InSTREAM-Gen: Modelling eco-evolutionary dynamics of trout populations under anthropogenic environmental change

Daniel Ayllón [a,*], Steven F. Railsback [b,c], Simone Vincenzi [d,e], Jürgen Groeneveld [a], Ana Almodóvar [f], Volker Grimm [a,g,h]

[a] *Helmholtz Centre for Environmental Research – UFZ, Department of Ecological Modelling, Permoserstr. 15, 04318 Leipzig, Germany*
[b] *Humboldt State University, Department of Mathematics, 1 Harpst Street, Arcata, CA 95521, USA*
[c] *Lang Railsback & Associates, 250 California Avenue, Arcata, CA 95521, USA*
[d] *University of California Santa Cruz, Center for Stock Assessment Research and Department of Applied Mathematics and Statistics, Santa Cruz, CA 95064, USA*
[e] *Politecnico di Milano, Dipartimento di Elettronica, Informazione e Bioingegneria, Via Ponzio 34/5, Milan 20133, Italy*
[f] *Complutense University of Madrid, Faculty of Biology, Department of Zoology, José Antonio Novais 2, 28040 Madrid, Spain*
[g] *University of Potsdam, Institute for Biochemistry and Biology, Maulbeerallee 2, 14469 Potsdam, Germany*
[h] *German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany*

ABSTRACT

Current rates of environmental change are exceeding the capacity of many populations to adapt to new conditions and thus avoid demographic collapse and ultimate extinction. In particular, cold-water freshwater fish species are predicted to experience strong selective pressure from climate change and a wide range of interacting anthropogenic stressors in the near future. To implement effective management and conservation measures, it is crucial to quantify the maximum rate of change that cold-water freshwater fish populations can withstand. Here, we present a spatially explicit eco-genetic individual-based model, *inSTREAM-Gen*, to predict the eco-evolutionary dynamics of stream-dwelling trout under anthropogenic environmental change. The model builds on a well-tested demographic model, which includes submodels of river dynamics, bioenergetics, and adaptive habitat selection, with a new genetic module that allows exploration of genetic and life-history adaptations to new environments. The genetic module models the transmission of two key traits, size at emergence and maturity size threshold. We parameterized the model for a brown trout (*Salmo trutta* L.) population at the warmest edge of its range to validate it and analyze its sensitivity to parameters under contrasting thermal profiles. To illustrate potential applications of the model, we analyzed the population's demographic and evolutionary dynamics under scenarios of (1) climate change-induced warming, and (2) warming plus flow reduction resulting from climate and land use change, compared to (3) a baseline of no environmental change. The model predicted severe declines in density and biomass under climate warming. These declines were lower than expected at range margins because of evolution towards smaller size at both emergence and maturation compared to the natural evolution under the baseline conditions. Despite stronger evolutionary responses, declining rates were substantially larger under the combined warming and flow reduction scenario, leading to a high probability of population extinction over contemporary time frames. Therefore, adaptive responses could not prevent extinction under high rates of environmental change. Our model demonstrates critical elements of next generation ecological modelling aiming at predictions in a changing world as it accounts for spatial and temporal resource heterogeneity, while merging individual behaviour and bioenergetics with microevolutionary adaptations.

© 2015 Elsevier B.V. All rights reserved.

* Corresponding author. Tel.: +49 341 235 1279; fax: +49 341 235 1473.
E-mail address: daniel.ayllon@ufz.de (D. Ayllón).

1. Introduction

Climate change and a wide range of interacting anthropogenic stressors are increasingly impacting global ecological systems and consequently causing elevated rates of population extinction (Brook et al., 2008). It is expected that without mitigation policies on-going climate change will push even common and widespread ecosystems and species beyond their capacity to recover (Warren et al., 2013). Quantifying the maximum rate of environmental change that populations can cope with becomes critical to devise adaptive management responses to global environmental change (Chevin et al., 2010; Brown et al., 2011). West et al. (2009) warned that successful management of natural resources under global environmental change will require managers and decision makers to cycle between "managing for resilience" and "managing for change", which involves identifying settings where management can influence the trajectory of ecosystem shifts towards new undesirable states. Ecological models are an indispensable tool for supporting environmental decision making by exploring the consequences of alternative policies or management scenarios (Schmolke et al., 2010; Stillman et al., 2015).

As the climate changes, species respond by adapting to the new conditions through either genetic evolution or phenotypic plasticity, by migrating towards favourable climates, or by going locally or globally extinct (Settele et al., 2014). Since migrating to track optimal environments is unfeasible for populations of many species, they will have to adapt locally to avoid extinction, particularly when demographic rescue from neighbouring populations is unlikely or impossible (Reed et al., 2011; Vedder et al., 2013). Local adaptation is the sole option for fully resident aquatic organisms living in freshwaters, land-locked networks where dispersal is limited and temperature is destiny. These ecosystems have already suffered more from human activities than marine and terrestrial ecosystems, and climate change will certainly pose additional threats directly (e.g., temperature and precipitation changes) and indirectly through interactions with other anthropogenic drivers (e.g., land use change) and stressors (e.g., water quality deterioration) (Jiménez Cisneros et al., 2014). In particular, freshwater fish species are experiencing higher extirpation rates than terrestrial organism as shifts in range towards higher elevation or latitude are not keeping pace with the rate of warming in streams and rivers (Comte and Grenouillet, 2013). Especially dramatic is the case of cold-water species such as salmonids, which have already experienced shrinking thermal habitat and will likely experience a strong contraction in distribution, decline in population size and extinction of isolated populations (see review by Comte et al., 2013). Global environmental change therefore sets hard challenges for monitoring, modelling and, ultimately, managing freshwater ecosystems.

Most studies assessing the impact of environmental change on species persistence and distribution rely on species distribution models (also referred to as habitat, niche, or climate envelope models), which are based on statistical approaches. Aside from some important methodological limitations, this approach does not account for the biological processes underlying adaptation of a species to its environment (Chevin et al., 2010). Local adaptation should lead to lower risks of extinction than predicted from statistical correlations between current distribution and climate (Botkin et al., 2007). Further, niche models cannot predict population demographic changes, but can only use shifts in suitable environments to infer where local populations might decline or increase.

Similarly, traditional population models based on empirical approaches are limited on their predictive scope because empirically determined demographic rates are valid only for the environmental conditions under which they were observed and may not hold for the new circumstances for which predictions are required (Evans, 2012; Stillman et al., 2015). In contrast, mechanistic population modelling allows identification of factors and processes that potentially limit population persistence in a changing environment (Chevin et al., 2010). Mechanistic models can simulate how direct changes in species' vital rates and indirect effects through consumer-resource interactions emerge from changing environments (Grimm and Railsback, 2005). However, most of such models focus so far on emerging changes in demography but do not take into account adaptation due to microevolution. Mechanistic eco-genetic modelling is a new approach that provides an integrative framework for studying demographic and life-history evolution at contemporary timescales and in realistically complex ecological settings (Dunlop et al., 2009), such as those posed by synergistic interactions among climate change and other anthropogenic drivers (e.g., land use change).

The genetic component of an eco-genetic model tracks the evolution of the distribution of heritable quantitative traits over generations, while the ecological component accounts for aspects of an individual's environment that are relevant to the evolutionary process (Dunlop et al., 2009). Although eco-genetic models need not be individual-based, individual-based modelling is a natural fit for eco-genetic modelling as it easily accounts for the demographic, genetic and spatial dimensions of individual variability (Frank et al., 2011). An increasing number of individual-based models (IBMs) incorporating a genetic structure have been recently developed and applied to salmonids (Thériault et al., 2008; Wang and Hook, 2009; Reed et al., 2011; Piou and Prévost, 2012; Vincenzi et al., 2012a, 2014; Frank and Baret, 2013). However, none of them represents the spatial dimension at the finest level (i.e., microhabitat scale) or model fish energetics.

Effects of habitat type and quality on individual fitness are strongest and best explained at the microhabitat spatial scale because riverscapes are highly spatially heterogeneous and trout are typically stationary feeders that hold relatively fixed positions from which they make short forays to feed (Fausch, 1984). Energetics are often critical for IBMs, because energy allocation is a key way in which organisms relate behaviour to fitness (Martin et al., 2013; Stillman et al., 2015). In spatially explicit IBMs that account for bioenergetics such as inSTREAM (Railsback et al., 2009) or inSALMO (Railsback et al., 2013), not only do population-level responses (e.g., demographic rates) emerge from the properties of the system but behavioural (e.g., habitat selection) and life-history (e.g., individual growth rate) traits of individuals also emerge from their interactions with other individuals and with their environment. These models therefore provide a strong mechanistic link between phenotypic traits and environmental conditions, which enhances their ability to model population demography in changing environments.

In addition, inSTREAM and inSALMO are underpinned by "state- and prediction-based theory" (Railsback and Harvey, 2013), a new approach that combines existing trade-off methods with routine updating: individuals make a prediction of the future growth and risk conditions over an entire time horizon under alternative behaviours, but update their decision daily by considering how their internal state and external conditions have changed, so that they can continually select alternatives providing high future fitness. This process enables individuals to respond adaptively to (1) feedbacks of their own behaviour and the behaviour of competitors, predators and food resources, and (2) other changes in their environment. It provides therefore a general method to model foraging in a way that both produces and responds to complex population-level dynamics, such as trait-mediated trophic interactions, in a biologically realistic manner (see Railsback and Harvey, 2013).

To provide the most realistic predictions under novel environmental conditions, next generation ecological modelling has to account for spatial and temporal resource heterogeneity at

different scales and levels of organization, while merging individual variability and behaviour with microevolution. In this work, we present the inSTREAM-Gen individual-based model, which was designed to model the effects of environmental conditions and anthropogenic disturbances on the evolution of demographics and life-history strategies of stream-dwelling trout populations. Therefore, it is particularly suited to simulate the eco-evolutionary consequences of river management decisions for fish population dynamics and persistence under a climate change context. InSTREAM-Gen is an eco-genetic version of inSTREAM, with genetic transmission of traits to allow evolutionary changes in trout life history. We describe the model and the calibration of its parameters to a brown trout (*Salmo trutta* L.) population at the warmest edge of its range, and then validate it against field observations and assess its sensitivity to model parameters under contrasting thermal profiles. To show potential applications of inSTREAM-Gen, we analyze the population's demographic and evolutionary dynamics under two simulation scenarios involving (1) warming resulting from climate change, and (2) climate change-induced warming plus stream flow reduction resulting from land use change, compared to (3) a baseline that includes the potential for evolutionary dynamics, but with no environmental change. We included the potential for evolution of heritable traits under the baseline scenario because we cannot exclude either that (a) evolutionary processes (i.e. adaptive evolution, genetic drift) are currently occurring in the population, or that (b) calibration may lead to life-history parameters which are not maximizing fitness under the given conditions.

2. Materials and methods

2.1. Model description

In the Supplementary Material (Appendix A), we provide a TRACE document ("TRAnsparent and Comprehensive model Evaluation"; Schmolke et al., 2010; Grimm et al., 2014; Augusiak et al., 2014) containing evidence that our model was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

InSTREAM-Gen was implemented in the freely available software platform NetLogo 5.0.4 (Wilensky, 1999). Computer code is provided in Appendix B. A detailed model description that follows the ODD (Overview, Design concepts, Details) protocol for describing individual-based models (Grimm et al., 2006, 2010) is provided in Section 2 ("Model description") of the aforementioned TRACE document. Here, we only give an overview of the model's overall structure and processes.

The model simulates the complete trout life cycle using a daily time step, with daily mean values of stream flow and water temperature as the driving environmental variables (Fig. 1). The model was designed with an individual-based eco-genetic structure and is spatially explicit. The ecological structure of the model is a replicate of the individual-based Stream Trout Research and Assessment Model (inSTREAM, version 4.2; Railsback et al., 2009). We thereby adopted existing model parameters and processes, with simplifications and minor modifications described in Sections 4 ("Conceptual model evaluation") and 5 ("Implementation verification") of the TRACE document (Appendix A). We added an inheritance model to allow for the genetic transmission of two fitness-related traits: size at emergence and size maturity threshold. The model represents one reach of a stream, typically a few hundred metres in length. It includes as entities cells, trout, and redds. Cells are objects that represent patches of relatively uniform habitat within the reach, and are characterized by both their physical habitat (mean depth and water velocity that are functions of stream flow, area of velocity shelter for drift feeding, spawning gravel area, and mean distance

to hiding cover), and their production rate of two different kinds of food, drift and search (stationary) food. Trout are modelled as individuals with unique values of body length, weight and condition, and both phenotypic and genotypic (or breeding) values for the heritable traits. Redds are spawning nests made by trout, which are modelled as individual objects with variables for the number and development status of the eggs they contain. Redds also carry the genetic information of the female spawner who created the redd and of the male spawners who fertilized the eggs, to be transmitted to the offspring. A complete and commented list of the model's entities and their variables can be found in Appendix C (worksheet "Entities state variables"). On each daily time step, the individual entities execute the following actions in the same predetermined order:

2.1.1. Habitat update

Reach's daily flow and temperature values, as well as the depth and velocity of each cell, are updated from input files. Food availability in each cell is calculated from its area, depth, velocity, and the reach's food parameters.

2.1.2. Trout spawning

Adult female trout determine whether they are ready to spawn, which depends on environmental conditions (date, temperature, and flow magnitude and steadiness) and on their own state (age, phenotypic maturity length threshold, length, and condition). If ready, female trout select and move to the cell having the best spawning quality and create a redd. The number of eggs increases with female length and is traded off with egg size, as female salmonids have limited energy resources available for egg production and limited body cavity for accommodation of the eggs (reviewed by Jonsson and Jonsson, 2011). In trout, egg size is strongly correlated with size of the offspring (Elliott, 1984; Einum and Fleming, 1999). To mimic this pattern, and since we modelled size at emergence as a heritable trait, egg size increases in our model with the genotypic value of size at emergence of the spawner (see emergence and genetic transmission of traits below). That is, females that have a larger genotypic value of size at emergence produce larger but fewer eggs than average females. Female trout spawn in descending order of length and the largest available male spawner plus a random number (between zero and three) of smaller males fertilize the eggs. The largest eligible male is always chosen because the largest males on the spawning ground usually achieve the highest reproductive success and monopolize most of the mating opportunities (summarized in Esteve, 2005, and Jonsson and Jonsson, 2011). Polygamy is a common mating strategy in trout breeding systems (e.g., García-Vázquez et al., 2001). The genotypic value of heritable traits of the mother and all fathers are stored in the genetic trait map of the redd. Spawners incur a weight loss to represent the energetic cost of spawning. While female trout can only spawn once per season, males can fertilize eggs multiple times during the reproductive season.

2.1.3. Trout habitat selection

This is the key adaptive behaviour in the model, which is modelled according to "state- and prediction-based" foraging theory (Railsback and Harvey, 2013). Each trout selects a cell for feeding from all wetted cells within a radius that increases with trout length. The trout predicts the growth and predation risk it would incur at each potential cell and moves to the cell offering the highest value of a fitness measure termed "Expected Maturity" (EM; Railsback et al., 1999). EM represents the expected probability of surviving both predation and starvation over a specified time horizon, multiplied by a term representing how growth affects fitness. This growth term represents the fitness benefits of reaching reproductive size for immature individuals. The habitat selection trait
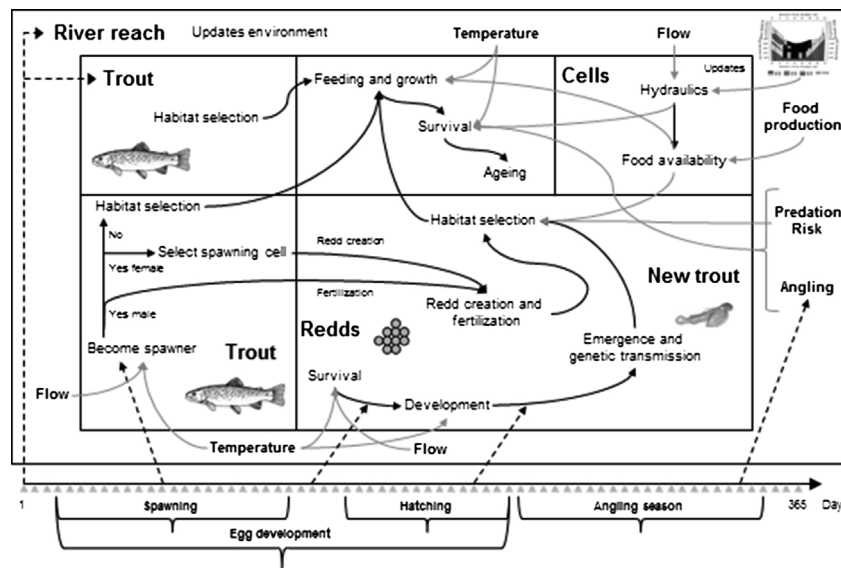
Fig. 1. Conceptual diagram of the life cycle of stream-dwelling trout represented in inSTREAM-Gen and of the actions executed by all entities in the model. Black lines link processes while grey lines represent factors influencing processes. All actions are executed in a daily time-step but dashed lines indicate the time of the year in which daily actions take place.

assumes a size-based dominance hierarchy: trout can only use resources (food and velocity shelters) that have not been consumed by larger trout.

2.1.4. Trout feeding and growth

The daily weight gain or loss of each trout is calculated using standard bioenergetics approaches. The feeding and growth sub-model calculates the potential food intake and metabolic costs a fish would experience in a cell, for both drift and search feeding. Fish growth is modelled as net energy intake, the difference between energy intake from food and metabolic costs. The rate of drift intake by a fish is modelled using a conventional drift-feeding approach, adapted from the models of Hughes (1992) and Hill and Grossman (1993). A fish is assumed to capture food only within a "reactive distance" that increases with body length but decreases with water velocity, while the amount of food passing within the reactive distance increases with velocity and drift concentration. Search food intake increases linearly with food production and decreases linearly to zero as water velocity increases to the fish's maximum sustainable swim speed. Metabolic costs increase with length, swimming speed, and temperature. Velocity shelters reduce swimming costs for drift-feeding fish. Length increases when trout in good condition gain weight; weight loss decreases condition.

2.1.5. Trout survival

Each trout determines stochastically whether it survives seven sources of mortality: starvation, high temperatures, high velocity, stranding, predation by terrestrial animals, predation by piscivorous trout, and angling; mortality sources are depicted as daily survival probabilities that depend on characteristics of the fish and its habitat. The risk of predation by terrestrial animals can be reduced by smaller size, high velocity or depth, and proximity of hiding cover; the risk of predation by other trout can be reduced by larger size, shallow depth, low temperature, and low density of large trout. The risk of starvation increases as body condition decreases. Angling and hooking mortality depends on fishing pressure, capture rate, and survival probability, which is a function of how many times a trout is hooked and whether it is kept vs. released each time hooked. Although none of these mortality risks

are directly density-dependent, density dependent survival often emerges from competition for safe feeding habitat.

2.1.6. Redd survival and development

Redds are subject to egg mortality (loss of some or all of their remaining viable eggs) owing to excessively cold or warm temperatures, dewatering in low flows, scouring in high flows, and superimposition of a new redd. Remaining viable eggs develop at a rate dependent on temperature.

2.1.7. Emergence and genetic transmission of traits

When a redd's eggs are fully developed, they "emerge" (hatch into new trout) over several days. Only length at emergence and the maturity size threshold are modelled as transmissible traits, although we additionally included a neutral trait (not affecting the fitness of individuals) used in evaluating whether genetic changes in heritable traits result from selection or from genetic drift. The maturity size threshold was genetically coded separately for males and females because it typically differs between sexes in wild populations (e.g., Parra et al., 2014). Details of how the transmission of this trait is modelled are reported in the extended version of the ODD protocol (Section 2.7 of the TRACE document). Heritable traits are independent of each other. We assume that each egg is fertilized by just one male spawner, so that each new trout inherits its traits from the mother and a father randomly assigned from the males contributing to the redd (the probability of fertilization is the same for all males). We model the phenotype of an individual as the sum of an inherited additive genetic effect and a non-heritable residual effect. Inheritance rules are based on the infinitesimal model of quantitative genetics theory (Lynch and Walsh, 1998). Each offspring's genotypic value for a trait under selection is drawn from a normal distribution centred on the arithmetic mean of the two parental values, while the variance of this distribution is equal to half the total additive genetic variance for the trait at the population level plus the variance potentially introduced by mutation (mutational variance). Theoretically, natural selection and genetic drift tend to decrease genetic variance, which is concurrently replenished by mutation. However, with moderate selection strength and sufficient population size, additive genetic variance for a polygenic trait to which a large number of loci are contributing tends to stay

relatively constant over contemporary times (Barton and Keightley, 2002; Vincenzi et al., 2012b; Vincenzi, 2014). Thus, as we do not explicitly model alleles and loci in our genetic module, we assumed the additive genetic variance remains constant across generations.

The choice of the life-history traits under genetic control was a critical step. We chose to explicitly model two heritable traits (see Carlson and Seamons, 2008), length-at-emergence and the maturity size threshold, which are key to population dynamics and are involved in several critical tradeoffs. While producing trout with a larger length at emergence increases offspring's survival (owing to increased ability to compete for food and shelter over the critical period of competition right after emergence), larger eggs result in lower fecundity of the female spawner (the total volume of eggs per female does not change). Females can transmit a competitive advantage to the offspring at the cost of producing fewer individuals. Given the clear benefits of being large for survival, growth, and fecundity, without tradeoffs with other fitness-related traits natural selection would lead to larger sizes at emergence. However, getting large requires energy that induces costs associated with growth. Metabolic rates should increase faster than intake rates at temperatures over a species' growth optimum, leading to increasingly lower growth efficiency as body size increases (see Rosenfeld, 2014 and references therein). Likewise, large fish would increase their selectivity for cooler water at a faster rate than smaller fish with decreasing per capita food availability (as it occurs with decreasing flow rates) (Hughes and Grand, 2000). It follows that the sensitivity of growth and survival rates to such environmental factors are highly size-dependent; therefore, changes in environmental conditions might strongly select against large individuals and thus reverse the direction of selection.

The maturity size threshold controls the reproductive strategy of the fish. Individuals with lower maturity size threshold will typically reproduce earlier in life, increasing their probability of reproducing at least once at a cost of producing fewer offspring and facing the higher post-spawning mortality due to the energetic costs of spawning. With earlier maturation, the lifetime fecundity of females may be lower as smaller spawners are expected to produce fewer offspring at first spawning than fish delaying reproduction. However, individuals with higher maturity size threshold face the risk of no reproduction, as they have to survive in-between spawning seasons. According to life-history theory, age at maturity should be adapted to age-specific survival rates and to maximize the overall lifetime reproductive rate (Jonsson and Jonsson, 2011).

Any anthropogenic disturbance that can decrease fitness or its components (e.g. survival up to maturity) will impose strong selection pressure on this fitness-related trait. For example, size-selective fishing might cause rapid evolution towards earlier maturation at smaller sizes (Jørgensen et al., 2007; Dunlop et al., 2009); likewise, adaptive responses to anthropogenic global change towards delayed maturity have been documented in anadromous salmonid populations (see Crozier et al., 2008; Crozier and Hutchings, 2014). Piou and Prévost (2013) showed that climate change would select for higher threshold values of river maturation as it increases sea survival in Atlantic salmon *Salmo salar*. However, adaptive responses in the opposite direction are expected in resident salmonid populations at low-latitude margins, where reduced survival rates and fitness are predicted under climate change (Jonsson and Jonsson, 2009). The maturity size threshold also affects the habitat-selection behaviour of juveniles in our model because they have a strong incentive to select cells with higher growth until they reach maturity. Therefore, adaptive changes in maturity thresholds may also involve behavioural responses.

A complete list and detailed description of the global parameters, the model entities' local variables, and all procedures can be found in Appendix C (worksheets "Globals", "Local variables" and "Procedures", respectively).

2.2. Test case

2.2.1. Study stream reach

To test and validate the model, we parameterized it for a resident brown trout population in the River Belagua, in the Aragón River basin (northern Spain). The study river corresponds to the Mediterranean medium-sized headwater mountain stream reach type described in Ayllón et al. (2010a), i.e., low stream order (2), short distance from the origin (13 km), relatively small catchment size (79 km²), high reach gradient (5%), narrow width (6.6 m), intermediate slow-to-fast-water ratio (0.6), and hence moderate mean reach depth (24 cm), maximum reach depth (77 cm) and width-to-depth ratio (30) at base flow. The length of the simulated reach is 305 m.

The model requires several kinds of input. Topographic, hydraulic, and channel structure (substrate, and feeding and hiding cover) data were collected following standard data collection procedures that are fully described elsewhere (e.g., Ayllón et al., 2010b, 2012). We calibrated PHABSIM v.1.5.1 (Milhous and Waddle, 2012) hydraulic models to predict depth and velocity in each cell at each simulated flow rate.

Time series input includes daily values for water temperature and stream flow. We used data collected by the closest meteorological (Urzainqui, AEMET [Spanish National Meteorological Agency]) and stream gauging (Isaba, Navarra Government) stations to generate the water temperature and flow time series.

2.2.2. Model parameterization and validation

Model parameterization is extensively described in elements 3 ("Data evaluation") and 6 ("Model output verification") of the TRACE document (Appendix A).

In inSTREAM-Gen, 20 parameters define the initial trout population; their values are site-specific because they define the abundance and age- and size-structure of the population at initialization. There are five parameters in the angler mortality model that are also site-specific because they characterize the legal restrictions to recreational fishing in the simulated reach. In addition, 20 trout parameters are highly site-specific; although their values are typically obtained from field studies, they can be obtained from the literature when not available for the simulated population. For all these parameters, we used population-specific values derived from field studies conducted in the study system (see Table A2 in Section 3 of the TRACE document). Additionally, there are 114 parameters in inSTREAM-Gen whose values are not reach- or population-specific so values suggested by Railsback et al. (2009) or other literature are typically used. The selected values and their data sources are detailed in the aforementioned element 3 of the TRACE document (Appendix A).

The values of six parameters (*habDriftRegenDist, habDriftConc, habSearchProd, habPreyEnergyDensity, mortFishAqPredMin*, and *mortFishTerrPredMin*) were derived via calibration. InSTREAM-Gen was calibrated within the pattern-oriented framework (Wiegand et al., 2003; Grimm et al., 2005) by using 12 years (1993–2004) of population data from the Belagua River (see Sections 3.2, pages 28–29, and 6 of the TRACE document for further details). We calibrated these parameters by attempting to reproduce six time-series patterns: length-at-age of age-1 trout (L1), age-2 trout (L2), and age-3 and older trout (age-3Plus; L3), and abundance of the same age classes (age-1, -2 and -3Plus; A1-3). After its calibration, the model was tested against the observed time series of population biomass of age-1 trout (B1) and age-2 and older trout (age-2Plus; B2). Calibration procedures summarized

below are explained in detail in Section 6 of the TRACE document (Appendix A).

The calibration simulations ran from 1 October 1993 through 30 September 2004. The population initialization parameters were derived from data observed in 1993 and global parameters were set to the values described in Section 3 of the TRACE document (Appendix A). We subsequently used a Latin hypercube sampling design (Iványi et al., 1979), optimizing the sample with a genetic algorithm, by means of the *lhs* R package v. 0.10 (Carnell, 2012) to draw 2000 parameter sets from the entire parameter space defined by the six parameters selected for calibration. Following Frank and Baret (2013), we used the sum of standardized squared errors (SSSE) to evaluate agreement between the observed and predicted patterns. This quantitative measure is computed as:

$$\sum_i \frac{(sim_i - obs_i)^2}{obs_i},$$

where *sim* and *obs* represent the simulated and observed values for each year *i* of the 1993–2004 time series, measured at September 1.

We next followed a Monte Carlo Filtering approach, by which tested patterns were applied as filters to separate good from bad sets of parameter values (Wiegand et al., 2003; Grimm and Railsback, 2005). The first patterns used as filters were lengths-at-age. We considered an observed field length-at-age pattern to be accurately reproduced by a model simulation when SSSE was equal to or less than the sum of yearly deviations corresponding to a maximum of 10% of the observed annual value. Parameter sets passing this filter were then filtered by abundance patterns. We only retained parameter sets producing a median SSSE lower than a value equal to a yearly deviation of 30% of the observed value. We selected the parameter set having the overall lowest SSSE values for tested abundance patterns. This process was replicated 5 times.

Using again a Latin-hypercube sampling design, we drew 2000 additional parameter sets around the final parameterization to verify possible parameterizations that would reproduce the six field patterns better than the "final parameter set" found according to the previous description. Therefore, we repeated the procedure explained above, using as well trial-and-error adjustment on all six parameters to find the final parameter set. The final parameter set was identified when the goodness-of-fit measure (SSSE) of the six patterns could not be improved by small parameter changes, and all analysis of variance tests of the comparison between observed and 10 replicates of simulated trout length-at-age and abundance distributions for the three age-classes were non-significant.

2.2.3. Sensitivity analysis

We conducted a global sensitivity analysis to identify those model parameters with the strongest influence on model outputs under two water temperature scenarios representing current non-stressful and projected climate-change stressful temperatures. We analyzed parameter sensitivity under two temperature scenarios because parameters controlling effects of high temperature on reproduction, survival or metabolism may have little effect under current conditions when temperatures are never extreme but could have strong effects at projected higher temperatures. A thorough description of the sensitivity analyses is provided in Section 7 ("Model analysis") of the TRACE document (Appendix A); here we outline the methods.

Since a full global sensitivity analysis was not computationally feasible, we followed a two-step protocol: (1) screening 72 selected model parameters to differentiate influential and non-influential parameters (remaining parameters were cast aside based on a first pre-analysis and results from previous sensitivity analyses described in Railsback et al., 2009; see TRACE document), and

then (2) a variance-decomposition technique to identify, among the eight most influential parameters, those that reduce the output variance most when fixed to their "true" values. For both analyses, we used the *sensitivity* R package v1.7 (Pujol et al., 2013) to generate the design of experiments and to estimate the sensitivity measures. In this paper, we only present the results from the screening step; a comprehensive description of the methodology and results of the sensitivity analyses using variance-decomposition methods is provided in Section 7 ("Model analysis"; Subsections 7.2 and 7.4) of the TRACE document (Appendix A).

The sensitivity analysis examined seven model outputs: mean total abundance and biomass of both young-of-the-year (YOY; age-0) and older (age-1 and older) trout, and the mean genotypic values of length at emergence and length maturity threshold (for both males and females) of breeders over a 12-year period. Each simulation was run from the 1st of October of 1993 to the 30th of September of 2004 using the same environmental and hydraulic input used in model calibration. One observation was obtained for each year (at September 1) and used to compute a mean for the entire model run.

The screening step used an improved version of Morris's elementary effects method (Morris, 1991; Campolongo et al., 2007). This method uses individually randomized one-factor-at-a-time designs to estimate the effects on model output of changes in parameter values; these effects are called elementary effects (EEs). The EEs are then statistically analyzed to measure their relative importance (see Thiele et al., 2014 for detailed description). We used the estimated mean of the distribution of the absolute values of the EEs, μ^*, as a sensitivity measure to establish the relative influence of each parameter. All 72 screened parameters were varied over five levels according to predefined ranges, the central value being the value used to calibrate the model (Table A19 in Section 7 of Appendix A). The number of tested settings was given by $r \times (k+1)$, where *r* is the number of EEs computed per parameter and *k* the number of parameters. As we chose 50 EEs, this led to $50 \times (72+1) = 3650$ model runs.

We repeated the analysis but using an increased-temperature input scenario. We created this scenario by adding 3 °C to daily temperatures all year round. According to regional climate change projections, this water temperature increase is expected to occur by 2100 under the ecologically friendly SRES scenario B2 (*Special Report on Emission Scenarios*, Nakicenovic et al., 2000; The B2 scenario emphasizes environmental preservation and social equity, with local solutions to economic, social and environmental sustainability, where the global population is expected to increase continuously, yet more slowly than in other scenarios). The high-temperature sensitivity analysis used the same seven demographic and genetic outputs. We selected the 36 parameters (half the number of the parameters selected for the first sensitivity analyses) identified as most influential by the Morris method using the original temperature profile. All parameters related to temperature were included in this selection. We then added the 13 temperature-related parameters not selected for the first sensitivity analyses (see Section 7 of Appendix A for further details). The 49 selected parameters were varied over five levels according to ranges shown in Table A27 in Section 7 of Appendix A. We chose again a value of 50 EEs, which led to $50 \times (49+1) = 2500$ new model runs.

2.2.4. Simulation scenarios

We allowed the model population to evolve between 1993 and 2100 under three different environmental scenarios. To do this, we generated time series for water temperature, flow, and cells' hydraulic conditions (water depth and velocity) for the simulated time frame. We used data collected by the closest meteorological (Urzainqui, AEMET) and stream gauging (Isaba, Navarra Government) stations to generate the water temperature and flow time

series for the 1993–2011 period. Time series for years 2012–2100 were thus projected as described below.

2.2.4.1. Scenario 1: Baseline. We modelled a baseline scenario that mimicked the observed variability in temperature and flow. We analyzed the historical flow time series (1992–2011) with the IHA v7.1 software (The Nature Conservancy, 2009) to estimate the probability that a hydrological year presented extreme low flows (probability = 0.158), small floods (0.368), large floods (0.053), and extreme low flows together with large floods (0.053). Thus the probability of a hydrological year having only low flows was 0.368. Each year of the 1992–2011 time series was assigned to one of these five categories. We then randomly selected the flow regime from one of those initial years every year for the 2012–2100 time period, the probability of selection depending on the probability of occurrence of the environmental flow event (extreme low flows, low flows, small floods, large floods, and extreme low flows together with large floods). Hydraulic time series were calculated using the projected flow time series by means of the depth-flow and velocity-flow relationships generated by the PHABSIM v.1.5.1 software.

We based water temperature time series on the air temperature time series collected by the Urzainqui meteorological station. To do this, water temperature was recorded daily at six sites next to meteorological stations within the Aragón River basin, from June of 2004 to November of 2005. We then fitted a linear regression model of daily water temperature (T_{water}) from mean air temperature during the previous seven days (T_{7d-air}). The resulting model $T_{water} = 3.331 + 0.633 \cdot T_{7d-air}$ was highly significant ($R^2 = 0.86$, $p < 0.0001$). Observed air temperature time series for our study reach were calculated by subtracting 1.03 °C from the Urzainqui meteorological station's daily time series. This correction factor was estimated from the regional air temperature model (T_{7d-air} [°C] = 323.25 – 6.914·*Latitude* [decimal degree] – 0.0044·*Altitude* [m]; $R^2 = 0.85$, $p < 0.0001$) described in Ayllón et al. (2013). We generated the temperature time series for 2012–2100 by using historic data from the same year as for the flow regime, so that both environmental variables did not get decoupled.

2.2.4.2. Scenario 2: Climate warming. Water temperatures were projected using the air temperature projections developed by AEMET for the Urzainqui meteorological station under the B2 SRES emission scenario (Brunet et al., 2009). We used the regional air temperature projections derived through statistical downscaling techniques based on the ECHAM4 Global Climate Model data (Brunet et al., 2009). Projected air temperatures were translated into water temperatures following the procedure explained for the baseline scenario. Because there is too much uncertainty on how flow patterns may respond in our study area to future climate change, we did not assume any changes in flow regime induced by climate change and instead used the flow time series generated for Scenario 1.

2.2.4.3. Scenario 3: Climate warming plus land use change. We simulated the combined effects of the climate-warming scenario described in the previous section and a future land use change scenario. Therefore, we used the water temperature time series estimated for the 1993–2100 period in Scenario 2. We based the land use change scenario on the land cover scenario described by López-Moreno et al. (2014) for the Aragón River basin for 2021–2050 under the A1B emission scenario. This land use change scenario is based on the expected evolution of land cover according to observed recent trends (see López-Moreno et al., 2014 and references therein): almost 90% of agricultural fields in the mountainous parts of the Aragón River basin were abandoned in recent decades, and natural re-vegetation has been accelerated by systematic afforestation, which adds to a significant decrease in livestock

pressure. The land cover scenario thus assumes that the remaining pasture and shrub areas in the basin will evolve into evergreen needle forests, and that the tree line will increase in elevation to 2000 m a.s.l., which is further facilitated by warmer climate conditions. Changes in forest type associated with the replacement of coniferous forests by more mature forest types (broadleaf forests) were not considered. López-Moreno and colleagues simulated changes in monthly streamflows in the Upper Aragón River basin across the 1970–2000 and 2021–2050 periods using the Regional Hydro-Ecologic Simulation System (RHESSys; Tague and Band, 2004) under these climatic and land cover scenarios. Simulations indicated a sustained decrease in runoff (owing to an increase in forest evapotranspiration) from late winter to the end of autumn, with reductions in river flows exceeding 30–40% relative to current levels.

We used the flow time series generated for Scenario 1, and then modified daily values for the 2012–2050 period at a rate reckoned to match changes projected by López-Moreno et al. (2014). López-Moreno et al. (2014) projected a decrease in both pasture (from 13.9 to 1.8% of the total area of the Aragón River basin) and shrub area (15.8–12.4%). However, the current area of pastures in the Belagua River sub-basin represents 23% of its total area, so we assumed that streamflows would keep on decreasing over 2051–2100 but at a lower rate (we arbitrarily set this rate as half the rate experienced over the 2012–2050 time period).

2.2.4.4. Population responses. We analyzed 12 population outputs produced every year (at September 1) from 20 replicate model runs for each scenario. Population outputs included density, biomass, and mean individual length and weight of three age-classes (1, 2, and 3 and older trout). We additionally recorded at the end of the spawning season the density and mean length of spawners, and their mean genotypic length maturity threshold broken out by sex, and the mean genotypic values of length at emergence and the neutral trait of all spawners.

2.2.4.5. Data analyses. We evaluated annual trends of model outputs using the Mann–Kendall trend test (Mann, 1945; Kendall, 1975). This non-parametric rank-based test determines whether there is an upward or downward trend over time, the null hypothesis being no trend (the data is independent and randomly ordered). An upward (downward) trend thus means that the variable consistently increases (decreases) through time, but the trend may or may not be linear. This test is widely used because it is robust to outliers and nonlinear trends, does not require the data to be normally distributed, and has low sensitivity to abrupt breaks due to non-homogeneous time series (Hirsch et al., 1982; Gilbert, 1987; Esterby, 1996). We used the *Kendall* R package v2.2 (McLeod, 2011) to estimate the Kendall's tau statistic and its probability. We also calculated the Sen's slope – the median linear slope joining all pairs of observations, expressed both by quantity per unit time and percent of the mean quantity per unit time, by means of the *wq* package for R v0.4-1 (Jassby and Cloern, 2014). However, despite the fact that no assumption of normality is required for this test, there must be no serial correlation for the resulting *p*-values to be correct (Yue and Wang, 2004). Therefore, *p*-values were corrected after accounting for serial autocorrelation using the package *fume* for R v1.0 (Santander Meteorology Group, 2012).

3. Results

3.1. Model parameterization and validation

The final parameter set, after using the six length-at-age and abundance patterns as filters, was: *habDriftRegenDist* = 600 cm, *habDriftConc* = 2.1E-10 g cm^{-3}, *habSearchProd* = 4.8E-7 g cm^{-2} h^{-1},
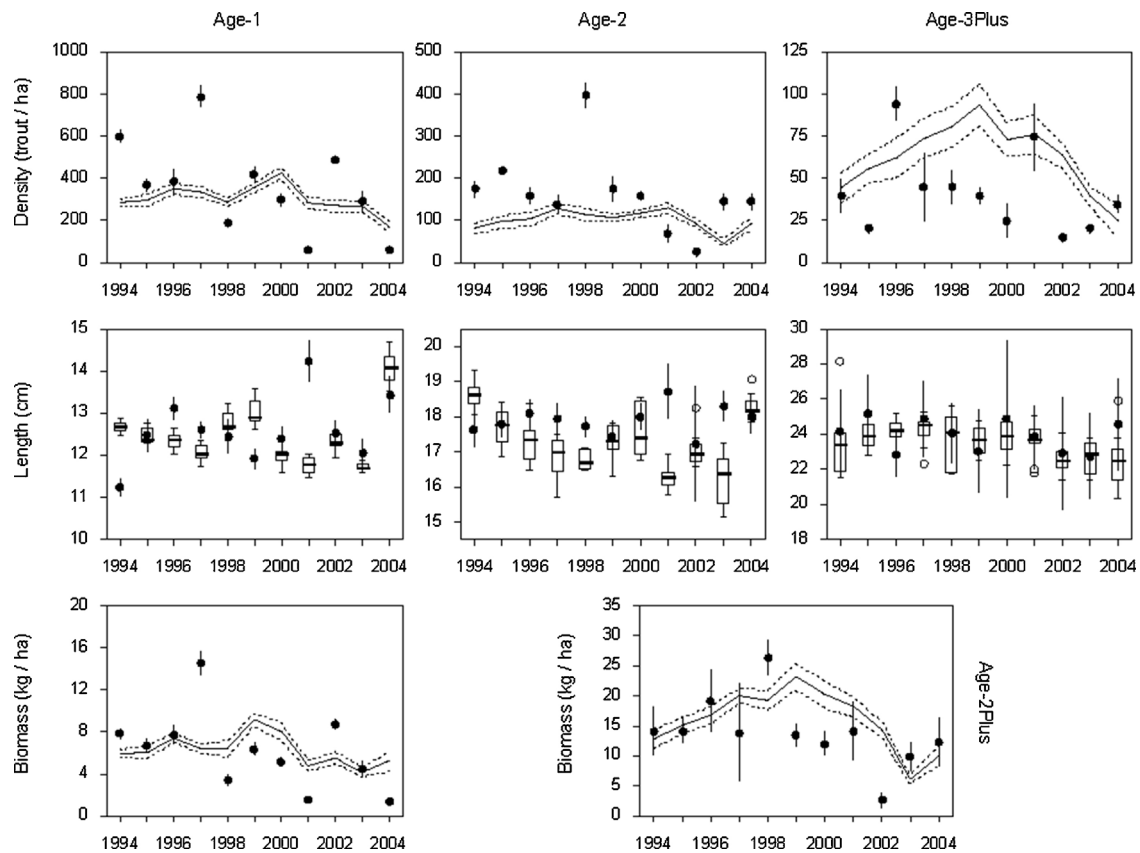
Fig. 2. Simulation results of 10 replicates with the final parameterization (black lines and box-plots) compared to field observations from the Belagua River (black circles). The three top graphs show the density of individuals of three age classes over 11 years. The graphs on the second row show the time series of mean length of individuals of three age classes. Box plots are the corresponding distribution of simulation replicates. The two bottom graphs show the biomass of two age classes, used as validation patterns.

$habPreyEnergyDensity = 5200\,\text{j g}^{-1}$, $mortFishAqPredMin = 0.984$, and $mortFishTerrPredMin = 0.996$. Results of the 10 replicates with the selected parameterization indicate that the model was able to reproduce relatively well the range of values of the eight time series taken as validation patterns (Fig. 2). Although some field observations lay outside the ranges of the replicates, the mean and range of variation of values observed in the Belagua population were reasonably well reproduced by inSTREAM-Gen for the sizes and numbers of individuals. The model showed lower accuracy to reproduce the actual deviation of some individual years around the mean values.

Regarding pattern A1, we observed small discrepancies for years 1997 (16% of the SSSE for this pattern) and 2004 (13%), and a higher one in 2001 (49%). As a consequence, the highest discrepancies for pattern A2 were for 1998 (30%) and 2002 (26%). This latter year was also problematic for A3 along with year 2000, since they contributed 32 and 22%, respectively, to the SSSE for this pattern. For L1, the fit between observed and simulated values was good except for 2001 (due to the extremely high discrepancy in numbers of age-1 trout that year) and 1994, whose contribution to the SSSE was as high as a 51 and 22%, respectively. Considering L2, most of the SSSE was from 2001 (44%) and 2003 (27%). Regarding L3, the bulk of SSSE was from 1995 (14%), 1996 (24%) and 2003 (35%).

Biomass time series, which were not used as filters for parameterization, were used as validation patterns. There were no significant differences in the mean values between observed and simulated patterns (ANOVA, $n = 22$, $p > 0.35$). Despite the fact that the overall scale of interannual variation in biomass was correctly predicted, the model did not accurately reproduce the

magnitude of the deviation above or below the mean in some specific years. The observed temporal distribution of discrepancies between observed and simulated values regarding abundance and length-at-age patterns, resulted in years 2004 and 2001 having the highest contribution to SSSE of pattern B1 (40 and 20%, respectively), while almost all SSSE of pattern B2 came from years 2002 (60%), 1999 and 2000 (both 12%).

3.2. Sensitivity analysis

3.2.1. Screening of influential parameters under observed-temperature scenario

The complete results from the screening analysis (Table A20 in Section 7 of Appendix A) show that the vast majority of parameters had little effect under the simulated conditions. However, the parameter *mortFishConditionK9* (which controls the relation between fish condition and starvation probability) appeared to be extremely important, controlling not only abundance and biomass of all life stages but also genotypic values of heritable traits (Fig. 3, Table 1). Three habitat parameters controlling prey energy availability, *habDriftRegenDist*, *habDriftConc*, and *habPreyEnergyDensity*, all had strong effects on model outputs, especially on demographic ones. Another food availability parameter, *habSearchProd*, was on the contrary only relatively important to abundance of both age-0 and older trout, but not to any other model output. Among the other parameters for feeding and growth processes, the model was sensitive only to the three respiration parameters, especially *fishRespParamB*. The parameter *mortFishTerrPredMin* (which controls the overall risk of predation by terrestrial animals) was the most important of all the survival-related parameters, its strongest effects
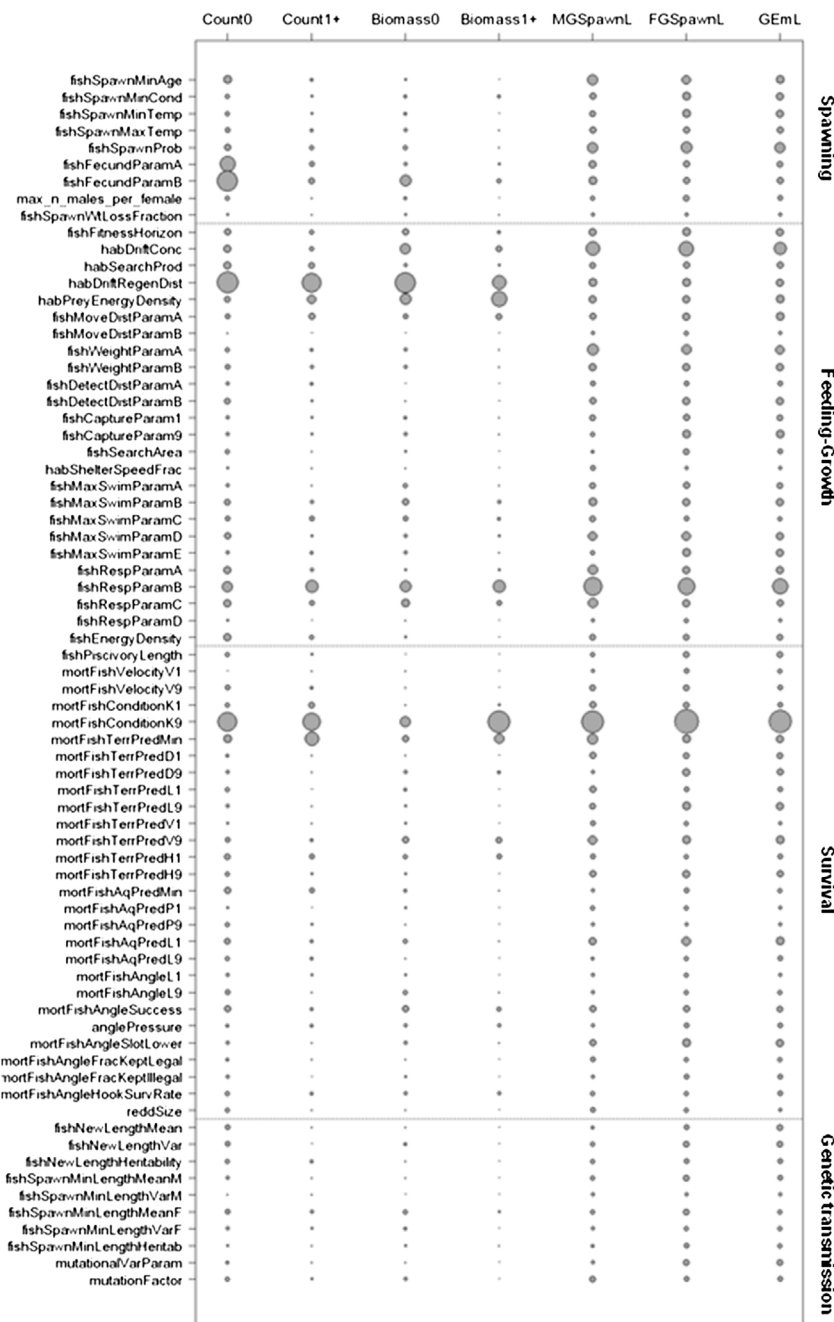
Fig. 3. Results of the sensitivity analysis conducted on inSTREAM-Gen under observed temperature conditions (Morris screening method). Parameters were grouped according to the spawning, feeding and growth, survival, and genetic transmission processes. For each parameter, the mean of absolute values of the elementary effects (μ^*) was estimated for seven model outputs: abundance of age-0 (Count0) and older trout (Count1+), biomass of age-0 (Biomass0) and older trout (Biomass1+), and the mean genotypic values of length at emergence (GEmL), and length maturity threshold for both female (FGSpawnL) and male (MGSpawnL) breeders. The size of the bubbles is proportional to the μ^* values.

being on numbers and biomass of adult trout. On the contrary, *mortFishAqPredMin* (controlling predation by fish, which affects only small trout) was only moderately important to abundance, without a strong effect on other model outputs. Other survival parameters to which the model was highly sensitivity were (ranked by global importance): *mortFishTerrPredV9*, *mortFishAqPredL1*, *mortFishTerrPredH1* and *mortFishConditionK1*. Fecundity parameters, *fishFecundParamA* and *B*, had strong effects on age-0 trout numbers and biomass, but only moderately important effects for older age classes. In contrast, three parameters involved in the angler model (*anglePressure*, *mortFishAngleSuccess*, and *mortFishAngleHookSurvRate*) affected biomass of older trout but not age-0

biomass. Parameters defining the maximum swimming speed for fish (especially *fishMaxSwimParamB*), which affects both bioenergetics and survival, had also a moderate influence on demographic outputs.

A few parameters had strong influence on genetic traits but not on demographic outputs. They were the parameters defining the criteria trout must meet to become spawners (*fishSpawnMinAge* and *fishSpawnMinCond*), and the probability of spawning once all spawning criteria are met, *fishSpawnProb*. The parameters governing the length-weight relationship for healthy fish, predominantly *fishWeightParamA*, were revealed as particularly influential to heritable traits.

Table 1
Parameters to which inSTREAM-Gen's assessed demographic and genetic outputs were found most sensitive in the global sensitivity analysis, in alphabetical order. We provide parameter's definition and sensitivity and uncertainty considerations. We indicate whether the parameter influences either demographic (D), genetic (G), both (DG) or none (0) model outputs under the observed (X/) and increased temperature profiles (/X).

Parameter	Influence	Definition/Sensitivity and uncertainty considerations
fishFecundParamA,B	(D/DG)	Parameters of the female length-number of eggs relationship/They affect population's fecundity. Values are highly site-specific.
fishFitnessHorizon	(DG/DG)	Number of days over which the terms of the expected maturity fitness measure equation are evaluated/It affect habitat selection and thus survival and growth. Values are not completely well-known.
fishMaxSwimParamB,C,D,E	(DG/DG)	Parameters of the fish maximum swim speed equation/These affect both food intake and velocity mortality. Consequently, they strongly affect how many cells offer positive growth and high survival. Values are from laboratory studies, but are moderately uncertain.
fishMoveDistParamA	(DG/DG)	Multiplier for the maximum movement distance/It limits potential destinations during habitat selection. It affects small trout above all, influencing the intensity of competition by limiting dispersal. Values are based on literature observations and there are some uncertainties in its values.
fishRespParamA,B,C	(DG/DG)	Parameters of the respiration equation/They strongly affect energy costs and growth. Values are relatively well-known from laboratory studies.
fishSpawnMaxTemp	(0/G)	Maximum temperature at which spawning occurs/Reliable values can be borrowed from the literature.
fishSpawnMinAge	(G/0)	Minimum age a fish must have to be able to spawn/Values can vary among sites and can often be estimated from site-specific census data.
fishSpawnMinCond	(G/0)	Minimum condition factor a fish must have to be able to spawn/Values are uncertain, but should be around a narrow range below 1.0.
fishSpawnProb	(DG/G)	Probability of spawning on the days when all the spawning criteria are met for a female/It gives the model user some control over what percent of spawning-sized fish actually spawn. Values are uncertain and really not well-known.
fishWeightParamA,B	(G/DG)	Parameters of the weight-length relationship for healthy fish/Seemingly small changes can greatly affect the growth in length that results from growth in weight. Values can vary among sites; using values from field data or literature will prevent significant error.
habDriftConc	(DG/DG)	Concentration of food items in the drift/Energy intake increases linearly with this parameter, until intake is limited by *Cmax*. Values are site-specific and rarely well-known. It is best evaluated via calibration to observed growth or size.
habDriftRegenDist	(DG/D)	Distance over which drift depleted by foraging fish is regenerated/It controls total food availability in a cell. Values are highly uncertain so they are best obtained via calibration of fish density in high-quality cells.
habPreyEnergyDensity	(DG/DG)	Prey energy density/Trout energy intake increases linearly with this parameter, and is not limited by the maximum daily intake (*Cmax*). Energy density of invertebrate prey can vary seasonally as prey types change, but the range of reasonable values is well-known.
habSearchProd	(D/DG)	Production rate of search food items/Search-feeding energy intake increases linearly with it, until intake is limited by *Cmax*. It mainly affects age-0 trout growth and survival. Values are site-specific and rarely well-known. It is best evaluated via calibration to observed growth rates.
mortFishAqPredT9	(0/DG)	Temperature at which fish survival increase function is 90% of maximum/It controls the aquatic predation survival increase function that describes how low temperatures reduce the metabolic demands and, therefore, feeding activity of piscivorous fish. Values are from laboratory studies, but there is relatively uncertainty around them.
mortFishConditionK9	(DG/DG)	Fish condition factor K at which fish survival is 90%/It controls the probability of surviving poor condition but it is highly interconnected to many different processes, so that it can have a strong effect not only on mortality but also on growth. Values are not well known.
mortFishHiTT9	(0/DG)	Temperature at which high-temperature fish survival is 90% of maximum/It controls fish mortality owing to the breakdown of physiological processes at high temperatures. Models of this mortality source remain variable and uncertain.
mortFishTerrPredMin	(DG/DG)	Fish daily survival probability due to terrestrial predators under most vulnerable conditions/Terrestrial predation is the most important mortality source for trout older than age-0. Values are highly uncertain and variable, so are best estimated via calibration to observed survival and abundance.
mortFishTerrPredV9	(DG/D)	Ratio of fish swimming speed to maximum swim speed at which fish high velocity survival is 90%/If this parameter is set to a low value (or close to *mortFishTerrPredV1*), velocity offers very high protection and terrestrial predation becomes negligible in many cells. The parameter is expected to have much less effect when set to higher values. Values are not well known and can vary with predator types and the size of the stream.
mortReddHiTT9	(0/D)	Temperature at which high-temperature egg survival is 90%/Values can be obtained from laboratory studies.

3.2.2. Screening of influential parameters under increased-temperature scenario

As expected, temperature-related parameters played a pervasive role on controlling both demographic and genetic outputs under this scenario (Fig. 4, Table 2). This was especially true for age-0 trout; eight and seven temperature-related parameters ranked amongst the 13 most influential parameters for abundance and biomass of age-0, respectively. While *mortFishConditionK9*, *fishFecundParamB*, and *fishRespParamB* were still the parameters exerting the strongest effects on demographic outputs of both age-0 and older trout, these model outputs were also highly sensitive to parameters controlling trout and redd mortality due to high temperatures (*mortFishHiTT9* and *mortReddHiTT9*) as well as to parameters controlling temperature effects on fish swimming performance (*fishMaxSwimParamC* and *fishMaxSwimParamD*).

Parameters driving temperature effects on survival of aquatic predation (*mortFishAqPredT9*) and on respiration costs (*fishRespParamC*) were additionally important for age-0 demographics.

The parameters *mortFishConditionK9* and *fishRespParamB* were also the most influential for genetic outputs. However, five temperature-related parameters ranked amongst the ten most influential. Aside from the temperature-related parameters previously identified as important for demographic outputs, the parameter defining the maximum temperature at which trout are able to spawn (*fishSpawnMaxTemp*) had strong effects on all genetic outputs. In contrast, none of demographic and genetic model outputs were sensitive to any of the parameters controlling the development of eggs within the redd, despite this process being dependent on temperature conditions.
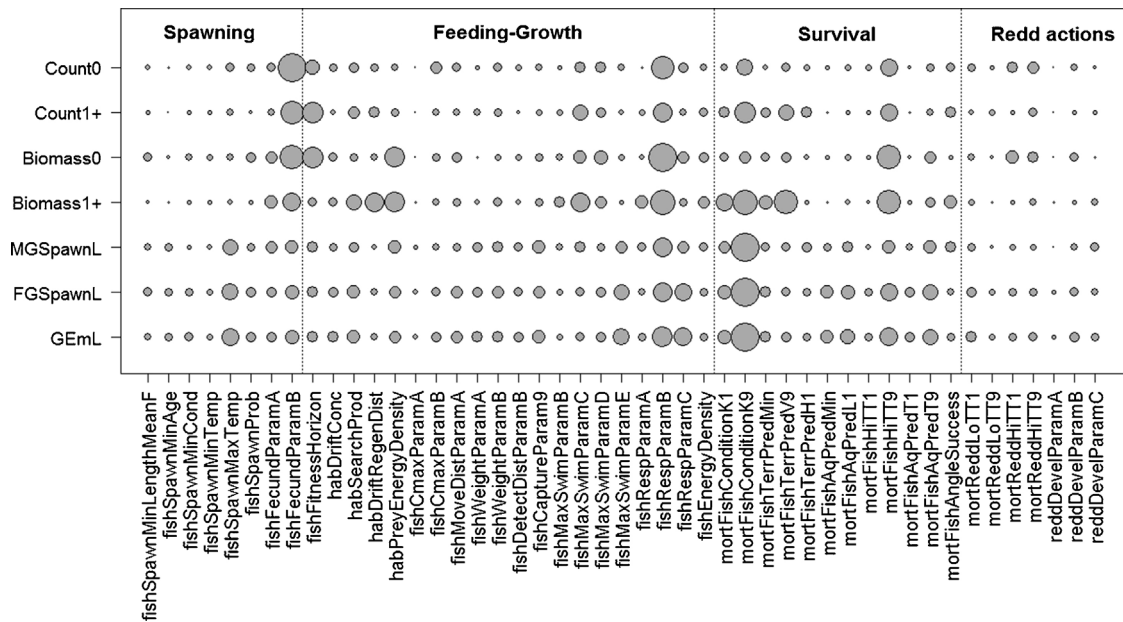
Spawning   **Feeding-Growth**   **Survival**   **Redd actions**

Rows: Count0, Count1+, Biomass0, Biomass1+, MGSpawnL, FGSpawnL, GEmL

Column labels: fishSpawnMinLengthMeanF, fishSpawnMinAge, fishSpawnMinCond, fishSpawnMinTemp, fishSpawnMaxTemp, fishSpawnProb, fishFecundParamA, fishFecundParamB, fishFitnessHorizon, habDriftConc, habDriftRegenDist, habSearchProd, habPreyEnergyDensity, fishCmaxParamA, fishCmaxParamB, fishMoveDistParamA, fishWeightParamA, fishWeightParamB, fishDetectDistParamB, fishCaptureParam9, fishMaxSwimParamB, fishMaxSwimParamC, fishMaxSwimParamD, fishMaxSwimParamE, fishRespParamA, fishRespParamB, fishRespParamC, fishEnergyDensity, mortFishConditionK1, mortFishConditionK9, mortFishTerrPredMin, mortFishTerrPredV9, mortFishTerrPredH1, mortFishAqPredMin, mortFishAqPredL1, mortFishHiTT1, mortFishHiTT9, mortFishAqPredT1, mortFishAqPredT9, mortFishAngleSuccess, mortReddLoTT1, mortReddLoTT9, mortReddHiTT1, mortReddHiTT9, reddDevelParamA, reddDevelParamB, reddDevelParamC

Fig. 4. Results of the sensitivity analysis conducted on inSTREAM-Gen under the increased temperature scenario (Morris screening method). Results are displayed as in Fig. 3.

Table 2

Trends of density, biomass, and length and weight-at-age for three age classes over the 1994–2100 time period for the climate change and climate change plus land use change simulation scenarios. Also shown are trends in density of spawners, phenotypic length-at-spawning and genotypic minimum length for spawning, length-at-emergence, and neutral trait values of spawners. Trends were analyzed using the Mann–Kendall test and p-values were corrected for serial correlation. Kendall's tau statistic and its standard error were estimated with 1000 bootstrap iterations. Significant p-values in bold ($\alpha = 0.05$) represent increasing or decreasing trends of magnitude over time, which is measured as the Sen's slope (both in units/decade and %/decade).

| Pattern	tau	p	Corrected p	Sen's slope	Sen's slope (%)
Climate change					
Density age-1 (trout/ha)	−0.36 (0.09)	<0.0001	**<0.0001**	−22.25	−2.74
Density age-2	−0.34 (0.09)	<0.0001	**<0.0001**	−8.68	−3.39
Density age-3Plus	−0.37 (0.11)	<0.0001	**<0.001**	−5.81	−3.60
Length age-1 (cm)	−0.03 (0.06)	0.62	0.58	<0.01	<0.01
Length age-2	0.26 (0.09)	<0.0001	**<0.01**	0.08	0.42
Length age-3Plus	−0.05 (0.09)	0.49	0.61	<0.01	<0.01
Weight age-1 (g)	−0.12 (0.06)	0.064	0.065	−0.17	−0.89
Weight age-2	0.09 (0.06)	0.16	**<0.05**	0.30	0.51
Weight age-3Plus	−0.30 (0.10)	<0.0001	**<0.001**	−2.67	−1.76
Biomass age-1 (kg/ha)	−0.35 (0.09)	<0.0001	**<0.0001**	−0.53	−3.44
Biomass age-2	−0.27 (0.07)	<0.0001	**<0.0001**	−0.46	−3.08
Biomass age-3Plus	−0.39 (0.11)	<0.0001	**<0.0001**	−1.25	−5.04
Density spawners (trout/ha)	−0.28 (0.09)	<0.0001	**<0.0001**	−9.83	−3.55
Spawning length female (cm)	−0.17 (0.09)	<0.05	0.051	−0.05	−0.23
Spawning length male	−0.06 (0.08)	0.35	0.37	−0.01	−0.06
Gen min spawn length female	0.88 (0.15)	<0.0001	**<0.001**	0.10	0.58
Gen min spawn length male	0.89 (0.15)	<0.0001	**<0.0001**	0.10	0.57
Gen emergence length	0.98 (0.15)	<0.0001	**<0.0001**	0.03	1.08
Gen neutral trait (unitless)	0.01 (0.14)	0.87	0.96	0.00	0.00
Climate + land use change					
Density age-1 (trout/ha)	−0.57 (0.12)	<0.0001	**<0.0001**	−46.97	−6.71
Density age-2	−0.61 (0.12)	<0.0001	**<0.0001**	−17.39	−8.12
Density age-3Plus	−0.67 (0.14)	<0.0001	**<0.0001**	−14.00	−11.46
Length age-1 (cm)	0.16 (0.07)	<0.05	**<0.01**	0.04	0.33
Length age-2	0.44 (0.11)	<0.0001	**<0.0001**	0.14	0.76
Length age-3Plus	−0.43 (0.11)	<0.0001	**<0.0001**	−0.18	−0.80
Weight age-1 (g)	0.03 (0.06)	0.70	0.62	0.03	0.17
Weight age-2	0.15 (0.08)	<0.05	**<0.05**	0.63	1.04
Weight age-3Plus	−0.58 (0.13)	<0.0001	**<0.0001**	−6.49	−4.91
Biomass age-1 (kg/ha)	−0.51 (0.11)	<0.0001	**<0.0001**	−0.84	−6.23
Biomass age-2	−0.51 (0.10)	<0.0001	**<0.0001**	−0.94	−7.30
Biomass age-3Plus	−0.67 (0.13)	<0.0001	**<0.0001**	−2.47	−14.29
Density spawners (trout/ha)	−0.53 (0.11)	<0.0001	**<0.0001**	−22.03	−9.83
Spawning length female (cm)	−0.54 (0.13)	<0.0001	**<0.0001**	−0.21	−1.00
Spawning length male	−0.47 (0.12)	<0.0001	**<0.0001**	−0.15	−0.76
Gen min spawn length female	0.70 (0.15)	<0.0001	**<0.01**	0.06	0.35
Gen min spawn length male	0.74 (0.15)	<0.0001	**<0.01**	0.06	0.37
Gen emergence length	0.96 (0.15)	<0.0001	**<0.0001**	0.02	0.77
Gen neutral trait (unitless)	−0.28 (0.10)	<0.0001	**<0.05**	0.00	0.00
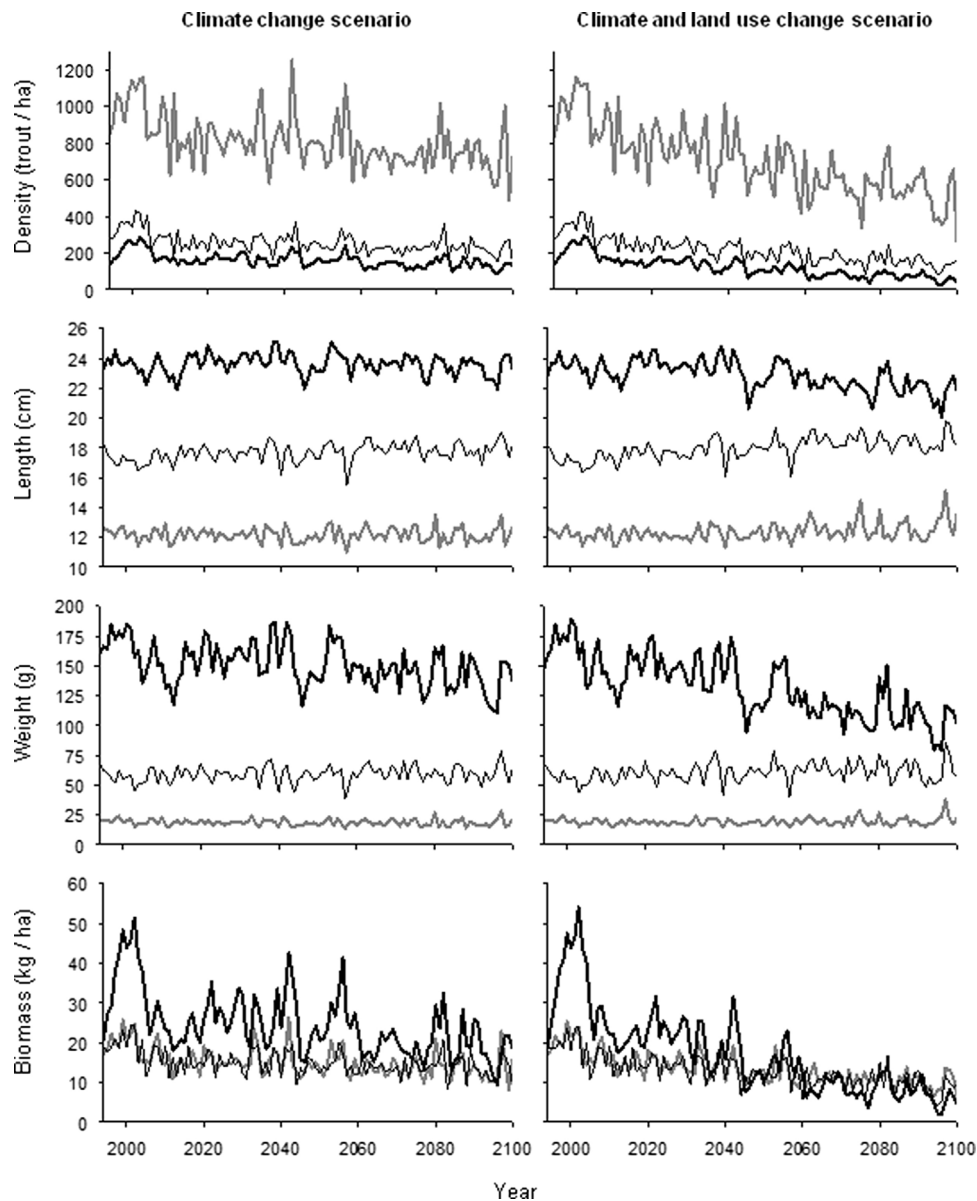
Fig. 5. Population density and biomass, and mean individual length and weight for three age classes (age 1, thin grey line; age 2, thin black line; age 3 and older trout, thick black line) over time under the climate change and climate change plus land use change simulation scenarios. Lines represent the mean of 20 replicates.

In spite of being somewhat less influential under limiting temperatures, the food-related parameters *habDriftRegenDist*, *habDriftConc*, *habSearchProd*, and *habPreyEnergyDensity*, as well as the fish parameter *mortFishTerrPredMin*, still had strong effects on model outputs, ranking amongst the twenty most determinant parameters across all model outputs. Interestingly, the relevance of the parameter *fishFitnessHorizon* increased under high temperature conditions.

3.3. Simulation scenarios

3.3.1. Evolution of life-history traits, and population abundance and biomass

Most of the demographic (density and biomass) and life-history (length and weight-at-age) outputs did not change significantly over time for any of the analyzed age-classes under the baseline scenario; we only detected, indeed, an increasing trend in length of spawners (Table D1 in Appendix D). In contrast, density of all age-classes decreased significantly over time under both climate change

(CC) and combined climate and land use change (CC + LUC) simulation scenarios, although the rate of decline was notably higher under the CC + LUC scenario (Table 1 and Figs. 5 and 6). While the rate of density decline was similar across age-classes under the CC scenario, it strongly increased with age under the CC + LUC scenario. Age-1 trout did show only a faint, though significant under the CC + LUC scenario, upward trend in body size. In contrast, age-2 trout significantly increased body length and weight over time under both simulation scenarios, while trout older than two years had a significantly lower mean weight over time. Nevertheless, we only detected a significant downward trend in body length of this age class under the CC + LUC scenario (Table 1 and Fig. 5). These opposing trends resulted in spawners having a significantly smaller size at spawning over time, but only under the CC + LUC scenario (Table 1). The combination of density and body size temporal patterns led to a significant negative trend in biomass of all age classes over time, the rate of decline increasing with age and being markedly higher under the CC + LUC scenario (Table 1 and Fig. 5).
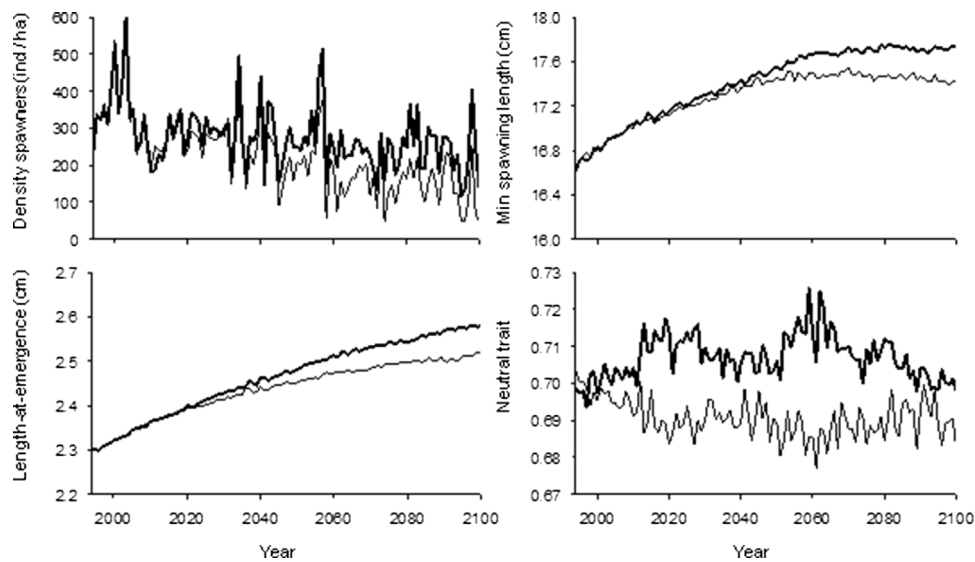
Fig. 6. Density of spawners, genotypic minimum length for spawning, length-at-emergence, and neutral trait value of spawners over time under the climate change and climate change plus land use change simulation scenarios; thick and thin lines, respectively). Lines represent the mean of 20 replicates.

3.3.2. Evolution of genetic traits

Values of both genetic traits showed a significant upward trend over time under the baseline scenario (Table D1 in Appendix D). The genotypic value of length at emergence showed also a significant upward trend through time under both CC and CC + LUC scenarios, but the rate of change was higher under the CC scenario (Table 1 and Fig. 6). In both cases, the rate of change in the trait was significantly lower than that observed under the baseline scenario (compare Sen's slopes from Tables 1 and 1D between scenarios). Therefore, the genotypic value of the trait was higher under the baseline conditions compared to the scenarios of change, the difference increasing over time (Fig. 7). The genotypic value of minimum length for spawning of both male and female spawners also increased significantly over time until reaching a plateau. Both time to reach this plateau and maximum genotypic value were higher under the CC scenario than under the CC + LUC scenario (Table 1 and Fig. 6). The rates of change in genotypic values under the change scenarios were again significantly lower than those observed under the baseline scenario (Tables 1 and 1D). Hence, maturity size thresholds were lower under the scenarios of change compared to the baseline, and the difference increased over time (Fig. 7). Consequently, while the number of spawners significantly decreased over time under both the baseline and environmental change scenarios, the proportion of mature age-2 trout at the beginning of the spawning season was higher under CC and CC + LUC scenarios compared to the baseline (Fig. 7). The neutral trait did not show any significant trend under either simulation scenario (the observed trend under the CC + LUC scenario is on the border of significance; Table 1 and Fig. 6), indicating the absence of genetic change not driven by natural selection.

4. Discussion

We developed, implemented, and "evaludated" (sensu Augusiak et al., 2014) an eco-genetic IBM representing the life cycle of stream-dwelling trout populations. We successfully parameterized inSTREAM-Gen to reproduce six time-series patterns observed in a Mediterranean brown trout population. The model was validated with two other field patterns. We analyzed the sensitivity of the model to 72 parameters to assess their relative influence on both demographic and genetic outputs and to understand how their role may change under increased temperature conditions. We finally presented a test case to show potential applications of the model in real settings.

4.1. Model structure and innovations

Our modelling approach incorporating both ecological and quantitative genetic processes provides a mechanistically rich framework in which to predict the rate of evolutionary change on ecological timescales. It enables distinguishing between plastic and evolutionary responses to environmental change as well. To our knowledge, inSTREAM-Gen is the first spatially explicit fish population model designed with an individual-based eco-genetic structure. Previous eco-genetic or demogenetic fish IBMs were not spatially explicit (e.g., Dunlop et al., 2007; Vincenzi et al., 2012a) or only considered two main generic compartments, such as "main river vs. tributary" (e.g., Frank and Baret, 2013) or "freshwater vs. ocean" (e.g., Thériault et al., 2008; Reed et al., 2011; Piou and Prévost, 2012). The model's detail, however, imposes limits on the spatial and temporal scales of the simulations, but resident trout populations can be modelled over smaller areas and times than can populations of anadromous salmonids that migrate over large distances and have longer and more complex reproductive cycles.

In inSTREAM-Gen, the inheritance rules for the transmission of evolving traits are based on a modified version of the infinitesimal model of quantitative genetics. The most common alternative model of inheritance is the allelic model, in which individual alleles are modelled as being passed on directly from parents to offspring. There are examples of effective implementation of a bi-allelic multilocus system for modelling the genetic coding of heritable traits in fish eco-genetic individual-based models (e.g., Piou and Prévost, 2012; Vincenzi, 2014). As argued by Piou and Prévost (2012), this type of genetic coding has been shown to be good tradeoff between a purely quantitative approach and the detailed multi-allelic multilocus reality. However, a quantitative genetics approach is typically used in eco-genetic modelling because most life-history traits are regarded as polygenic quantitative characteristics affected by a large number of genetic loci, each with small effects, and the explicit modelling of genes and alleles is thus not necessary (see Dunlop et al., 2009 and references therein).

Natural selection and genetic drift are the main potential drivers of genetic evolution in inSTREAM-Gen. We did not account for the contribution of gene flow to trait evolution; such mechanisms
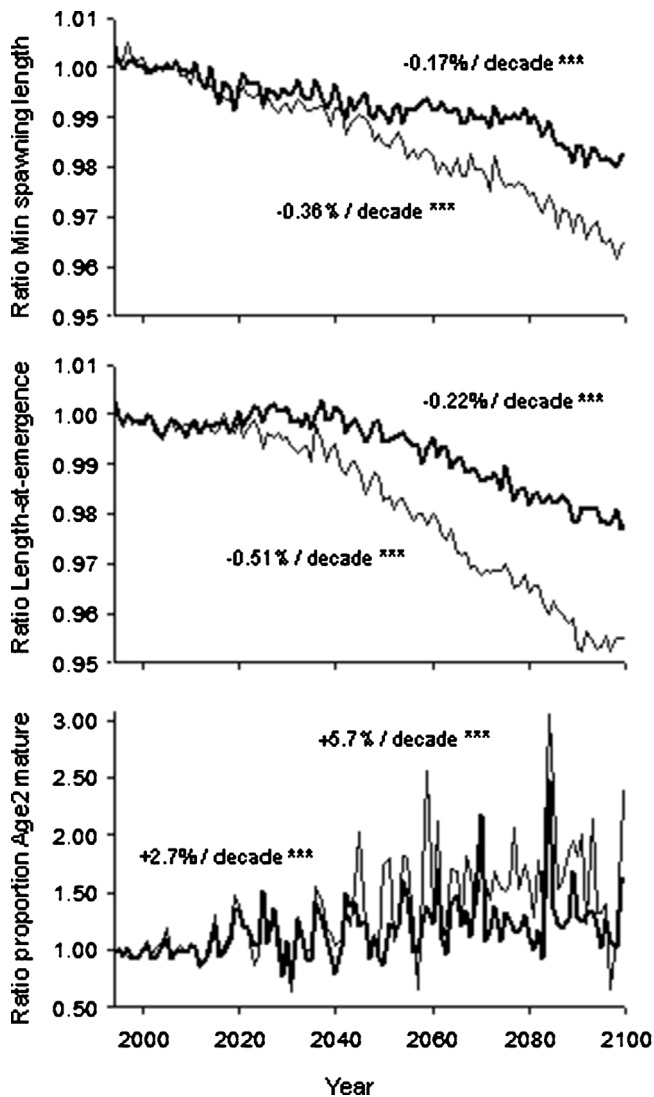
Fig. 7. Ratio of genotypic minimum length for spawning, length-at-emergence and proportion of age-2 trout mature at the beginning of the spawning season under two simulation scenarios (climate change vs. climate change plus land use change; thick and thin lines, respectively) to the baseline scenario over time. Lines represent the mean of 20 replicates. Significant trends measured as the Sen's slope (%/decade) and their *p*-values (*** indicates $\alpha < 0.0001$) are provided (trends for the climate change scenario are highlighted in bold).

2013, and Piou and Prévost, 2012, respectively). However, there are other quantitative genetic traits related to life history, behaviour, or physiology that may be subject to rapid evolution under selection and thus important for adaptation to climate change (see Carlson and Seamons, 2008 and Crozier and Hutchings, 2014).

Previous fish eco-genetic IBMs have allowed evolution in a variety of such other traits. Evolution in reproductive strategy has been modelled via a heritable age-at-maturity parameter (Jager, 2001) and probabilistic maturation reaction norm (Dunlop et al., 2007, 2009; Thériault et al., 2008; Wang and Hook, 2009). When individual growth rates have been modelled as under genetic control, they evolved rapidly under strong selection (e.g., Dunlop et al., 2009; Wang and Hook, 2009; Vincenzi et al., 2012a). Phenological events in salmonids (e.g., reproductive migration timing) are often highly adapted to local thermal conditions, generally heritable, and subject to rapid microevolution under global warming (Crozier et al., 2011; Kovach et al., 2012). Through eco-genetic individual-based modelling, Reed et al. (2011) predicted that stream warming would select for earlier upstream migration of sockeye salmon *Oncorhynchus nerka*, in agreement with observed long-term shifts in natural populations (Crozier et al., 2011).

In contrast to the above models, inSTREAM-Gen represents phenological events (e.g., spawn and emergence timing) and growth as emerging from environmental conditions, habitat, competition, and adaptive behaviour. Therefore, plastic responses in growth rates and phenological traits can emerge in inSTREAM-Gen from environmental change. Most traits of salmonids are highly plastic, and observed shifts in distribution of trait values are typically more consistent with plastic responses to environmental conditions than to evolutionary changes (Crozier and Hutchings, 2014). The current structure of inSTREAM-Gen can provide realistic predictions of future population dynamics since it allows for evolution only in two key traits but also includes phenotypic plasticity in other traits that have been shown to play an important role in local adaptations of salmonids. Of course, inSTREAM-Gen could be modified to include adaptive potential in additional traits, such as both physiological mechanisms (e.g., metabolic rates) and behavioural traits (e.g., boldness) that affect growth, given that such traits might co-evolve under selection (Biro and Post, 2008). Doing so would certainly make predictions of demographic and genetic response to climate change more interesting and potentially more accurate, especially when selective forces operating in opposite directions make it difficult to predict the evolutionary trajectory.

4.2. Model parameterization and validation

The calibrated model reproduced the magnitude and overall scale of interannual variations in length of three age-classes without significant deviations, but patterns in abundance were less well reproduced. In particular, the model tended to slightly underestimate numbers of age-2 trout and overestimate those of age-3 and older trout. In general, the model was not able to reproduce certain density peaks that were subsequently spread throughout cohort lifetime; those peaks seemed to result from processes not in inSTREAM-Gen, most likely emigration and immigration. Further, any real population can be assumed to have buffer mechanisms that reduce the effect of environmental extremes on abundance (Grimm et al., 2003). Moreover, the relative effect of different environmental factors (e.g., predation intensity) may vary from year to year more than assumed by inSTREAM-GEN. Because the model is an intentional simplification of real streams and trout, it cannot reproduce all observations.

We validated the model against two extra demographic patterns that were not used during the calibration process. Despite the inability of the model to mimic such density peaks – and thus, to predict specific interannual variation, it did fit the mean and

would be very hard to model in a realistic way, as the determinants of immigration and emigration are rarely known, and thus typically not represented in eco-genetic IBMs. Nevertheless, we modelled input of new genetic variation in the population via mutation. Our results have shown that the mutational variance introduced over such a short number of generations (ca 115) is probably unimportant for adaptation. Our study agrees with others in concluding that adaptation to a novel environment would be fuelled more by standing variation (pre-existing segregating genetic variant) than by de novo mutation (Barrett and Schluter, 2008).

This version of inSTREAM-Gen has two evolving traits, length-at-emergence and the maturity size threshold (minimum length for spawning), plus a non-fitness-related trait to test whether traits change due to selection and not to genetic drift. The two evolving traits are key to population dynamics as they control survival during the critical period after emergence and the reproductive strategy of the fish (affecting an individual's lifetime fecundity), respectively, and they have been already modelled as heritable traits in previous fish demo/eco-genetic IBMs (Frank and Baret,

Table 3
Patterns theoretically expected or observed in real trout populations reproduced by the inSTREAM IBM.

Pattern	Reference
Habitat selection behaviour:	
Hierarchical feeding in heterogeneous habitat, responses to high flow, interspecific competition and predatory fish, seasonal shifts in velocity preferences, and changes in habitat use with food availability and energy reserves	Railsback and Harvey (2002)
Diel foraging behaviour:	
Variations in individual diel activity and habitat use, and responses to temperature, competition, food availability and habitat quality	Railsback et al. (2005)
Demographic and life-history population-level behaviour:	
Self-thinning, the critical survival time after emergence, density-dependent growth, and age-specific quantitative patterns in population variation over space and time	Railsback et al. (2002)
Adult trout individual growth rates and streamflow effects on growth rates	Harvey and Railsback (2014)
Population biomass below vs. above a flow diversion	Harvey et al. (2014)

range of variation of observed biomass of both juvenile and adult trout (i.e., the additional validation patterns) relatively well. The structural realism and robustness of inSTREAM have been tested, validated, and improved by Railsback and colleagues over the last 15 years (Table 3). Further details are provided in Section 8 of Appendix A.

4.3. Model sensitivity

The fish parameter controlling how the probability of surviving starvation and disease varies with fish condition (weight relative to length) was the most important parameter under both temperature scenarios used in the sensitivity analysis, influencing all model outputs. Because habitat selection is modelled as a tradeoff between survival of starvation and predation, this parameter affects many processes and can have strong effects not only on mortality but also on habitat selection and thus growth. (E.g., making starvation more likely can cause fish to use riskier habitat to maintain growth, resulting in higher predation mortality.) This parameter also affects genetic traits by filtering the number and quality of spawners: fish can only spawn if their condition is above a threshold.

A few fish parameters were fairly influential to all model outputs under both temperature scenarios. Three food-related parameters had strong effects on demographic outputs because they control the energy available to the population. The parameter controlling terrestrial predation mainly affected numbers and biomass of adult trout. Terrestrial predation is normally the most important mortality source for older trout, affecting the number of spawners, and consequently having also strong effects on heritable traits and number of new recruits. Parameters defining the length-fecundity relationship were the main drivers of age-0 trout numbers and biomass; that is understandable because recruitment and early individual growth rates are strongly constrained by factors driving reproductive output in natural systems (Jonsson and Jonsson, 2011).

Parameters governing the length–weight relationship for healthy fish were particularly influential on evolving traits. These parameters strongly define how much energy a trout needs to grow in length, so their values affect the strength of selection on both heritable traits. Frank and Baret (2013) did not find any influence of these parameters on demogenetic outputs, probably because they modelled growth using observed rates of growth in length instead of bioenergetics. Parameters driving respiration costs and fish swimming capacity were strongly influential to all model outputs, especially at higher water temperatures, as they affect energy costs and food intake, and thus growth and survival. Parameters controlling the swimming costs and capture success functions typically exert the most influence on net energy intake predictions from bioenergetics models (Rosenfeld et al., 2014). Finally, parameters defining the conditions under which spawning occurs had large effects only on genetic outputs, as observed in previous fish IBMs (Frank and Baret, 2013).

The high sensitivity of inSTREAM-Gen's outputs to *fishFitnessHorizon* under our high-temperature scenario was probably a complex consequence of higher temperatures causing sharper tradeoffs between starvation and predation survival in the habitat selection decision. In this decision, the time horizon is the future time period over which fish balance the potential for starvation against predation risk. With higher temperatures, starvation is more likely in less time, which makes model results more sensitive to the decision time horizon.

We found demographic and genetic outputs insensitive to the heritability and mutation rate of the evolving traits. Frank and Baret (2013) and Piou and Prévost (2012) also found a similar lack of effects of heritability of length-at-emergence or size maturity threshold on outputs from their models.

It is not surprising that sensitivity analysis results were different under different temperature scenarios; we expect parameters for effects of high temperature to be important when, and only when, temperatures are high or over a certain threshold. This understanding reminds us that sensitivity analysis results are context-dependent and should be applied with caution to conditions different from those assumed in the sensitivity analysis. Detailed interpretation and further consideration of results are in Section 7 ("Model analysis") of the TRACE document (Appendix A).

4.4. Model application

Our application of inSTREAM-Gen to the investigation of demographic and evolutionary impacts of anthropogenic change on stream trout populations predicted a decline in numbers in all age classes (up to 3.6% per decade in the oldest age class) under projected warming. Abundance of the oldest and largest individuals declined the most. Density and biomass declined substantially more when we combined the warming scenario with a land use change scenario involving sustained flow reductions, especially in summer and autumn. This combined scenario lead to a high probability of population extinction over contemporary time frames, indicated by predicted declines in the number of spawners. As expected, synergies among climate warming and other anthropogenic drivers sped the dynamics of extinction (Brook et al., 2008; Ayllón et al., 2013).

Our predictions under the warming scenario are consistent with the expected responses of salmonid populations living at the warmest edge of their distribution (Jonsson and Jonsson, 2009). Our simulations predicted larger body sizes early but smaller body sizes late in the ontogeny (Fig. 5 and Table 2), which suggests that under warming conditions energy intake increases more quickly than increased respiration costs for smaller fish, but not larger ones. This result is likely because the allometries of metabolism and consumption may have divergent temperature sensitivities and the negative effect of high temperature on growth should be stronger for larger fish (see Rosenfeld, 2014 and references cited therein). It also supports the third ecological response to global warming in aquatic systems proposed by Daufresne et al. (2009). However, our predicted population declines were lower than we would have expected in the absence of evolution, taking into account that the study population is projected to experience systematic stressful temperature conditions for feeding and growth from year 2050 onwards (see Almodóvar et al., 2012). Evolutionary changes

increased the simulated population's capacity to cope with warming conditions.

We observed selection towards larger sizes at emergence and higher size maturity threshold values under the baseline scenario. We did not hypothesize that such microevolution would occur in our simulations or is actually happening in the modelled river, but this outcome was not surprising. Previous IBMs suggest that there could be microevolution occurring in fish populations. Results from Piou and Prévost (2012) revealed changes to the proportion of fish with different reproductive tactics after 50 years of simulations under stable environmental conditions. Likewise, Wang and Hook (2009) showed that growth and maturation schedules could co-evolve under baseline conditions over a relatively short time period (<200 years). Our results do not indicate that microevolutionary changes under the baseline are caused by genetic drift instead of natural selection (e.g. there was strong directional selection for the fitness-related traits but not in the neutral trait). However, we cannot exclude that they emerge from a sub-optimal parameterization of the model: either the heritable traits were not initialized at their "true" values, so that they evolved towards their evolutionary equilibrium (which is unlikely); or the final parameter set was sub-optimal. The model does not contain all the same evolutionary forces that occur in reality, and its assumptions and parameter values are by nature intentional simplifications based on observations of many different populations in many different conditions, so there is no reason to expect them to be "optimal" for any particular study site or set of environmental conditions. Predicted trends would just occur as the natural evolution of the population to maximize fitness under the best possible parameterization of the model.

The evolution towards larger size at emergence in our baseline simulations presumably occurred because larger size increases competitive ability over the critical period of competition among newly emerged juveniles. The evolution towards delayed maturity makes sense because terrestrial predation is very low in our study system, so the cost of surviving for another year is likely offset by the benefit of greater size and fecundity.

The trajectory of these heritable traits under baseline temperature conditions was maladaptive under simulated environmental change: larger size at emergence and delayed maturity reduced fitness and survival under high-temperature conditions. Under the environmental-change scenarios, maturity thresholds evolved until they stabilized at lower values than those predicted under the baseline scenario (Figs. 6 and 7). Under the combined climate and land use change scenario, maturity thresholds even start to decline. Therefore, the proportion of age-2 trout that are already mature at the beginning of the spawning season increases over time compared to the baseline scenario (Fig. 7). The evolution of length-at-emergence slows down under environmental change (Fig. 6). Under increased temperatures, being large at emergence still provides a competitive advantage and increases survival and growth, but later in the ontogeny being "too large" is deleterious as metabolic costs increase. That is, being large could be adaptive early in the ontogeny but maladaptive later, so that projected environmental change would select for intermediate body sizes. However, negative population growth rates are so high under the combined warming and flow reduction scenario that evolutionary responses cannot keep track of environmental changes to avoid population collapse and ultimate extinction.

This study is only one of many potential applications of inSTREAM-Gen and eco-genetic models in general. Eco-evolutionary approaches are poised not only to improve our basic understanding of the mechanisms driving the adaptation of populations to their natural environments but also to support decision making and assist managers in devising strategies for mitigating anthropogenic threats to global ecological systems.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2015.07.026

References

Almodóvar, A., Nicola, G.G., Ayllón, D., Elvira, B., 2012. Global warming threatens the persistence of Mediterranean brown trout. Global Change Biol. 18, 1549–1560.

Augusiak, J., Van den Brink, P.J., Grimm, V., 2014. Merging validation and evaluation of ecological models to 'evaludation': A review of terminology and a practical approach. Ecol. Model. 280, 117–128.

Ayllón, D., Almodóvar, A., Nicola, G.G., Elvira, B., 2010a. Ontogenetic and spatial variations in brown trout habitat selection. Ecol. Freshw. Fish 19, 420–432.

Ayllón, D., Almodóvar, A., Nicola, G.G., Elvira, B., 2010b. Modelling brown trout spatial requirements through physical habitat simulations. River Res. Appl. 26, 1090–1102.

Ayllón, D., Almodóvar, A., Nicola, G.G., Parra, I., Elvira, B., 2012. Modelling carrying capacity dynamics for the conservation and management of territorial salmonids. Fish. Res. 134–136, 95–103.

Ayllón, D., Nicola, G.G., Elvira, B., Parra, I., Almodóvar, A., 2013. Thermal carrying capacity for a thermally-sensitive species at the warmest edge of its range. PLoS ONE 8, e81354.

Barrett, R.D.H., Schluter, D., 2008. Adaptation from standing genetic variation. Trends Ecol. Evol. 23, 38–44.

Barton, N.H., Keightley, P.D., 2002. Understanding quantitative genetic variation. Nat. Rev. Genet. 3, 11–21.

Biro, P.A., Post, J.R., 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. Proc. Natl. Acad. Sci. U. S. A. 105, 2919–2922.

Botkin, D.B., Saxe, H., Araujo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R., Faith, D.P., Ferrier, S., Guisan, A., Hansen, A.S., Hilbert, D.W., Loehle, C., Margules, C., New, M., Sobel, M.J., Stockwell, D.R.B., 2007. Forecasting the effects of global warming on biodiversity. Bioscience 57, 227–236.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. Trends Ecol. Evol. 23, 453–460.

Brown, C.J., Schoeman, D.S., Sydeman, W.J., Brander, K., Buckley, L.B., Burrows, M.T., Duarte, C.M., Moore, P.J., Pandolfi, J.M., Poloczanska, E.S., Venables, W., Richardson, A.J., 2011. Quantitative approaches in climate change ecology. Global Change Biol. 17, 3697–3713.

Brunet, M., Casado, M.J., de Castro, M., Galán, P., López, J.A., Martín, J.M., Pastor, A., Petisco, E., Ramos, P., Ribalaygua, J., Rodríguez, E., Sanz, I., Torres, L., 2009. Regional climate change scenarios for Spain. Spanish Meteorol. Agency (in Spanish).

Campolongo, F., Cariboni, J., Saltelli, A., 2007. An effective screening design for sensitivity analysis of large models. Environ. Model. Softw. 22, 1509–1518.

Carlson, S.M., Seamons, T.R., 2008. A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. Evolut. Appl. 1, 222–238.

Carnell, R., 2012. Lhs: Latin Hypercube Samples. R package version 0.10.

Chevin, L.M., Lande, R., Mace, G.M., 2010. Adaptation plasticity, and extinction in a changing environment: towards a predictive theory. PLoS Biol. 8.

Comte, L., Grenouillet, G., 2013. Do stream fish track climate change? Assessing distribution shifts in recent decades. Ecography 36, 1236–1246.

Comte, L., Buisson, L., Daufresne, M., Grenouillet, G., 2013. Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. Freshw. Biol. 58, 625–639.

Crozier, L.G., Hendry, A.P., Lawson, P.W., Quinn, T.P., Mantua, N.J., Battin, J., Shaw, R.G., Huey, R.B., 2008. Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. Evolut. Appl. 1, 252–270.

Crozier, L.G., Scheuerell, M.D., Zabel, R.W., 2011. Using time series analysis to characterize evolutionary and plastic responses to environmental change: a case

study of a shift toward earlier migration date in sockeye salmon. Amer. Nat. 178, 755–773.

Crozier, L.G., Hutchings, J.A., 2014. Plastic and evolutionary responses to climate change in fish. Evolut. Appl. 7, 68–87.

Daufresne, M., Lengfellner, K., Sommer, U., 2009. Global warming benefits the small in aquatic ecosystems. Proc. Natl. Acad. Sci. U. S. A. 106, 12788–12793.

Dunlop, E.S., Shuter, B.J., Dieckmann, U., 2007. Demographic and evolutionary consequences of selective mortality: predictions from an eco-genetic model for small-mouth bass. Trans. Am. Fish. Soc. 136, 749–765.

Dunlop, E.S., Heino, M., Dieckmann, U., 2009. Eco-genetic modeling of contemporary life-history evolution. Ecol. Appl. 19, 1815–1834.

Einum, S., Fleming, I.A., 1999. Maternal effects of egg size in brown trout (Salmo trutta): norms of reaction to environmental quality. Proc. R. Soc. B 266, 2095–2100.

Elliott, J.M., 1984. Numerical changes and population regulation in young migratory trout Salmo trutta in a Lake District stream, 1966–83. J. Anim. Ecol. 53, 327–350.

Esterby, S.R., 1996. Review of methods for the detection and estimation of trends with emphasis on water quality applications. Hydrol. Process. 10, 127–149.

Esteve, M., 2005. Observations of spawning behaviour in Salmoninae: Salmo, Oncorhynchus and Salvelinus. Rev. Fish Biol. Fish. 15, 1–21.

Evans, M.R., 2012. Modelling ecological systems in a changing world. Philos. Trans. R. Soc. B 367, 181–190.

Fausch, K.D., 1984. profitable stream positions for salmonids – relating specific growth-rate to net energy gain. Can. J. Zool. 62, 441–451.

Frank, B.M., Baret, P.V., 2013. Simulating brown trout demogenetics in a river/nursery brook system: the individual-based model DemGenTrout. Ecol. Model. 248, 184–202.

Frank, B.M., Piccolo, J.J., Baret, P.V., 2011. A review of ecological models for brown trout: towards a new demogenetic model. Ecol. Freshw. Fish 20, 167–198.

García-Vázquez, E., Morán, P., Martínez, J., Pérez, B., de Gaudemar, B., Beall, E., 2001. Alternative mating strategies in Atlantic salmon and brown trout. J. Hered. 92, 146–149.

Gilbert, R.O., 1987. Statistical Methods for Environmental Pollution Monitoring. Wiley, New York.

Grimm, V., Dorndorf, N., Frey-Roos, F., Wissel, C., Wyszomirski, T., Arnold, W., 2003. Modelling the role of social behavior in the persistence of the alpine marmot Marmota marmota. Oikos 102, 124–136.

Grimm, V., Railsback, S., 2005. Individual-based Modeling and Ecology. Princeton University Press, Princeton, NJ.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310, 987–991.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jorgensen, C., Mooij, W.M., Muller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Ruger, N., Strand, E., Souissi, S., Stillman, R.A., Vabo, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. Ecol. Model. 198, 115–126.

Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: a review and first update. Ecol. Model. 221, 2760–2768.

Grimm, V., Augusiak, J., Focks, A., Frank, B.M., Gabsi, F., Johnston, A.S.A., Liu, C., Martin, B.T., Meli, M., Radchuk, V., Thorbek, P., Railsback, S.F., 2014. Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. Ecol. Model. 280, 129–139.

Harvey, B.C., Railsback, S.F., 2014. Feeding modes in stream salmonid population models: is drift feeding the whole story? Environ. Biol. Fishes 97, 615–625.

Harvey, B.C., Nakamoto, R.J., White, J.L., Railsback, S.F., 2014. Effects of streamflow diversion on a fish population: combining empirical data and individual-based models in a site-specific evaluation. N. Am. J. Fish. Manag. 34, 247–257.

Hill, J., Grossman, G.D., 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. Ecology 74, 685–698.

Hirsch, R.M., Slack, J.R., Smith, R.A., 1982. Techniques of trend analysis for monthly water quality data. Water Resour. Res. 18, 107–121.

Hughes, N.F., 1992. Selection of positions by drift-feeding salmonids in dominance hierarchies: model and test for arctic grayling (Thymallus arcticus) in subarctic mountain streams, interior Alaska. Can. J. Fish. Aquatic Sci. 49, 1999–2008.

Hughes, N.F., Grand, T.C., 2000. Physiological ecology meets the ideal-free distribution: predicting the distribution of size-structured fish populations across temperature gradients. Environ. Biol. Fishes 59, 285–298.

Iványi, M., Beckman, R., Conover, W., 1979. A comparison of three methods for selecting values of input variables in the analysis of output from a computer code. Technometrics 21, 239–245.

Jager, H.I., 2001. Individual variation in life history characteristics can influence extinction risk. Ecol. Model. 144, 61–76.

Jassby, A.D., Cloern, J.E., 2014. Wq: Exploring Water Quality Monitoring Data R Package version 0.4-1.

Jiménez Cisneros, B.E., Oki, T., Arnell, N.W., Benito, G., Cogley, J.G., Döll, P., Jiang, T., Mwakalila, S.S., 2014. Freshwater resources. In: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.), Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge and New York, pp. 229–269.

Jonsson, B., Jonsson, N., 2009. A review of the likely effects of climate change on anadromous Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular reference to water temperature and flow. J. Fish Biol. 75, 2381–2447.

Jonsson, B., Jonsson, N., 2011. Ecology of Atlantic Salmon and Brown Trout: Habitat as a Template for Life Histories. Springer, Dordrecht.

Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Gardmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M., Rijnsdorp, A.D., 2007. Ecology: managing evolving fish stocks. Science 318, 1247–1248.

Kendall, M., 1975. Multivariate Analysis. Charles Griffin & Company, London.

Kovach, R.P., Gharrett, A.J., Tallmon, D.A., 2012. Genetic change for earlier migration timing in a pink salmon population. Proc. R. Soc. B 279, 3870–3878.

López-Moreno, J.I., Zabalza, J., Vicente-Serrano, S.M., Revuelto, J., Gilaberte, M., Azorin-Molina, C., Morán-Tejeda, E., García-Ruiz, J.M., Tague, C., 2014. Impact of climate and land use change on water availability and reservoir management: scenarios in the Upper Aragón River, Spanish Pyrenees. Sci. Total Environ. 493, 1222–1231.

Lynch, M., Walsh, J.B., 1998. Genetics and Analysis of Quantitative Traits. Sinauer Associates Inc., Sunderland, USA.

Martin, B., Jager, T., Nisbet, R.M., Preuss, T.G., Grimm, V., 2013. Predicting population dynamics from the properties of individuals: a cross-level test of dynamic energy budget theory. Am. Nat. 181, 506–519.

Mann, H.B., 1945. Nonparametric tests against trend. Econometrica 13, 245–259.

McLeod, A.I., 2011. Kendall: Kendall Rank Correlation and Mann–Kendall Trend Test R Package Version 2.2.

Milhous, R.T., Waddle, T.J., 2012. Physical Habitat Simulation (PHABSIM) Software for Windows (v.1.5.1). USGS Fort Collins Science Center, Fort Collins, CO.

Morris, M.D., 1991. Factorial sampling plans for preliminary computational experiments. Technometrics 33, 161–174.

Nakicenovic, N., Alcamo, J., Davis, G., de Vries, B., Fenhann, J., Gaffin, S., Gregory, K., Grübler, A., Jung, T.Y., Kram, T., Lebre-La Rovere, E., Michaelis, L., Mori, S., Morita, T., Pepper, W., Pitcher, H., Price, L., Riahi, K., Roehrl, A., Rogner, H., Sankovski, A., Schlesinger, M., Shukla, P., Smith, S., Swart, R., van Rooijen, S., Victor, N., Dadi, Z., 2000. Special Report on Emissions Scenarios: A Special Report of Working Group III of the IPCC. Cambridge University Press, Cambridge.

Parra, I., Nicola, G.G., Vøllestad, L.A., Elvira, B., Almodóvar, A., 2014. Latitude and altitude differentially shape life history trajectories between the sexes in non-anadromous brown trout. Evol. Ecol. 28, 707–720.

Piou, C., Prévost, E., 2012. A demo-genetic individual-based model for Atlantic salmon populations: model structure, parameterization and sensitivity. Ecol. Model. 231, 37–52.

Piou, C., Prévost, E., 2013. Contrasting effects of climate change in continental vs oceanic environments on population persistence and microevolution of Atlantic salmon. Global Change Biol. 19, 711–723.

Pujol, G., Iooss, B., Janon, A., 2013. Sensitivity: Sensitivity Analysis. R Package version 1.7.

Railsback, S.F., Harvey, B.C., 2002. Analysis of habitat selection rules using an individual-based model. Ecology 83, 1817–1830.

Railsback, S.F., Harvey, B.C., 2013. Trait-mediated trophic interactions: is foraging theory keeping up? Trends Ecol. Evol. 28, 119–125.

Railsback, S.F., Lamberson, R.H., Harvey, B.C., Duffy, W.E., 1999. Movement rules for individual-based models of stream fish. Ecol. Model. 123, 73–89.

Railsback, S.F., Harvey, B.C., Lamberson, R.H., Lee, D.E., Claasen, N.J., Yoshihara, S., 2002. Population-level analysis and validation of an individual-based cutthroat trout model. Nat. Resour. Model. 15, 83–110.

Railsback, S.F., Harvey, B.C., Hayes, J.W., LaGory, K.E., 2005. Tests of theory for diel variation in salmonid feeding activity and habitat use. Ecology 86, 947–959.

Railsback, S.F., Harvey, B.C., Jackson, S.K., Lamberson, R.H., 2009. InSTREAM: The Individual-based Stream Trout Research and Environmental Assessment Model. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

Railsback, S.F., Gard, M., Harvey, B.C., White, J.L., Zimmerman, J.K.H., 2013. Contrast of degraded and restored stream habitat using an individual-based salmon model. N. Am. J. Fish. Manag. 33, 384–399.

Reed, T.E., Schindler, D.E., Hague, M.J., Patterson, D.A., Meir, E., Waples, R.S., Hinch, S.G., 2011. Time to Evolve? Potential evolutionary responses of Fraser river sockeye salmon to climate change and effects on persistence. PLoS ONE 6, e20380.

Rosenfeld, J.S., 2014. Modelling the effects of habitat on self-thinning, energy equivalence, and optimal habitat structure for juvenile trout. Can. J. Fish. Aquatic Sci. 71, 1395–1406.

Rosenfeld, J.S., Bouwes, N., Wall, C.E., Naman, S.M., 2014. Successes, failures, and opportunities in the practical application of drift-foraging models. Environ. Biol. Fishes 97, 551–574.

Santander Meteorology Group, 2012. FUME Package: A Set of Functions for the Analysis of Climate/Weather Fire Danger. R package version 1.0.

Schmolke, A., Thorbek, P., DeAngelis, D.L., Grimm, V., 2010. Ecological models supporting environmental decision making: a strategy for the future. Trends Ecol. Evol. 25, 479–486.

Settele, J., Scholes, R., Betts, R., Bunn, S., Leadley, P., Nepstad, D., Overpeck, J.T., Taboada, M.A., 2014. Terrestrial and inland water systems. In: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.), Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel

on Climate Change. Cambridge University Press, Cambridge and New York, pp. 271–359.

Stillman, R.A., Railsback, S.F., Giske, J., Berger, U., Grimm, V., 2015. Making predictions in a changing world: the benefits of individual-based ecology. Bioscience, http://dx.doi.org/10.1093/biosci/biu192 (in press).

Tague, C., Band, L., 2004. RHESSys: regional hydro-ecologic simulation system: an object-oriented approach to spatially distributed modeling of carbon, water and nutrient cycling. Earth Interact. 8, 1–42.

The Nature Conservancy, 2009. Indicators of Hydrologic Alteration Version 7.1. Olympia, WA.

Thériault, V., Dunlop, E.S., Dieckmann, U., Bernatchez, L., Dodson, J.J., 2008. The impact of fishing-induced mortality on the evolution of alternative life-history tactics in brook charr. Evolut. Appl. 1, 409–423.

Thiele, J.C., Kurth, W., Grimm, V., 2014. Facilitating parameter estimation and sensitivity analysis of agent-based models: a cookbook using NetLogo and 'R'. J. Artif. Soc. Soc. Simul. 17, 11.

Vedder, O., Bouwhuis, S., Sheldon, B.C., 2013. Quantitative assessment of the importance of phenotypic plasticity in adaptation to climate change in wild bird populations. PLoS Biol. 11, e1001605.

Vincenzi, S., 2014. Extinction risk and eco-evolutionary dynamics in a variable environment with increasing frequency of extreme events. J. R. Soc. Interface 11.

Vincenzi, S., Crivelli, A.J., Giske, J., Satterthwaite, W., Mangel, M., 2012a. Selective consequences of catastrophes for growth rates in a stream-dwelling salmonid. Oecologia 168, 393–404.

Vincenzi, S., De Leo, G.A., Bellingeri, M., 2012b. Consequences of extreme events on population persistence and evolution of a quantitative trait. Ecol. Inf. 8, 20–28.

Vincenzi, S., Crivelli, A.J., Satterthwaite, W.H., Mangel, M., 2014. Eco-evolutionary dynamics induced by massive mortality events. J. Fish Biol. 85, 8–30.

Wang, H.Y., Hook, T.O., 2009. Eco-genetic model to explore fishing-induced ecological and evolutionary effects on growth and maturation schedules. Evolut. Appl. 2, 438–455.

Warren, R., VanDerWal, J., Price, J., Welbergen, J.A., Atkinson, I., Ramirez-Villegas, J., Osborn, T.J., Jarvis, A., Shoo, L.P., Williams, S.E., Lowe, J., 2013. Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. Nat. Climate Change 3, 678–682.

West, J.M., Julius, S.H., Kareiva, P., Enquist, C., Lawler, J.J., Petersen, B., Johnson, A.E., Shaw, M.R., 2009. U.S. natural resources and climate change: concepts and approaches for management adaptation. Environ. Manag. 44, 1001–1021.

Wiegand, T., Jeltsch, F., Hanski, I., Grimm, V., 2003. Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. Oikos 100, 209–222.

Wilensky, U., 1999. NETLOGO, Centre for Connected Learning and Computer-Based Modelling. Northwestern University, Evanston, IL, http://ccl.northwestern.edu/netlogo

Yue, S., Wang, C., 2004. The Mann–Kendall test modified by effective sample size to detect trend in serially correlated hydrological series. Water Resour. Manag. 18, 201–218.