of the normal distribution for condition factor of trout in stream C	0.98	-
mean-bcf-L	Mean of the normal distribution for condition factor of trout in stream L	0.99	-

Table 6.2: Initial values for stream and trout variables of the DemGenTrout model (continued).

Variable name	Description	Value	Unit
sd-bcf-C	Std dev. of the normal distribution for condition factor of trout in stream C	0.13	-
sd-bcf-L	Std dev. of the normal distribution for condition factor of trout in stream L	0.09	-

[a] *prop-L* = 1− *prop-C*

[b] *prop-age3-C* = 1− (*prop-age0-C* + *prop-age1-C* + *prop-age2-C*)

[c] *prop-age3-L* = 1− (*prop-age0-L* + *prop-age1-L* + *prop-age2-L*)

2.2.3.2 Input data

The following time series of observations were available for the Lesse River / Chicheron Brook hydrological system: water temperatures in both streams, flow rates in stream L, and water heights in stream C. Water temperatures (°C) in both streams were automatically measured and recorded every hour with loggers, from years 2004 to 2009. For the Lesse River, daily flow rates ($m^3.s^{-1}$) were available from a nearby permanent gauging station located in Daverdisse (Q_D) for the years 2004 to 2009. We used the following equation to compute the flow at the study 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 both streams, 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 both streams, 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 6.3 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).

Table 6.3: 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; VBE, von Bertalanffy equation; LWR, length-weight relationship; std dev., standard deviation). 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				
streamC-age0-survival	Survival rate for age-0 trout in stream C	0.39	year^{-1}	E[a]
streamC-age1-survival	Survival rate for age-1 trout in stream C	0.37	year^{-1}	E[a]
streamC-age2-survival	Survival rate for age-2 trout in stream C	0.85	year^{-1}	E[a]
streamC-age3-survival	Survival rate for trout of age 3 to 6 in stream C	0.70	year^{-1}	G
streamL-age0-survival	Survival rate for age-0 trout of in stream L	0.38	year^{-1}	E[a]
streamL-age1-survival	Survival rate for age-1 trout of in stream L	0.74	year^{-1}	E[a]
streamL-age2-survival	Survival rate for age-2 trout of in stream L	0.87	year^{-1}	E[a]
streamL-age3-survival	Survival rate for trout of age 3 to 6 in stream L	0.69	year^{-1}	E[a]
predation-factor	Division factor for survival rate of spawners moving from stream L to C	2	-	G
Growth				
streamC-parK	von Bertalanffy growth coefficient for trout in stream C	0.012	week^{-1}	E[b]

Table 6.3: List of parameters involved in the DemGenTrout model (continued).

Parameter name	Description	Value	Unit	Source
streamL-parK	von Bertalanffy growth coefficient for trout in stream L	0.011	$week^{-1}$	E[b]
streamC-max-length	Asymptotic length for trout in stream C	179.80	mm	E[b]
streamL-max-length	Asymptotic length for trout in stream L	267.00	mm	E[b]
streamC-parA	Parameter a of the LWR for trout in stream C	14×10^{-6}	-	E[c]
streamL-parA	Parameter a of the LWR for trout in stream L	13×10^{-6}	-	E[c]
streamC-parB	Parameter b of the LWR for trout in stream C	2.95	-	E[c]
streamL-parB	Parameter b of the LWR for trout in stream L	2.96	-	E[c]
Spawning				
spawn-start	Start of the spawning period	6	week	O[d]
spawn-end	End of the spawning period	17	week	O[d]
spawn-min-age	Minimum age at which trout spawn	3	year	O[d]
spawn-mean-length	Mean of the normal distribution for length of spawners	222.90	mm	O[d]
spawn-sd-length	Std dev. of the normal distribution for length of spawners	33.82	mm	O[d]
spawn-mean-cond	Mean of the normal distribution for condition factor of spawners	0.936	-	O[d]
spawn-sd-cond	Std dev. of the normal distribution for condition factor of spawners	0.108	-	O[d]
moved-prop	Proportion of trout born in stream L moving to stream C for spawning	0.45	-	O[d]
spawn-mean-flow	Mean of the log-normal distribution for flow rate in stream L	6.85	$m^3.s^{-1}$	O[d]
spawn-sd-flow	Std dev. of the log-normal distribution for flow rate in stream L	5.15	$m^3.s^{-1}$	O[d]
offprod-min-length	Minimum length at which trout spawn in both streams	120.00	mm	O[d]
offprod-max-length	Maximum length at which trout spawn in both streams	388.00	mm	O[d]
offprod-min	Minimum number of offspring produced in both streams	0	-	E[e]
offprodC-max	Maximum number of offspring produced in stream C	168	-	C
offprodL-max	Maximum number of offspring produced in stream L	5	-	C
length-heritability	Heritability of length at age for fry	0.18	-	E[f]
Hatching				
hatch-start	Start of the hatching period	16	week	G
hatch-end	End of the hatching period	27	week	G
Downstream movement				
move-start	Start of the migration period for juveniles	23	week	O[d]
move-end	End of the migration period for juveniles	48	week	O[d]
move-min-age	Minimum age at which trout of stream C move downstream	1	year	O[d]

Table 6.3: List of parameters involved in the DemGenTrout model (continued).

Parameter name	Description	Value	Unit	Source
move-max-age	Maximum age at which trout of stream C move downstream	2	year	O[d]
move-mean-length	Mean of the normal distribution for length of juveniles	88.49	mm	O[d]
move-sd-length	Std dev. of the normal distribution for length of juveniles	20.98	mm	O[d]
move-age1-varA	Variable A of the logistic function for the probability of moving for age-1 juveniles	0.0026	-	C
move-age1-varB	Variable B of the logistic function for the probability of moving for age-1 juveniles	-4.8	-	C
move-age2-varA	Variable A of the logistic function for the probability of moving for age-2 juveniles	-0.0007	-	C
move-age2-varB	Variable B of the logistic function for the probability of moving for age-2 juveniles	0.1	-	C
move-mean-temperature	Mean of the normal distribution for water temperature in stream C	9.72	°C	O[d]
move-sd-temperature	Std dev. of the normal distribution for water temperature in stream C	3.72	°C	O[d]
move-mean-flow	Mean of the log-normal distribution for flow rate in stream C	0.040	$m^3.s^{-1}$	O[d]
move-sd-flow	Std dev. of the log-normal distribution for flow rate in stream C	0.038	$m^3.s^{-1}$	O[d]
Leaving stream L forever				
leaving-propC	Proportion of juveniles migrated from stream C that do not settle in stream L	0.57	-	C
leaving-propL	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 females 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) with an animal model (Kruuk, 2004; Wilson *et al.*, 2010).

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.

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 $\pm$ 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 and Almodovar, 2002).

Each week of the spawning period (i.e., week 6 to 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. Upswimming 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): $L^{\text{off}} = \mu^{\text{par}} + dev_P^{\text{off}} = \mu^{\text{par}} + dev_G^{\text{off}} + dev_E^{\text{off}}$, where μ^{par} is the parental population mean, dev_P^{off} is the total phenotypic deviance of the offspring population, dev_G^{off} and dev_E^{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 $\sqrt{h^2} \times (dev_\mu^{\text{par1}} + dev_\mu^{\text{par2}})$, where h^2 is the narrow-sense heritability, dev_μ^{par1} and dev_μ^{par2} 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 *meanl-birth-X* and *sdl-birth-X* initial conditions (see Table 6.2), truncated at $\pm$ 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* parameter - 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 to 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 to 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).

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; Stuart, 1957). 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; Wiegand *et al.*, 2003; Grimm *et al.*, 2005). After identifying the submodels to consider as key processes, parameter values of the model were first determined directly to reduce the parameter space (Table 6.3). 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: $\sum_i (\mathrm{sim}_i - \mathrm{obs}_i)^2 / \mathrm{obs}_i$. 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,

Table 6.4: 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.

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

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 6.2) and 8 parameters (Table 6.3). 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 6.4).

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 A3.3 of Appendix 3, page 261). Patterns C3 to C5 were derived from observations at the trapping facility (Table A3.1 of Appendix 3).

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 A3.4 of Appendix 3, page 262) 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 A3.1 and A3.3 of Appendix 3, 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 A3.1 of Appendix 3). Values of V4 were derived from length measurements of trout electrofished in autumn in both streams (Table A3.3 of Appendix 3).

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 6.3 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.

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.

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 A3.5 of Appendix 3, page 262). 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. 6.4(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. 6.4(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. 6.4(c)), the year 2010-2011 contributed the most to the SSSE of the pattern (36%). For V4 (Fig. 6.4(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 ($> 26\%$).

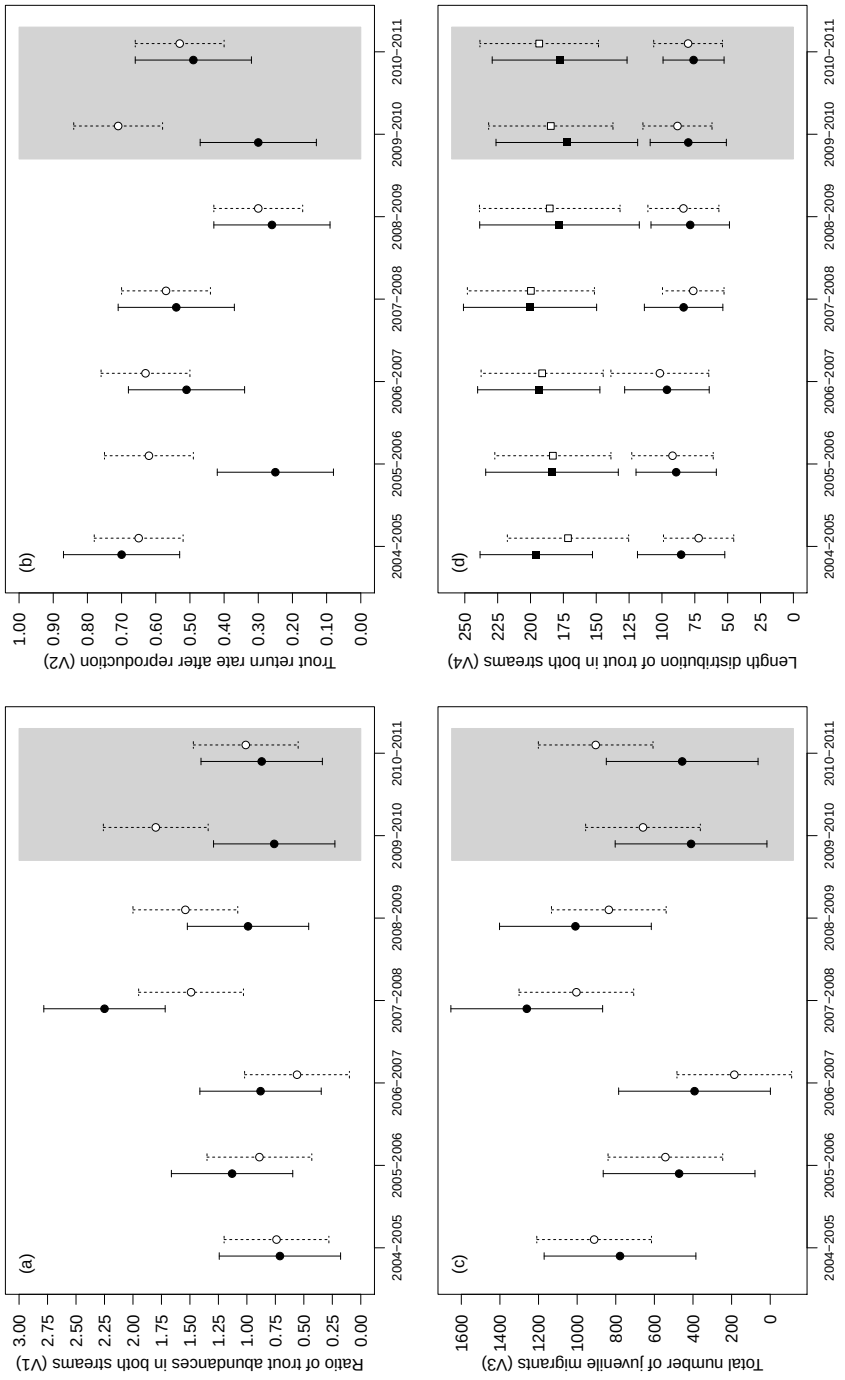

Figure 6.4: Pattern-matching validation performed on the DemGenTrout individual-based model, with observed (solid circles) and simulated (open circles) patterns within one standard deviation range. Four patterns were considered: (a) ratio of trout abundances in both streams, (b) trout return rate after 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).

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. 6.5). 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.

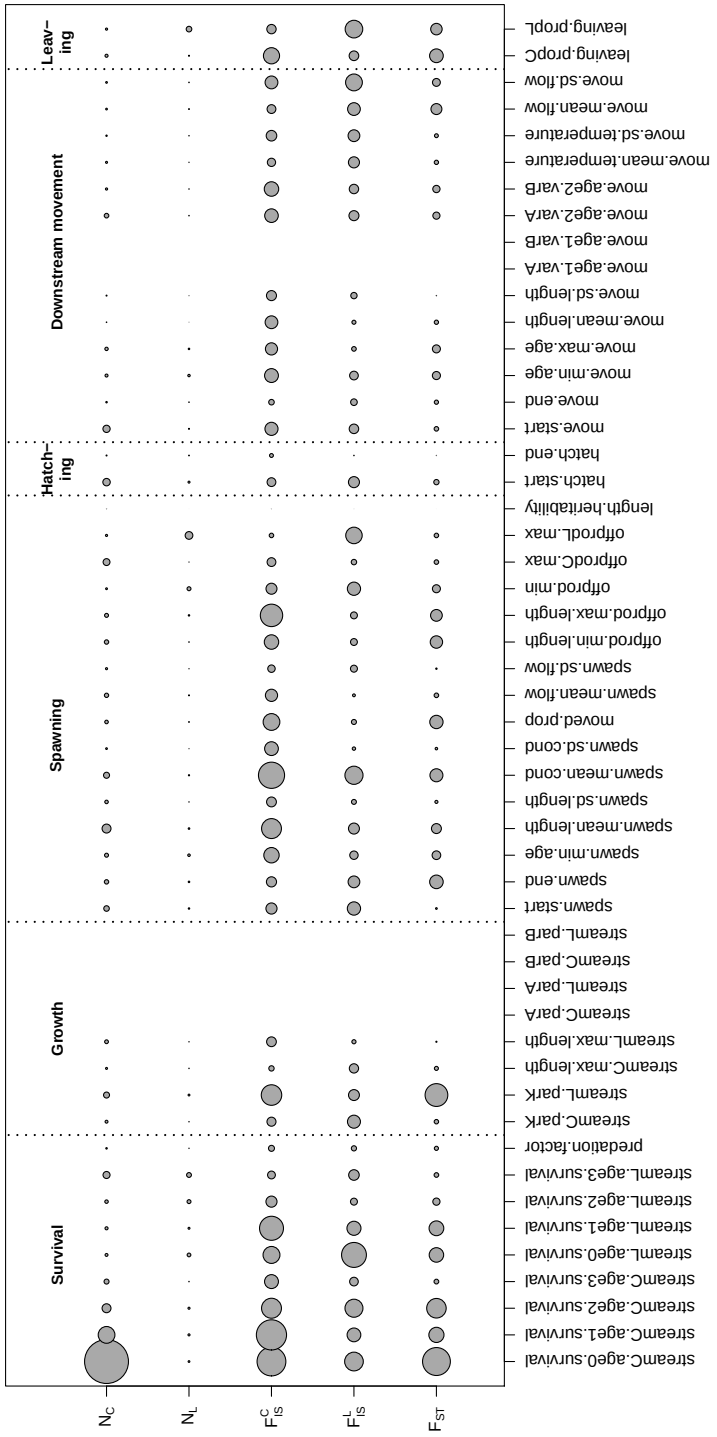

Figure 6.5: Results of the sensitivity analysis conducted on the DemGenTrout individual-based model (Morris method). All 51 parameters were varied over five levels and 50 trajectories or elementary effects were randomly selected. Parameters were grouped according to the survival, growth, spawning, hatching 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.

3.2.2 Prioritization of parameters

The six parameters of DemGenTrout identified as the most influential by the Morris method were analysed using the Sobol 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. 6.6(a)). In the case of abundance in stream L, *spawn-mean-cond* explained 89% of the output variance (Fig. 6.6(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. 6.6(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.

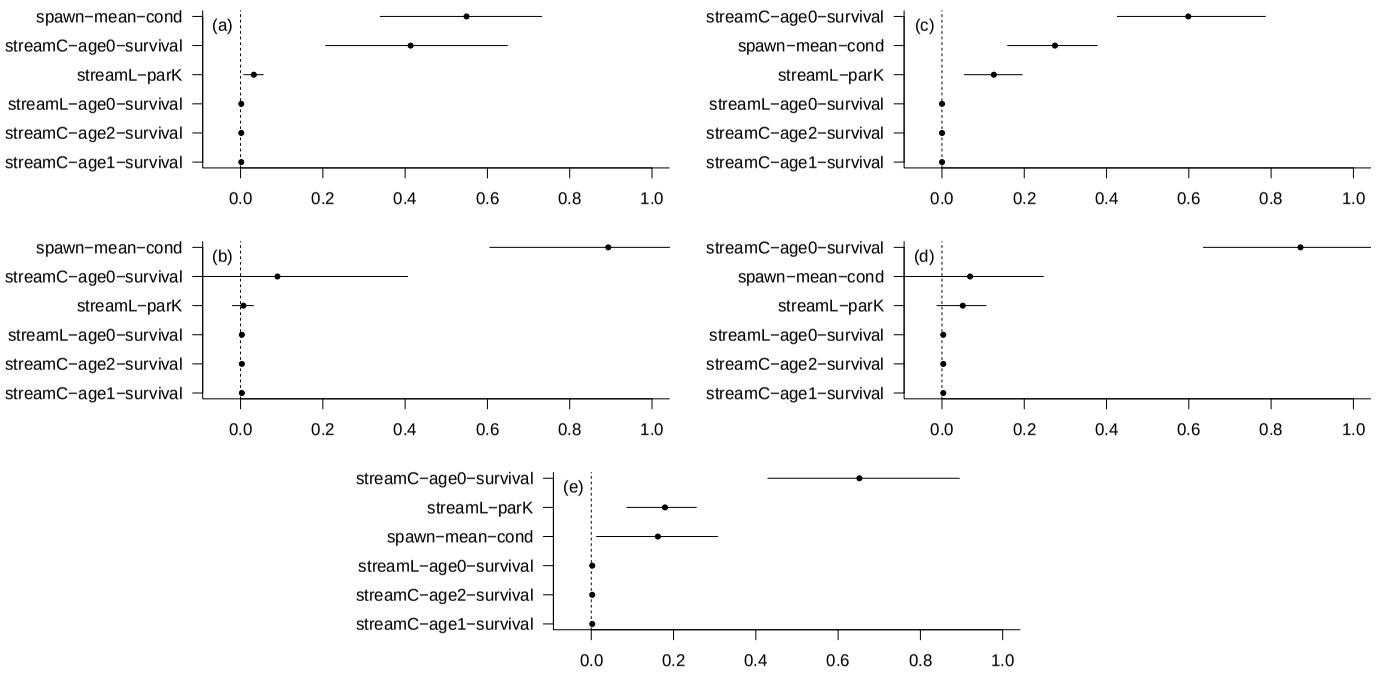

Figure 6.6: Sobol first-order indices of sensitivity for the seven parameters of the DemGenTrout individual-based model identified as the most influential by the Morris method. Each index was computed for the five following demogenetic outputs: (a) trout abundance in stream C, (b) trout abundance in 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 6.5). In the scenario with migration barrier, trout abundance in both streams has drastically decreased (Fig. 6.7(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 6.5).

Table 6.5: 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}).

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

C, Chicheron Brook; L, Lesse River; W, wild trout; H, hybrids; S, stocked trout.

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 0% stocked trout in both streams the last 5 years of simulation.

When a 90% stocking coefficient was considered, 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. 6.7(b)). For the 50 and 70% stocking coefficients, peaks of 104 and 132 hybrids were reached at years

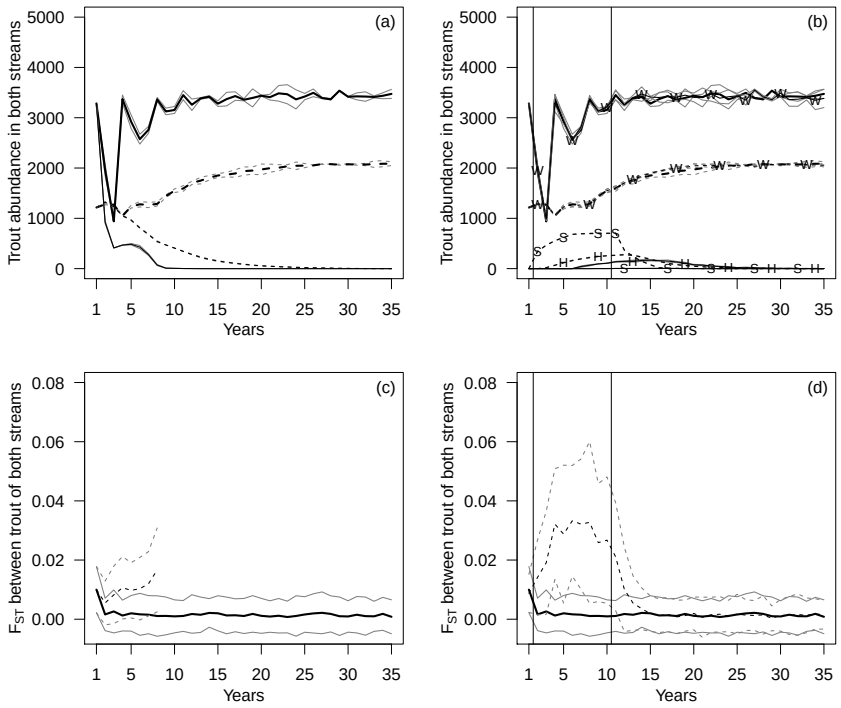

Figure 6.7: Comparison of two scenarios simulating anthropogenic disturbances for brown trout over 35 years. Impacts of (a) migration barrier and (b) stocking with a coefficient of 90% on the abundance of trout in stream C (solid lines) and abundance in stream L (dashed lines). Impacts of (c) migration 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 (c) and (d), vertical lines represent the 10-year stocking period.

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 6.5). 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. 6.7(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 6.5). 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 *versus* -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. 6.7(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. 6.7(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 6.5).

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 improve-

ments 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 5 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.

6 Acknowledgements

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Conclusions and perspectives

"The purpose of models is not to fit the data but to sharpen the questions." – Samuel Karlin, 20 April 1983, 11th Fisher Memorial Lecture, Royal Society, London.

The general objective of the present thesis was to contribute to the conservation of the brown trout species, by providing (i) a descriptive tool to study the functioning of a brown trout population at the stream scale, (ii) a predictive tool to evaluate the impacts of anthropogenic disturbances on native populations. To this end, an individual-based model called DemGenTrout was designed for answering the following research question: "Can we predict the evolution of the demogenetic structure of brown trout populations at a local scale?"

During the two last decades, there has been a shift away from statistical methods emphasizing formal hypothesis testing to an approach called model selection, in which several competing hypotheses are simultaneously confronted with observed data (Johnson and Omland, 2004; Hobbs and Hilborn, 2006). With advances in computing technologies, this shift has led to the progressive use of object-based simulations to the detriment of procedural, equation-based models (Parry and Evans, 2008). Fitting competing models to observed data is thus the actual trend in ecology.

The development of individual-based models, which allow to analyse ecological systems based upon the actions of individuals, can be based on a reductionist or holistic approach. On the one hand, a highly simplified model is built, and new variables and processes are then added in order to increase its realism. On the other hand, the model is first built by including every important aspect of the system, and then, as the modelling cycle proceeds, inessential elements are discarded. During

the development of the DemGenTrout model, only characteristics that were useful to achieve the general objective were included. Our approach tends thus towards the reductionist approach.

After summarizing the steps followed to achieve the general objective of this thesis in Section A, we present its main contributions. Methodological contributions are first identified in Section B, while the next Section C deals with contributions to the study of brown trout populations. Finally, perspectives of further development for the DemGenTrout model are presented in Section D.

A Main results

In this work, the stream fish literature was first reviewed to highlight the modelling efforts that have already been made, by integrating (Chapter 1): (i) stream scale habitat characteristics into population dynamics, with spatial dynamics models, (ii) landscape ecology into population genetics, with landscape genetics models, (iii) population dynamics and population genetics, with demogenetic models. We showed that further developments were needed to integrate the spatial dimension into demogenetic models, and we demonstrated that individual-based simulation techniques were particularly well-suited for this task.

Such an individual-based model for brown trout, called DemGenTrout, was then designed. Survival, growth, spawning and movement were the processes constituting the skeleton of the model. They were parameterized using data from a field study conducted since 2003 on a river and its spawning tributary in the Belgian Ardennes, the Lesse River / Chicheron Brook system. A methodology for assigning a birth year to most of the tagged trout of this hydrological system was developed (Chapter 4). This information was used to determine the values of several parameters of the main four processes of the model (Chapter 5).

The DemGenTrout model was optimized and validated using the POM strategy, which consists of systematically testing how well the model reproduces multiple patterns observed in the field (Grimm *et al.*, 2005; Grimm and Railsback, 2012). On the one hand, the model was calibrated with genetic algorithms, then the most appropriate submodel for the spawning process was selected. Random mating and polyandry were the two spawning modes for brown trout included in the model, and we eventually demonstrated that the second one was the most plausible. The model was then validated, and a sensitivity analysis was conducted.

Two scenarios mimicking anthropogenic disturbances during 35 years were finally simulated (Chapter 6).

From the sensitivity analysis of DemGenTrout, 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 comparison of results obtained for the two simulation scenarios. Barrier to upstream spawning migration and stocking with hatchery-reared fish showed a strong short-term impact on the demogenetic structure of the population. Obstacle to migration 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.

B Methodological contributions

Three methodological contributions arose from the achievement of the thesis objective. The main contribution was of course the DemGenTrout model itself (Section B.1). A secondary contribution was the development of the systematic methodology to decompose trout length frequencies into age classes (Section B.2). A further secondary methodological contribution of this thesis was the design of a multistate capture-recapture model combining two sources of data, i.e., trapping and electrofishing (Section B.3).

B.1 The DemGenTrout individual-based model

The extensive collection of demographic, genetic, and environmental data available for the studied system allowed us to design a demogenetic model for brown trout with a fairly complex structure (i.e., 9 submodels and 91 parameters, see Chapter 6). As the model was optimized and validated within the POM 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. To our knowledge, this is the first attempt of such a model for brown trout.

Although our work yielded interesting results about impacts caused on wild brown trout populations by migration barriers and stocking from hatcheries (see Section C.2), DemGenTrout presents some limitations.

First, all processes included in the model were chosen so that our objective of simulating anthropogenic disturbances could be addressed. All limitations mentioned in the Introduction and objectives (see Section D.3, page 17) could be overcome to further improve the DemGenTrout model. In particular, mortality sources such as high water temperatures could be explicitly taken into account in the model or additional sources could be considered, 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.

Second, the model was parametrized for a specific river / nursery brook system. 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, individual-based models often require a high number of parameters (see Chapter 1, Section 3.3.1, page 52). The parameterization of our model was ideal since extensive and precise data were available for the studied hydrological system. Almost three quarters of the DemGenTrout parameters were directly 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. However, results of the sensitivity analysis showed that the structure of the model 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 offspring length inheritance.

B.2 The systematic methodology for birth year assignment

The purpose of this methodology was to assign a birth year to as many individuals caught and tagged in the Lesse River / Chicheron Brook hydrological system as possible (see Chapter 4).

To this end, trout length frequencies obtained from capture-recapture data over a period of 6 years were first decomposed into age classes. Then, the means and standard deviations of the length distributions were estimated with finite mixture distribution models. The birth year of the trout was finally determined by simply subtracting the estimated age class from the observed year of capture.

A birth year was assigned to 70% of the trout of the studied system. In comparison with other "by hand" methods, the one we developped is standardized and reproducible, and is thus especially valuable for analysing data that continuously accumulate over time.

B.3 The multistate capture-recapture model

To better study brown trout spawning behaviour, we proposed to combine two sources of data (i.e., trapping and electrofishing in the Lesse River / Chicheron Brook hydrological system) in a multistate capture-recapture model (see Chapter 2).

The performance of the multistate model and its sensitivity to the level of data integration were first evaluated. We found that a lack of trapping data could lead to an underestimation of movement probabilities, and that this effect could be compensated by an additional source of data such as electrofishing samplings.

Second, trout movement rates obtained from the model were compared with field observations using more traditional methods, and were found realistic enough to be biologically interpreted (see next section).

C Specific contributions to the study of brown trout populations

In this section, the findings of our thesis are presented in terms of contributions to the ecological and genetic knowledge of brown trout populations.

First, observations obtained since 1957 by Huet, Timmermans and Dupont on the role of the spawning and juvenile downstream movement processes in shaping the brown trout population of the studied system are described (Section C.1). Results obtained in this thesis allowed to confirm these observations and to precisely quantify some of them, as well as to provide new findings.

Then, as the DemGenTrout model was created to simulate the demogenetic structure of a brown trout population at a stream scale and to predict medium-term impacts of human activities on this population, Section C.2 is devoted to this topic.

C.1 Population dynamics

From all previous field studies carried out on the studied system (Huet and Timmermans, 1979; Dupont, 2004, 2009), we can summarize the dynamics of the brown trout population as follows: each winter, 80 to 530 mature adults spawn in the Chicheron Brook. Post-spawning homing behaviour is exclusive but spawners face predation by herons during their stay in the brook, and consequently only 62% of them return to the main river (30 to 200 individuals). The young born in the Chicheron Brook either establish territories or migrate to the Lesse River during the successive spring and summer (280 to 1320 individuals). If juveniles stay in the brook, they face cannibalism by spawners during the reproduction period. On the contrary, if they migrate, they may benefit from the higher food capacity offered by the main stream.

Results presented in Chapter 2 of this thesis are consistent with these findings. First, the mean numbers of trout moving from the Lesse River to the Chicheron Brook or vice-versa are in the same ranges, confirming the migration pattern of brown trout in this hydrological system. Second, spawning (from November to January) and downstream migration (from March to September) periods observed nowadays are roughly identical than 50 years ago. Third, results about post-spawning behaviour were also in accordance, as we computed an average return rate of spawners equal to 58%.

Complementary findings about the downstream migration of juveniles were also provided. It was shown that (i) a young trout has a probability of 44% to migrate from the brook to the main stream, (ii) 82% of the individuals that did migrate stayed in the main stream during 1 or 2 years on average before returning to their natal brook for spawning. We also estimated that 55% of the spawners performed natal homing (Chapter 2), a behaviour not observed by Huet and Timmermans but suspected by Dupont. It is noteworthy that this behaviour was probably only possible to highlight with the techniques currently in use and that did not exist at that time (i.e., PIT-tagging *vs* fin removal, and trapping with a catch efficiency of 98% *vs* 70%). This natal homing behaviour predisposes for the development of genetically different populations in different spawning locations, and could be under genetic control. We indeed found in Chapter 3 that the genetic structure of the population was mainly determined by the respective spawning events in which the trout were involved .

Finally, additional knowledge about brown trout ecology were given in this thesis (Chapter 5). For instance, it was shown that most mature

adults spawn in the Chicheron Brook when they are aged from 3 to 5 years old, and that the average generation interval for trout of the studied system is equal to 3.52 years. The von Bertalanffy growth curves fitted to field data indicated that trout growth in the Lesse River was higher than in the Chicheron Brook, and this bears out the higher food capacity of the river. Furthermore, we observed that annual survival rates of age-0 and 1 trout in the Chicheron Brook (values around 0.40) were lower than the rate estimated for age-2 trout (0.85). This confirms the cannibalism of spawners on young trout during their stay in the brook.

C.2 Evolution of population demogenetic structure under different scenarios

In the DemGenTrout model, five indicators were chosen to monitor the changes occurring in the demogenetic structure of the studied brown trout population: two demographic outputs (i.e., trout abundance in the Chicheron Brook and the Lesse River), and three genetic outputs (i.e., inbreeding coefficients F_{IS} for trout in each stream, and fixation index F_{ST} between trout of both streams).

The sensitivity analysis conducted on the model showed that parameters of survival and spawning processes influenced the most the demogenetic structure of the Lesse River/Chicheron Brook trout population, on a short-term (i.e., 7 years of simulation). More precisely, two parameters were identified as the most influential: (i) the survival rate of fry in the brook, (ii) the mean of the spawner condition factor distribution. Such parameters are highly variable in nature, and availability of data can therefore compromise the applicability of the DemGenTrout model to less informative systems.

The two scenarios of anthropogenic disturbances were medium-term, as they were simulated over 35 years. Hereafter, we summarize their main impacts on the demogenetic structure of the population, by comparing their results to those obtained in a situation with no disturbances.

In the Chicheron Brook, the main effect was observed in the scenario simulating a barrier to upstream spawning migration, which caused the extinction of the brook population after only 13 years. A significant increase in the F_{IS} values was also observed, reflecting the loss of genetic diversity in this population. However, values remained negative throughout the simulation, keeping the trout in a safe outbreeding situation. Impacts from stocking with hatchery trout during a 10-year period were relatively weak provided that stocked trout had lower survival

and spawning probabilities than wild trout. Otherwise, we observed an inbreeding situation between years 7 and 17, and a drastic reduction in abundance of wild trout at the end of the simulation, due to the reduction in the reproductive potential of wild trout induced by the production of hybrids.

In the Lesse River, a drastic decrease of trout abundance was observed when the brook was isolated (only 2 individuals remained in the river after 35 years). This effect was linked to the reduction of the pool of adults available for reproduction in the river, which thus seemed in great part composed of trout native of the brook. This result is however biased since in the real system, trout from other tributaries can settle in the river. Stocking was responsible for a diminution of the interindividual differentiation in the main river, which led to a slight inbreeding situation during the 10 years of stocking (F_{IS} values between 0.09 and 0.12). If a significant number of stocked fish survived in the wild or if hatchery and wild trout had a similar spawning probability, the inbreeding persisted until years 15 to 18. If hatchery and wild trout had similar survival and spawning probabilities, a drastic reduction in wild trout abundance was also observed.

The overall genetic differentiation among trout of both streams stayed negligible in the first scenario (F_{ST} values below 0.02). In the second scenario, a medium effect was observed during the stocking period when a significant number of hatchery trout survived in the wild (values close to 0.10).

D Perspectives

Possibilities for improving the realism of the DemGenTrout individual-based model are (i) the consideration of density-dependence in other submodels than the downstream movement of juveniles, (ii) the integration of the quantitative genetics dimension, (iii) the inclusion of additional environmental factors. These three elements are tackled in Section D.1.

As our initial intention was to switch from a 6 km^2 system comprising the Lesse River / Chicheron Brook, to a 1343 km^2 system formed by the Lesse watershed, the extension of the model spatial scale is the subject of Section D.2.

These are only a few examples, among infinite possibilities of extension. For instance, the entire Meuse basin could be considered or the model could include other fish species.

D.1 Possibilities for model extension

Like the downstream movement of juveniles, trout survival and growth could also be modelled as density-dependent processes.

In the first case, stock-recruitment relationships could be used (see Section 3.1.1 in Chapter 1). With increasing fish density, competition for limited resources such as food and space also increases, and this results in lower survival (Hayes *et al.*, 1996; Cattaneo *et al.*, 2002). Density-dependence mortality in salmonids occur during the first few months of their life (Mortensen, 1977).

Second, the decline of average growth with increasing density is often described for juvenile freshwater salmonids (Grant and Kramer, 1990; Klemetsen *et al.*, 2003). This negative density-growth relationship is explained in the literature by two main factors, in potential interaction: (i) exploitative competition, i.e., the depletion of food by competitors (Keddy, 1989; Imre and Boisclair, 2005), (ii) spatial competition, i.e., individuals competing for foraging sites that vary spatially in quality (Ward *et al.*, 2007). To include this effect, the growth process of DemGenTrout could be modified, for example by adding age-specific negative power curves relating the length of the individuals with trout density.

Inheritance of quantitative traits could be integrated as in eco-genetic models like IBASAM. For instance, individual decisions intervening in processes such as growth or maturation, if considered, could be simulated from probabilistic reaction norms (Heino *et al.*, 2002). This would allow the evaluation of individual fitness-related traits, but would necessitate the use of non-neutral molecular markers such as allozymes.

Water temperature and flow are the only environmental factors considered in DemGenTrout, and they currently intervene in the spawning, survival (although indirectly) and downstream movement processes. Integrating these two factors in the growth and survival processes would be interesting to simulate a climate change scenario. For instance, water temperature could be integrated into the von Bertalanffy growth equation (e.g., Kielbassa *et al.*, 2010). Supplementary factors such as rainfall could be included in the model as well.

D.2 Extending the spatial scale of the model

The spatial scale of the DemGenTrout model could be extended to consider an entire watershed, the Lesse watershed (Fig. 1) for instance, in which several brown trout populations interact. In that case, we enter the

field of landscape genetics (see Section 3.3.3 in Chapter 1). The impact of brown trout behaviour on the exchange of genetic material among populations could therefore be studied. Indeed, the trout is a territorial species and shows a strong natal stream fidelity (Stuart, 1957; Elliott, 1994), and this could limit gene flow and lead to a high genetic differentiation among populations. In particular, the hypothesis of reproductive isolation (Costello *et al.*, 2003; Antunes *et al.*, 2006) could be checked against isolation by distance (Poissant *et al.*, 2005; Dionne *et al.*, 2008).

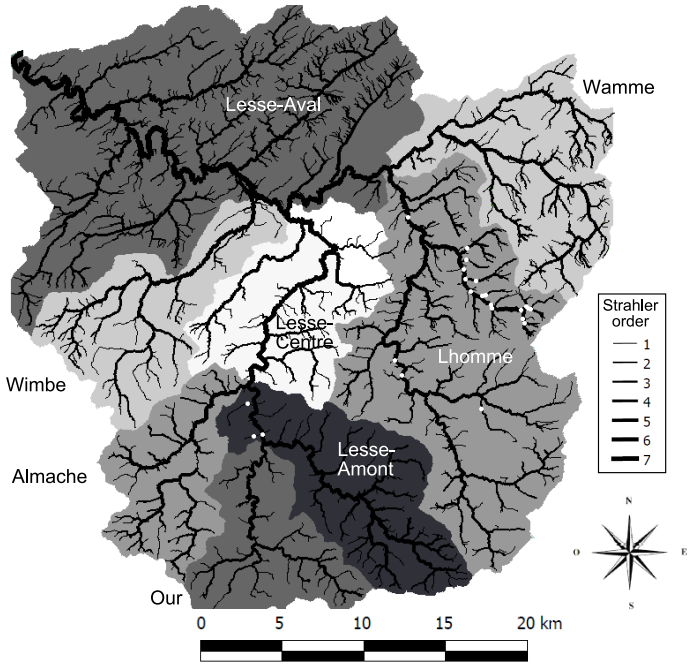

Figure 1: The Lesse watershed is subdivided into eight sub-basins: Lesse-Aval, Wamme, Wimbe, Lesse-Centre, Lhomme, Almache, Our, Lesse-Amont. The thickness of the lines representing the rivers follows the Strahler ordination (Strahler, 1957), from first- to seventh-order. Genetic sampling sites are represented by white circles.

The main challenge of this extension is the scaling up of the model, which takes place at the biological level and at spatial and temporal levels (Parasiewicz, 2003). Indeed, moving up the organisational hierarchy from one biological level to the next (i.e., from the individual to the population level) usually implies a change in the spatio-temporal scale (Ewert *et al.*, 2006).

First, biological results obtained for one population should be scaled up to several populations. The purpose is to retain only elements essential for larger-scale applications (Urban, 2005). The relative importance

of factors explaining fish-environment relationships can indeed vary between local and multi-scale studies, and relationships prevailing at small scales might either completely disappear or be replaced at large scales (Schneider, 2001; Wiens, 2002; Durance *et al.*, 2006). For instance, site-based experiments suggested that brown and brook trout stream communities in Michigan were shaped by site-specific variables such as habitat quality, competition and predation, while studies conducted at the catchment scale showed that large-scale variables such as geology, climate and land cover were prevalent (Wiley *et al.*, 1997).

The second level is the articulation of model processes that can occur at very different spatial and temporal scales. On the one hand, a spatial resolution of 1 km is sufficient for modelling trout activities such as spawning, but movements of individuals over several kilometres have also been observed (Ovidio, 1999; Young *et al.*, 2010). Furthermore, anthropogenic impacts intervene at several spatial scales, e.g., pollution at the local scale and flow control at the catchment scale. On the other hand, individual interactions generally occur at a fast time scale (i.e., daily or weekly), but hydromorphological phenomenons such as floods and droughts are observed at the scale of the decade. Several approaches could be used to face these scale issues, for instance hierarchy theory, nested modelling, or aggregation methods. Hierarchy theory techniques such as meta-modelling and scale separation consist of first aggregating source scale variables to target scale variables, then derive the associated target scale model functions (Lischke *et al.*, 2007). Nested modelling allow fine resolution models (both in the time and the space domains) to be nested into models operating at larger scales (Molnar *et al.*, 2002). In approximate aggregation techniques, a reduced model that summarises the dynamics of a complex system is constructed to approximate this system (Auger *et al.*, 2008).

We propose a four-step procedure that could be followed to extend the spatial scale of the model from stream to watershed. The first step is the genetic characterization of each brown trout population of the watershed. The delineation of the different populations could be performed with STRUCTURE (see Chapter 3). Second, the life history and population dynamics of each genetically identified population should be modelled. Strahler ordination (Strahler, 1957) of reaches could be used to identify headwater streams, which are privileged spawning areas for brown trout. In the third step, trout movements are modelled, including spawning movements to neighbouring streams and long-distance movements among sub-basins. The last step is the validation and calibration of the model. The pattern-oriented modelling strategy should be used,

with patterns carefully selected from field observations. Some applications could then be performed such as sensibility analysis or comparison of simulation scenarios, like we did with the DemGenTrout model at the stream scale.

From a practical point of view, this rescaling would lead to several modifications in the model structure, and would of course require supplementary data. To our opinion, this improved model should include two types of agents, with the following state variables:

- Trout: code, age, sex, length, genotype, birth date, natal reach, current reach;
- Reach: code, Strahler order, length, width, discharge, temperature, carrying capacity.

Two supplementary processes should be considered, in addition to those described in the previous implementation of the model. The first one would trigger trout movement if the actual number of individuals in a reach exceeds its corresponding carrying capacity. The second process would orchestrate trout movements among sub-basins.

Extending the model at a watershed scale would necessitate following a very large number of individuals, and this would require excessive computer memory and computational time. One strategy for resolving this problem is to use parallel computing, which has the advantage of maintaining the model structure (Parry and Evans, 2008). Another efficient strategy is the "super-individual" approach where the population is treated as a collection of groups, within which individuals are identical (Grimm and Railsback, 2005). This technique has already been applied in several individual-based models of fish (Rose *et al.*, 1993; Scheffer *et al.*, 1995; Van Nes *et al.*, 2002).

We also anticipate that five types of data would be required to extend the spatial scale of the model (Table 1): cartographic, environmental, biological, genetic, and data associated with the anthropogenic dimension.

The hydrographic network and the digital terrain model of the watershed are the minimal cartographic data required. Environmental data should include land use maps, rainfall and hydraulic characteristics of each stream (e.g., flow rate, physico-chemical quality). Biological and genetic data are based on fish inventories conducted by regional services on rivers. Data related to anthropogenic activities comprise recreational fishing, stocking and obstacles.

An exhaustive inventory of the data available at the watershed scale should be first realised, then these data could be gathered in a spatial

Table 1: Available field data for the Lesse River watershed that could be used to extend the spatial scale of the DemGenTrout individual-based model.

Type	**Data**	**Sources**
Cartographic	Hydrographic network at 1/1000	ELI/UCL[a]
	Digital terrain model at 1/1000	PICC[b]
Environmental	Land cover maps, aerial photographs	PCNOSW[c]
	Rainfall and hydraulic measurements	PAMESEB[d], Wacondah network (DGMVH[e]), Aquaphyc network (DGARNE[f])
Biological	Trout inventories	DGARNE
Genetic	Trout genotypes	ISV/UCL[g], ELI/UCL, DGARNE
Recreational fishing	Fishermen booklets	ELI/UCL, local fishing societies
Stocking from hatcheries	Stocking records	ELI/UCL, local fishing societies, DGARNE
Obstacles to fish movements	Obstacles inventories	DGARNE

[a] Earth and Life Institute, Université catholique de Louvain.
[b] Projet Informatique de Cartographie Continue, Service public de Wallonie.
[c] Projet de Cartographie Numérique de l'Occupation du Sol en Wallonie, Service public de Wallonie.
[d] Non-profit organization for the promotion of Agrometeorology in the Walloon Region.
[e] Direction Générale de la Mobilité et des Voies Hydrauliques, Service public de Wallonie.
[f] Direction Générale de l'Agriculture, des Ressources Naturelles et de l'Environnement, Service public de Wallonie.
[g] Institut des Sciences de la Vie, Université catholique de Louvain.

database, which could finally be visualised with a geographic information system (GIS). NetLogo could still be used as a modelling tool, with the GIS extension.

In function of the quantity of available data, new sampling campaigns should be programmed. For instance, among trout genotypes currently available for the Lesse River drainage, 90% are coming from the Lhomme sub-basin and 10% from the Lesse-Amont sub-basin (Fig. 1). Spatial statistical techniques such geostatistic tools (Rossi *et al.*, 1992) could be used to establish the sampling protocol (Johnson and Gage, 1997).

D.3 A further step towards a demogenetic model for brown trout

This thesis showed that individual-based models were able to simulate relatively well the demogenetic structure of a brown trout population at the stream scale. The DemGenTrout individual-based model was particularly useful as a predictive simulation tool for testing hypotheses concerning the response of a population to anthropogenic scenarios.

The development of this model was only made possible by the earlier studies conducted by Huet, Timmermans and Dupont. Analytical approaches should thus not be dropped in favour of individual-based ones. The potential that these latter have to offer will indeed increase as more individual-level data become available through laboratory and field experiments.

In the future, we hope that the DemGenTrout model will be used and extended by other scientists. Results derived from simulation scenarios could be of interest for industry actors, such as hatcheries, fishing companies, and government officials. To this end, the model was uploaded to the NetLogo User Community Models public Web space[1], under a Creative Commons License.

[1] `http://ccl.northwestern.edu/netlogo/models/community`

Appendix 1

This appendix contains supplementary material for Chapter 2 "Assessing brown trout spawning movements with multistate capture-recapture models: a case study in a fully controlled Belgian brook":

- Mathematical formulation and instructions for implementing the multistate capture-recapture models in program E-SURGE (Section S1);
- Goodness-of-fit test for the Jolly-Move model applied to total and partial capture histories (Section S2);
- Simple analysis of trout movements at the trapping facility applied to the reduced data set (Section S3);
- Parameters estimates from multistate capture-recapture models applied to total and partial capture histories (Section S4).

S1 Mathematical formulation and instructions for implementing the multistate capture-recapture models in program E-SURGE

At each sampling occasion A (i.e., by electrofishing), an individual may be non-spawner in the brook (state NS1), non-spawner in the main river (state NS2) or dead (state D). The following observations may be made: 1 (if caught NS1), 2 (if caught NS2) and 0 (if not caught). At each sampling occasion B (i.e. by trapping), an individual may be young trout migrating out of the brook (state YT), spawner moving from the main river to the brook but not coming back (state SP1), spawner moving from the main river to the brook and coming back (state SP2) or dead (state D). The following observations may be made: 3 (if caught YT), 4 (if caught SP1), 5 (if caught SP2) and 0 (if not caught).

We defined the initial state vector ($\mathbf{p}$), the transition matrix (which is decomposed into two matrices: survival matrix $\mathbf{S}$ and movement matrix $\mathbf{M}$) and the event matrix ($\mathbf{R}$):

$$\mathbf{p} = \begin{pmatrix} p_1 & p_2 & p_3 & p_4 & 1-p_1-p_2-p_3-p_4 & 0 \end{pmatrix}$$

$$\mathbf{S} = \begin{pmatrix} S_1 & 0 & 0 & 0 & 0 & 1-S_1 \\ 0 & S_2 & 0 & 0 & 0 & 1-S_2 \\ 0 & 0 & S_3 & 0 & 0 & 1-S_3 \\ 0 & 0 & 0 & S_3 & 0 & 1-S_3 \\ 0 & 0 & 0 & 0 & S_3 & 1-S_3 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

$$\mathbf{M} = \begin{pmatrix} 1-M_1 & 0 & M_1 & 0 & 0 & 0 \\ 0 & 1-M_2-M_3 & 0 & M_2 & M_3 & 0 \\ 0 & M_4 & 1-M_4 & 0 & 0 & 0 \\ M_4 & 0 & 0 & 1-M_4 & 0 & 0 \\ 0 & M_4 & 0 & 0 & 1-M_4 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

$$\mathbf{R} = \begin{pmatrix} 1-R_1 & R_1 & 0 & 0 & 0 & 0 \\ 1-R_2 & 0 & R_2 & 0 & 0 & 0 \\ 1-R_3 & 0 & 0 & R_3 & 0 & 0 \\ 1-R_3 & 0 & 0 & 0 & R_3 & 0 \\ 1-R_3 & 0 & 0 & 0 & 0 & R_3 \\ 1 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

Columns of matrices **p**, **S** and **M** correspond respectively to state NS1, NS2, YT, SP1, SP2 and D. Columns of the matrix **R** correspond to the observations 'not caught', 'caught as NS1', 'caught as NS2', 'caught as YT', 'caught as SP1' and 'caught as SP2'. Rows of matrices **R**, **S** and **M** correspond respectively to state NS1, NS2, YT, SP1, SP2 and D. According to the occasion considered, some probabilities were set equal in order to simplify the parameter fixation with the IVFV interface (see later). For instance, recapture probabilities of individuals caught in states YT, SP1 and SP2 were all equal to R_3, and this parameter was fixed to 0 at occasions A.

Multistate capture-recapture models (see Lebreton *et al.*, 2009, for a recent review) can be implemented in program E-SURGE (Choquet *et al.*, 2009b), which is freely downloadable at `http://www.cefe.cnrs.fr/biom/En/softwares.htm`. The first step is to load the data into the program and specify the number of groups (2 here), states (6 here), events (6 here), age classes (2 here) and covariate (0 here). Then, the model specification procedure is decomposed into (i) implementing the basic structural form of the matrices using the GEPAT interface, (ii) setting linear model of each parameter using the GEMACO interface, (iii) fixing initial parameters using the IVFV interface.

Matrices **p**, **S**, **M** and **R** introduced above are specified as follows in the GEPAT module ('*' entries denote the complement of the sum of positive rows entries, and '-' entries denote zero):

```
\%\%\%\% Initial state \%\%\%\%\%\%
1
1 5 IS
p p p p *

\%\%\%\% Transition \%\%\%\%\%\%
2
6 6 S
f - - - - *
- f - - - *
- - f - - *
```

```
- - - f - *
- - - - f *
- - - - - *

6 6 M
* - y - - -
- * - y y -
- y * - - -
y - - * - -
- y - - * -
- - - - - *

\%\%\%\% Event \%\%\%\%\%\%
1
6 6 R
* b - - - -
* - b - - -
* - - b - -
* - - - b -
* - - - - b
* - - - - -
```

In the GEMACO interface (Choquet, 2008), the general structure of the model is constrained in order to fit the desired model. Predefined shortcuts are used to specify which parameters are time-constant, time-specific or state-specific (e.g., 'i' denotes constancy, 't' means time effect, 'g' denotes a group effect, 'f' and 'to' mean that parameters are not equal in each matrix row and column, respectively). For the events, the first capture occasions are distinguished from the following ones using the shortcuts 'firste' and 'nexte', because the capture history of individuals is conditional on being caught in the first period and the following recapture probabilities depend on the state and the time occasions. The phrases used to construct the four models are presented in Table A1.1.

In the IVFV interface, the following constraints should be set before running the models. At occasions A (i.e., 1, 3, 5, 7, 9, 11), beta values associated with survival parameter S_3 and first capture parameters R_1 and R_2 should be constrained to 1, and movement parameter M_4 and recapture parameter R_3 for first and next periods to 0. At occasions B (i.e., 2, 4, 6, 8, 10, 12), beta values associated with survival parameters S_1, S_2 and S_3 as well as movement parameter M_4 and first capture parameter R_3 should be constrained to 1, and movement parameters M_1, M_2 and M_3 as well as recapture parameters R_1 and R_2 for first and next periods to 0.

Table A1.1: GEMACO sentences used to construct the four multistate models.

Effect	Phrases
A. Initial State IS	
constant	i
B. Event R	
constant	firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(1 3 5 7 9 11) +firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(2 4 6 8 10 12) +nexte.[f(1)+f(2)+f(3)&f(4)&f(5)].t(3 5 7 9 11) +nexte.[f(1)&f(2)+f(3)&f(4)&f(5)].t(4 6 8 10 12)
time	firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(1 3 5 7 9 11) +firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(2 4 6 8 10 12) +nexte.[f(1)+f(2)+f(3)&f(4)&f(5)].t(3, 5, 7, 9, 11) +nexte.[f(1)&f(2)+f(3)&f(4)&f(5)].t(4, 6, 8, 10, 12)
constant × group	firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(1 3 5 7 9 11) +firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(2 4 6 8 10 12) +nexte.[f(1)+f(2)+f(3)&f(4)&f(5)].t(3 5 7 9 11).g +nexte.[f(1)&f(2)+f(3)&f(4)&f(5)].t(4 6 8 10 12).g
time × group	firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(1 3 5 7 9 11) +firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(2 4 6 8 10 12) +nexte.[f(1)+f(2)+f(3)&f(4)&f(5)].t(3, 5, 7, 9, 11).g +nexte.[f(1)&f(2)+f(3)&f(4)&f(5)].t(4, 6, 8, 10, 12).g
C. Transition S - Step 1	
constant	[f(1)+f(2)+f(3)&f(4)&f(5)].t(1 3 5 7 9 11) +[f(1)&f(2)&f(3)&f(4)&f(5)].t(2 4 6 8 10 12)
time	[f(1)+f(2)+f(3)&f(4)&f(5)].t(1, 3, 5, 7, 9, 11) +[f(1)&f(2)&f(3)&f(4)&f(5)].t(2 4 6 8 10 12)
constant × group	[f(1)+f(2)+f(3)&f(4)&f(5)].t(1 3 5 7 9 11).g +[f(1)&f(2)&f(3)&f(4)&f(5)].t(2 4 6 8 10 12)
time × group	[f(1)+f(2)+f(3)&f(4)&f(5)].t(1, 3, 5, 7, 9, 11).g +[f(1)&f(2)&f(3)&f(4)&f(5)].t(2 4 6 8 10 12)
D. Transition M - Step 2	
constant	[f(1).to(3)+f(2).to(4)+f(2).to(5)+f(3 4 5)].t(1 3 5 7 9 11) +[f(1).to(3)&f(2).to(4)&f(2).to(5)+f(3 4 5)].t(2 4 6 8 10 12)
time	[f(1).to(3)+f(2).to(4)+f(2).to(5)+f(3 4 5)].t(1, 3, 5, 7, 9, 11) +[f(1).to(3)&f(2).to(4)&f(2).to(5)+f(3 4 5)].t(2, 4, 6, 8, 10, 12)
constant × group	[f(1).to(3)+f(2).to(4)+f(2).to(5)+f(3 4 5)].t(1 3 5 7 9 11).g +[f(1).to(3)&f(2).to(4)&f(2).to(5)+f(3 4 5)].t(2 4 6 8 10 12)
time × group	[f(1).to(3)+f(2).to(4)+f(2).to(5)+f(3 4 5)].t(1, 3, 5, 7, 9, 11).g +[f(1).to(3)&f(2).to(4)&f(2).to(5)+f(3 4 5)].t(2, 4, 6, 8, 10, 12)

S2 Goodness of fit test for the Jolly-Move model applied to total and partial capture histories

Goodness of fit (GoF) tests are used to measure the adequacy between the data and the various assumptions underlying the statistical models. The lack of fit of a model is approximated by the variance inflation factor: $\hat{c} \cong \frac{\text{Dev}}{\text{df}}$, where Dev is the deviance of the model and df is the number of degrees of freedom of the model. The deviance is equal to $-2\ ln$ Likelihood.

Two general models are used for GoF tests: the Cormack-Jolly-Seber (CJS; Cormack, 1964; Jolly, 1965; Seber, 1965) model and variants for single-state data, and the Jolly-Move (JMV; Brownie *et al.*, 1993) model and variants for multistate data (Pradel *et al.*, 2005). If the general model fits the data, the value of the deviance of this model is equal to the number of degrees of freedom and $\hat{c}$ value equals 1. When the $\hat{c}$ value of a model is greater than 1, it means that the model is not properly fitted to the data. There are two reasons for this (Burnham and Anderson, 2002; Choquet *et al.*, 2009a): (1) the model structure is not suitable for the data, for example because one of the assumptions underlying the capture-recapture method was not respected; (2) the sample variance exceeds the theoretical variance, i.e., the data show an extra binomial variation (overdispersion). In the first case, the model is biologically unrealistic and has simply to be corrected, then the $\hat{c}$ of the new obtained model is checked. In the second case, the cause is purely statistical and the only solution is to take into account the noise, by using the $\hat{c}$ value to calculate the QAIC of the model.

Results of goodness of fit tests for the JMV model applied to total and partial capture histories 1, 2 and 3 are presented in Table A1.2.

S3 Simple analysis of trout movements at the trapping facility applied to the reduced data set

Proportions of trout performing movement types I to III and the annual return rates of adults to their location of origin after the reproduction period were computed from the reduced data set (Table A1.3).

Table A1.2: Goodness of fit test for (a) total capture histories, (b) partial capture histories 1, (c) partial capture histories 2 and (d) partial capture histories 3 calculated by adding the individual X^2 values and degrees of freedom (df) for each group (individuals born in CB and of unknown origin). The variance inflation factor ($\hat{c}$), computed as the ratio of X^2 to df, is given for each test component and for the global test.

(a) Total capture histories

Test component	X^2	**p**	**df**	$\hat{c}$
WBWA	0.000	1.000	3	0.000
3G.SR	33.387	0.001	12	2.782
3G.SM	21.919	0.857	30	0.731
M.ITEC	18.488	0.005	6	3.081
M.LTEC	0.835	0.841	3	0.278
TOTAL	74.629	0.033	54	1.382

(b) Partial capture histories 1

Test component	X^2	**p**	**df**	$\hat{c}$
WBWA	1.519	0.823	4	0.380
3G.SR	27.972	0.014	14	1.998
3G.SM	58.445	0.023	39	1.499
M.ITEC	4.432	0.816	8	0.554
M.LTEC	4.048	0.400	4	1.012
TOTAL	96.416	0.016	69	1.397

(c) Partial capture histories 2

Test component	X^2	**p**	**df**	$\hat{c}$
WBWA	5.031	0.540	6	0.839
3G.SR	31.814	0.004	14	2.272
3G.SM	50.271	0.088	38	1.323
M.ITEC	20.830	0.004	7	2.976
M.LTEC	1.325	0.723	3	0.442
TOTAL	109.271	0.001	68	1.607

(d) Partial capture histories 3

Test component	X^2	**p**	**df**	$\hat{c}$
WBWA	14.554	0.042	7	2.079
3G.SR	28.423	0.019	15	1.895
3G.SM	63.009	0.012	40	1.575
M.ITEC	11.363	0.124	7	1.623
M.LTEC	2.572	0.462	3	0.857
TOTAL	119.919	0.000	72	1.666

Table A1.3: Number (and associated percentage) of tagged individuals performing various movement types during the 6 years of the study (reduced data set). Movement types are as follows: I, strict immigration; II, strict emigration; III, immigration then emigration; III / (I+III), return rate of spawners to their original site after reproduction. The last column presents results over the years 2004-2010.

Type	**2004-2005**	**2005-2006**	**2006-2007**	**2007-2008**	**2008-2009**	**2009-2010**	**2004-2010**
I	55 (13)	64 (20)	82 (21)	76 (11)	55 (9)	57 (25)	248 (10)
II	340 (79)	240 (77)	266 (69)	592 (85)	539 (90)	159 (70)	2300 (89)
III	33 (8)	9 (3)	36 (9)	25 (4)	5 (1)	12 (5)	39 (2)
III / (I+III)	- (38)	- (12)	- (31)	- (25)	- (8)	- (17)	- (14)

S4 Parameters estimates from multistate capture-recapture models applied to total and partial capture histories

In total, ten parameters were estimated by multistate capture-recapture (MSCR) models applied to total capture histories: trout recapture probabilities in both streams, the Chicheron brook (CB) and the Lesse river (LR) (R_{CB} and R_{LR}) as well as at the trapping facility (R_{TF}), trout survival probabilities in both streams (S_{CB} and S_{LR}), trout probabilities to stay in both streams (M_{CB} and M_{LR}), young trout movement probability to emigrate out of CB to LR ($M_{CB\ to\ LR}$), movement probabilities for spawners of LR to go reproduce in CB and to not come back or to come back ($M_{LR\ to\ CB}$ and $M_{LR\ to\ LR}$). Estimates obtained from models 1 and 8 are shown in Table A1.4 and those from models 9 and 16 in Table A1.5.

For the three partial capture histories, the number of parameters is twelve in each case because recapture parameter R_{TF} is split into three to take into account the states of individuals caught in the traps (YT, young trout migrating out of the brook; SP1, spawner moving from the main river to the brook but not coming back; SP2, spawner moving from the main river to the brook and coming back): $R_{TF\ as\ YT}$, $R_{TF\ as\ SP1}$ and $R_{TF\ as\ SP2}$. Tables A1.6, A1.7 and A1.8 show estimates obtained from models 9 and 16.

Table A1.4: Survival (S), recapture (R) and movement (M) estimates from (a) time-independent and (b-f) time-dependent models with group effect applied to total capture histories with lower (CI-) and upper (CI+) 95% confidence intervals and standard error (SE). Superscripts *a* and *b* stand for the group of trout born in the brook and the group of unknown origin trout, respectively.

(a) 2004-2010

Parameter	Estimate	CI-	CI+	SE
S^a_{CB}	0.9459	0.9273	0.9599	0.0082
S^a_{LR}	0.5883	0.5537	0.6221	0.0175
R^a_{CB}	0.3255	0.2522	0.4084	0.0401
R^a_{LR}	0.2213	0.2080	0.2353	0.0070
R^a_{TF}	1.0000	1.0000	1.0000	0.0000
M^a_{CB}	0.0869	0.0685	0.1097	0.0104
M^a_{LR}	0.9005	0.8858	0.9136	0.0071
$M^a_{CB\ to\ LR}$	0.9131	0.8903	0.9315	0.0104
$M^a_{LR\ to\ CB}$	0.0447	0.0369	0.0542	0.0044
$M^a_{LR\ to\ LR}$	0.0548	0.0458	0.0653	0.0049
S^b_{CB}	0.4396	0.4037	0.4762	0.0185
S^b_{LR}	0.4990	0.4772	0.5208	0.0111
R^b_{CB}	0.3948	0.3526	0.4387	0.0220
R^b_{LR}	0.6104	0.5773	0.6425	0.0167
R^b_{TF}	0.6300	0.4866	0.7536	0.0697
M^b_{CB}	0.9904	0.9829	0.9947	0.0029
M^b_{LR}	0.7591	0.7074	0.8041	0.0247
$M^b_{CB\ to\ LR}$	0.0096	0.0053	0.0171	0.0029
$M^b_{LR\ to\ CB}$	0.0874	0.0720	0.1057	0.0085
$M^b_{LR\ to\ LR}$	0.1535	0.1176	0.1980	0.0204

(b) 2004-2005

Parameter	Estimate	CI-	CI+	SE
S^a_{CB}	1.0000	1.0000	1.0000	0.0000
S^a_{LR}	0.5000	0.5000	0.5000	0.0000
R^a_{CB}	1.0000	1.0000	1.0000	0.0000
R^a_{LR}	1.0000	1.0000	1.0000	0.0000
R^a_{TF}	1.0000	1.0000	1.0000	0.0000
M^a_{CB}	0.0272	0.0086	0.0825	0.0158
M^a_{LR}	0.3333	0.3333	0.3333	0.0000
$M^a_{CB\ to\ LR}$	0.9728	0.9175	0.9914	0.0158
$M^a_{LR\ to\ CB}$	0.3333	0.3333	0.3333	0.0000
$M^a_{LR\ to\ LR}$	0.3333	0.3333	0.3333	0.0000
S^b_{CB}	0.5176	0.4281	0.6059	0.0458
S^b_{LR}	0.4974	0.4518	0.5430	0.0233
R^b_{CB}	1.0000	1.0000	1.0000	0.0000
R^b_{LR}	1.0000	1.0000	1.0000	0.0000
R^b_{TF}	1.0000	1.0000	1.0000	0.0000
M^b_{CB}	0.9826	0.9161	0.9966	0.0143
M^b_{LR}	0.0000	0.0000	0.0000	0.0000
$M^b_{CB\ to\ LR}$	0.0174	0.0034	0.0839	0.0143
$M^b_{LR\ to\ CB}$	0.0526	0.0312	0.0875	0.0139
$M^b_{LR\ to\ LR}$	0.9474	0.9125	0.9688	0.0139

(c) 2005-2006

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^a_{CB}	1.0000	1.0000	1.0000	0.0000
S^a_{LR}	0.4457	0.3603	0.5344	0.0449
R^a_{CB}	1.0000	1.0000	1.0000	0.0000
R^a_{LR}	0.2175	0.1810	0.2591	0.0199
R^a_{TF}	1.0000	1.0000	1.0000	0.0000
M^a_{CB}	0.0083	0.0016	0.0410	0.0068
M^a_{LR}	0.9319	0.8835	0.9611	0.0191
$M^a_{CB\ to\ LR}$	0.9917	0.9590	0.9984	0.0068
$M^a_{LR\ to\ CB}$	0.0568	0.0308	0.1022	0.0174
$M^a_{LR\ to\ LR}$	0.0114	0.0030	0.0423	0.0077
S^b_{CB}	0.3763	0.2980	0.4618	0.0421
S^b_{LR}	0.4062	0.3631	0.4506	0.0224
R^b_{CB}	0.5485	0.4518	0.6417	0.0490
R^b_{LR}	0.5893	0.5310	0.6451	0.0292
R^b_{TF}	0.9396	0.7484	0.9879	0.0479
M^b_{CB}	0.9897	0.9481	0.9980	0.0086
M^b_{LR}	0.7707	0.7145	0.8187	0.0266
$M^b_{CB\ to\ LR}$	0.0103	0.0020	0.0519	0.0086
$M^b_{LR\ to\ CB}$	0.1606	0.1214	0.2094	0.0224
$M^b_{LR\ to\ LR}$	0.0687	0.0435	0.1067	0.0158

(d) 2006-2007

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^a_{CB}	0.9171	0.8523	0.9550	0.0253
S^a_{LR}	0.5377	0.4509	0.6223	0.0442
R^a_{CB}	0.1765	0.0471	0.4817	0.1088
R^a_{LR}	0.2499	0.2124	0.2916	0.0202
R^a_{TF}	1.0000	1.0000	1.0000	0.0000
M^a_{CB}	0.0859	0.0459	0.1549	0.0268
M^a_{LR}	0.8586	0.8084	0.8972	0.0225
$M^a_{CB\ to\ LR}$	0.9141	0.8451	0.9541	0.0268
$M^a_{LR\ to\ CB}$	0.0278	0.0138	0.0553	0.0099
$M^a_{LR\ to\ LR}$	0.1137	0.0797	0.1595	0.0201
S^b_{CB}	0.5774	0.4556	0.6903	0.0610
S^b_{LR}	0.6341	0.5665	0.6969	0.0334
R^b_{CB}	0.3438	0.2716	0.4240	0.0391
R^b_{LR}	0.6863	0.6098	0.7539	0.0370
R^b_{TF}	0.7034	0.5015	0.8483	0.0913
M^b_{CB}	0.9735	0.9411	0.9882	0.0109
M^b_{LR}	0.7234	0.6361	0.7964	0.0411
$M^b_{CB\ to\ LR}$	0.0265	0.0118	0.0589	0.0109
$M^b_{LR\ to\ CB}$	0.0879	0.0594	0.1282	0.0173
$M^b_{LR\ to\ LR}$	0.1887	0.1283	0.2689	0.0358

(e) 2007-2008

Parameter	Estimate	CI-	CI+	SE
S^a_{CB}	0.9773	0.9425	0.9913	0.0109
S^a_{LR}	0.7289	0.6120	0.8209	0.0538
R^a_{CB}	0.6211	0.3834	0.8120	0.1164
R^a_{LR}	0.2492	0.2149	0.2869	0.0184
R^a_{TF}	1.0000	1.0000	1.0000	0.0000
M^a_{CB}	0.1138	0.0795	0.1603	0.0204
M^a_{LR}	0.8352	0.7922	0.8707	0.0200
$M^a_{CB\ to\ LR}$	0.8862	0.8397	0.9205	0.0204
$M^a_{LR\ to\ CB}$	0.0473	0.0309	0.0718	0.0102
$M^a_{LR\ to\ LR}$	0.1175	0.0887	0.1541	0.0166
S^b_{CB}	0.3506	0.2754	0.4341	0.0408
S^b_{LR}	0.5293	0.4584	0.5990	0.0361
R^b_{CB}	0.4443	0.3559	0.5363	0.0465
R^b_{LR}	0.5935	0.5256	0.6580	0.0340
R^b_{TF}	0.9272	0.5607	0.9922	0.0792
M^b_{CB}	0.9969	0.9695	0.9997	0.0036
M^b_{LR}	0.7806	0.7129	0.8360	0.0314
$M^b_{CB\ to\ LR}$	0.0031	0.0003	0.0305	0.0036
$M^b_{LR\ to\ CB}$	0.0729	0.0466	0.1124	0.0164

(f) 2008-2009

Parameter	Estimate	CI-	CI+	SE
S^a_{CB}	0.9113	0.8507	0.9488	0.0243
S^a_{LR}	0.6995	0.5662	0.8060	0.0621
R^a_{CB}	0.3898	0.2662	0.5294	0.0687
R^a_{LR}	0.2253	0.2020	0.2504	0.0124
R^a_{TF}	1.0000	1.0000	1.0000	0.0000
M^a_{CB}	0.0916	0.0537	0.1520	0.0244
M^a_{LR}	0.9392	0.9183	0.9551	0.0093
$M^a_{CB\ to\ LR}$	0.9084	0.8480	0.9463	0.0244
$M^a_{LR\ to\ CB}$	0.0403	0.0283	0.0570	0.0072
$M^a_{LR\ to\ LR}$	0.0205	0.0128	0.0327	0.0049
S^b_{CB}	1.0000	0.0000	1.0000	0.0003
S^b_{LR}	0.6965	0.3611	0.9031	0.1511
R^b_{CB}	0.4599	0.3633	0.5597	0.0507
R^b_{LR}	0.5594	0.4788	0.6371	0.0407
R^b_{TF}	0.6787	0.3392	0.8968	0.1574
M^b_{CB}	0.9976	0.9857	0.9996	0.0022
M^b_{LR}	0.9312	0.8655	0.9661	0.0243
$M^b_{CB\ to\ LR}$	0.0024	0.0004	0.0143	0.0022
$M^b_{LR\ to\ CB}$	0.0501	0.0241	0.1012	0.0184

Table A1.5: Survival (S'), recapture (R') and movement (M') estimates from (a) time-independent and (b-f) time-dependent models without group effect applied to total capture histories with lower (CI-) and upper (CI+) 95% confidence intervals and standard error (SE).

(a) 2004-2010

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S'_{CB}	0.5125	0.4919	0.5331	0.0105
S'_{LR}	0.5625	0.5432	0.5816	0.0098
R'_{CB}	0.4882	0.4519	0.5247	0.0186
R'_{LR}	0.3039	0.2908	0.3173	0.0068
R'_{TF}	0.9669	0.9402	0.9819	0.0101
M'_{CB}	0.5556	0.5279	0.5828	0.0140
M'_{LR}	0.8792	0.8676	0.8899	0.0057
$M'_{CB\ to\ LR}$	0.4444	0.4172	0.4721	0.0140
$M'_{LR\ to\ CB}$	0.0521	0.0458	0.0594	0.0035
$M'_{LR\ to\ LR}$	0.0687	0.0608	0.0774	0.0042

(b) 2004-2005

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S'_{CB}	0.7773	0.7004	0.8389	0.0354
S'_{LR}	0.5545	0.5036	0.6042	0.0257
R'_{CB}	1.0000	1.0000	1.0000	0.0000
R'_{LR}	1.0000	1.0000	1.0000	0.0000
R'_{TF}	1.0000	1.0000	1.0000	0.0000
M'_{CB}	0.3987	0.3308	0.4708	0.0359
M'_{LR}	0.0000	0.0000	0.0000	0.0000
$M'_{CB\ to\ LR}$	0.6013	0.5292	0.6692	0.0359
$M'_{LR\ to\ CB}$	0.0438	0.0259	0.0732	0.0116
$M'_{LR\ to\ LR}$	0.9562	0.9268	0.9741	0.0116

(c) 2005-2006

Parameter	Estimate	CI-	CI+	SE
S'_{CB}	0.5155	0.4649	0.5659	0.0258
S'_{LR}	0.4355	0.3914	0.4806	0.0228
R'_{CB}	0.5931	0.4977	0.6819	0.0475
R'_{LR}	0.3537	0.3206	0.3881	0.0172
R'_{TF}	0.9470	0.8980	0.9731	0.0181
M'_{CB}	0.4000	0.3375	0.4659	0.0329
M'_{LR}	0.8494	0.8132	0.8797	0.0169
$M'_{CB\ to\ LR}$	0.6000	0.5341	0.6625	0.0329
$M'_{LR\ to\ CB}$	0.1087	0.0837	0.1401	0.0143
$M'_{LR\ to\ LR}$	0.0418	0.0272	0.0639	0.0091

(d) 2006-2007

Parameter	Estimate	CI-	CI+	SE
S'_{CB}	0.5624	0.5015	0.6214	0.0307
S'_{LR}	0.6052	0.5457	0.6616	0.0297
R'_{CB}	0.4009	0.3271	0.4796	0.0392
R'_{LR}	0.3649	0.3286	0.4027	0.0189
R'_{TF}	1.0000	1.0000	1.0000	0.0000
M'_{CB}	0.6563	0.5954	0.7125	0.0300
M'_{LR}	0.8368	0.8041	0.8650	0.0155
$M'_{CB\ to\ LR}$	0.3437	0.2875	0.4046	0.0300
$M'_{LR\ to\ CB}$	0.0494	0.0351	0.0691	0.0085
$M'_{LR\ to\ LR}$	0.1138	0.0907	0.1418	0.0130

(e) 2007-2008

Parameter	Estimate	CI-	CI+	SE
S'_{CB}	0.4915	0.4482	0.5350	0.0222
S'_{LR}	0.6799	0.6065	0.7454	0.0356
R'_{CB}	0.5837	0.5031	0.6601	0.0404
R'_{LR}	0.3496	0.3169	0.3837	0.0171
R'_{TF}	0.9899	0.9411	0.9983	0.0093
M'_{CB}	0.5217	0.4691	0.5739	0.0268
M'_{LR}	0.8364	0.8053	0.8633	0.0148
$M'_{CB\ to\ LR}$	0.4783	0.4261	0.5309	0.0268
$M'_{LR\ to\ CB}$	0.0505	0.0371	0.0685	0.0079
$M'_{LR\ to\ LR}$	0.1131	0.0914	0.1392	0.0121

(f) 2008-2009

Parameter	Estimate	CI-	CI+	SE
S'_{CB}	0.6159	0.5031	0.7174	0.0555
S'_{LR}	0.8837	0.6769	0.9650	0.0676
R'_{CB}	0.5283	0.4537	0.6017	0.0380
R'_{LR}	0.2672	0.2441	0.2916	0.0121
R'_{TF}	0.9857	0.8763	0.9985	0.0164
M'_{CB}	0.6388	0.5637	0.7076	0.0370
M'_{LR}	0.9563	0.9435	0.9663	0.0058
$M'_{CB\ to\ LR}$	0.3612	0.2924	0.4363	0.0370
$M'_{LR\ to\ CB}$	0.0299	0.0221	0.0402	0.0045
$M'_{LR\ to\ LR}$	0.0138	0.0091	0.0209	0.0029

Table A1.6: Survival (S^1), recapture (R^1) and movement (M^1) estimates from (a) time-independent and (b-f) time-dependent models without group effect applied to partial capture histories 1 with lower (CI-) and upper (CI+) 95% confidence intervals and standard error (SE). *YT*, *SP1* and *SP2* notation stand for the following states: young trout migrating out of the brook (CB to LR), spawner moving from the main river to the brook but not coming back (LR to CB), spawner moving from the main river to the brook and coming back (LR to LR), respectively.

(a) 2004-2010

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^1_{CB}	0.5233	0.4976	0.5489	0.0131
S^1_{LR}	0.5573	0.5353	0.5790	0.0112
R^1_{CB}	0.4678	0.4281	0.5080	0.0204
R^1_{LR}	0.3320	0.3154	0.3490	0.0086
$R^1_{TF\ as\ YD}$	0.6948	0.6389	0.7456	0.0273
$R^1_{TF\ as\ SP1}$	0.8560	0.7679	0.9143	0.0368
$R^1_{TF\ as\ SP2}$	0.0457	0.0385	0.0542	0.0040
M^1_{CB}	0.5764	0.5434	0.6086	0.0166
M^1_{LR}	0.0000	0.0000	0.0000	0.0000
$M^1_{CB\ to\ LR}$	0.4236	0.3914	0.4566	0.0166
$M^1_{LR\ to\ CB}$	0.0573	0.0492	0.0667	0.0045
$M^1_{LR\ to\ LR}$	0.9427	0.9333	0.9508	0.0045

(b) 2004-2005

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^1_{CB}	0.7081	0.6254	0.7790	0.0394
S^1_{LR}	0.5186	0.4644	0.5724	0.0277
R^1_{CB}	1.0000	1.0000	1.0000	0.0000
R^1_{LR}	1.0000	1.0000	1.0000	0.0000
$R^1_{TF\ as\ YD}$	1.0000	1.0000	1.0000	0.0000
$R^1_{TF\ as\ SP1}$	1.0000	1.0000	1.0000	0.0000
$R^1_{TF\ as\ SP2}$	1.0000	1.0000	1.0000	0.0000
M^1_{CB}	0.4643	0.3827	0.5479	0.0425
M^1_{LR}	0.0000	0.0000	0.0000	0.0000
$M^1_{CB\ to\ LR}$	0.5357	0.4521	0.6173	0.0425
$M^1_{LR\ to\ CB}$	0.0536	0.0308	0.0919	0.0150
$M^1_{LR\ to\ LR}$	0.9464	0.9081	0.9692	0.0150

(c) 2005-2006

Parameter	Estimate	CI-	CI+	SE
S^1_{CB}	0.4886	0.4304	0.5471	0.0299
S^1_{LR}	0.4357	0.3841	0.4888	0.0268
R^1_{CB}	0.5469	0.4475	0.6428	0.0505
R^1_{LR}	0.4086	0.3667	0.4519	0.0218
$R^1_{TF\ as\ YD}$	0.6421	0.5422	0.7311	0.0487
$R^1_{TF\ as\ SP1}$	0.8854	0.6783	0.9659	0.0672
$R^1_{TF\ as\ SP2}$	0.1497	0.0820	0.2574	0.0440
M^1_{CB}	0.4248	0.3514	0.5017	0.0386
M^1_{LR}	0.7149	0.5986	0.8083	0.0541
$M^1_{CB\ to\ LR}$	0.5752	0.4983	0.6486	0.0386
$M^1_{LR\ to\ CB}$	0.0890	0.0630	0.1243	0.0155
$M^1_{LR\ to\ LR}$	0.1961	0.1119	0.3208	0.0531

(d) 2006-2007

Parameter	Estimate	CI-	CI+	SE
S^1_{CB}	0.6035	0.5264	0.6757	0.0383
S^1_{LR}	0.5797	0.5139	0.6428	0.0331
R^1_{CB}	0.4409	0.3526	0.5330	0.0465
R^1_{LR}	0.3917	0.3471	0.4382	0.0233
$R^1_{TF\ as\ YD}$	0.8328	0.6837	0.9198	0.0593
$R^1_{TF\ as\ SP1}$	0.7978	0.5999	0.9122	0.0797
$R^1_{TF\ as\ SP2}$	0.1836	0.1418	0.2343	0.0236
M^1_{CB}	0.6928	0.6218	0.7558	0.0343
M^1_{LR}	0.4488	0.4044	0.4940	0.0229
$M^1_{CB\ to\ LR}$	0.3072	0.2442	0.3782	0.0343
$M^1_{LR\ to\ CB}$	0.0698	0.0492	0.0981	0.0123
$M^1_{LR\ to\ LR}$	0.4814	0.4249	0.5384	0.0291

(e) 2007-2008

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^1_{CB}	0.5018	0.4467	0.5569	0.0282
S^1_{LR}	0.6737	0.5885	0.7488	0.0412
R^1_{CB}	0.5283	0.4431	0.6119	0.0435
R^1_{LR}	0.3903	0.3490	0.4332	0.0215
$R^1_{TF\ as\ YD}$	0.7790	0.6785	0.8548	0.0451
$R^1_{TF\ as\ SP1}$	1.0000	1.0000	1.0000	0.0000
$R^1_{TF\ as\ SP2}$	0.9997	0.9995	0.9998	0.0001
M^1_{CB}	0.5660	0.5036	0.6264	0.0315
M^1_{LR}	0.8501	0.8149	0.8796	0.0165
$M^1_{CB\ to\ LR}$	0.4340	0.3736	0.4964	0.0315
$M^1_{LR\ to\ CB}$	0.0649	0.0470	0.0891	0.0106
$M^1_{LR\ to\ LR}$	0.0850	0.0639	0.1121	0.0122

(f) 2008-2009

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^1_{CB}	0.6241	0.4753	0.7527	0.0725
S^1_{LR}	0.9228	0.5051	0.9929	0.0895
R^1_{CB}	0.4748	0.3974	0.5535	0.0401
R^1_{LR}	0.2955	0.2661	0.3267	0.0155
$R^1_{TF\ as\ YD}$	0.7321	0.5728	0.8478	0.0713
$R^1_{TF\ as\ SP1}$	0.6976	0.4514	0.8661	0.1110
$R^1_{TF\ as\ SP2}$	0.1041	0.0699	0.1524	0.0208
M^1_{CB}	0.6641	0.5687	0.7478	0.0461
M^1_{LR}	0.8729	0.8310	0.9056	0.0189
$M^1_{CB\ to\ LR}$	0.3359	0.2522	0.4313	0.0461
$M^1_{LR\ to\ CB}$	0.0334	0.0222	0.0500	0.0069
$M^1_{LR\ to\ LR}$	0.0936	0.0643	0.1345	0.0177

Table A1.7: Survival (S^2), recapture (R^2) and movement (M^2) estimates from (a) time-independent and (b-f) time-dependent models without group effect applied to partial capture histories 2 with lower (CI-) and upper (CI+) 95% confidence intervals and standard error (SE). *YT*, *SP1* and *SP2* notation stand for the following states: young trout migrating out of the brook (CB to LR), spawner moving from the main river to the brook but not coming back (LR to CB), spawner moving from the main river to the brook and coming back (LR to LR), respectively.

(a) 2004-2010

Parameter	Estimate	CI-	CI+	SE
S^2_{CB}	0.5075	0.4808	0.5341	0.0136
S^2_{LR}	0.5432	0.5212	0.5650	0.0112
R^2_{CB}	0.4750	0.4337	0.5167	0.0212
R^2_{LR}	0.3815	0.3620	0.4014	0.0100
$R^2_{TF\ as\ YT}$	0.5152	0.4611	0.5689	0.0276
$R^2_{TF\ as\ SP1}$	0.8438	0.7442	0.9094	0.0416
$R^2_{TF\ as\ SP2}$	0.0334	0.0270	0.0411	0.0036
M^2_{CB}	0.6322	0.5988	0.6644	0.0168
M^2_{LR}	0.0000	0.0000	0.0000	0.0000
$M^2_{CB\ to\ LR}$	0.3678	0.3356	0.4012	0.0168
$M^2_{LR\ to\ CB}$	0.0549	0.0465	0.0648	0.0047
$M^2_{LR\ to\ LR}$	0.9451	0.9352	0.9535	0.0047

(b) 2004-2005

Parameter	Estimate	CI-	CI+	SE
S^2_{CB}	0.6428	0.5648	0.7139	0.0383
S^2_{LR}	0.4859	0.4344	0.5376	0.0264
R^2_{CB}	1.0000	1.0000	1.0000	0.0000
R^2_{LR}	1.0000	1.0000	1.0000	0.0000
$R^2_{TF\ as\ YT}$	1.0000	1.0000	1.0000	0.0000
$R^2_{TF\ as\ SP1}$	1.0000	1.0000	1.0000	0.0000
$R^2_{TF\ as\ SP2}$	1.0000	1.0000	1.0000	0.0000
M^2_{CB}	0.5250	0.4389	0.6097	0.0440
M^2_{LR}	0.0000	0.0000	0.0000	0.0000
$M^2_{CB\ to\ LR}$	0.4750	0.3903	0.5611	0.0440
$M^2_{LR\ to\ CB}$	0.0513	0.0286	0.0902	0.0151
$M^2_{LR\ to\ LR}$	0.9487	0.9098	0.9714	0.0151

(c) 2005-2006

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^2_{CB}	0.4596	0.4025	0.5177	0.0295
S^2_{LR}	0.4296	0.3785	0.4822	0.0265
R^2_{CB}	0.5708	0.4706	0.6656	0.0504
R^2_{LR}	0.4581	0.4113	0.5057	0.0241
$R^2_{TF\ as\ YT}$	0.5221	0.4229	0.6196	0.0509
$R^2_{TF\ as\ SP1}$	0.8822	0.6365	0.9697	0.0770
$R^2_{TF\ as\ SP2}$	0.0353	0.0180	0.0681	0.0120
M^2_{CB}	0.4598	0.3826	0.5390	0.0402
M^2_{LR}	0.3341	0.2591	0.4186	0.0410
$M^2_{CB\ to\ LR}$	0.5402	0.4610	0.6174	0.0402
$M^2_{LR\ to\ CB}$	0.0784	0.0535	0.1136	0.0151
$M^2_{LR\ to\ LR}$	0.5874	0.4919	0.6768	0.0477

(d) 2006-2007

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^2_{CB}	0.6287	0.5410	0.7087	0.0432
S^2_{LR}	0.5733	0.5091	0.6351	0.0323
R^2_{CB}	0.4776	0.3813	0.5756	0.0502
R^2_{LR}	0.4417	0.3914	0.4933	0.0261
$R^2_{TF\ as\ YT}$	0.7260	0.5632	0.8448	0.0731
$R^2_{TF\ as\ SP1}$	0.7332	0.5224	0.8735	0.0920
$R^2_{TF\ as\ SP2}$	0.5318	0.3239	0.7291	0.1096
M^2_{CB}	0.7694	0.7035	0.8244	0.0309
M^2_{LR}	0.7846	0.7055	0.8470	0.0361
$M^2_{CB\ to\ LR}$	0.2306	0.1756	0.2965	0.0309
$M^2_{LR\ to\ CB}$	0.0723	0.0502	0.1031	0.0133
$M^2_{LR\ to\ LR}$	0.1431	0.0880	0.2244	0.0344

(e) 2007-2008

Parameter	Estimate	CI-	CI+	SE
S^2_{CB}	0.4685	0.4122	0.5256	0.0291
S^2_{LR}	0.6511	0.5693	0.7248	0.0400
R^2_{CB}	0.4954	0.4126	0.5785	0.0427
R^2_{LR}	0.4594	0.4112	0.5083	0.0248
$R^2_{TF\ as\ YT}$	0.5784	0.4779	0.6728	0.0504
$R^2_{TF\ as\ SP1}$	1.0000	1.0000	1.0000	0.0000
$R^2_{TF\ as\ SP2}$	0.3046	0.0714	0.7139	0.1880
M^2_{CB}	0.6216	0.5566	0.6826	0.0323
M^2_{LR}	0.7395	0.4409	0.9108	0.1259
$M^2_{CB\ to\ LR}$	0.3784	0.3174	0.4434	0.0323
$M^2_{LR\ to\ CB}$	0.0580	0.0403	0.0829	0.0107
$M^2_{LR\ to\ LR}$	0.2025	0.0523	0.5386	0.1257

(f) 2008-2009

Parameter	Estimate	CI-	CI+	SE
S^2_{CB}	0.7613	0.4842	0.9155	0.1134
S^2_{LR}	1.0000	1.0000	1.0000	0.0000
R^2_{CB}	0.5083	0.4241	0.5920	0.0432
R^2_{LR}	0.3472	0.3115	0.3846	0.0187
$R^2_{TF\ as\ YT}$	0.4484	0.3278	0.5753	0.0645
$R^2_{TF\ as\ SP1}$	0.7116	0.4567	0.8786	0.1127
$R^2_{TF\ as\ SP2}$	0.0120	0.0037	0.0381	0.0071
M^2_{CB}	0.7240	0.6179	0.8096	0.0493
M^2_{LR}	0.5419	0.1843	0.8610	0.2097
$M^2_{CB\ to\ LR}$	0.2760	0.1904	0.3821	0.0493
$M^2_{LR\ to\ CB}$	0.0308	0.0205	0.0461	0.0064
$M^2_{LR\ to\ LR}$	0.4272	0.1219	0.8003	0.2099

Table A1.8: Survival (S^3), recapture (R^3) and movement (M^3) estimates from (a) time-independent and (b-f) time-dependent models without group effect applied to partial capture histories 3 with lower (CI-) and upper (CI+) 95% confidence intervals and standard error (SE). *YT*, *SP1* and *SP2* notation stand for the following states: young trout migrating out of the brook (CB to LR), spawner moving from the main river to the brook but not coming back (LR to CB), spawner moving from the main river to the brook and coming back (LR to LR), respectively.

(a) 2004-2010

Parameter	Estimate	CI-	CI+	SE
S^3_{CB}	0.4624	0.4377	0.4874	0.0127
S^3_{LR}	0.5173	0.4965	0.5380	0.0106
R^3_{CB}	0.5387	0.4937	0.5830	0.0228
R^3_{LR}	0.4819	0.4583	0.5057	0.0121
$R^3_{TF\ as\ YD}$	0.3794	0.3313	0.4300	0.0253
$R^3_{TF\ as\ SP1}$	0.7175	0.5979	0.8126	0.0554
$R^3_{TF\ as\ SP2}$	0.0153	0.0112	0.0210	0.0025
M^3_{CB}	0.6846	0.6531	0.7145	0.0157
M^3_{LR}	0.0000	0.0000	0.0000	0.0000
$M^3_{CB\ to\ LR}$	0.3154	0.2855	0.3469	0.0157
$M^3_{LR\ to\ CB}$	0.0454	0.0373	0.0551	0.0045
$M^3_{LR\ to\ LR}$	0.9546	0.9449	0.9627	0.0045

(b) 2004-2005

Parameter	Estimate	CI-	CI+	SE
S^3_{CB}	0.5594	0.4908	0.6258	0.0347
S^3_{LR}	0.4324	0.3882	0.4778	0.0229
R^3_{CB}	1.0000	1.0000	1.0000	0.0000
R^3_{LR}	1.0000	1.0000	1.0000	0.0000
$R^3_{TF\ as\ YD}$	1.0000	1.0000	1.0000	0.0000
$R^3_{TF\ as\ SP1}$	1.0000	1.0000	1.0000	0.0000
$R^3_{TF\ as\ SP2}$	1.0000	1.0000	1.0000	0.0000
M^3_{CB}	0.6258	0.5392	0.7050	0.0427
M^3_{LR}	0.0000	0.0000	0.0000	0.0000
$M^3_{CB\ to\ LR}$	0.3742	0.2950	0.4608	0.0427
$M^3_{LR\ to\ CB}$	0.0495	0.0276	0.0873	0.0146
$M^3_{LR\ to\ LR}$	0.9505	0.9127	0.9724	0.0146

(c) 2005-2006

Parameter	Estimate	CI-	CI+	SE
S^3_{CB}	0.3853	0.3355	0.4377	0.0261
S^3_{LR}	0.4224	0.3746	0.4716	0.0248
R^3_{CB}	0.6478	0.5439	0.7393	0.0504
R^3_{LR}	0.5950	0.5409	0.6469	0.0271
$R^3_{TF\ as\ YD}$	0.3703	0.2772	0.4742	0.0509
$R^3_{TF\ as\ SP1}$	0.6739	0.3968	0.8665	0.1283
$R^3_{TF\ as\ SP2}$	0.0201	0.0075	0.0528	0.0100
M^3_{CB}	0.5319	0.4512	0.6110	0.0411
M^3_{LR}	0.1209	0.0024	0.8879	0.2198
$M^3_{CB\ to\ LR}$	0.4681	0.3890	0.5488	0.0411
$M^3_{LR\ to\ CB}$	0.0553	0.0339	0.0890	0.0136
$M^3_{LR\ to\ LR}$	0.8238	0.1917	0.9893	0.2208

(d) 2006-2007

Parameter	Estimate	CI-	CI+	SE
S^3_{CB}	0.6111	0.5295	0.6869	0.0405
S^3_{LR}	0.5859	0.5232	0.6460	0.0315
R^3_{CB}	0.5471	0.4411	0.6489	0.0538
R^3_{LR}	0.5373	0.4805	0.5932	0.0289
$R^3_{TF\ as\ YD}$	0.5148	0.3710	0.6562	0.0748
$R^3_{TF\ as\ SP1}$	0.5409	0.3502	0.7203	0.0991
$R^3_{TF\ as\ SP2}$	0.0865	0.0000	0.9987	0.3621
M^3_{CB}	0.7908	0.7272	0.8428	0.0295
M^3_{LR}	0.4628	0.0000	1.0000	1.9363
$M^3_{CB\ to\ LR}$	0.2092	0.1572	0.2728	0.0295
$M^3_{LR\ to\ CB}$	0.0741	0.0510	0.1064	0.0139
$M^3_{LR\ to\ LR}$	0.4631	0.0000	1.0000	1.9352

(e) 2007-2008

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^3_{CB}	0.4431	0.3894	0.4980	0.0278
S^3_{LR}	0.6062	0.5300	0.6776	0.0379
R^3_{CB}	0.5611	0.4727	0.6458	0.0446
R^3_{LR}	0.5465	0.4902	0.6016	0.0285
$R^3_{TF\ as\ YD}$	0.4618	0.3694	0.5568	0.0484
$R^3_{TF\ as\ SP1}$	1.0000	1.0000	1.0000	0.0000
$R^3_{TF\ as\ SP2}$	0.0398	0.0149	0.1019	0.0196
M^3_{CB}	0.6618	0.5989	0.7194	0.0309
M^3_{LR}	0.3498	0.0559	0.8303	0.2561
$M^3_{CB\ to\ LR}$	0.3382	0.2806	0.4011	0.0309
$M^3_{LR\ to\ CB}$	0.0424	0.0272	0.0655	0.0095
$M^3_{LR\ to\ LR}$	0.6079	0.1579	0.9276	0.2569

(f) 2008-2009

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^3_{CB}	0.6787	0.4060	0.8672	0.1255
S^3_{LR}	1.0000	1.0000	1.0000	0.0000
R^3_{CB}	0.5368	0.4491	0.6223	0.0446
R^3_{LR}	0.4261	0.3814	0.4720	0.0232
$R^3_{TF\ as\ YD}$	0.2637	0.1808	0.3674	0.0479
$R^3_{TF\ as\ SP1}$	0.8795	0.3686	0.9892	0.1366
$R^3_{TF\ as\ SP2}$	0.0019	0.0004	0.0077	0.0014
M^3_{CB}	0.7401	0.6187	0.8333	0.0552
M^3_{LR}	0.0657	0.0000	0.9927	0.2370
$M^3_{CB\ to\ LR}$	0.2599	0.1667	0.3813	0.0552
$M^3_{LR\ to\ CB}$	0.0148	0.0089	0.0247	0.0039
$M^3_{LR\ to\ LR}$	0.9194	0.0209	0.9998	0.2374

Appendix 2

This appendix contains supplementary material for Chapter 4 "A systematic methodology to determine birth years of fish from length measurements":

- Length criteria used to attribute a birth year to trout electrofished in autumn and spring in the Chicheron Brook (Tables A2.1 and A2.2);
- Length criteria used to attribute a birth year to juveniles caught in the downstream trap (Table A2.3);
- Length criteria used to attribute a birth year to trout electrofished in autumn in the Lesse River (Table A2.4).

Table A2.1: Length criteria for trout of age classes 0 and 1 of the Chicheron Autumn data set (2004-2009), according to the year of capture (means μ and standard deviations σ in centimetres).

Year	μ **age 0**	σ **age 0**	**Interval age 0**	μ **age 1**	σ **age 1**	**Interval age 1**
2004	5.8836	0.6768	[3.23; 7.54]	10.7983	1.3690	[8.05; 13.48]
2005	6.0242	0.6885	[3.33; 7.38]	9.9743	1.1754	[7.85; 12.28]
2006	6.5216	0.6810	[3.85; 8.03]	11.0435	1.2568	[8.52; 13.51]
2007	6.8497	0.8460	[3.53; 8.86]	11.1566	1.2013	[9.37; 13.51]
2008	5.9003	0.7361	[3.01; 7.62]	9.6751	0.9489	[8.04; 11.53]
2009	5.7414	0.6041	[3.37; 6.98]	9.2650	1.1687	[7.42; 11.56]

Table A2.2: Length criteria for trout of age classes 1 and 2 of the Chicheron Spring data set (2005-2009), according to the year of capture (means μ and standard deviations σ in centimetres).

Year	μ **age 1**	σ **age 1**	**Interval age 1**	μ **age 2**	σ **age 2**	**Interval age 2**
2005	7.3174	0.8396	[4.03; 9.39]	11.5945	1.0188	[9.85; 13.59]
2006	8.1374	0.8371	[4.86; 9.92]	11.4714	0.7098	[10.31; 12.86]
2007	7.7182	0.9202	[4.11; 9.44]	11.4952	0.9789	[9.92; 13.41]
2008	8.2598	1.0992	[3.95; 10.87]	12.7429	0.8146	[11.35; 14.34]
2009	6.9100	0.8557	[4.39; 8.72]	10.3851	0.8445	[9.15; 12.04]

Table A2.3: Length criteria for trout of age classes 0, 1 and 2 of the Juveniles Trap data set (2003-2009), according to the year and month of capture (age intervals in centimetres).

Data set	Age	Nov.	Dec.	Jan.	Feb.	March	April
2003	0	NA	NA	NA	NA	NA	NA
	1	[3.0; 6.6]	[3.0; 7.5]	[3.0; 7.5]	[3.0; 7.5]	[6.5; 8.6]	[6.5; 9.1]
	2	[8.9; 14.0]	[9.6; 14.0]	[9.3; 14.0]	[10.4; 14.0]	[11.2; 14.0]	[10.4; 14.0]
2004	0	NA	NA	NA	NA	NA	NA
	1	NA	NA	[7.0; 8.5]	[4.5; 6.5]	[4.0; 7.5]	[6.5; 9.1]
	2	NA	NA	[8.9; 14.0]	[9.0; 14.0]	[9.0; 14.0]	[10.5; 14.0]
2005	0	NA	NA	NA	NA	NA	NA
	1	NA	NA	[4.5; 6.8]	[4.5; 7.4]	[4.9; 8.2]	[5.5; 9.4]
	2	NA	NA	[8.5; 14.0]	[8.1; 14.0]	[9.8; 14.0]	[10.5; 14.0]
2006	0	NA	NA	NA	NA	NA	NA
	1	NA	[4.4; 8.6]	[4.5; 8.5]	[5.0; 8.5]	[4.9; 7.9]	[5.0; 8.3]
	2	NA	[9.0; 14.0]	[8.9; 14.0]	[9.4; 14.0]	[9.1; 14.0]	[9.5; 14.0]
2007	0	NA	NA	NA	NA	NA	NA
	1	[4.0; 8.0]	[4.5; 7.4]	[5.0; 7.5]	[5.5; 8.5]	[5.4; 8.4]	[5.4; 9.0]
	2	[11.0; 14.0]	[9.9; 14.0]	[9.0; 14.0]	[9.9; 14.0]	[9.6; 14.0]	[10.5; 15.0]
2008	0	NA	NA	NA	NA	NA	NA
	1	NA	[4.4; 8.5]	[4.5; 8.9]	[4.4; 9.6]	[4.5; 9.4]	[5.0; 9.7]
	2	NA	[10.0; 12.0]	[10.0; 14.0]	[11.7; 14.0]	[10.6; 14.0]	[10.9; 14.0]
2009	0	NA	NA	NA	NA	NA	NA
	1	NA	[4.0; 7.1]	[5.0; 7.4]	[5.0; 7.0]	[5.0; 8.3]	[4.0; 8.4]
	2	NA	[8.5; 11.5]	[8.5; 12.0]	[9.8; 12.5]	[9.6; 12.5]	[9.5; 13.5]

Data set	Age	May	June	July	Aug.	Sep.
2003	0	NA	[2.0; 5.0]	[2.0; 6.0]	NA	NA
	1	[6.0; 9.4]	[6.0; 10.1]	[7.0; 10.6]	NA	NA
	2	[10.5; 14.0]	[11.2; 14.0]	NA	NA	NA
2004	0	NA	NA	[2.0; 6.0]	[2.0; 6.0]	[2.0; 6.0]
	1	[6.5; 9.4]	[6.5; 10.0]	[7.0; 11.4]	NA	NA
	2	[10.5; 14.0]	[11.5; 14.0]	NA	NA	NA
2005	0	NA	NA	[2.0; 5.0]	[2.0; 6.5]	[2.0; 7.0]
	1	[6.0; 10.1]	[6.0; 11.0]	[6.5; 11.4]	[8.5; 11.0]	[7.6; 11.0]
	2	[11.5; 14.0]	NA	NA	[12.0; 15.0]	NA
2006	0	NA	[2.0; 5.5]	NA	NA	NA
	1	[6.0; 9.4]	[7.5; 10.4]	NA	NA	NA
	2	[10.6; 14.0]	[11.5; 13.5]	NA	NA	NA
2007	0	[2.0; 6.0]	[2.0; 7.0]	[2.0; 6.8]	[2.0; 7.4]	[2.0; 8.1]
	1	[6.9; 10.4]	[7.4; 14.0]	[8.4; 14.0]	[9.5; 13.0]	NA
	2	[11.8; 15.0]	NA	NA	NA	NA
2008	0	NA	[2.0; 6.3]	[2.0; 5.9]	[2.0; 6.4]	NA
	1	[5.9; 9.9]	[6.8; 11.4]	[6.9; 11.5]	[8.6; 10.0]	NA
	2	[11.1; 14.0]	[12.5; 15.0]	NA	NA	NA
2009	0	NA	[2.0; 5.6]	[2.0; 5.6]	NA	NA
	1	[4.0; 9.5]	[5.9; 10.4]	[6.4; 10.6]	NA	NA
	2	[10.4; 13.5]	[11.5; 15.0]	[11.7; 13.5]	NA	NA

Table A2.4: Length criteria for trout of age classes 0, 1, 2 and 3 of the Lesse Autumn data set (2003-2009), according to the year of capture (means μ and standard deviations σ in centimetres).

Year	μ **age 0**	σ **age 0**	**Interval age 0**	μ **age 1**	σ **age 1**	**Interval age 1**
2003	8.3013	0.8517	[7.44; 9.16]	11.8432	1.2346	[10.61; 13.07]
2004	8.3730	0.7918	[7.59; 9.16]	12.9389	1.2162	[11.72; 14.16]
2005	8.4812	1.0426	[7.54; 9.42]	12.9922	2.2557	[10.71; 15.28]
2006	8.4233	1.0151	[7.42; 9.43]	12.8110	0.8005	[11.96; 13.66]
2007	8.0867	0.5727	[7.27; 8.90]	12.5885	1.8814	[11.20; 13.98]
2008	7.6507	0.7699	[6.88; 8.42]	13.3825	2.1076	[12.33; 14.44]
2009	7.2913	0.8874	[6.43; 8.15]	12.6085	1.4605	[11.13; 14.09]
Data set	μ **age 2**	σ **age 2**	**Interval age 2**	μ **age 3**	σ **age 3**	**Interval age 3**
2003	15.3851	1.6175	[14.59; 16.18]	18.9271	2.0004	[17.75; 20.11]
2004	17.5048	1.6406	[16.68; 18.33]	22.0708	2.0650	[20.83; 23.32]
2005	17.5033	1.7792	[16.64; 18.36]	22.0144	1.7602	[20.91; 23.12]
2006	17.1987	1.7950	[16.31; 18.09]	21.5864	1.5556	[20.68; 22.49]
2007	17.0902	1.4934	[16.32; 17.86]	21.5920	1.9589	[20.31; 22.88]
2008	16.5561	1.4548	[15.82; 17.29]	19.9599	1.7441	[18.94; 20.98]
2009	16.5932	1.9745	[15.62; 17.57]	20.3786	2.4355	[18.94; 21.81]

Appendix 3

This appendix contains supplementary material for Chapter 6 "Simulating brown trout demogenetics in a river / nursery brook system: the individual-based model DemGenTrout":

- Annual number of brown trout caught and tagged at the trapping facility, Table A3.1;
- Alleles and allelic frequencies used to initialise trout genotypes in the model, Table A3.2;
- Annual population size and length distribution of brown trout in autumn in each stream, Table A3.3;
- Values of effective number of alleles, inbreeding coefficients, and fixation index, Table A3.4;
- Alleles and allelic frequencies used to initialise the genotypes of stocked trout in the model, Table A3.5.

Table A3.1: Annual number of brown trout caught and tagged at the trapping facility (2004-2011). Individuals passing through the upstream trap are mature adults, swimming from the Lesse River to the Chicheron Brook for reproduction. Individuals caught at the downstream trap (i.e., moving from the brook to the Lesse River) are either spawners coming back from the brook, or young trout migrating from it for the first time.

Year	Upswimming spawners	Downswimming spawners	Downswimming age-1 trout	Downswimming age-2 trout
2004-2005	167	117	519	259
2005-2006	145	36	168	304
2006-2007	216	111	205	187
2007-2008	222	120	1044	217
2008-2009	124	32	813	196
2009-2010	142	43	260	150
2010-2011	168	83	276	180

Table A3.2: Alleles and allelic frequencies used to initialise the trout genotypes in each stream, derived from the 144 individuals sampled in 2003 in the downstream trap, and in autumn 2004 in the brook and the river (C: Chicheron Brook, L: Lesse River).

Locus	Stream C	Stream L	Locus	Stream C	Stream L
SsoSL417	168/174 (0.03)	168/176 (0.02)	SsoSL438	095/099 (0.03)	095/097 (0.04)
	168/176 (0.04)	172/174 (0.02)		095/107 (0.01)	095/099 (0.02)
	168/183 (0.01)	172/176 (0.02)		097/097 (0.01)	095/105 (0.02)
	168/189 (0.01)	174/176 (0.08)		097/099 (0.06)	097/097 (0.02)
	170/181 (0.01)	174/189 (0.02)		097/101 (0.03)	097/099 (0.08)
	172/176 (0.02)	176/176 (0.52)		097/105 (0.14)	097/101 (0.04)
	172/183 (0.01)	176/178 (0.02)		097/107 (0.07)	097/105 (0.02)
	174/174 (0.01)	176/181 (0.08)		099/099 (0.04)	099/099 (0.13)
	174/176 (0.13)	176/183 (0.04)		099/101 (0.04)	099/101 (0.04)
	174/181 (0.02)	176/187 (0.06)		099/105 (0.29)	099/105 (0.17)
	176/176 (0.57)	176/189 (0.04)		099/107 (0.05)	099/107 (0.10)
	176/178 (0.01)	176/191 (0.04)		101/101 (0.01)	099/125 (0.02)
	176/181 (0.04)	191/191 (0.02)		101/105 (0.04)	101/101 (0.04)
	176/183 (0.02)			105/105 (0.13)	101/105 (0.02)
	176/189 (0.03)			105/107 (0.04)	105/105 (0.13)
	176/191 (0.01)				105/107 (0.08)
	181/191 (0.01)				107/125 (0.02)
	183/183 (0.01)				
SsoSL85	176/180 (0.02)	178/180 (0.17)	Ssa197	128/128 (0.02)	128/128 (0.02)
	176/182 (0.01)	178/182 (0.04)		128/132 (0.18)	128/132 (0.17)
	178/178 (0.07)	178/188 (0.02)		128/136 (0.02)	128/136 (0.04)
	178/180 (0.11)	178/192 (0.02)		128/140 (0.04)	128/140 (0.02)
	178/182 (0.03)	180/180 (0.44)		128/156 (0.01)	128/144 (0.02)
	178/196 (0.01)	180/182 (0.10)		132/132 (0.51)	128/156 (0.04)
	180/180 (0.51)	180/190 (0.02)		132/136 (0.15)	132/132 (0.40)
	180/182 (0.19)	180/192 (0.06)		132/140 (0.01)	132/136 (0.15)
	180/196 (0.02)	182/182 (0.08)		132/144 (0.01)	132/140 (0.13)
	182/182 (0.01)	182/190 (0.02)		132/152 (0.03)	132/148 (0.02)

Table A3.2: Alleles and allelic frequencies used to initialise trout genotypes in each stream (continued).

Locus	Stream C	Stream L	Locus	Stream C	Stream L
	194/210 (0.01)	192/192 (0.02)		132/156 (0.02)	
Ssa85	105/113 (0.01)	105/109 (0.02)	Str15	211/219 (0.01)	219/219 (0.27)
	111/113 (0.15)	105/111 (0.02)		219/219 (0.28)	219/221 (0.06)
	111/115 (0.01)	105/115 (0.02)		219/221 (0.22)	219/223 (0.08)
	111/117 (0.04)	109/113 (0.02)		219/223 (0.06)	219/225 (0.25)
	113/113 (0.42)	111/113 (0.04)		219/225 (0.16)	221/221 (0.02)
	113/115 (0.20)	113/113 (0.40)		221/221 (0.02)	221/223 (0.10)
	113/117 (0.13)	113/115 (0.33)		221/223 (0.07)	221/225 (0.19)
	113/119 (0.03)	113/117 (0.02)		221/225 (0.09)	223/229 (0.02)
	115/115 (0.01)	113/119 (0.04)		221/227 (0.02)	
	117/117 (0.01)	115/115 (0.04)		223/225 (0.02)	
		115/117 (0.04)		225/225 (0.04)	
Str73	138/138 (0.01)	138/142 (0.10)	Str60	094/094 (0.16)	094/094 (0.10)
	138/142 (0.25)	138/144 (0.04)		094/098 (0.43)	094/098 (0.46)
	138/144 (0.07)	140/142 (0.02)		098/098 (0.42)	098/098 (0.44)
	142/142 (0.38)	142/142 (0.42)			
	142/144 (0.19)	142/144 (0.33)			
	144/144 (0.10)	144/144 (0.08)			
Ssa171	225/225 (0.46)	225/225 (0.48)	Str85	148/148 (0.16)	148/148 (0.23)
	225/227 (0.14)	225/227 (0.09)		148/160 (0.51)	148/158 (0.02)
	225/229 (0.04)	225/229 (0.04)		148/168 (0.06)	148/160 (0.26)
	225/231 (0.01)	225/231 (0.02)		158/160 (0.03)	148/168 (0.02)
	225/235 (0.01)	225/239 (0.02)		160/160 (0.17)	148/174 (0.04)
	225/237 (0.04)	225/242 (0.11)		160/164 (0.01)	158/160 (0.02)
	225/240 (0.01)	227/227 (0.02)		160/168 (0.03)	158/168 (0.06)
	225/242 (0.07)	227/237 (0.02)		160/174 (0.02)	160/160 (0.17)
	227/227 (0.05)	227/242 (0.04)		168/174 (0.01)	160/168 (0.06)
	227/239 (0.01)	229/249 (0.02)			160/174 (0.04)
	227/242 (0.04)	237/237 (0.02)			168/172 (0.02)
	229/237 (0.01)	237/245 (0.02)			168/174 (0.02)
	237/237 (0.01)	239/239 (0.02)			168/176 (0.02)
	237/242 (0.01)	239/244 (0.02)			
	239/242 (0.01)	240/253 (0.02)			
	242/242 (0.04)	243/243 (0.02)			
	242/244 (0.01)				
	242/259 (0.01)				
	244/258 (0.01)				
Ssa408	202/245 (0.01)	206/278 (0.02)	T3-13	186/199 (0.01)	186/199 (0.04)
	206/238 (0.01)	214/238 (0.02)		186/203 (0.01)	193/199 (0.02)
	210/230 (0.01)	214/242 (0.02)		186/219 (0.02)	195/199 (0.02)
	210/242 (0.01)	214/246 (0.02)		188/203 (0.01)	195/227 (0.02)
	210/257 (0.01)	214/257 (0.02)		193/193 (0.01)	197/199 (0.02)
	214/226 (0.01)	214/278 (0.02)		193/199 (0.01)	197/203 (0.02)
	214/242 (0.04)	218/242 (0.02)		193/203 (0.01)	197/215 (0.02)

Table A3.2: Alleles and allelic frequencies used to initialise trout genotypes in each stream (continued).

Locus	Stream C	Stream L	Locus	Stream C	Stream L
	214/250 (0.01)	218/253 (0.02)		197/199 (0.03)	199/199 (0.33)
	214/278 (0.01)	218/266 (0.02)		197/219 (0.03)	199/203 (0.06)
	222/238 (0.01)	222/238 (0.02)		199/199 (0.42)	199/205 (0.04)
	222/266 (0.01)	222/242 (0.02)		199/203 (0.07)	199/217 (0.02)
	226/230 (0.01)	226/266 (0.02)		199/205 (0.01)	199/221 (0.02)
	226/242 (0.01)	230/230 (0.02)		199/215 (0.02)	199/227 (0.06)
	226/250 (0.02)	230/246 (0.02)		199/217 (0.01)	199/231 (0.10)
	226/257 (0.01)	230/250 (0.02)		199/219 (0.07)	203/211 (0.02)
	226/261 (0.01)	230/258 (0.02)		199/227 (0.02)	203/219 (0.02)
	230/230 (0.01)	232/242 (0.02)		199/231 (0.07)	205/211 (0.02)
	230/238 (0.02)	234/238 (0.02)		199/235 (0.03)	217/231 (0.02)
	230/242 (0.01)	234/242 (0.02)		201/201 (0.03)	219/223 (0.02)
	230/250 (0.01)	236/242 (0.02)		203/203 (0.01)	219/231 (0.04)
	230/257 (0.01)	238/238 (0.02)		203/219 (0.01)	221/231 (0.02)
	230/261 (0.01)	238/242 (0.04)		203/221 (0.01)	227/231 (0.02)
	230/266 (0.01)	238/246 (0.02)		203/227 (0.01)	
	230/274 (0.02)	238/258 (0.02)		205/233 (0.01)	
	230/278 (0.01)	238/261 (0.02)		219/219 (0.02)	
	234/242 (0.02)	242/242 (0.04)		219/231 (0.01)	
	234/246 (0.01)	242/246 (0.04)		231/231 (0.01)	
	234/250 (0.01)	242/257 (0.02)			
	234/265 (0.01)	242/261 (0.02)			
	234/274 (0.02)	242/274 (0.02)			
	238/242 (0.02)	242/278 (0.02)			
	238/245 (0.02)	245/266 (0.02)			
	238/246 (0.03)	246/246 (0.02)			
	238/257 (0.01)	246/258 (0.02)			
	238/261 (0.04)	246/261 (0.04)			
	238/265 (0.02)	250/254 (0.02)			
	238/266 (0.01)	250/278 (0.02)			
	238/274 (0.01)	253/278 (0.02)			
	238/278 (0.01)	254/261 (0.02)			
	242/242 (0.01)	257/278 (0.02)			
	242/245 (0.02)	258/258 (0.02)			
	242/246 (0.02)	261/265 (0.02)			
	242/250 (0.01)	261/278 (0.04)			
	242/254 (0.01)				
	242/258 (0.02)				
	242/261 (0.04)				
	242/278 (0.02)				
	245/245 (0.01)				
	246/261 (0.02)				
	250/250 (0.03)				
	250/257 (0.01)				

Table A3.2: Alleles and allelic frequencies used to initialise trout genotypes in each stream (continued).

Locus	Stream C	Stream L	Locus	Stream C	Stream L
	250/258 (0.02)				
	250/261 (0.01)				
	250/270 (0.01)				
	250/278 (0.01)				
	253/266 (0.01)				
	253/274 (0.01)				
	254/257 (0.01)				
	254/258 (0.02)				
	257/257 (0.01)				
	257/261 (0.01)				
	258/261 (0.02)				
	261/274 (0.01)				
	261/278 (0.02)				
	262/278 (0.01)				
	270/274 (0.01)				

Table A3.3: Annual population size and length distribution (mean ± standard deviation in mm) of brown trout in autumn in each stream, over the years 2004-2011 (C: Chicheron Brook, L: Lesse River). Population sizes were estimated by fitting capture-recapture models to electrofishing data, and length distributions were obtained from measurements of these electrofished individuals.

Year	Population size (stream C)	Population size (stream L)	Length distribution (stream C)	Length distribution (stream L)
2004-2005	818	1152	85.41 ± 33.22	195.62 ± 42.77
2005-2006	1419	1253	89.18 ± 30.55	183.66 ± 50.44
2006-2007	905	1027	96.21 ± 32.16	193.73 ± 46.51
2007-2008	2196	975	83.52 ± 29.86	200.36 ± 50.66
2008-2009	1365	1375	78.49 ± 29.84	177.95 ± 60.71
2009-2010	1094	1448	79.98 ± 28.98	172.37 ± 53.88
2010-2011	1232	1416	75.95 ± 23.21	177.85 ± 51.30

Table A3.4: Values of (a) effective number of alleles E_A and inbreeding coefficient F_{IS} in each of the five groups of trout, CRa, CRb, CMa, EXa and EXb, and (b) fixation index F_{ST} between groups. The groups correspond to residents born in the Chicheron Brook sampled in 2004 (CRa) and 2008 (CRb), migrants born in the Chicheron Brook sampled in 2003 (CMa), and individuals native to the Lesse River or another tributary with unknown behaviour sampled in 2004 (EXa) and 2008 (EXb).

(a)

Group	E_A	F_{IS}
CRa	1.66	0.0466
CRb	1.73	0.1017
CMa	1.77	0.0360
EXa	1.62	0.0671
EXb	1.57	0.0136

(b)

Compared groups	F_{ST}
CRa *vs* CMa	0.0068
CRa+CMa *vs* EXa	0.0018
CRa *vs* CRb	0.0019
EXa *vs* EXb	0.0024

Table A3.5: Alleles and allelic frequencies used to initialise the stocked trout genotypes, derived from the 48 individuals sampled in 2008 in the Mirwart Hatchery (Saint-Hubert, Belgium).

Locus	**Values**	**Locus**	**Values**	**Locus**	**Values**
SsoSL417	170/174 (0.04)	Ssa197	128/132 (0.02)	Str85	148/148 (0.13)
	170/176 (0.02)		128/140 (0.04)		148/158 (0.02)
	170/181 (0.02)		132/132 (0.15)		148/168 (0.23)
	170/191 (0.02)		132/136 (0.13)		148/172 (0.06)
	172/172 (0.04)		132/140 (0.10)		148/174 (0.04)
	172/174 (0.08)		132/144 (0.06)		148/176 (0.02)
	172/185 (0.02)		132/152 (0.02)		148/178 (0.08)
	172/189 (0.02)		132/160 (0.02)		158/172 (0.02)
	172/191 (0.04)		136/136 (0.02)		158/178 (0.02)
	174/174 (0.06)		136/140 (0.10)		160/164 (0.04)
	174/176 (0.15)		136/144 (0.02)		160/168 (0.02)
	174/181 (0.04)		136/148 (0.04)		160/176 (0.02)
	174/183 (0.04)		136/156 (0.02)		164/168 (0.06)
	174/185 (0.02)		140/140 (0.06)		168/172 (0.06)
	174/187 (0.08)		140/144 (0.08)		168/176 (0.02)
	174/189 (0.04)		140/148 (0.02)		172/172 (0.04)
	174/191 (0.02)		140/156 (0.02)		172/174 (0.02)
	176/176 (0.06)		144/152 (0.02)		172/178 (0.04)
	176/181 (0.04)		148/148 (0.02)		174/176 (0.02)
	176/185 (0.02)		148/156 (0.02)		176/176 (0.02)
	176/187 (0.02)				
	176/191 (0.02)				
	181/183 (0.02)				
	181/191 (0.02)				
	183/187 (0.02)				
SsoSL438	098/098 (0.02)	SsoSL85	166/178 (0.02)	Ssa85	103/109 (0.02)

Table A3.5: Alleles and allelic frequencies used to initialise the stocked trout genotypes (continued).

Locus	Values	Locus	Values	Locus	Values
	098/100 (0.15)		166/180 (0.06)		103/113 (0.04)
	098/102 (0.02)		166/182 (0.02)		105/105 (0.02)
	098/104 (0.08)		168/182 (0.02)		105/111 (0.15)
	098/106 (0.08)		176/178 (0.04)		105/113 (0.15)
	098/108 (0.06)		178/178 (0.33)		105/115 (0.06)
	100/100 (0.02)		178/180 (0.17)		109/111 (0.02)
	100/102 (0.02)		178/182 (0.02)		109/113 (0.02)
	100/106 (0.15)		178/186 (0.06)		111/111 (0.02)
	100/108 (0.02)		178/190 (0.02)		111/113 (0.15)
	102/102 (0.04)		178/192 (0.02)		111/115 (0.02)
	102/106 (0.10)		180/180 (0.13)		113/113 (0.08)
	102/108 (0.02)		180/182 (0.02)		113/115 (0.19)
	104/106 (0.04)		180/186 (0.02)		115/115 (0.06)
	104/108 (0.02)		180/192 (0.02)		
	106/106 (0.10)		182/186 (0.02)		
	106/108 (0.02)				
	108/108 (0.02)				
Str15	219/221 (0.13)	Str73	138/138 (0.02)	Str60	093/093 (0.42)
	219/223 (0.02)		138/140 (0.02)		093/097 (0.40)
	219/225 (0.08)		138/142 (0.04)		093/103 (0.02)
	221/221 (0.04)		138/144 (0.10)		097/097 (0.17)
	221/223 (0.17)		140/142 (0.08)		
	221/225 (0.15)		140/144 (0.02)		
	221/227 (0.02)		142/142 (0.06)		
	223/223 (0.19)		142/144 (0.29)		
	223/225 (0.15)		144/144 (0.35)		
	225/225 (0.06)				
Ssa408	206/214 (0.02)	T3-13	186/193 (0.04)	Ssa171	225/225 (0.08)
	206/246 (0.02)		186/195 (0.02)		225/229 (0.04)
	210/214 (0.02)		186/197 (0.02)		225/234 (0.02)
	210/282 (0.04)		186/203 (0.02)		225/239 (0.02)
	214/214 (0.04)		186/215 (0.02)		225/241 (0.02)
	214/218 (0.02)		186/223 (0.02)		227/229 (0.02)
	214/230 (0.02)		186/227 (0.04)		227/236 (0.02)
	214/234 (0.02)		188/201 (0.02)		229/229 (0.15)
	214/242 (0.08)		188/205 (0.02)		229/239 (0.06)
	214/246 (0.06)		193/193 (0.02)		229/240 (0.02)
	214/249 (0.02)		193/195 (0.06)		229/247 (0.02)
	214/270 (0.02)		193/197 (0.02)		231/239 (0.02)
	218/218 (0.02)		193/199 (0.02)		232/247 (0.02)
	218/236 (0.02)		193/201 (0.04)		236/240 (0.02)
	218/258 (0.02)		193/221 (0.04)		237/239 (0.06)
	222/236 (0.02)		193/227 (0.04)		237/251 (0.02)
	230/236 (0.02)		195/197 (0.02)		239/251 (0.02)

Table A3.5: Alleles and allelic frequencies used to initialise the stocked trout genotypes (continued).

Locus	Values	Locus	Values	Locus	Values
	230/238 (0.02)		195/199 (0.04)		239/258 (0.15)
	230/242 (0.06)		195/201 (0.06)		239/266 (0.02)
	230/250 (0.02)		195/215 (0.02)		240/261 (0.02)
	236/238 (0.02)		195/221 (0.02)		241/250 (0.02)
	236/246 (0.02)		197/201 (0.02)		247/250 (0.02)
	236/254 (0.02)		199/215 (0.02)		247/258 (0.02)
	238/254 (0.02)		199/221 (0.04)		249/251 (0.02)
	242/242 (0.08)		199/227 (0.04)		249/257 (0.02)
	242/246 (0.02)		199/246 (0.02)		253/255 (0.02)
	242/250 (0.02)		201/209 (0.02)		255/263 (0.02)
	242/254 (0.02)		201/221 (0.06)		258/261 (0.02)
	242/257 (0.02)		205/221 (0.02)		
	242/258 (0.02)		205/227 (0.02)		
	242/262 (0.04)		217/223 (0.02)		
	246/250 (0.02)		219/225 (0.02)		
	246/254 (0.02)		219/227 (0.02)		
	250/250 (0.02)		221/227 (0.02)		
	250/258 (0.02)				

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Université catholique de Louvain
Faculté d'ingénierie biologique, agronomique et environnementale
Earth and Life Institute – Agronomy
Genetics, Reproduction, Population

Croix du Sud 2, boîte L7.05.14, 1348 Louvain-la-Neuve
Tél. : + 32 (0) 10 47 37 23 – fax : + 32 (0) 10 47 24 28
E-mail : Beatrice.Frank@gmail.com
www.uclouvain.be/gena-pops

The brown trout (*Salmo trutta* L.) is one of the vertebrate species presenting the highest degree of intraspecific biological diversity. 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, by providing (i) a descriptive tool to study the functioning of a brown trout population at the stream scale, (ii) a predictive tool to evaluate the medium-term impacts of anthropogenic disturbances on native populations.

The DemGenTrout model was first parameterized with demographic, genetic, and environmental data collected over 5 years on the Lesse River drainage (Belgium). A methodology for attributing a birth year to tagged trout of this hydrological system was developed. This information was used to determine the values of several parameters of the main four processes of the model (i.e., survival, growth, reproduction, movement). Second, the model was optimized and validated using the Pattern-oriented modelling strategy, which consists of systematically testing how well the model reproduces multiple patterns observed in the field. Third, the sensitivity of the model to its parameters was analysed.

Two scenarios mimicking anthropogenic disturbances were simulated over 35 years: (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, whereas 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.

Béatrice Frank was born in Ottignies (Belgium) in 1984. She received her Master of Environmental Bio-engineering from UCL in 2007.