



**HAL**  
open science

## Using eco-evolutionary models to improve management of introgression in brown trout

Dorinda Marie Folio, Arnaud Caudron, Laure Vigier, Sylvie Oddou-Muratorio, Jacques Labonne

► **To cite this version:**

Dorinda Marie Folio, Arnaud Caudron, Laure Vigier, Sylvie Oddou-Muratorio, Jacques Labonne. Using eco-evolutionary models to improve management of introgression in brown trout. *Ecology of Freshwater Fish*, 2024, 33 (4), pp.e12789. 10.1111/eff.12789 . hal-04736999

**HAL Id: hal-04736999**

**<https://univ-pau.hal.science/hal-04736999v1>**

Submitted on 15 Oct 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

1 TITLE

2 Using eco-evolutionary models to improve management of introgression in brown trout.

3

4 AUTHORS

5 Dorinda Folio<sup>1,2</sup>, Arnaud Caudron<sup>2</sup>, Laure Vigier<sup>2</sup>, Sylvie Oddou-Muratorio<sup>1</sup>, Jacques Labonne<sup>1</sup>.

6

7 AFFILIATIONS

8 1 - UMR INRAE-UPPA, ECOBIOP, Université de Pau et des Pays de l'Adour, 64310 Saint-Pée-sur-  
9 Nivelle, France

10 2 - SCIMABIO Interface, Thonon-les-Bains, France

11

12 CORRESPONDING AUTHOR

13 [jacques.labonne@inrae.fr](mailto:jacques.labonne@inrae.fr)

14

15 RUNNING TITLE

16 Eco-evolutionary modelling of introgression management in brown trout.

17

18 ABSTRACT

19 The management of intraspecific diversity in many species is usually disconnected from eco-  
20 evolutionary processes happening *in natura*. A classic example is embodied in the problem of  
21 introgression in hybridised fish populations, wherein management practices are generally unaware of  
22 any selective process at work, and therefore generally rely on numbers (adding or removing  
23 individuals) to reduce introgression. Such an example can be observed in the French Alps, where  
24 native Mediterranean (MED) brown trout have been highly introgressed through decades of stocking  
25 with domesticated Atlantic (ATL) brown trout. Recently however, new results shed light on a  
26 potential selective mechanism that may affect differentially the fitness of MED and ATL genes  
27 depending on the environment (GxE interaction). Using a demogenetic agent-based model able to  
28 account for such GxE interaction, we simulate a management scenario implemented in 2005 by some  
29 biodiversity managers and scientists, who attempted to restore the Mediterranean gene pool using  
30 translocation of near pure MED individuals in Atlantic dominated areas. We show that the model is  
31 unable to recreate the observed introgression dynamics if the GxE interaction is not included. This  
32 finding implies that i/ eco-evolutionary mechanisms can have large effects on introgression dynamics  
33 on very short time scales and ii/, management of intraspecific diversity should increasingly rely on  
34 these natural mechanisms, so as to improve management targets and facilitate adaptation to rapid  
35 environmental changes.

36

37

38

39 KEYWORDS

40 Hybridization; *Salmo trutta*; intraspecific diversity; genotype environment interaction;

41

42 INTRODUCTION

43 Management and conservation of intraspecific diversity has the complex task to maximise the  
44 protection of standing diversity, a legacy of millions of years of evolution, and to also ensure that this  
45 diversity is up to challenge the current environmental change. In the midst of the biodiversity crisis,  
46 scientists have become increasingly aware that intraspecific diversity is not only an intrinsic value  
47 of species and populations in itself (Piccolo, 2017; Soulé, 1985). It is also, as specified by the tenets of  
48 evolutionary biology, the fuel of adaptation, through response to natural selection. In short, the very  
49 thing that we seek to protect is also the one thing that might help populations to cope with climate  
50 and global change effects (Carroll et al., 2007; Reznick et al., 2019). Paralleling that growing  
51 understanding, many recent studies analysed to what extent evolutionary change in populations is  
52 caused by human activities and interference (Godineau et al., 2023; Hendry et al., 2017). Their results  
53 are generally consistent, and indicate that such evolutionary change is real, massive, and happening  
54 on ecological time scales. Hence, selection associated with local anthropogenic pressure can interact  
55 with that associated with global change. It is therefore paramount to investigate these interactions  
56 so that biological production systems and conservation programs can benefit from and care for  
57 evolutionary processes.

58 One such human interference is embodied by anthropogenic hybridization, defined here as the  
59 accidental or deliberate admixture of previously isolated genetic pools (Crispo & Chapman, 2010;  
60 Rhymer & Simberloff, 1996). One of the most common cause of anthropogenic hybridization (55% of  
61 the studies reviewed in (Todesco et al., 2016) is related to the assisted migration of - or 'restocking  
62 by' - non-native individuals (either wild or domesticated) or to escapes from livestock (Champagnon  
63 et al., 2013). Known negative effects spans from the loss of genetic and phenotypic variation (e.g.  
64 through competition, disease transmission, or reduced reproductive success of native individuals), to  
65 breakdowns of local adaptations in recipient populations as well as negative demographic effects  
66 though lower hybrid fitness (Allendorf et al., 2001; Bohling, 2016; Daupagne et al., 2021; Garant et  
67 al., 2007; Verhoeven et al., 2010). In a given restocking situation, it can therefore be difficult to  
68 understand or predict the net outcome on population evolutionary dynamics of these various risks.  
69 This is all the more problematic that follow-up monitorings after restocking are rare, particularly  
70 from a genetic perspective (Kurland et al., 2022; Weeks et al., 2011). Conversely, it is equally  
71 challenging to counteract the effects of past anthropogenic hybridization: attempting to bolster the  
72 native gene pools by simply restocking with similar gene pools generally leads to disappointing  
73 outcomes, notably because each situation might be unique (Allendorf et al., 2001; Bohling, 2016;  
74 Genovart, 2009; Gil et al., 2016a). Obviously, knowledge of impacts of restocking on population  
75 adaptive potential, their underlying mechanisms, and, whenever possible, a quantitative assessment  
76 of these impacts are urgently needed to elaborate exploratory scenarios covering a wide range of  
77 plausible outcomes to guide management decisions.

78 Provided some of the above-mentioned elements are available, demo-genetic agent-based models  
79 (DG-ABM) are efficient tools to address these challenges (Lamarins et al., 2022). The philosophy of  
80 such modelling approaches is to represent explicitly an eco-evolutionary loop, wherein traits involved  
81 in fitness variation have a genetic basis that is intergenerationally transmitted. Fitness itself arises

82 from interactions between individuals with regard to their environment. DG–ABM proved to be  
83 useful for the exploration of fundamental questions in evolutionary ecology, and also as effective  
84 prospective and decision support tools to investigate the interactions between management and  
85 natural eco-evolutionary processes (Coulson et al., 2006; Lamarins et al., 2022), notably in the  
86 fisheries domain (e.g., Ayllón et al., 2016; Nathan et al., 2019; Piou & Prévost, 2012).

87 The salmonids, as exploited species for both consumption and recreational angling, concentrate a  
88 significant part of the historical efforts of restocking and stocking outside their original distribution  
89 range (Laikre, 1999; McIntosh, 2011). Among them, *Salmo trutta* L. (Brown trout) is well-  
90 appropriated to investigate the impacts of restocking on population adaptive potential. At least five  
91 genetically and phenotypically distinct lineages of this widely-distributed species evolved in allopatry  
92 during Pleistocene glaciations (Bernatchez, 2001) with possible secondary contacts (Hashemzadeh  
93 Segherloo et al., 2021). Since the end of the 19th century, the Atlantic (ATL) lineage has been  
94 intensively used for fish farming and intensive river stocking to sustain recreational fishing. In the  
95 Mediterranean region, where the eponymic lineage is native (MED), the outcome of these ATL  
96 (re)stocking activities varies from total extirpation of native MED populations, to partial or full  
97 hybridization and eventually introgression of native MED populations by non-native ATL alleles  
98 (Behnke, 1992; Caudron et al., 2009; Gil et al., 2016a). Additionally, these stocking efforts also  
99 targeted segments of rivers usually located in upstream high-altitude areas, previously fish-free for  
100 reasons related to either biogeography (ice cover of the last glacial maximum, see Splendiani et al.,  
101 2016) or to the presence of natural or non-natural barriers. More rarely, native populations managed  
102 to remain genetically pure. Across decades, the goals of fish populations managers has however  
103 progressively shifted from maximising density and catches, to protecting native diversity (Laikre,  
104 1999). Consequently and more recently, managers have tried to mitigate the effect of non-native  
105 stocking, through either stopping said stocking, starting native stocking, removing potential non-  
106 native and/or hybrid fish, or translocating native fish between rivers (Caudron et al., 2011; Gil et al.,  
107 2016a).

108 In the French Alps, located in the Mediterranean basin, biodiversity managers elected in 2005 to  
109 translocate native MED fish to an ATL dominated stretch on the River Borne, hoping to significantly  
110 reduce the introgression rate (Gil et al., 2016a). Later, in another close river system, a quantitative  
111 genetics study shed light on an eco-evolutionary mechanism that may be involved in the dynamics of  
112 hybridization in wild populations (D. M. Folio et al., 2021): it was found that eggs sired by MED native  
113 females had a higher survival at hatching than eggs sired by ATL females in cold temperatures (2 to  
114 4.5°C). This advantage however was fully cancelled when average temperatures were raised (7.5°C).  
115 In combination with local heterogeneity in river temperatures, this genotype by environment (GxE)  
116 interaction was a potential candidate to explain the observed spatial heterogeneity of the  
117 distribution of population introgression rates. The present study takes the opportunity of the well-  
118 documented translocation action on the River Borne to investigate the impacts of a translocation  
119 management scenario with the higher egg survival of MED females at low temperature on the  
120 dynamics of introgression in the MED-ATL trout system. To that aim, we built a DG-ABM coupling (1)  
121 a model of resident brown trout population dynamics simulating the effect of competition and  
122 temperature on growth and survival, and (2) a simple quantitative genetics model describing the  
123 effect of individual introgression rate on survival at hatching in relation to water temperature. Using  
124 this model, we simulated the translocation of MED population from the lower part of a watershed to  
125 its ATL-dominated upper part, and we tracked the simulated dynamics of introgression and  
126 intraspecific diversity changes, accounting (or not) for the GxE interaction relating survival of  
127 offspring at hatching, river temperature, and maternal genotype. Thanks to the managers' data and  
128 monitoring, we also compare the outcome of our model with the outcome of their management

129 action, so to actually assess whether the inclusion of eco-evolutionary mechanisms allows for better  
130 predictions.

131

## 132 METHODS

### 133 **Model overview**

134 The MEDITERRANEA model is a demogenetic agent-based model (DG-ABM), implementing the  
135 guidelines described in Lamarins et al. ((Lamarins et al., 2022). Its general purpose is to simulate the  
136 demographic and evolutionary dynamics of brown trout populations in a spatially explicit  
137 environment (a hydrographic dendritic network), with a strong focus on interactions between  
138 individuals (e.g., competition driven survival at different life stages and mating systems), and  
139 between individuals and environment (e.g., temperature-dependent survival at different life stages).  
140 It is particularly suited to simulate these interactions in the context of hybridization between  
141 evolutionary lineages (here, MED and ATL) because the individual introgression rate directly  
142 determines two key life history traits (egg survival and female preference). The underlying hypothesis  
143 is that the same seven quantitative trait loci linearly control the genetic variation in egg survival and  
144 female preference, a gross simplification that is yet justified by (1) the absence of detailed knowledge  
145 on the genetic architecture of these traits and (2) the opportunity to compare the simulated  
146 variation in introgression across time and populations with field observation of introgression rate (Gil  
147 et al., 2016a). Additionally, the model integrates tools to simulate the effects of various management  
148 actions on the dynamics of the system, such as stocking, fishing, or habitat modification.

149 The model can be downloaded freely at <https://doi.org/10.57745/LIKOGD>. A comprehensive  
150 installation guide is available at: [https://capsis.cirad.fr/capsis/documentation/installation\\_guide](https://capsis.cirad.fr/capsis/documentation/installation_guide). A  
151 full description of the model is accessible (Folio, 2022), <https://theses.hal.science/tel-04122411>).  
152 Additionally, the model provides a user friendly interface with an online help assistance. The model is  
153 coded in JAVA language, on the CAPSIS-4 platform (<https://capsis.cirad.fr>). We here provide a brief  
154 overview of its structure and characteristics.

### 155 **Model architecture**

156 The hydrographic dendritic network is composed of reaches of homogenous habitat. Limits between  
157 reaches are such that any reach is big enough to host the home range of a typical adult trout  
158 (minimum 200m long), but they locate major differences in habitat continuity (slope, confluences,  
159 obstacles, etc). The quality of habitat (for growth, reproduction and carrying capacity) can be  
160 specified for each reach. Local temperature dynamics in each reach are modelled as functions of  
161 season and altitude. Between reaches, weirs can be placed and may influence connectivity in both  
162 directions.

163 Fish are modelled in two ways: either a collection (or group) of individuals sharing similar  
164 characteristics (a coding trick to improve memory use), or an individual with its own characteristics.  
165 Collections of individuals are used from fertilisation up to 8 months old, covering egg stage, hatching,  
166 emergence, and early growth. Beyond 8 months old, each fish is modelled individually with its own  
167 traits and genetic data (Supplementary File 1). Individuals are diploids and possess a nuclear genome  
168 composed of seven bi-allelic unlinked loci for which each allele is related to a specific lineage. Alleles  
169 value can either be 0 (MED) or 1 (ATL) at each locus. This simplified genetic architecture is in relation  
170 to the data generated by managers that use 7 SNPs to genotype and assign brown trout individuals  
171 to their lineage of origin ((D. M. Folio et al., 2021). It allows to compute an introgression score for

172 each individual, which is used at some points in the simulation as an abstract genetic component of  
173 traits involved in reproduction and mortality processes (see below).

174 The model updates all information on reaches, weirs, collections of fish or individual fish on a  
175 monthly scale, which allows it to depict the within-year changes in environment, biological functions  
176 and life stages (growth, movements, mortality, reproduction).

## 177 **Process overview**

178 The life cycle is modelled as a series of processes at each time step for each individual or groups of  
179 individuals (Fig. 1). Ageing and developing allows individuals to change life stages. Eggs hatch at 380  
180 degree-days and larvae emerge at 700 degree.days, producing juveniles. At 12 months old, juveniles  
181 produce sub-adults, and at 24 months old, sub-adults turn to adult fish.

182 The monthly survival rate  $S_{stage}$  is controlled by a stage dependent value ( $C_{stage}$ ) and is also influenced  
183 by the local density of the considered stage ( $D_{stage, reach}$ ):

184

$$185 \quad S_{stag, reach} = D_{stage, reach} \times \frac{e^{(C_{stage})}}{(1+e^{(C_{stage})})} \quad \text{with} \quad D_{stage, reach} = \frac{1}{(1+\frac{Density_{stage, reac}}{K_{max}})}$$

186 Before emergence from the gravel however,  $D_{stage, reach} = 1$ .  $C_{stage}$  is calibrated using empirical data  
187 (Folio 2022). Additionally,  $C_{stage}$  at hatching is modelled as a quantitative genetic trait, whose inter-  
188 individual variation depends on a genetic component (the maternal introgression rate), on an  
189 environmental component (temperature) and on their interactions, so as to reflect the available  
190 knowledge regarding the GxE interaction in post-zygotic selection:

$$191 \quad C_{stage=hatching} = \alpha + \beta \times T + (Maternal \text{ introgression} - 0.5) \times (\gamma + \delta \times T)$$

192 In the present study,  $\alpha$ ,  $\beta$ ,  $\gamma$  and  $\delta$  are directly extracted from empirical estimates in the field (Fig. 2,  
193 Supplementary file 2), and  $T$  is the mean winter temperature in the considered reach over the  
194 incubation period. This implies that offspring of MED females have higher survival in cold  
195 temperature than offspring from ATL females (data from Folio et al., 2021). Note that the paternal  
196 component of offspring genotype does not affect egg survival.

197

198

199 Individual growth is both temperature and density dependent, following a Von Bertalanffy model.  
200 Body Size ( $BS_{t+1}$ ) at time  $t+1$  is a function of previous body size, growth factor  $k$  and maximum body  
201 size  $L_{inf}$ :

$$202 \quad BS_{t+1} = BS_t + BS_t \times k \times (1 - \frac{BS_t}{L_{inf}})$$

$$203 \quad \text{with } k = b \times e^{(-a_{stage} \times density_{stage})} \times ME \times e^{\frac{(optT-T)^2}{2 \times rangeT^2}}$$

204 Where  $b$  is the base growth parameter,  $a$  is a stage factor for density effect on growth,  $ME (=0.7)$  is  
205 maturation effect slowing down somatic growth when individuals reach reproductive age,  $optT$  is the  
206 optimal growth temperature (Elliott et al., 1995; Forseth et al., 2009; Forseth & Jonsson, 1994),  $T$  is  
207 the monthly mean temperature, and  $rangeT$  is an amplitude parameter describing how quickly

208 growth is reduced when  $T$  goes farther from  $optT$ . None of these parameters are genetically  
209 controlled in the model.

210 Movement probability between reaches in growth season depends on local density:

$$211 \quad \theta_{stage,reach} = \frac{Density_{stage,reach} * \theta_{max}}{Density_{max} * GQ}$$

212

213 with  $\theta_{max}$  and  $Density_{max}$  are user-determined and  $GQ$  is the habitat quality of the reach for somatic  
214 growth.

215 Fish then move to the next reach with an equal probability to go upstream or downstream, provided  
216 no obstacle is met. If an obstacle is met, the probability to cross said obstacle is ruled by the  
217 characteristics of the obstacle. Just before reproduction season, individuals can undertake homing  
218 migration, trying to move back to their birth reach. Again, obstacles might prevent them from doing  
219 so.

220 Reproduction occurs in December each year. Mature individuals in a reach undergo a process of  
221 random encounters. Each female is then associated with a number of males (this number depends on  
222 the Operational Sex Ratio defined by user). Females then express a mating preference  $p$  based on the  
223 dissimilarity  $D$  between their own phenotype and the potential partner's phenotype (Gil et al.,  
224 2016b) :

$$225 \quad p = \frac{GC * \left( \frac{e^{(x+y \times D)}}{1 + e^{(x+y \times D)}} \right) + ((100 - GC) \times q)}{100}$$

226 where  $x$  and  $y$  are parameters defining the strength of preference (extracted from Gil et al., 2016b),  
227 and  $GC$  is a scaling factor between the introgression rate and the phenotype (since differences in  
228 phenotypes between lineages are only partly related to genetic differences between lineages). In the  
229 present case,  $GC=35$ , and  $D$  is computed as the absolute difference between the introgression rate of  
230 the target female and of its potential partner.  $q$  is a random decimal drawn in a uniform distribution  
231 between 0 and 1.  $(100-GC)*q$  can be viewed as the environmental component of the variation in  
232 mating preference. For each successful mating, a batch of eggs of size  $nEggs$  is created such as:

$$233 \quad nEggs = F \times (10 \times BS)^f \times \frac{RQ}{(h * SC)}$$

234 With  $F$  and  $f$  fecundity parameters,  $BS$  the body size of the female,  $RQ$  the habitat quality of the reach  
235 for reproduction,  $SC$  a user defined parameter that describes the number of potential mating within  
236 a season per female, and  $h$  a parameter describing potential oophagy effects on the redd.

237 All parameters values are provided in Supplementary Information 3.

### 238 **Simulation scenario(s)**

239 We used the MEDITERRANEA model to simulate a real management action undertaken on brown  
240 trout populations in the River Borne, French alps, in the Mediterranean region where the MED  
241 lineage is native. This river, as many in the Alps region and in Europe, has been stocked for decades  
242 using domestic ATL trout (Caudron et al., 2009; Gil et al., 2016a). In particular, following a major flash  
243 flood in 1987 that wiped out populations upstream of an impassable dam, ATL stocking in the  
244 upstream part of the river was intensive until 2005, leading to a pure ATL population located

245 upstream. Below the dam however, nearly pure and thriving MED populations remained (mean  
246 introgression = 0.2). Then, from 2005 to 2007, managers and scientists elected to translocate weakly  
247 introgressed MED trout from the downstream part (altitude ranging from 698 to 784m) to the  
248 upstream part (altitude ranging from 838 to 1039m), hoping to restore the MED native lineage in the  
249 upstream part of the river. At the time, they hoped that 1/ the translocation would create a MED  
250 gene flow in the upstream part and 2/ the translocated population with MED genes could be more  
251 adapted to the local environment. Although they had no evidence at this date, behavioural and eco-  
252 evolutionary interactions supporting this prediction were discovered later (Folio et al., 2021; Gil et  
253 al., 2016a).

254 We modelled this exact scenario, starting from known initial conditions in terms of population  
255 structure : near pure MED populations downstream, pure ATL populations upstream. The  
256 environment was also recreated: the dendritic structure of the river, the presence of dams that  
257 might block movement and, the local habitat quality (see Fig. 3). Of specific importance was the  
258 temporal and spatial variation of temperature: we assumed that temperature was negatively  
259 correlated with altitude, and could therefore be variable between reaches, reflecting the minimum  
260 and maximum temperature provided by the managers (see Supplementary File 3). We then  
261 envisioned two alternative scenarios: a neutral scenario, where all individuals survive hatching with  
262 the same probability whatever their genotype and therefore introgression, and a selective scenario,  
263 based on Folio et al. (2021)'s results, wherein offspring from MED females have higher chance of  
264 survival in cold water, and where this advantage cancels at 8°C (see Fig. 2). Our goal was to  
265 investigate whether the inclusion of GxE mechanism i/ changes the model's prediction and ii/  
266 provides predictions closer to reality than a neutral model would.

267 The model was first run for a decade in order to establish demographic and genetic equilibrium in  
268 the downstream and upstream parts of the river (introgression per reach, age, size and maturation  
269 variation). Then, during three years, respectively 125, 610 and 370 nearly pure MED individuals were  
270 translocated from reach D to reach B, and respectively 135, 282 and 110 from reach D to reach A.  
271 Notably, amateur fishing was not allowed in reaches B and B1, but authorised in reaches A and A1.

272 We then monitored population eco-evolutionary dynamics in reaches A and B, as well as in two  
273 neighbouring accessible reaches (A1 and B1), during 11 years (2 to 3 generations). More specifically,  
274 we looked at the mean introgression per reach, and at the distribution of individual introgression,  
275 two measures often used by managers to assess results. The simulations were replicated 20 times.

276

## 277 RESULTS

### 278 **Dynamics of mean introgression**

279 Following translocation, the introgression rate decreases slowly from 100% down to 95% when  
280 considering a neutral scenario. However, when the GxE interaction is simulated, the introgression  
281 rate quickly decreases down to 50% in 10 years (Fig. 4). It is worth noting that this decrease is  
282 observed directly in the reaches where the translocations occurred (A and B), but also to some extent  
283 in the contiguous reaches (A1 and B1), indicating that the simulated movement rates allow for some  
284 spatial homogenization.

### 285 **Distribution of individual introgression**

286 Looking at the dynamics of individual introgression 4 years and 11 years after translocation (Fig. 5),  
287 we notice two very different situations again between the neutral and the GxE scenarios. In the



288 neutral scenario, we observe a production of hybrid genotypes, with individual introgression ranging  
289 from 0.5 to 1, 4 years after the translocation. Then, after 11 years, the distribution of individual  
290 introgression clearly converges towards mostly pure ATL genotypes. In the GxE scenario however,  
291 the initial genotypic diversity is much larger, with even some pure MED genotypes being observed.  
292 After 11 years, the distribution is mostly composed of HYB genotypes variously introgressed, and  
293 with nearly no pure MED or ATL genotypes in the translocated area.

#### 294 **Comparison with real data**

295 Using data provided by managers on each reach studied (Caudron et al., 2012), we were able to  
296 compare the observed mean introgression per reach in 2009 with the mean introgression predicted  
297 from the neutral and the GxE scenarios (Fig. 6). First, the neutral scenario was unable to  
298 approximate the real results, nor to reproduce spatial heterogeneity in introgression. The GxE  
299 scenario provided introgression patterns substantially closer to reality, but it generally overpredicted  
300 the mean introgression rate. Additionally, the GxE scenario was able to predict some spatial  
301 heterogeneity in introgression between reaches, wherein the mean introgression was higher  
302 downstream and lower upstream (in relationship to the altitudinal temperature gradient simulated in  
303 the model). To some extent, the same pattern was observed in the real results, but with much more  
304 contrast between reaches (lower introgression in translocated reaches than in neighbouring  
305 reaches).

306

## 307 DISCUSSION

308 The present study aimed at using a demogenetic agent-based modelling approach to simulate and  
309 predict the results of management practices on introgression dynamics in brown trout. Our findings  
310 indicate that neutral and GxE driven scenarios generate very different introgression dynamics on a  
311 short time scale. Additionally, GxE scenarios are better at predicting such dynamics than neutral  
312 models: a logical conclusion, and yet, it stems from different key points: (1) the existence and the  
313 discovery of eco-evolutionary mechanisms involved in the dynamics of introgression; (2) the ability to  
314 include these mechanisms in a consistent population model accounting available knowledge in  
315 ecology, demography, behaviour, development, and genetics, in interface with human activities, so  
316 as to actually quantify the strength of these eco-evolutionary forces in the system dynamics; (3) a  
317 detailed description of the management practices, as well as actual data on initial conditions and  
318 environmental variation in time and space. This last point is mandatory, because we aimed at  
319 reproducing relatively realistic dynamics that generate patterns in limited time and space, often in  
320 non-equilibrium situations.

#### 321 **The strength of the GxE interaction**

322 Our results clearly indicate that the neutral scenario and the GxE scenario make two very different  
323 predictions. Under the neutral scenario, as intuitively expected, the impact of the translocation is  
324 reduced, and depends mostly on the number of translocated individuals with respect to the  
325 population size of the upstream reaches. Including the GxE interaction in the model however  
326 completely changes the prediction in a handful of years.

327 The parameters used to simulate the GxE interaction were directly extracted from Folio et al. (2021),  
328 and they therefore represent actual values estimated in a field experiment, in three natural rivers of  
329 the same region presenting contrasted temperatures. In that way, we expect our GxE model to be a  
330 possible realisation of what is generally happening in natural populations. It is however only one

331 situation, and it could vary much depending on other factors of environment and on the populations  
332 considered throughout the whole Mediterranean area inhabited by the MED lineage. Sensitivity  
333 analyses not presented here also indicate that the strength of the GxE interaction has a substantial  
334 effect on the evolutionary dynamics (for instance, on mean introgression). It is thus paramount to  
335 provide field-based estimates related to the populations and environment of interest to the  
336 managers.

### 337 **Quality of the predictions**

338 Because our case study was based on a management strategy already implemented, it was possible  
339 to somewhat compare our predictions to observed results in the field (see Caudron et al., 2012). The  
340 neutral scenario performed very poorly, unable to predict the sharp decrease observed in mean  
341 introgression following the translocation of MED individuals. The GxE scenario provided a much  
342 better fit. This should indicate that the selective mechanism at work in relation to temperature  
343 variation is a very likely candidate to explain what actually happened during the translocation. Yet we  
344 must temper that fact with several other observations. First, in general, our predictions still tended  
345 to underestimate the general speed of change in the observed introgression: this might be due to a  
346 stronger GxE interaction, or to lower winter temperatures than those communicated by the  
347 managers, but it could also be linked to other non-elucidated selective events along the life cycle, still  
348 favouring the MED genes. Second, the fit was not as spatially variable as the observed data. It is  
349 noteworthy that the fit was better in translocated reaches than in neighbouring reaches. It is thus  
350 very possible that the movement rate in our model was overestimated.

### 351 **Implications for biodiversity managers**

352 Here, the effect of the GxE interaction indicates that actual conservation efforts must be ecologically  
353 allocated: some parts of the rivers where temperature remains colder should be prioritised. In  
354 warmer waters, the cost-benefit balance of translocation could be much lower to inexistent. It is  
355 equally important to develop models to predict the evolution of these thermal conditions in relation  
356 to climate change effects. An important consideration is also the fact that the mating system is  
357 generally slightly heterogamous: this implies that even in very cold waters, it might be near  
358 impossible to produce pure MED genotypes using translocation without removing the local  
359 introgressed populations before, if such a thing is feasible (Rytwinski et al., 2019).

360 It is noteworthy that the present case study is illustrative of other similar case studies performed in  
361 the same region (D. Folio, 2022), which generally provide the same results, where translocation is a  
362 relatively successful strategy in cold waters. It is also interesting to note that the selective advantage  
363 of the MED genes in cold waters included in the MEDITERRANEA model could also be at work in  
364 other regions: for instance Vera et al. (2023) have found that the MED genes were more frequent in  
365 rivers presenting cold waters in winter (but also in summer) in Spain. In Italy, MED genes were  
366 dominating in areas presenting more stable hydrogeological conditions, but the correlation with  
367 temperature gradients has not been investigated (Splendiani et al., 2016). In another lineage, the  
368 marble trout, it has also been demonstrated that in introgressed areas, the native genes were  
369 transmitted by females, as observed in our case, but no eco-evolutionary mechanisms were  
370 investigated (Pujolar et al., 2011).

371 The speed of phenotypic and genetic change under selection is very substantial in the present study,  
372 and it echoes several other studies on other biological models and under different anthropogenic  
373 pressures (Hendry et al., 2017; Kurland et al., 2022; Lamarins et al., 2022). These results point at eco-  
374 evolution as a likely efficient force to cope with rapid environmental change, leading to potential  
375 rescue effects (Fitzpatrick et al., 2020; Frankham, 2015). As a consequence, we advise that the

376 management of biodiversity should now quickly integrate eco-evolutionary considerations. The  
377 MEDITERRANEA model embodies such an approach, resulting from a collaboration between  
378 managers and researchers. It provides a comprehensive framework, accessible to expert managers,  
379 to simulate management scenarios, and implement management practices based on actual  
380 predictions.

381

## 382 ACKNOWLEDGEMENTS

383 This research was funded by the OFB (Office Français pour la Biodiversité) and the ANRT (Association  
384 Nationale Recherche Technologie). We thank François de Coligny for his continuous help during the  
385 development of the MEDITERRANEA model.

386

387

388

389

390

391

392

393

394

395

396

397

398

399

400

401

402

403

404

405

406

407

408

409  
410  
411  
412  
413  
414  
415  
416  
417  
418  
419  
420  
421  
422  
423  
424  
425  
426  
427  
428  
429  
430  
431  
432  
433  
434  
435  
436  
437  
438  
439  
440  
441  
442  
443  
444  
445  
446  
447  
448

## REFERENCES

- Allendorf, F. W., Leary, R. F., Spruell, P., & Wenburg, J. K. (2001). The problems with hybrids : Setting conservation guidelines. *Trends in Ecology & Evolution*, *16*(11), 613-622.  
[https://doi.org/10.1016/S0169-5347\(01\)02290-X](https://doi.org/10.1016/S0169-5347(01)02290-X)
- Ayllón, D., Railsback, S. F., Vincenzi, S., Groeneveld, J., Almodóvar, A., & Grimm, V. (2016). InSTREAM-Gen : Modelling eco-evolutionary dynamics of trout populations under anthropogenic environmental change. *Ecological Modelling*, *326*, 36-53. <https://doi.org/10.1016/j.ecolmodel.2015.07.026>
- Behnke, R. (1992). *American Fisheries Society Monograph no. 6*. American Fisheries Society (AFS).
- Bernatchez, L. (2001). THE EVOLUTIONARY HISTORY OF BROWN TROUT (SALMO TRUTTA L.) INFERRED FROM PHYLOGEOGRAPHIC, NESTED CLADE, AND MISMATCH ANALYSES OF MITOCHONDRIAL DNA VARIATION. *Evolution*, *55*(2), 351-379. <https://doi.org/10.1111/j.0014-3820.2001.tb01300.x>
- Bohling, J. H. (2016). Strategies to address the conservation threats posed by hybridization and genetic introgression. *Biological Conservation*, *203*, 321-327.  
<https://doi.org/10.1016/j.biocon.2016.10.011>
- Carroll, S. P., Hendry, A. P., Reznick, D. N., & Fox, C. W. (2007). Evolution on ecological time-scales. *Functional Ecology*, *21*(3), 387-393. <https://doi.org/10.1111/j.1365-2435.2007.01289.x>
- Caudron, A., Champigneulle, A., & Guyomard, R. (2009). Evidence of two contrasting brown trout *Salmo trutta* populations spatially separated in the River Borne (France) and shift in management towards conservation of the native lineage. *Journal of Fish Biology*, *74*(5), 1070-1085.  
<https://doi.org/10.1111/j.1095-8649.2008.02168.x>
- Caudron, A., Champigneulle, A., Guyomard, R., & Largiadèr, C. R. (2011). Assessment of three strategies practiced by fishery managers for restoring native brown trout (*Salmo trutta*) populations in Northern French Alpine Streams. *Ecology of Freshwater Fish*, *20*(3), 478-491.  
<https://doi.org/10.1111/j.1600-0633.2010.00458.x>
- Caudron, A., Champigneulle, A., Vigier, L., Hamelet, V., & Guyomard, R. (2012). Early effects of the strategies of creating a genetic refuge and direct translocation for conserving and restoring populations of native brown trout. *Freshwater Biology*, *57*(8), 1702-1715.  
<https://doi.org/10.1111/j.1365-2427.2012.02823.x>
- Champagnon, J., Crochet, P.-A., Kreisinger, J., Čížková, D., Gauthier-Clerc, M., Massez, G., Söderquist, P., Albrecht, T., & Guillemain, M. (2013). Assessing the genetic impact of massive restocking on wild mallard. *Animal Conservation*, *16*(3), 295-305. <https://doi.org/10.1111/j.1469-1795.2012.00600.x>
- Coulson, T., Benton, T., Lundberg, P., Dall, S., & Kendall, B. (2006). Putting evolutionary biology back in the ecological theatre : A demographic framework mapping genes to communities. *EVOLUTIONARY ECOLOGY RESEARCH*, *8*(7). <https://ora.ox.ac.uk/objects/uuid:4774c437-baf5-4d9c-87cc-25ef51881953>

449 Crispo, E., & Chapman, L. J. (2010). Geographic variation in phenotypic plasticity in response to  
450 dissolved oxygen in an African cichlid fish. *Journal of Evolutionary Biology*, 23(10), Article 10.  
451 <https://doi.org/10.1111/j.1420-9101.2010.02069.x>

452 Daupagne, L., Rolan-Meynard, M., Logez, M., & Argillier, C. (2021). Effects of fish stocking and fishing  
453 pressure on fish community structures in French lakes. *Fisheries Management and Ecology*, 28(4),  
454 317-327. <https://doi.org/10.1111/fme.12476>

455 Elliott, J. M., Hurley, M. A., & Fryer, R. J. (1995). A New, Improved Growth Model for Brown Trout,  
456 *Salmo trutta*. *Functional Ecology*, 9(2), 290-298. <https://doi.org/10.2307/2390576>

457 Fitzpatrick, S. W., Bradburd, G. S., Kremer, C. T., Salerno, P. E., Angeloni, L. M., & Funk, W. C. (2020).  
458 Genomic and Fitness Consequences of Genetic Rescue in Wild Populations. *Current Biology*, 30(3),  
459 Article 3.

460 Folio, D. (2022). *Evolutionary management of brown trout intraspecific diversity* [Phdthesis,  
461 Université de Pau et des Pays de l'Adour]. <https://theses.hal.science/tel-04122411>

462 Folio, D. M., Gil, J., Caudron, A., & Labonne, J. (2021). Genotype-by-environment interactions drive  
463 the maintenance of genetic variation in a *Salmo trutta* L. hybrid zone. *Evolutionary Applications*,  
464 14(11), 2698-2711. <https://doi.org/10.1111/eva.13307>

465 Forseth, T., & Jonsson, B. (1994). The Growth and Food Ration of Piscivorous Brown Trout (*Salmo*  
466 *trutta*). *Functional Ecology*, 8(2), 171. <https://doi.org/10.2307/2389900>

467 Forseth, T., Larsson, S., Jensen, A. J., Jonsson, B., Näslund, I., & Berglund, I. (2009). Thermal growth  
468 performance of juvenile brown trout *Salmo trutta* : No support for thermal adaptation hypotheses.  
469 *Journal of Fish Biology*, 74(1), 133-149. <https://doi.org/10.1111/j.1095-8649.2008.02119.x>

470 Frankham, R. (2015). Genetic rescue of small inbred populations : Meta-analysis reveals large and  
471 consistent benefits of gene flow. *Molecular Ecology*, 24(11), Article 11.  
472 <https://doi.org/10.1111/mec.13139>

473 Garant, D., Forde, S. E., & Hendry, A. P. (2007). The multifarious effects of dispersal and gene flow on  
474 contemporary adaptation. *Functional Ecology*, 434-443.

475 Genovart, M. (2009). Natural hybridization and conservation. *Biodiversity and Conservation*, 18(6),  
476 1435-1439. <https://doi.org/10.1007/s10531-008-9550-x>

477 Gil, J., Caudron, A., & Labonne, J. (2016). Can female preference drive intraspecific diversity dynamics  
478 in brown trout (*Salmo trutta*, L.)? *Ecology of Freshwater Fish*, 25(3), Article 3.

479 Gil, J., Labonne, J., & Caudron, A. (2016). Evaluation of strategies to conserve and restore  
480 intraspecific biodiversity of brown trout : Outcomes from genetic monitoring in the French Alps.  
481 *Reviews in fish biology and fisheries*, 26(1), Article 1.

482 Godineau, C., Fririon, V., Beudez, N., de Coligny, F., Courbet, F., Ligoit, G., Oddou-Muratorio, S.,  
483 Sanchez, L., & Lefèvre, F. (2023). A demo-genetic model shows how silviculture reduces natural  
484 density-dependent selection in tree populations. *Evolutionary Applications*, 16(11), 1830-1844.  
485 <https://doi.org/10.1111/eva.13606>

486 Hashemzadeh Segherloo, I., Freyhof, J., Berrebi, P., Ferchaud, A.-L., Geiger, M., Laroche, J., Levin, B.  
487 A., Normandeau, E., & Bernatchez, L. (2021). A genomic perspective on an old question : *Salmo*

488 trouts or *Salmo trutta* (Teleostei: Salmonidae)? *Molecular Phylogenetics and Evolution*, 162, 107204.  
489 <https://doi.org/10.1016/j.ympev.2021.107204>

490 Hendry, A. P., Gotanda, K. M., & Svensson, E. I. (2017). Human influences on evolution, and the  
491 ecological and societal consequences. *Philosophical Transactions of the Royal Society B: Biological*  
492 *Sciences*, 372(1712), 20160028. <https://doi.org/10.1098/rstb.2016.0028>

493 Kurland, S., Rafati, N., Ryman, N., & Laikre, L. (2022). Genomic dynamics of brown trout populations  
494 released to a novel environment. *Ecology and Evolution*, 12(7), e9050.  
495 <https://doi.org/10.1002/ece3.9050>

496 Laikre, L. (1999). *Conservation genetic management of brown trout (Salmo trutta) in Europe : [Report*  
497 *by the concerted action on identification, management and exploitation of genetic resources in the*  
498 *brown trout (Salmo trutta), TROUTCONCERT ; EU FAIR CT97-3882]*. Danmarks Fiskeriundersøgelse,  
499 Afd. for Ferskvandsfiskeri.

500 Lamarins, A., Fririon, V., Folio, D., Vernier, C., Daupagne, L., Labonne, J., Buoro, M., Lefèvre, F., Piou,  
501 C., & Oddou-Muratorio, S. (2022). Importance of interindividual interactions in eco-evolutionary  
502 population dynamics : The rise of demo-genetic agent-based models. *Evolutionary Applications*,  
503 15(12), 1988-2001. <https://doi.org/10.1111/eva.13508>

504 McIntosh, A. (2011). Brown Trout (*Salmo trutta*). In *A handbook of global freshwater invasive species*  
505 (R. A. Francis, editor, p. Pages 285-296). Earthscan, London.

506 Nathan, L. R., Mamoozadeh, N., Tumas, H. R., Gunselman, S., Klass, K., Metcalfe, A., Edge, C., Waits, L.  
507 P., Spruell, P., Lowery, E., Connor, E., Bearlin, A. R., Fortin, M.-J., & Landguth, E. (2019). A spatially-  
508 explicit, individual-based demogenetic simulation framework for evaluating hybridization dynamics.  
509 *Ecological Modelling*, 401, 40-51. <https://doi.org/10.1016/j.ecolmodel.2019.03.002>

510 Piccolo, J. J. (2017). The Land Ethic and conservation of native salmonids. *Ecology of Freshwater Fish*,  
511 26(1), 160-164. <https://doi.org/10.1111/eff.12263>

512 Piou, C., & Prévost, E. (2012). A demo-genetic individual-based model for Atlantic salmon  
513 populations : Model structure, parameterization and sensitivity. *Ecological Modelling*, 231, 37-52.  
514 <https://doi.org/10.1016/j.ecolmodel.2012.01.025>

515 Pujolar, J. M., Lucarda, A. N., Simonato, M., & Patarnello, T. (2011). Restricted gene flow at the micro-  
516 and macro-geographical scale in marble trout based on mtDNA and microsatellite polymorphism.  
517 *Frontiers in Zoology*, 8(1), 7. <https://doi.org/10.1186/1742-9994-8-7>

518 Reznick, D. N., Bassar, R. D., Handelsman, C. A., Ghalambor, C. K., Arendt, J., Coulson, T., Potter, T.,  
519 Ruell, E. W., Torres-Dowdall, J., Bentzen, P., & Travis, J. (2019). Eco-Evolutionary Feedbacks Predict  
520 the Time Course of Rapid Life-History Evolution. *The American Naturalist*, 194(5), Article 5.  
521 <https://doi.org/10.1086/705380>

522 Rhymer, J. M., & Simberloff, D. (1996). Extinction by Hybridization and Introgression. *Annual Review*  
523 *of Ecology and Systematics*, 27(1), 83-109. <https://doi.org/10.1146/annurev.ecolsys.27.1.83>

524 Rytwinski, T., Taylor, J. J., Donaldson, L. A., Britton, J. R., Browne, D. R., Gresswell, R. E., Lintermans,  
525 M., Prior, K. A., Pellatt, M. G., Vis, C., & Cooke, S. J. (2019). The effectiveness of non-native fish  
526 removal techniques in freshwater ecosystems : A systematic review. *Environmental Reviews*, 27(1),  
527 71-94. <https://doi.org/10.1139/er-2018-0049>

528 Soulé, M. E. (1985). What Is Conservation Biology? *BioScience*, 35(11), 727-734.  
529 <https://doi.org/10.2307/1310054>

530 Splendiani, A., Ruggeri, P., Giovannotti, M., Pesaresi, S., Occhipinti, G., Fioravanti, T., Lorenzoni, M.,  
531 Nisi Cerioni, P., & Caputo Barucchi, V. (2016). Alien brown trout invasion of the Italian peninsula : The  
532 role of geological, climate and anthropogenic factors. *Biological Invasions*, 18(7), 2029-2044.  
533 <https://doi.org/10.1007/s10530-016-1149-7>

534 Todesco, M., Pascual, M. A., Owens, G. L., Ostevik, K. L., Moyers, B. T., Hübner, S., Heredia, S. M.,  
535 Hahn, M. A., Caseys, C., Bock, D. G., & Rieseberg, L. H. (2016). Hybridization and extinction.  
536 *Evolutionary Applications*, 9(7), 892-908. <https://doi.org/10.1111/eva.12367>

537 Vera, M., Aparicio, E., Heras, S., Abras, A., Casanova, A., Roldán, M.-I., & García-Marin, J.-L. (2023).  
538 Regional environmental and climatic concerns on preserving native gene pools of a least concern  
539 species : Brown trout lineages in Mediterranean streams. *Science of The Total Environment*, 862,  
540 160739. <https://doi.org/10.1016/j.scitotenv.2022.160739>

541 Verhoeven, K. J. F., Macel, M., Wolfe, L. M., & Biere, A. (2010). Population admixture, biological  
542 invasions and the balance between local adaptation and inbreeding depression. *Proceedings of the*  
543 *Royal Society B: Biological Sciences*, 278(1702), 2-8. <https://doi.org/10.1098/rspb.2010.1272>

544 Weeks, A. R., Sgro, C. M., Young, A. G., Frankham, R., Mitchell, N. J., Miller, K. A., Byrne, M., Coates,  
545 D. J., Eldridge, M. D. B., Sunnucks, P., Breed, M. F., James, E. A., & Hoffmann, A. A. (2011). Assessing  
546 the benefits and risks of translocations in changing environments : A genetic perspective.  
547 *Evolutionary Applications*, 4(6), 709-725. <https://doi.org/10.1111/j.1752-4571.2011.00192.x>

548

549

550

551

552

553

554

555

556

557

558

559

560

561

562

563

564 FIGURE LEGENDS

565

566 Figure 1: Representation of the life cycle, with the different processes modelled and their order. In  
567 the MEDITERRANEA model, splitted between the individual and the group phase.

568 Figure 2: Offspring survival rate at hatching as a function of maternal introgression and mean daily  
569 water temperature over incubation period.

570 Figure 3: Spatial representation of fish translocation carried out in the MEDITERRANEA model based  
571 on the structure of the River Borne.

572 Figure 4: Mean introgression as a function of time in the neutral scenario (blue curve) and in the GxE  
573 scenario (red curve) in the upstream part of the River Borne.

574 Figure 5: Distribution of individual introgression in the translocated area, at years 14 and 21 after the  
575 beginning of the simulation, for the neutral and the GxE scenario.

576 Figure 6: Comparison of mean introgression per reach in the translocated area between observed  
577 data (red pentagons) and simulated data (summarised as boxplots to display the 2.5, 25,50,75,97.5%  
578 quantiles of the simulated trajectories, with blue boxplots for the neutral scenario and red boxplots  
579 for the GxE scenario).

580

581

582

583

584

585

586

587

588

589

590

591

592

593

594

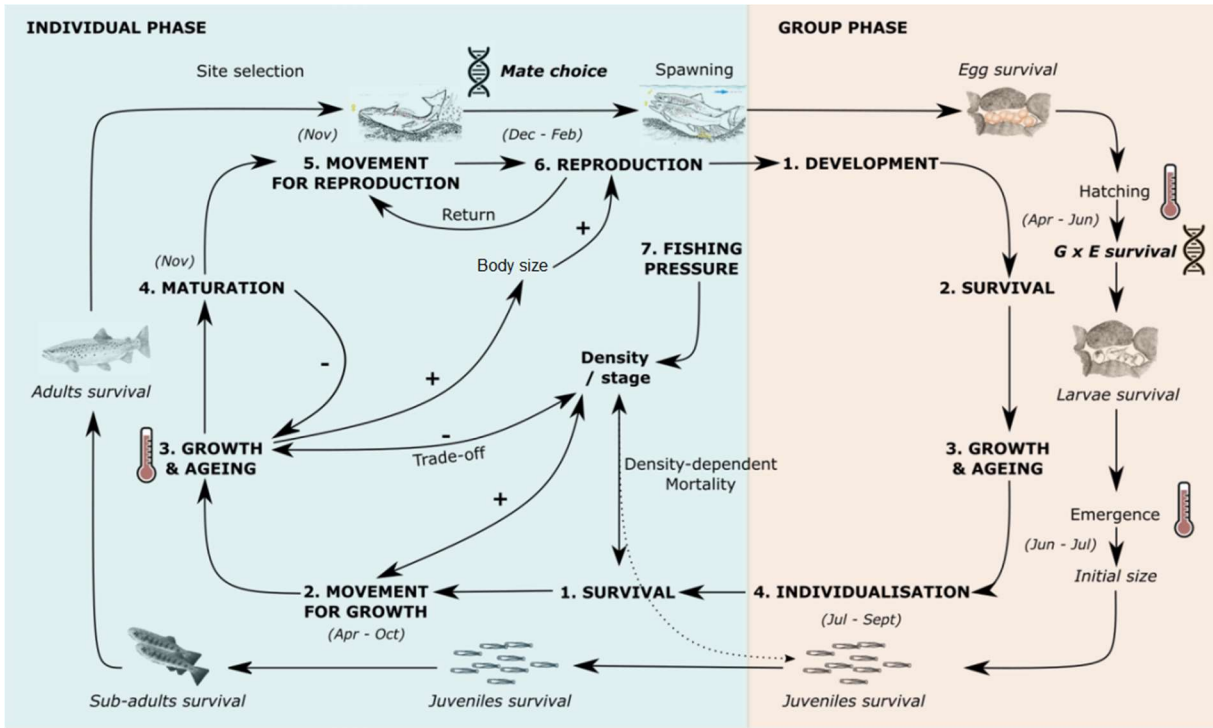
595

596

597

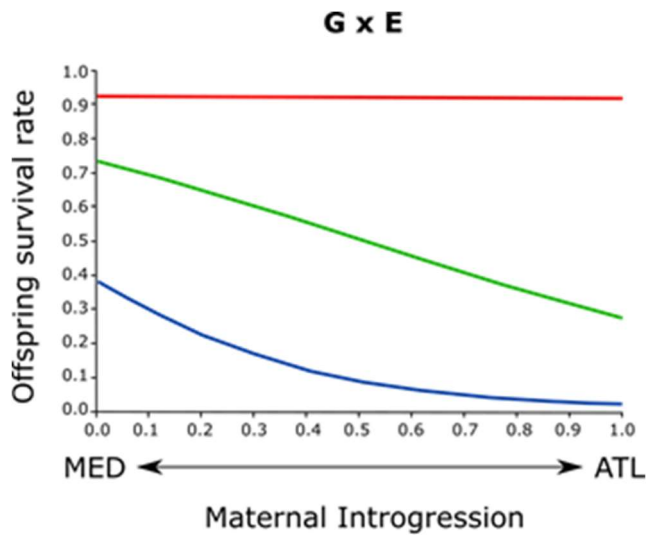


598 FIGURE 1



599  
 600  
 601  
 602  
 603  
 604  
 605  
 606  
 607  
 608  
 609  
 610  
 611  
 612  
 613  
 614  
 615  
 616  
 617

618 FIGURE 2



619 — 8°C — 5°C — 2°C

620

621

622

623

624

625

626

627

628

629

630

631

632

633

634

635

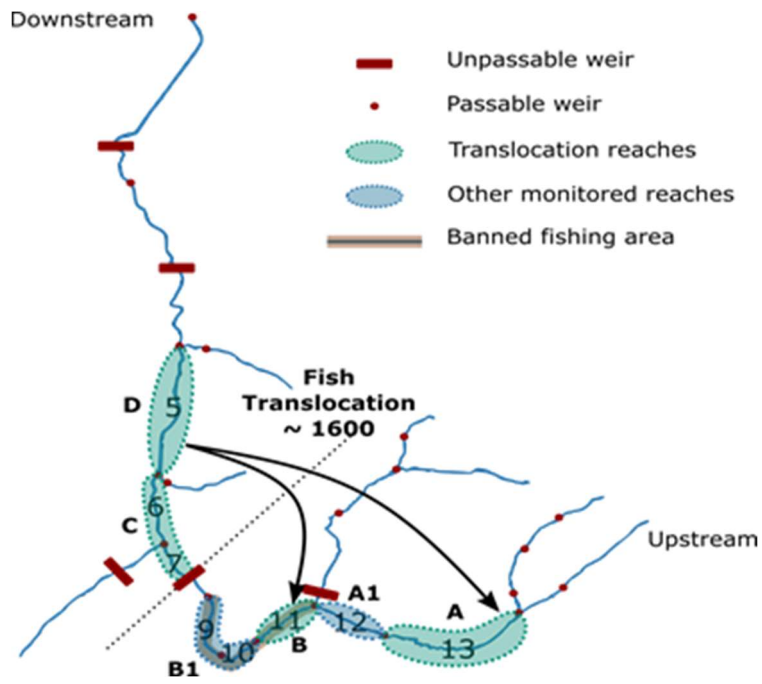
636

637

638

639

640 FIGURE 3



641

642

643

644

645

646

647

648

649

650

651

652

653

654

655

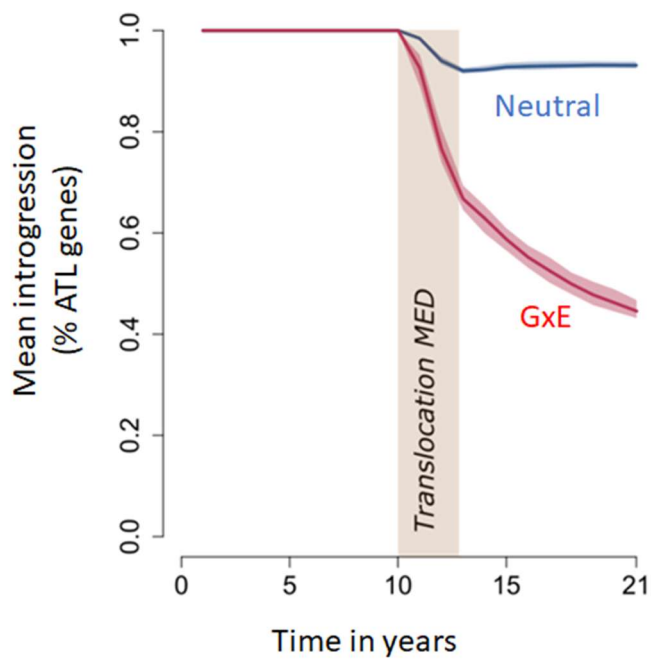
656

657

658

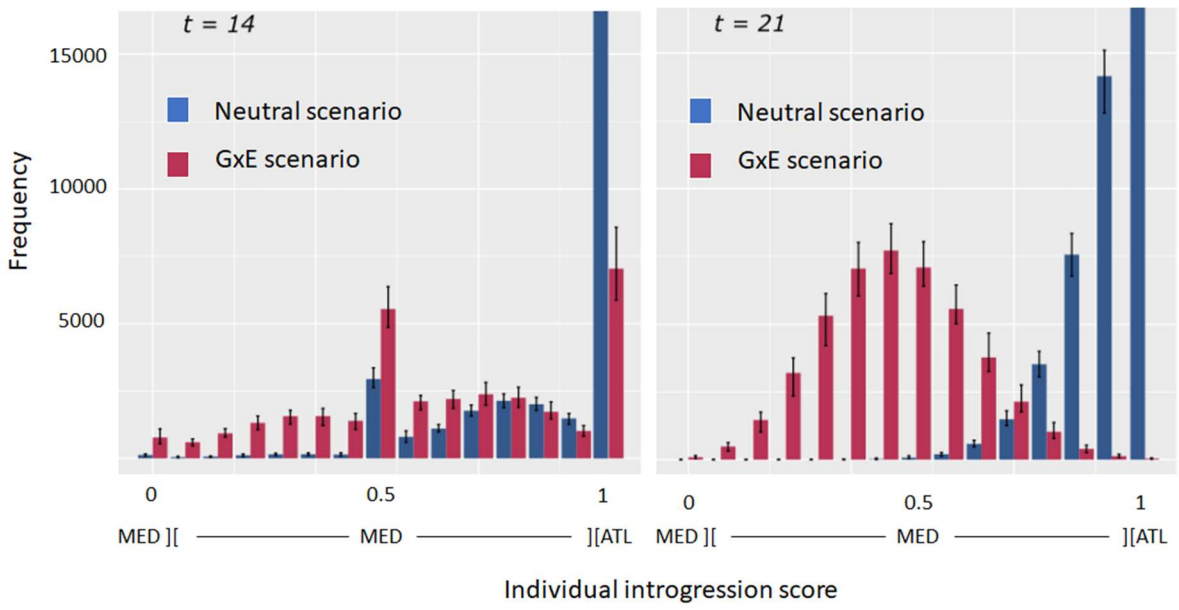
659

660 FIGURE 4



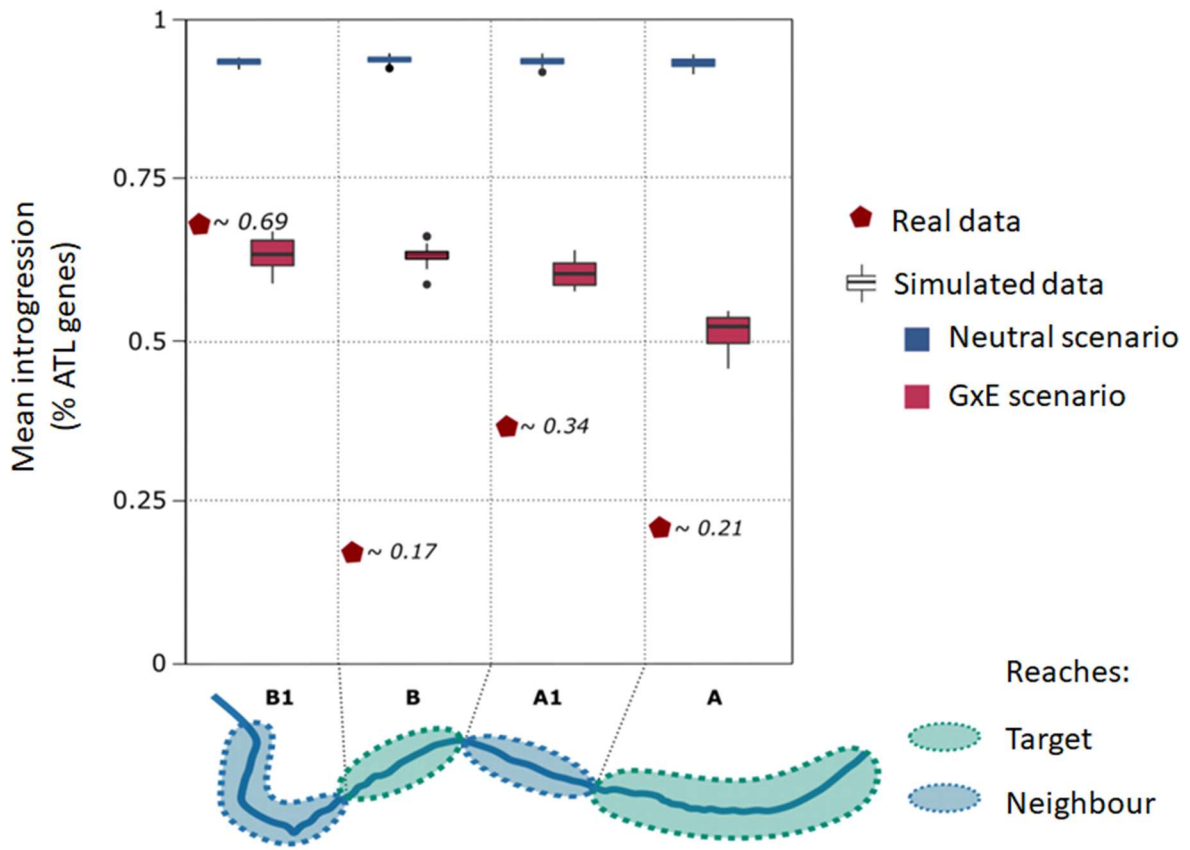
661  
662  
663  
664  
665  
666  
667  
668  
669  
670  
671  
672  
673  
674  
675  
676  
677  
678  
679

680 FIGURE 5



681  
682  
683  
684  
685  
686  
687  
688  
689  
690  
691  
692  
693  
694  
695  
696  
697  
698  
699  
700

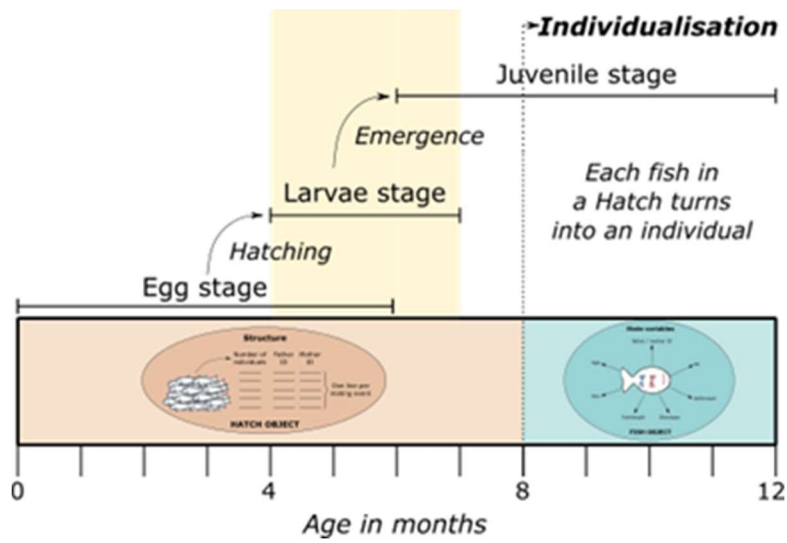
701 FIGURE 6



702  
703  
704  
705  
706  
707  
708  
709  
710  
711  
712  
713  
714  
715  
716  
717

Supplementary Information 1: Early life stages description in the model.

718



719

720

721

722 Individual life stages from egg stage up to juvenile stage and corresponding objects. Individuals are  
723 within a Hatch object for 8 months. Then they are individualised into fish objects. The timing and  
724 windows for hatching and emergence are indicated in yellow.

725

726

727

728

729

730

731

732

733

734

735

736

737

738

739

740

741 **Supplementary Information 2: Model parameters values.**

742

743

Parameter	Value, range of values, variation domain.	Description
$C_{stage}$	{2.197;1.386;2.197;2.944;2.944}	Monthly survival coefficient per stage.
$Density_{stage, reach}$	[0-10000]	Density per reach and stage.
$K_{max}$	2	Controls for maximum density in a reach. A value of 2 implies a carrying capacity of 3500 ind.ha <sup>-1</sup>
$\alpha$	{2.197;0.5}	Base survival at hatching (neutral/GxE)
$\beta$	{0;-3.2}	Additive temperature effect on survival (neutral/GxE)
$\gamma$	{0;-0.03}	Effect of genotype on survival (neutral/GxE)
$\delta$	{0;0.55}	Interaction of temperature and genotype on survival (neutral/GxE)
$T$	[2-20]	Mean monthly temperature
$L_{inf}$	50	Theoretical maximum body size (cm) in the considered habitat.
$a$	{0.45;0.45;0.45}	Density effect on growth.
$b$	0.23	Base growth parameter.
$ME$	0.7	Accounts for sexual maturation in the growth model.
$optT$	15	Optimal growth temperature.
$rangeT$	4	Amplitude parameter describing how quickly growth is reduced when $T$ goes farther from $optT$ .



$\vartheta_{max}$	0.2	A constant determining maximum movement probability.
$Density_{max}$	[0-10000]	Maximum density per reach
$GQ$	[0-1]	Reach habitat quality for growth.
$GC$	[0-1]	Correlation between genotype and phenotype for sexual preference.
$x$	1.5	Intercept parameter for female preference on male phenotype.
$y$	-0.2	Slope parameter for female preference on male phenotype.
$D$	[0-1]	Dissimilarity between the female and the male phenotype
$q$	[0-1]	Random component of the selection of male phenotype by females.
$f$	0.0011236	Fecundity coefficient
$F$	2.36	Fecundity exponent
$RQ$	[0-1]	Habitat quality of the reach for reproduction
$h$	2	Oophagy effect on the redd
$SC$	2	Number of egg batch laid by a female each year

744

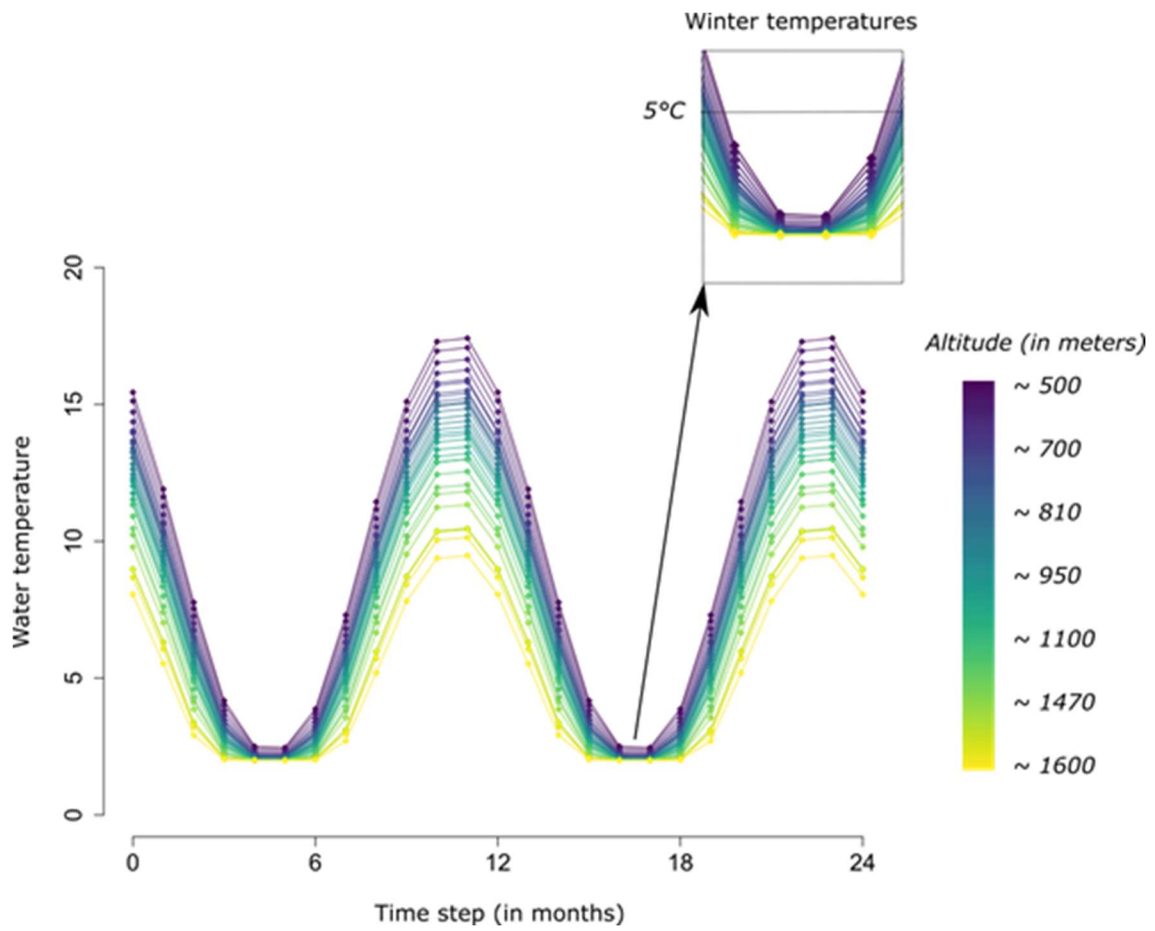
745

746

747

748 **Supplementary Information 3: Temperature model.**

749



750

751 Temperature model used for simulations carried out on the River Borne. One water temperature is  
 752 calculated per reach each month based on altitude. A zoom of winter temperatures shows the  
 753 temperature from December to March.

754

755

756

757