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## Cause or consequence? Exploring the role of phenotypic plasticity and genetic polymorphism in the emergence of phenotypic spatial patterns of the European eel

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1 Cause or consequence? Exploring the role of phenotypic plasticity and genetic polymorphism in the  
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3

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## 34 **1 Abstract**

35           The European eel (*Anguilla anguilla*), and generally, temperate eels, are relevant species for  
36 studying adaptive mechanisms to environmental variability because of their large distribution areas  
37 and their limited capacity of local adaptation. In this context, GenEveel, an individual-based  
38 optimization model, was developed to explore the role of adaptive phenotypic plasticity and genetic-  
39 dependent habitat selection, in the emergence of observed spatial life-history traits patterns for eels.  
40 Results suggest that an interaction of genetically and environmentally controlled growth may be the  
41 basis for genotype-dependent habitat selection, whereas plasticity plays a role in changes in life-  
42 history traits and demographic attributes. Therefore, this suggests that those mechanisms are  
43 responses to address environmental heterogeneity. Moreover, this brings new elements to explain  
44 the different life strategies of males and females. A sensitivity analysis showed that the parameters  
45 associated with the optimization of fitness and growth genotype were crucial in reproducing the  
46 spatial life-history patterns. Finally, it raises the question of the impact of anthropogenic pressures  
47 that can cause direct mortalities but also modify demographic traits, and act as a selection pressure.

48

49           Keywords: phenotypic plasticity, *Anguilla anguilla*, genetic polymorphism, life history theory,  
50 modeling

## 51 2 Introduction

52 Life-history theory posits that the schedule and duration of life-history traits are the result of  
53 natural selection to optimize individual fitness (Clark 1993; Giske et al. 1998). Optimal solutions  
54 greatly depend on environmental conditions, and consequently, living organisms have developed  
55 different adaptive mechanisms to address environmental variability. Among them, local adaptation  
56 theory posits that natural selection favors the most well adapted genotypes in each type of  
57 environment. In a context of limited genetic exchange between environments, this may lead to  
58 isolation and speciation (Williams 1996; Kawecki and Ebert 2004). Phenotypic plasticity might also be  
59 an adaptive response to an heterogeneous environment (Levins 1963; Gotthard and Nylin 1995;  
60 Pigliucci 2005). Phenotypic plasticity refers to the possibility of a genotype to produce different  
61 phenotypes depending on environmental conditions. In some cases, increases in fitness occur  
62 because of plastic phenotypes compared to non-plastic ones, and that consequently, phenotypic  
63 plasticity may be selected by natural selection (Schlichting 1986; Sultan 1987; Travis 1994).

64 Adaptation to environment heterogeneity is a key issue for temperate anguillids, *Anguilla*  
65 *anguilla*, *A. japonica*, *A. rostrata*, three catadromous species that display remarkable similarities in  
66 their life-history traits (Daverat et al. 2006; Edeline 2007). The European eel (*A. anguilla*) is widely  
67 distributed from Norway to Morocco, grows in contrasting environments, and displays considerable  
68 phenotypic variation. The species displays a complex life cycle: reproduction takes place in the  
69 Sargasso Sea, larvae (or leptocephali) are transported by ocean currents to European and North  
70 African waters, where they experience their first metamorphosis to become glass eels. These  
71 juveniles colonize continental waters and undergo progressive pigmentation changes to become  
72 yellow eels. The growth phase lasts between two and 20 years depending upon the region and sex of  
73 the eels (Vollestad 1992). At the end of this stage, yellow eels metamorphose again into silver eels,  
74 which mature during the migration to their spawning area in the Sargasso Sea. The population is  
75 panmictic, resulting in a homogeneous population, from a genetic viewpoint (Palm et al. 2009; Als et

76 al. 2011; Côté et al. 2013). This panmixia combined with a long and passive larval drift limit the  
77 possibility of adaptation to local environments. However, spatial patterns of different life traits,  
78 including growth rate (Daverat et al. 2012; Geffroy and Bardonnnet 2012), sex (Helfman et al. 1987;  
79 Tesch 2003; Davey and Jellyman 2005), length at maturity (Vollestad 1992; Oliveira 1999), and habitat  
80 use (De Leo and Gatto 1995; Daverat et al. 2006; Edeline 2007) are observed and correlated with  
81 environmental patterns.

82         Growth rates greatly vary depending on latitude, temperature, sex (Helfman et al. 1987) but  
83 also on habitat characteristics (Cairns et al. 2009). Indeed, eel can settle in a wide range of habitats  
84 (De Leo and Gatto 1995; Daverat et al. 2006; Geffroy and Bardonnnet 2012) and faster growth is  
85 observed in brackish waters than in freshwater (Daverat et al. 2012). Slower growth in freshwater  
86 habitats is sometimes assumed to be compensated for by lower mortalities and Edeline (2007)  
87 suggested that habitat choice could be the result of a conditional evolutionary stable strategy.  
88 However, Cairns et al. (2009) questioned this assumption because they did not observe strong  
89 variation in mortality rates between habitats. Spatial patterns were also observed with respect to sex  
90 ratios, with female biased sex ratios in the upper part of river catchments (Tesch 2003) and in the  
91 northern part of the distribution range (Helfman et al. 1987; Davey and Jellyman 2005). However, sex  
92 is not determined at birth but is determined by environmental factors (Oliveira 2001; Davey and  
93 Jellyman 2005; Geffroy and Bardonnnet 2012). Population density also plays a role in this mechanism:  
94 males are favored at high densities, whereas low densities favor females (Tesch 2003). This is  
95 important because males and females have different life-history strategies (Helfman et al. 1987). The  
96 reproductive success of a male does not vary with body size, and consequently, males are assumed  
97 to follow a time-minimizing strategy, leaving continental waters as soon as they have enough energy  
98 to migrate to the spawning grounds (Vollestad 1992). However, a female's reproductive success is  
99 constrained by a trade-off between fecundity, which increases with length, and survival, which  
100 decreases with length. Consequently, females are assumed to adopt a size-maximizing strategy

101 (Helfman et al. 1987). Strong differences in female length at silvering were observed among habitats  
102 and latitudes (Oliveira 1999).

103           Because local adaptation is impossible, this raises two questions: (i) are those life-history  
104 trait patterns resulting from an adaptive response to environmental heterogeneity, and (ii) which  
105 adaptation mechanisms have been selected. Despite panmixia, previous researchers (Gagnaire et al.  
106 2012; Ulrik et al. 2014; Pavey et al. 2015) have detected genetic differences correlated with  
107 environmental gradients and assumed that those differences were reshuffled at each generation.  
108 Common garden experiments have been used to test the respective contributions of genetic and  
109 plastic mechanisms on phenotypic differences observed in glass eels found in distinct locations. The  
110 results revealed genetic patterns related to geographic zones in American eels, whereas individual  
111 growth rates had a genetic basis and could be sex-dependent (Côté et al. 2009, 2014, 2015). Building  
112 on this, Boivin et al. (2015) studied the influence of salinity preferences and geographic origin on  
113 habitat selection and growth in American eels, demonstrating genetic-based differences for growth  
114 between glass eels from different origins. However, these experiments also confirmed the  
115 contribution of phenotypic plasticity that allowed individuals to develop quick and effective  
116 responses to environmental variability (Hutchings et al. 2007). Several traits have been proposed as  
117 plastic: growth habitats (Daverat et al. 2006; Edeline 2007), growth rates (Geffroy and Bardonnnet  
118 2012), and length at silvering (Vollestad 1992). Understanding the adaptive mechanisms that explain  
119 this diversity is crucial to environmental conservation and management (Brodersen and Seehausen  
120 2014).

121           As a result of a decline observed since the 1980s, the European eel is now listed as critically  
122 endangered in the IUCN Red List (Jacoby and Gollock 2014) and the European Commission enforced a  
123 European Regulation, which requires a reduction in all sources of anthropogenic mortality (obstacles,  
124 loss of habitat, fisheries, pollution, and global change) (Council of the European Union 2007).  
125 However, those anthropogenic pressures are not uniformly distributed (Dekker 2003) and acts on  
126 specific fractions of the stock isolated in river catchments (Dekker 2000), with heterogeneous life-

127 history traits because of the spatial phenotypic variability. This strong spatial heterogeneity of  
128 anthropogenic pressures affecting the eel population in Europe combined with this spatial  
129 phenotypic variability at both the distribution area and river catchment scales causes specific  
130 challenges for management, because it impairs our ability to assess the effect of anthropogenic  
131 pressures on the whole stock and to coordinate management actions (Dekker 2003, 2009).

132         Recently, a model called EvEel (evolutionary ecology-based model for eel) was developed to  
133 explore the contribution of adaptive phenotypic plasticity in the emergence of observed phenotypic  
134 patterns: sex ratio, length at silvering, and habitat use (Drouineau et al. 2014). Assuming fitness  
135 maximization, the model was able to mimic most observed patterns at both river catchment and  
136 distribution area scales. The result confirmed the probable role of adaptive phenotypic plasticity in  
137 response to environmental variability. However, recent findings demonstrated the existence of  
138 genetic differences in growth traits in a wide range of different habitats (Côté et al. 2009, 2014, 2015;  
139 Boivin et al. 2015). Building on these new results, we developed GenEveel, a new version of EvEel,  
140 which introduces a bimodal growth distribution (fast and slow growers) for individuals, as observed  
141 by Côté et al. (2015), and considers phenotypic plasticity in life-history traits and demographic  
142 attributes as in EvEel. Because individuals have different intrinsic growth and mortality rates, they  
143 can be favored differently among environments, opening the door to conditional habitat selection. In  
144 this study, we used GenEveel to test whether simultaneously considering genetically distinct  
145 individuals and phenotypic plasticity improves model performance. Pattern orienting modelling was  
146 used to detect the reproduced spatial patterns of EvEel and other patterns based on the distribution  
147 of the different types of individuals.

148



## 149 **3 Materials and methods**

### 150 **3.1 Model description**

151 The model description follows the Overview, Design concepts, and Details (ODD) protocol  
152 (Grimm et al. 2006, 2010):

#### 153 **3.1.1 Overview**

##### 154 **3.1.1.1 Purpose**

155 GenEveel is a model based on a former model called EvEel (Drouineau et al. 2014), but  
156 includes a genetic component. It is an individual-based population model that predicts emergent life-  
157 history spatial patterns depending on adaptive mechanisms and environmental heterogeneity.  
158 Emergent patterns can later be compared to observed spatial patterns in freshwater life stages of  
159 European eels in order to (i) confirm that observed phenotypic patterns can plausibly result from  
160 adaptive responses to environmental heterogeneity, (ii) validate that phenotypic plasticity for length  
161 at silvering, sex determination, habitat choice, and genetic polymorphism (slow growers and fast  
162 growers) with conditional habitat selection can explain those patterns.

##### 163 **3.1.1.2 State variables and scales**

164 *Temporal scales:* the model simulates a population generation. It has no *sensu stricto* time  
165 steps, but rather successive events: sex-determination and habitat selection, survival, and growth  
166 until maturation.

167 *Entities and spatial scales:* a Von Bertalanffy growth function is assumed for individual  
168 growth. Each individual  $i$  is characterized by an intrinsic Brody growth coefficient  $K_i$  and a natural  
169 mortality rate  $M_i$ . Based on Côté et al. (2015), who observed two clusters in growth rates, we build a  
170 simple quantitative-genetic model assuming that growth is coded for by a single gene with two  
171 variations. Therefore, we assumed that there are two types of individuals called (i) fast-growing

172 individuals for which  $K_i = K_{fast}$  and  $M_i = M_{fast}$  and (ii) slow-growing individuals for which  $K_i = K_{slow}$   
173 and  $M_i = M_{slow}$ . At the end of the simulation, individuals are characterized by a sex, length at  
174 silvering, corresponding fecundity (if female), position in the river catchment, and survival rate until  
175 silvering.

176 The river catchment environment was represented by a sequence of cells of the same size.  
177 The first cell represents the river mouth, whereas the  $n$ th cell represents the source of the river.  
178 Because it was observed that an individual grows faster downstream than upstream (Acou et al.  
179 2003; Melià et al. 2006), we assumed that realized growth rate in a cell depends on both intrinsic  
180 growth rate and position in the catchment (i.e., cell) (see submodel section). Realized natural  
181 mortalities depend both on individual intrinsic mortality rates, position of the cell in the catchment,  
182 and number of individuals in the catchment (to mimic density-dependent mortality).

### 183 3.1.1.3 Process overview and scheduling

184 The model has two main steps. In a first step, individuals select their growth habitat (a cell in  
185 the catchment) and determine a sex (male or female) one after another (random order). To do that,  
186 fitness is calculated for each combination of sex and cell (a quasi-Newton algorithm is used to  
187 estimate the lengths at silvering that optimize female fitness in each cell). Individuals are assumed to  
188 select the combination with highest fitness given the choices made by former individuals. Once this  
189 step is finished (i.e., all individuals have a growth habitat and sex), using the quasi-Newton algorithm  
190 we estimated the optimal length at silvering for all females (males have a constant length at silvering)  
191 given the positions of fishes from step 1, and then compute corresponding survival rates until  
192 silvering and fecundity determination (Fig. 1). The process mentioned above is defined by the  
193 computer algorithm (Figure 2):

- 194 (1) For each individual  $i$ :
- 195 - For each cell  $x$ :
  - 196 · Compute  $\pi_m(x)$  given positions of individuals  $\{1, \dots, i-1\}$

- 197       · Compute  $\max_{L_s f} \pi_f(x, L_s f)$  given positions of individuals  $\{1, \dots, i-1\}$
- 198       - Put individual and determine sex by selecting maximum values within  $\max_{L_s f} \pi_f(x, L_s f)$  and  $\pi_m(x)$
- 199 (2) For each individual i:
- 200       - For each cell x:
- 201       · if sex(i) = male
- 202              $L_s(i) = L_{sm}$
- 203       · else
- 204              $L_s(i) = \arg_L \max (\pi_f(x, L_s f))$  given positions of individuals  $\{1, \dots, n\}$
- 205 where fitness is defined in equations 9 and 10 for females and males respectively.

## 206 **3.1.2 Design concept**

### 207 **3.1.2.1 Basic principles**

208       Consistent with life-history theory and optimal foraging theory, the model uses an  
209 optimization approach in which individuals “respond to choices” so as to select and fix the adaptive  
210 traits, maximizing their expected fitness given their environment (Parker and Maynard Smith 1990;  
211 McNamara and Houston 1992; Giske et al. 1998; Railsback and Harvey 2013).

### 212 **3.1.2.2 Emergence**

213       Using the pattern-oriented modelling approach (Grimm and Railsback 2012), GenEveel  
214 compares predicted spatial patterns with those observed in real river catchments. Five emergent  
215 population spatial patterns were analyzed from the literature:

- 216 (i) higher density downstream than upstream
- 217 (ii) higher length at silvering upstream than downstream
- 218 (iii) male-biased sex ratio downstream and female-biased sex ratio upstream

219 (iv) more individuals characterized with the fast-growing genotype downstream than upstream,  
220 which was mainly characterized by the slow-growing genotype  
221 (v) the phenotypic response led to faster growth rate downstream than upstream.

### 222 **3.1.2.3 Adaptation**

223 Individuals have three adaptive traits: sex-determination, length at silvering for females, and  
224 choice of growth habitat (cell in the grid). These traits are assumed to maximize the predicted  
225 objective function (i.e., the individual fitness).

### 226 **3.1.2.4 Predictions**

227 We assumed that individuals could perfectly predict expected fitness given previous choices  
228 and could make the most appropriate choices.

### 229 **3.1.2.5 Sensing**

230 In the model, individuals are able to “sense” fitness, which was a function of a density-  
231 dependent mortality and growth rate. In the real world, temperature and density would probably be  
232 the proximal cues because natural mortality and growth rates are strongly influenced by temperature  
233 (Bevacqua et al. 2011; Daverat et al. 2012).

### 234 **3.1.2.6 Interaction**

235 Interactions occurred through growth habitat selection, sex determination, and density-  
236 dependent mortality.

### 237 **3.1.2.7 Stochasticity**

238 Stochasticity occurred at two levels. First, individuals were randomly affected by a slow-  
239 growing genotype ( $Pr = 0.5$ ) or by a fast-growing genotype ( $Pr = 0.5$ ). Then stochasticity occurred in  
240 the order of individuals for step 1.

### 241 **3.1.2.8 Observations**

242 Five spatial patterns were computed at the end of the simulation:

243 (i) number of individuals per cell

244 (ii) mean length at silvering per cell

245 (iii) sex ratio (proportion of females) per cell

246 (iv) ratio of fast-growing genotype per cell

247 (v) phenotypic response of mean realized growth rate per cell.

248 These five patterns corresponded to five patterns available in the literature. Simulated patterns (i),  
249 (iv), (v) was said to be consistent with the literature when a negative trend from downstream to  
250 upstream was observed, whereas patterns (ii), (iii) were said to be consistent with the literature  
251 when a positive trend was observed from downstream to upstream.

### 252 **3.1.3 Details**

#### 253 **3.1.3.1 Initialization**

254 At the beginning of the simulation, the catchment was empty.  $N$  individuals were created and  
255 attributed to the slow-growing or fast-growing genotype with probability 0.5 and had a length 7.5  
256 cm. They had not yet entered the river catchment.

#### 257 **3.1.3.2 Input data**

258 We tested the model using a reference simulation. Values of parameters were obtained from  
259 the literature (Table 1). The outputs of the model were identified based on spatial patterns as  
260 previously defined in *Observations*.

261 **3.1.3.3 Submodels**

262 Most of the submodels were similar to submodels from EvEel. Consequently, we provide  
 263 here only the novelties and the equations that are required for a better understanding of the model.  
 264 Further details are provided in Drouineau et al. (2014).

- 265 • Growth and silvering

266 Growth rate was assumed the outcome of an intrinsic Brody growth coefficient ( $K_i$ ), which is  
 267 modulated by an environmental effect. This combination resulted in a phenotypic growth rate.  
 268 Within the river, growth rates were significantly faster downstream than upstream (even for the  
 269 same individual). Therefore, we assumed that individual  $i$  would have a growth rate  $K(i, x)$  in cell  $x$   
 270 given by:

271 (1) 
$$K(i, x) = r_K \cdot K(i, n) + (K(i, 1) - r_K \cdot K(i, n)) \cdot \text{cauchit}\left(\frac{x}{n}, \gamma_K\right)$$

272 (2) 
$$\text{cauchit}(x, \gamma) = 1 - \frac{2}{\pi} \cdot \text{atan}\left(\frac{x^2}{\gamma}\right)$$

273 where  $r_k$  defined the ratio between upstream and downstream growth rate,  $K(i, 1)$  is the growth rate  
 274 in cell 1,  $n$  is the total cells in the river catchment and *cauchit* was a mathematical function similar to  
 275 the sigmoid function, but which allowed asymmetrical patterns (by modifying the parameter  $\gamma$ ) to  
 276 model, for example, a small brackish area in the downstream part of the catchment and a large  
 277 freshwater zone upstream.

278 Individual's growth was simulated by a Von Bertalanffy function:

279 (3) 
$$L(t, i, x) = L_\infty \left[ 1 - e^{-K(i, x)(t-t_0)} \right]$$

280 where  $L(t, i, x)$  was the length at time  $t$  and  $L_\infty$  and  $K(i, x)$ , the Von Bertalanffy parameters in cell  $x$  for  
 281 individual  $i$ .

282 From this equation, we could calculate the time required to reach the length at silvering.

283 (4) 
$$\text{As}(i, x) = \frac{1}{K(i, x)} \cdot \log\left(\frac{L_\infty - L_g}{L_\infty - L_s(i, x)}\right)$$

284 where  $L_g$  was the length at recruitment and  $L_s(i, x)$  was the length at silvering, which was constant  
285 for males, and a fitness maximizing variable for females.

286 • Survival

287 Mortality rate was assumed the result of three factors: density-dependence, intrinsic growth  
288 rate, and  $M_i$  modulated by an environmental effect. Because natural mortality was sometimes  
289 assumed to be smaller upstream than downstream (Moriarty 2003; Daverat and Tomás 2006), we  
290 assumed that the instantaneous natural mortality without density-dependence in cell  $x$  for individual  
291  $i$ ,  $M(i, x)$  was:

292 (5)  $M(i, x) = r_M \cdot M(i, n) + (M(i, 1) - r_M \cdot M(i, n)) \cdot \text{cauchii}\left(\frac{x}{n}, \gamma_M\right)$

293 where  $r_m$  is the ratio between upstream and downstream instantaneous mortality rate and  $M(i, 1)$   
294 was the natural mortality in cell 1.

295 To account for the additional density-dependent mortality, we assumed that natural mortality  
296 increased linearly with an intensity of density  $\alpha$  as in EvEel:

297 (6)  $M_d(i, x) = M(i, x) + N(i, x) \cdot \alpha$

298 where  $N$  was the number of competitors in cell  $x$ . An eel was assumed a competitor if it had an  
299 intrinsic growth rate greater or equal to  $K_i$ . This corresponded to an asymmetric growth rate with  
300 larger individuals harassing smaller individuals. The basis of this assumption was the intraspecific  
301 competition, which leads to compete for limited resources between individuals of different sizes  
302 (Francis 1983; Juanes et al. 2002).

303 Given equation (4) and this survival rate, we could calculate the probability of surviving until silvering  
304 as:

305 (7)  $p(i, x) = e^{-M_d(i, x) \cdot \Delta t} = \left(\frac{L_\infty - L_g}{L_\infty - L_s(i, x)}\right)^{\frac{-M_d(i, x)}{K(i, x)}}$

306 • Fitness

307 In any optimization model, an important component is the computation of the fitness.  
308 Because sexes adopt different life strategies, and following Drouineau et al. (2014), we assumed sex-

309 specific fitness functions. Males were known to adopt a time minimizing strategy (Helfman et al.  
 310 1987), with constant length at silvering. Therefore, male fitness was proportional to survival rate  
 311 until length at silvering. However, females follow a size-maximizing strategy in which length at  
 312 silvering was constrained by a trade-off between survival and fecundity (Helfman et al. 1987).  
 313 Consequently, we assumed that female fitness was the product of fecundity at an optimal length at  
 314 silvering (based on an allometric relationship, fecundity is assumed to be a power function of length)  
 315 multiplied by the probability of survival until this length at silvering. In the model, individuals were  
 316 assumed to determine their sex according to the relative potential male and female fitness. To make  
 317 fitness values comparable, we rescaled male fitness (which was the probability of survival) into an  
 318 expectation of egg production (the scale of female fitness). To do that, we multiplied the male  
 319 survival by a constant that would be similar to fertility. Hence, we had to specify a value for fertility  
 320 with an order of magnitude similar to fecundity. The first solution might be to fix the fertility value  
 321 equal to the fecundity of silver females having a length equal to male length at silvering. However,  
 322 with this solution, female fitness will always be greater (because females can optimize their length at  
 323 silvering). Consequently, fertility has to be slightly greater such that male fitness can be sometimes  
 324 be greater than female fitness (but not too much, to avoid male fitness always being superior). These  
 325 resulted in the following equations:

326 (8)  $fecundity(L_{s_f}(i, x)) = (a_1 + a \cdot L_{s_f}(i, x)^b)$

327 where  $a_1$ ,  $a$  and  $b$  are the parameters of the allometric relationship linking fecundity and female  
 328 length at silvering  $L_{s_f}(i, x)$  (Andrello et al. 2011; Melia et al. 2006).

329 (9)  $\pi_f(i, x) = fecundity(L_{s_f}(i, x)) \cdot \left[ \frac{L_\infty - L_g}{L_\infty - L_{s_f}(i, x)} \right]^{\frac{-M_f(i, x)}{K(i, x)}}$

330 (10)  $\pi_m(i, x) = fertility \cdot \left[ \frac{L_\infty - L_g}{L_\infty - L_{s_m}(i, x)} \right]^{\frac{-M_m(i, x)}{K(i, x)}}$



## 331 **3.2 Model exploration**

### 332 **3.2.1 Reference simulation**

333 The reference simulation consisted of a simulation using parameter values in Table 1, i.e. the  
334 best set of values found in the literature. After simulating this scenario, we analyzed the different  
335 patterns. Mann-Kendall tests were implemented on each pattern to detect a monotonic upward or  
336 downward trend of the variable of interest confirming the spatial patterns previously defined. The  
337 correlation coefficient of this non-parametric test was denoted by  $\tau$ .

### 338 **3.2.2 Experimental design**

339 Simulation design is a classical tool to explore complex models. Typically, the goal is to assess  
340 the sensitivity of results to uncertain model parameters. We developed such an experimental design  
341 to (i) assess the influence of uncertain parameters on the simulated patterns (Table 1) and (ii) derive  
342 environmental and population dynamics for all the patterns that were correctly modelled.  
343 Seventeen uncertain parameters were identified in the model (Table 1) and they were dispatched  
344 into twelve groups: number of glass eel entering the catchment freshwater ( $N$ ), parameters that  
345 impact the male fitness (fertility and male length at silvering,  $L_{sm}$ ), fast growing genotype ( $K_{fast}(i, 1)$   
346 and  $M_{fast}(i, 1)$ ), slow-growing genotype ( $K_{slow}(i, 1)$  and  $M_{slow}(i, 1)$ ), proportion of individuals that grow  
347 slowly ( $propK$ ), intensity of density-dependence ( $\alpha$ ), cells of river catchment ( $n$ ), regression  
348 coefficient from fecundity at length ( $b$ ), asymptotic length ( $L_{\infty}$ ), length at recruitment ( $L_g$ ), ratio  
349 between upstream and downstream instantaneous growth and mortality rates ( $r_k$  and  $r_m$ ), and the  
350 shape parameter of growth and mortality ( $\gamma_k$  and  $\gamma_m$ ). Groups were composed of parameters that  
351 have are assumed to influence the model in similar directions, a method called group-screening  
352 (Kleijnen 1987). A low and high value was set for each parameter around the reference value, with  
353 20% variation (Drouineau et al. 2006; Rougier et al. 2015), except for three sets of parameters:  
354 *fertility* and  $L_{sm}$ (as a minimum value, *fertility* corresponded to the fecundity of a female with a length

355 at silvering equals to male length at silvering; otherwise, female fitness would always be superior to  
356 male fitness), and growth genotypes (to avoid overlap between them), where the range of variation  
357 was less. We then conducted a fractional factorial design of resolution V ( $2^{12-4} = 256$  combinations).  
358 This kind of orthogonal designs allows to explore main effects and first order interactions without  
359 confusion. To account for model stochasticity, we conducted 10 replicates for each of the 256  
360 combinations leading to 2560 simulations. The five patterns were calculated for each simulation  
361 producing an output table with 2560 lines (one per simulation) and five columns containing the tau  
362 value of the Mann-Kendall trend tests for each pattern (a negative tau value indicates a negative  
363 trend from downstream to upstream while a positive tau indicates a positive trend from downstream  
364 to upstream).

365

## 366 **4 Results**

### 367 **4.1 Reference simulation**

368 In the reference simulation, GenEveel mimicked the five spatial patterns at the catchment  
369 scale (Fig. 3). Males were concentrated in the downstream section of the river where density was  
370 higher (Helfman et al. 1987; Tesch 2003; Davey and Jellyman 2005). Fast growers preferentially  
371 settled in downstream habitats, whereas slow growers tended to move upstream to avoid  
372 competition (De Leo and Gatto 1995; Daverat et al. 2006, 2012; Drouineau et al. 2006; Edeline 2007;  
373 Geffroy and Bardonnnet 2012). Regarding mean length at silvering (for males and females), a smaller  
374 size at maturity was simulated in the downstream section of the river, whereas larger lengths were  
375 occurred gradually throughout the catchment (Vollestad 1992; Oliveira 1999).

376 The Mann-Kendall test confirmed that the five patterns were mimicked in the simulation.  
377 More specifically, negative tau values confirmed a decreasing trend for density, ratio of fast growers

378 and mean realized growth rate; while positive tau values pointed to an increasing trend for ratio of  
379 females and mean length at silvering (Table 2).

## 380 **4.2 Model exploration**

381 For each combination, the 10 replicates provided the same results, confirming that the  
382 patterns were not sensitive to stochasticity.

383 Interestingly, 310 simulations produced only females while 640 simulations produced only  
384 males. Simulations with only females corresponded to simulation where density-dependence  $\alpha$ ,  $L_{\infty}$   
385 and the fecundity exponent  $b$  were simultaneously strong. Conversely, simulations with only males  
386 corresponded to simulations with a low  $b$  and a low  $L_{\infty}$ . With only one sex, it was not possible to  
387 calculate a spatial trend in sex ratio and with only males, it was not possible to calculate a trend of  
388 length at silvering.

389 Two questions were addressed here. In a first time, we compared the five patterns to see  
390 which of those patterns were frequently mimicked and which were less frequently mimicked. Then,  
391 we compared the sensitivity of the model to each group of parameters. To quantify this sensitivity to  
392 a group of parameters values, we compared the number of simulations that reproduce a given  
393 pattern when the group had modality (-) with the number of simulations and when the group had  
394 modality (+). A strong discrepancy indicated a high sensitivity to the group of parameters.

395 The Mann-Kendall tests of spatial patterns confirmed that the simulated patterns of  
396 abundance, ratio of fast growers, and mean realized growth rate were consistent with the literature  
397 in each of the 2560 combinations (Table 3). This result indicates that these model outputs do not  
398 depend on parameters values in the parameter space considered. Consequently, the assumptions  
399 about asymmetrical density-dependence and growth genotypes were enough to simulate catchment  
400 colonization.

401 Regarding length at silvering pattern, patterns were consistent in 1300 simulations of the  
402 1920 simulations for which it was possible to calculate a pattern (Table 3, Fig. 4 for several examples).

403 This meant that, in situations where some females were produced, the pattern was consistent in  
404 about  $\frac{2}{3}$  of the simulations. Length at silvering pattern appeared to be sensitive to most of the  
405 parameters. The two most important were  $L_{\infty}$  and  $b$ : consistent pattern were much more frequent  
406 with a modality (+) (respectively 990 and 940 simulations) for these two parameters than with  
407 modality (-) (respectively 310 and 360 simulations). This is not surprising since with modality (-) for  
408 those parameters, the model produced only males in 640 simulations. Two other groups of  
409 parameters had a strong influence: male fertility/ male length at silvering and density-dependence.  
410 Consistent patterns were more frequent with low male fertility and length at silvering (800 with  
411 modality (-) vs 500 with modality (+)), and with limited density dependence (810 with modality (-) vs  
412 490 with modality (+)).

413 For the female ratio pattern, 130 simulations produced consistent patterns over the 1610  
414 simulations for which it was possible to calculate a pattern (Table 3). This pattern was mostly  
415 sensitive to four groups of parameters which correspond to the four most influential groups for the  
416 pattern of length at silvering. Patterns were consistent only when male fertility/length at silvering  
417 had modality (-) whereas  $K_{slow}/M_{slow}$  had modality (+). Moreover, consistent patterns were more  
418 frequent when  $L_{\infty}$  had a modality (-) and  $b$  a modality (+).

419 On the whole, 130 of the 2560 combinations produced results which were consistent for all  
420 the five patterns (Table 4, Fig. 4 and Table S1). These 130 simulations corresponded exactly to the  
421 130 simulations that produced consistent sex ratio patterns, demonstrating that this last pattern was  
422 the more constraining (Fig. 5). Consequently, the interpretation regarding sensitive parameters was  
423 similar.

424 To make a summary of those results: in situations where females' fitness was favored  
425 because of a strong  $L_{\infty}$  or a strong  $b$ , i.e. a high fecundity, the model produced only females.  
426 Conversely, when females were too penalised, model produced only males. Therefore, an equilibrium  
427 was required between males and females fitnesses to mimic all patterns. The patterns in length at  
428 silvering and sex ratio were the two most constraining patterns and were mainly sensitive to four

429 groups of patterns. These groups of parameters set the equilibrium between males and females  
430 fitnesses (male fertility and length at silvering,  $b$  and  $L_{\infty}$ ) and the advantages between slow and fast  
431 growers. Density-dependence was also important regarding the pattern on length at silvering. We  
432 can observed that the five patterns were consistent mostly when slow growers and females were not  
433 too penalized with respect to males and fast-growers.

434         Some of the patterns were indeed very constrained by model assumptions so it is hardly  
435 surprising that they were mimicked by the model. For example, our constraints on mortality and  
436 growth really constrained the distribution of fishes and probably the pattern of realized growth rates  
437 in the catchment. However, those constraints were based on various observations in the literature  
438 that have rarely been considered together to see if they make sense in a context of adaptive  
439 response. We do not specify any constraints on the sex ratio, length at maturity and relationships  
440 between sex ratio and slow/fast growers. Those results are really emerging patterns that are  
441 consistent with the literature.

442

## 443 **5 Discussion**

### 444 ***5.1 Adaptation to environmental variability: phenotypic plasticity and*** 445 ***genetic polymorphism of European eel***

446         The European eels, and more generally, temperate eels, display fascinating characteristics:  
447 catadromy with a long larval drift, large distribution area with contrasted growth habitats, panmixia,  
448 and strong phenotypic and tactic variability at different spatial scales. Consequently, this species is  
449 relevant to explore adaptive mechanisms to environmental variability. Phenotypic plasticity has been  
450 proposed as one such mechanism because of random mating and larval dispersal that prevent local  
451 selection pressures to generate habitat-specific adaptations, or local adaptation, from one generation  
452 to the next. Drouineau et al. (2014) developed the first model to explore the major role of

453 phenotypic plasticity in both life-history traits and tactical choices as an adaptive response to  
454 spatially structured environments and density dependence. However, recently Gagnaire et al. (2012),  
455 Pujolar et al. (2014), Boivin et al. (2015), Côté et al. (2015) and Pavey et al. (2015) demonstrated the  
456 existence of genetic differences correlated with the environment, suggesting that part of the  
457 observed phenotypic variability had a genetic basis.

458         Based on the approach developed by Drouineau et al. (2014), the objective of this study was  
459 to propose a model based on life-history theory and optimal foraging theory to explore the role of  
460 both adaptive phenotypic plasticity and genetic polymorphism with genetic-dependent habitat  
461 selection, in the emergence of phenotypic patterns. To that end, we used a pattern-oriented  
462 modelling approach, as developed by Grimm et al. (1996). This kind of approach compared field  
463 observed patterns to simulated patterns and postulated that those patterns are similar, the model is  
464 likely to contain the mechanisms generating these patterns.

## 465 **5.2 *In which conditions were the patterns mimicked?***

466         Similarly to Eveel, a main limitation of our approach was that it was based on a simulation  
467 model with a pattern-oriented approach. Consequently, our results demonstrated that our  
468 assumptions were plausible, but did not demonstrate that they were correct. Such a demonstration  
469 would require demonstrating underlying mechanisms, for example by conducting complementary  
470 controlled experiments.

471         We built a full experimental design to explore the model. This type of approach is classical in  
472 complex model exploration (de Castro et al. 2001; Faivre et al. 2013). For example, in the context of  
473 sensitivity analysis of complex simulation models (Drouineau et al. 2006). Our exploration goals were  
474 to generate simulations from the parameter space and analyze the qualitative differences in the  
475 model output to (i) study the impact of parameters on the model output, (ii) determine which  
476 parameters were the most important, and (iii) identify the combinations of parameters required to

477 mimic all observed spatial patterns. In this study, 17 parameters grouped in 12 set of parameters,  
478 were chosen to define the region of the parameter space where all spatial patterns were reproduced.

479 To assess the influence of stochasticity, we made 10 replicates per combination. This can  
480 appear limited, however, it was impossible to increase the number of simulations and we preferred  
481 to have a better exploration of uncertainty due to uncertain parameters rather than on stochasticity  
482 which is rather limited in our model. Stochasticity occurs during the initialization process when  
483 randomly building slow or fast value with a given probability. This corresponds to a binomial  
484 distribution which has, given the large number of individuals, a very small variance. Stochasticity also  
485 occurs in the order of individuals for step 1, but this is closely linked to the previous process and  
486 consequently also has a limited variability. This limited effect of stochasticity was confirmed by our  
487 results since patterns per combination were always consistent among replicates (Fig. 4 and 5).

488 One hundred thirty simulations among the 2560 mimicked the five spatial patterns. The  
489 fourth pattern stated that fast growers and slow growers had different spatial distributions. Fulfilling  
490 this pattern demonstrated that genetically different individuals have different habitat selection  
491 strategies to maximize their respective fitnesses. Consequently, fulfilling the five patterns suggested  
492 that, at least in certain conditions, genotype-dependent habitat selection and phenotypic plasticity  
493 could explain observed phenotypic patterns. The level of sensitivity was variable among groups of  
494 parameters, but four main groups of parameters were crucial: males' fertility and length at silvering,  
495 growth and mortality rates of slow growers, fecundity, and  $L_{\infty}$ . Density-dependence was also an  
496 important parameter regarding length at silvering. In summary, the patterns were mimicked in  
497 simulations with dominants and dominated but when dominated individuals, mainly females, were  
498 not too penalized with respect to dominants, mainly males.

499 Regarding the spatial patterns, higher density, higher proportions of fast growers, and faster  
500 growth rates in downstream regions were mimicked for all combinations of parameters. This  
501 suggested that in the range of variation considered, none of the parameters had effects on model  
502 outputs. This probably means that the gradient in environmental conditions and the population

503 dynamics in the model were sufficient to reproduce these patterns, regardless of the competitive  
504 advantage of fast growers with respect to slow growers, confirming that phenotypic plasticity plays  
505 an important role in environmentally induced changes in life-history traits and demographic  
506 attributes. Concerning the two other patterns (sex ratio and length at silvering), additional  
507 hypotheses are needed regarding competition and genetic polymorphism. They were fulfilled in  
508 conditions of weak competition and when growth differences were not too strong between the two  
509 genotypes.

### 510 ***5.3 Consequences of intra-specific competition***

511 In our model, we assumed the existence of asymmetrical density dependence between fast  
512 and slow growers. We assumed that smaller individuals would avoid engaging in competition with  
513 larger ones (regardless of sex) and would consequently be more affected by density dependence.  
514 This assumption seems ecologically realistic. Asymmetrical density dependence has been observed in  
515 plants (Weiner 1990), insects (Varley et al. 1973), and fish (Dingsøer et al. 2007). Intraspecific  
516 competition is a very common mechanism of density dependence, favoring large body size in fishes  
517 (Francis 1983; Juanes et al. 2002). In anguillid eels, this may be manifested through agonistic  
518 interactions (Knights 1987; Bardonnnet et al. 2005), including cannibalism (Edeline and Elie 2004).  
519 Such behaviors have been observed in yellow eels under artificial rearing conditions (Peters et al.  
520 1980; Degani and Levanon 1983; Knights 1987).

521 We modelled this asymmetric competition by specifying different levels of density-  
522 dependent mortality for slow and fast growers. Interestingly, the spatial patterns were still  
523 reproduced when setting these parameters to a similar value (not presented here). Indeed, even with  
524 similar intensity of density dependence, slow growers needed more time to reach their length at  
525 silvering and consequently, suffered competition longer. Thus, even if competition has the same  
526 impact on instantaneous mortality rates of slow and fast-growers, density dependence produces  
527 asymmetric impacts on their respective fitness. In EvEel, Drouineau et al. (2014) assumed the



528 existence of asymmetric competition between males and females, with females being more affected  
529 by competition. Interestingly, we observed in our results that females had a higher proportion of  
530 slow growers than males. This means that the gender-based asymmetry proposed by Drouineau et al.  
531 (2014) may be an indirect result of an asymmetry between two genetically distinct types of  
532 individuals with respect to growth.

533         The asymmetric competition implies that fitness of individuals having a given growth  
534 genotype depends on the number of individuals having the other growth genotype, which may lead  
535 to frequency-dependent selection (Heino et al. 1998). This has several implications. In the model, we  
536 assumed that individual fitness corresponded to the lifetime reproductive success called  $R_0$ , and that  
537 this fitness is maximized. However, in a frequency-dependent selection context (i) natural selection  
538 does not necessarily lead in fitness maximization (Mylius and Diekmann 1995; Metz et al. 2008), and  
539 (ii) fitness may need to be defined as an invasion criterion (Metz et al. 1992). Even when fitness  
540 maximization applies,  $r$ , the population growth rate, may be a more appropriate measure of fitness  
541 than  $R_0$  depending on how density-dependence acts (Mylius and Diekmann 1995). To ensure that  
542 our assumptions about fitness definition and maximization were valid would require a multi-  
543 generational model at the scale of the population distribution area. This would allow computing  
544 fitness for the whole life-cycle across all potential habitat types of the distribution area while  
545 accounting for population structure in terms of genotypes or clusters. At this point, it would be  
546 interesting to explore the heritability of the different traits and the intra-generational spatially  
547 varying selection, a mechanism suggested by the SNP differences according to latitude (Pujolar et al.  
548 2011; Gagnaire et al. 2012; Ulrik et al. 2014).

549         This was not possible because of difficulties to develop a whole life-cycle model. More  
550 specifically, the fractal dimension of the eel population makes it very difficult to develop a population  
551 dynamics model for the continental phase at the distribution area scale. Moreover, such a model  
552 would require the use of stock-recruitment relationships, which is very difficult for the European eels  
553 because of insufficient data, long larval drift, and different recruitment trends through the

554 distribution area. In this context, we had to use intra-generational model and a R0 fitness function,  
555 restricted to a single catchment and a portion of the whole life-cycle, and to postulate that this R0  
556 was maximized.

#### 557 **5.4 Reinterpreting the time-minimizing and size-maximizing strategies**

558 To summarize the results for combinations of parameters that mimicked observed patterns,  
559 we observed a high proportion of individuals, mainly fast growers, in the downstream environment,  
560 which corresponded to marine or brackish water. These individuals were mainly males with a  
561 constant length at silvering. In upstream areas, we found mainly slow growers, primarily females with  
562 higher length at silvering. This can aid in the reinterpretation of gender difference in life tactics (i.e.,  
563 males with a time-maximizing strategy and females with a size-maximizing strategy). Our results  
564 suggest that these tactics were possibly based on the existence of two genotypes for growth. Fast  
565 growers grow fast but suffer higher mortality (because they inhabit downstream habitats with higher  
566 mortality and density); a time-minimizing strategy is suitable for them. Slow growers grow slowly but  
567 suffer lower mortality, consequently they can stay longer in continental habitats, and a size-  
568 maximizing strategy is suitable for them.

569 Another interesting question is whether cues are used by individuals to select their growth  
570 habitat. In the model, individuals were omnipotent and omniscient: they were able to assess the  
571 potential fitness in each cell and move in the most suitable cell. This would mean that they were able  
572 to assess the natural mortality, growth rate, and density in each cell. Drouineau et al. (2014)  
573 suggested that temperature might be one of the main proximal cue used by individuals to assess the  
574 suitability. Regarding density-dependence, reaction to aggressiveness (Geffroy and Bardonnnet, 2012)  
575 or cons-specific odors (Schmucker et al. 2016) were observed on growth and propensity to migrate.  
576 Vélez-Espino and Koops (2010) also revealed temperature as main factor explaining variation in life-  
577 history traits. Our model suggested that density in various habitats was also probably a main cue,  
578 especially for slow growers, which tended to minimize competition.

## 579 **5.5 Perspectives**

### 580 **5.5.1 Exploring conditions in which phenotypic plasticity is adaptive**

581 It has been demonstrated that phenotypic plasticity allows short-term adaptation to  
582 environmental heterogeneity for many species (Schlichting 1986; Sultan 1987; Scheiner 1993;  
583 Pigliucci 2005). However, the fitness gain arising from phenotypic plasticity should overcome its cost  
584 to be selected. This last point has not been demonstrated for eels. One possibility would be to  
585 simulate the evolution of a plastic reaction norm, for example length at silvering, close to the model  
586 developed by Marty et al. (2011). Following Ernande et al. (2004) and based on adaptive dynamics  
587 models (Mylius and Diekmann 1995), it would be interesting to explore in which environmental and  
588 density-dependence conditions, phenotypic plasticity may be selected as an adaptive mechanism  
589 despite its costs, and if plasticity is still adaptive in a context of low densities after a population  
590 collapse.

### 591 **5.5.2 Assessing the impact of anthropogenic pressures at the distribution**

#### 592 **area scale**

593 Another perspective is to assess the impact of anthropogenic pressures on eel populations.  
594 Drouineau et al. (2014) mentioned that, because of phenotypic plasticity, anthropogenic pressures  
595 are not only a source of mortality, but may also affect sex ratio or mean length at silvering. The  
596 existence of two genotypes for growth suggests that anthropogenic activities may act as selective  
597 forces. Recently, Podgorniak et al. (2015) demonstrated that human-induced obstacles to migration  
598 could act as an evolutionary pressure. Concerning this, Boulenger et al. (2016) highlighted that  
599 human pressures impact survival, leading to different life-history strategies.

600

601 To conclude, our model provided new insights on eel adaptive mechanisms to heterogeneous  
602 environments. Phenotypic plasticity and genotype-dependent habitat selection are two types of  
603 mechanisms that can explain the patterns in life-history traits observed in natural environments at  
604 the river catchment scale. A better understanding of these mechanisms is crucial to interpret the  
605 observations made in the environment, the effects of anthropogenic pressures on the population,  
606 and to understand if eels are still adapted in the context of depleted population size and climate  
607 change.

608

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613

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- 829

830 **Tables**

831 **Table 1.** GenEveel parameter descriptions with reference values and modalities (- and +) for the 17  
 832 parameters involved in the experimental design.

Parameter	Description	Reference value	(-) modality	(+) modality	Reference
$n$	Cells of river catchment	30	24	36	(Drouineau et al. 2014)
$N$	Number of glass eels that colonize freshwater	30 000	24 000	36 000	(Drouineau et al. 2014)
$a1$	Regression coefficient from fecundity at length	8 846	-	-	(Andrello et al. 2011)
$a$	Regression coefficient from fecundity at length	1.3877119	-	-	(Melià et al. 2006, Andrello et al. 2011)
$b$	Regression exponent from fecundity at length	3.22	2.576	3.864	(Melià et al. 2006)
$L_{\infty}$ (cm)	Asymptotic length	76.2	60.96	91.44	(De Leo and Gatto 1995)
$L_{sm}$ (cm)	Male length at silvering	40.5	38.15	42.85	(Vollestad 1992)
$L_g$ (cm)	Length at recruitment	7.5	6	9	(Desaunay and Guerault 1997, Dekker 1998, Desaunay et al. 2012)
$fertility$	Constant of male fertility	43	40.5	45.5	-
$K_{fast}(i,1), year^{-1}$	Fast intrinsic growth rate	0.315	0.295	0.335	(De Leo and Gatto 1995)
$K_{slow}(i,1), year^{-1}$	Slow intrinsic growth rate	0.253	0.233	0.273	(De Leo and Gatto 1995)
$propK$	Proportion of individuals that grow slowly	0.5	0.4	0.6	-
$M_{fast}(i,1), year^{-1}$	Fast intrinsic mortality rate	0.38	0.405	0.355	-
$M_{slow}(i,1), year^{-1}$	Slow intrinsic mortality rate	0.138	0.15	0.127	(Dekker 2000)
$\alpha$	Intensity of density-dependence	0.0001	0.00008	0.00012	(Drouineau et al. 2014)
$r_K$	Ratio between upstream and downstream growth rate	0.5	0.4	0.6	(Drouineau et al. 2014)
$r_M$	Ratio between upstream and downstream mortality	1	0.8	1.02	(Drouineau et al. 2014)

	rate				
$Y_K$	Shape parameter of growth	0.05	0.049	0.051	(Drouineau et al. 2014)
$Y_M$	Shape parameter of mortality	0.05	0.049	0.051	(Drouineau et al. 2014)

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834 **Table 2.** Results of Mann-Kendall test of reference simulation.

Spatial pattern	Tau
Abundance	-1
Mean length at silvering	0.98
Sex ratio (proportion of females)	0.57
Ratio of fast growers	-0.78
Mean realized growth rate	-1

835

836 **Table 3.** Number of simulations with consistent patterns for each modality of the groups of  
 837 parameters, over the number of simulations for which it was possible to calculate a pattern. The  
 838 columns represent the spatial patterns and the numbers of simulations for which it was possible to  
 839 estimate a pattern.

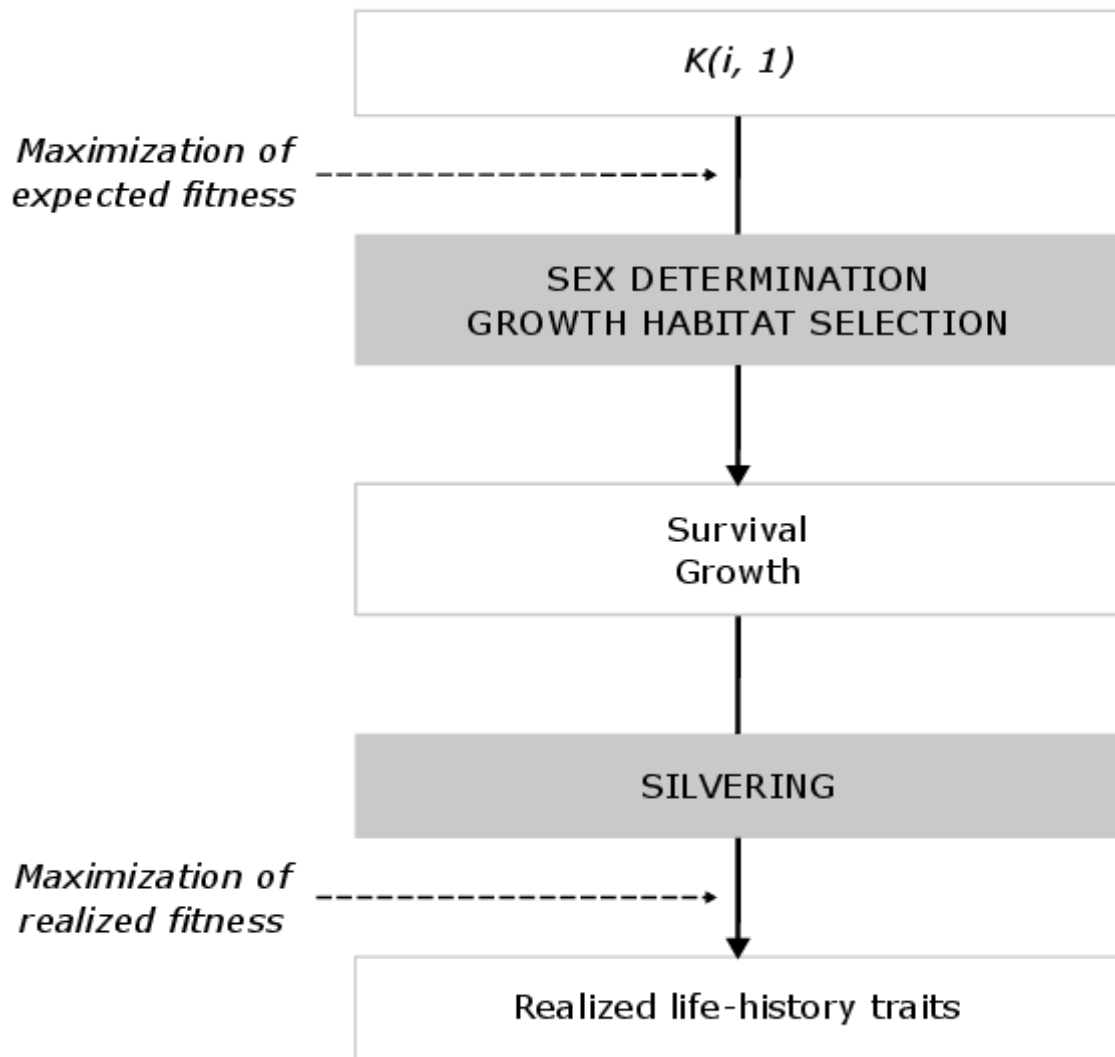
Parameters group	Abundance 2560	Mean length at silvering 1920	Sex ratio	Ratio of fast	Mean	The five
			(proportion of females) 1610	growers 2560	realized growth rate 2560	spatial patterns 1610
<i>N</i>	(-) 1280/1280	(-) 650/960	(-) 70/800	(-) 1280/1280	(-) 1280/1280	(-) 70/800
	(+) 1280/1280	(+) 650/960	(+) 60/810	(+) 1280/1280	(+) 1280/1280	(+) 60/810
<i>fertility</i> and <i>L<sub>sm</sub></i>	(-) 1280/1280	(-) 800/960	(-) 130/800	(-) 1280/1280	(-) 1280/1280	(-) 130/800
	(+) 1280/1280	(+) 500/960	(+) 0/810	(+) 1280/1280	(+) 1280/1280	(+) 0/810
<i>K<sub>fast</sub>(i, 1)</i> and <i>M<sub>fast</sub>(i, 1)</i>	(-) 1280/1280	(-) 650/960	(-) 70/810	(-) 1280/1280	(-) 1280/1280	(-) 70/810
	(+) 1280/1280	(+) 650/960	(+) 60/800	(+) 1280/1280	(+) 1280/1280	(+) 60/800
<i>K<sub>slow</sub>(i, 1)</i> and <i>M<sub>slow</sub>(i, 1)</i>	(-) 1280/1280	(-) 710/960	(-) 0/810	(-) 1280/1280	(-) 1280/1280	(-) 0/810
	(+) 1280/1280	(+) 590/960	(+) 130/800	(+) 1280/1280	(+) 1280/1280	(+) 130/800
<i>propK</i>	(-) 1280/1280	(-) 650/960	(-) 90/810	(-) 1280/1280	(-) 1280/1280	(-) 90/810
	(+) 1280/1280	(+) 650/960	(+) 40/800	(+) 1280/1280	(+) 1280/1280	(+) 40/800
<i>α</i>	(-) 1280/1280	(-) 810/960	(-) 60/960	(-) 1280/1280	(-) 1280/1280	(-) 60/960
	(+) 1280/1280	(+) 490/960	(+) 70/650	(+) 1280/1280	(+) 1280/1280	(+) 70/650
<i>n</i>	(-) 1280/1280	(-) 660/960	(-) 60/810	(-) 1280/1280	(-) 1280/1280	(-) 60/810
	(+) 1280/1280	(+) 640/960	(+) 70/800	(+) 1280/1280	(+) 1280/1280	(+) 70/800
<i>b</i>	(-) 1280/1280	(-) 360/640	(-) 10/640	(-) 1280/1280	(-) 1280/1280	(-) 10/640
	(+) 1280/1280	(+) 940/1280	(+) 120/970	(+) 1280/1280	(+) 1280/1280	(+) 120/970
<i>L<sub>∞</sub></i>	(-) 1280/1280	(-) 310/640	(-) 120/640	(-) 1280/1280	(-) 1280/1280	(-) 120/640
	(+) 1280/1280	(+) 990/1280	(+) 10/970	(+) 1280/1280	(+) 1280/1280	(+) 10/970
<i>L<sub>g</sub></i>	(-) 1280/1280	(-) 650/960	(-) 60/800	(-) 1280/1280	(-) 1280/1280	(-) 60/800
	(+) 1280/1280	(+) 650/960	(+) 70/810	(+) 1280/1280	(+) 1280/1280	(+) 70/810
<i>r<sub>k</sub></i> and <i>r<sub>m</sub></i>	(-) 1280/1280	(-) 630/960	(-) 40/810	(-) 1280/1280	(-) 1280/1280	(-) 40/810
	(+) 1280/1280	(+) 670/960	(+) 90/800	(+) 1280/1280	(+) 1280/1280	(+) 90/800
<i>γ<sub>k</sub></i> and <i>γ<sub>m</sub></i>	(-) 1280/1280	(-) 730/960	(-) 60/810	(-) 1280/1280	(-) 1280/1280	(-) 60/810
	(+) 1280/1280	(+) 570/960	(+) 70/800	(+) 1280/1280	(+) 1280/1280	(+) 70/800

840 **Table 4.** Results of the 13 combinations that generated five consistent patterns. The signs +/- refer to  
 841 the modalities of the parameters groups. The two last columns represent the five spatial patterns. An  
 842 ascendant arrows stands for positive Mann-Kendall tau value (increasing trend from downstream to  
 843 upstream). Conversely, a descendant arrow stands for a negative Mann-Kendall tau value.

N	fertility,		$K_{fast}(i, 1),$	$K_{slow}(i, 1),$	propK	$\alpha$	n	b	$L_{\infty}$	$L_g$	$r_K,$	$\gamma_K,$	Abundance	
	$L_{sm}$	$M_{fast}(i, 1)$	$M_{slow}(i, 1)$	Ratio of fast growers $\overline{K(l, x)}$									Sex ratio $\overline{Ls}$	
1	-	-	-	+	+	+	+	+	-	-	+	+	↘	↗
2	+	-	-	+	-	+	+	+	-	+	+	+	↘	↗
3	+	-	-	+	+	-	+	+	-	+	+	-	↘	↗
4	-	-	-	+	-	-	+	+	-	-	+	-	↘	↗
5	+	-	+	+	+	-	-	+	-	-	+	-	↘	↗
6	+	-	-	+	-	-	-	+	-	+	-	-	↘	↗
7	-	-	-	+	-	+	+	-	+	+	+	+	↘	↗
8	-	-	+	+	-	-	-	+	-	+	+	-	↘	↗
9	-	-	+	+	+	+	-	+	-	+	+	+	↘	↗
10	-	-	+	+	-	+	+	+	-	+	-	+	↘	↗
11	+	-	+	+	-	+	-	+	-	-	+	+	↘	↗
12	-	-	-	+	-	+	-	+	-	-	-	+	↘	↗
13	+	-	+	+	-	-	+	+	-	-	-	-	↘	↗

844

845 **Figures**

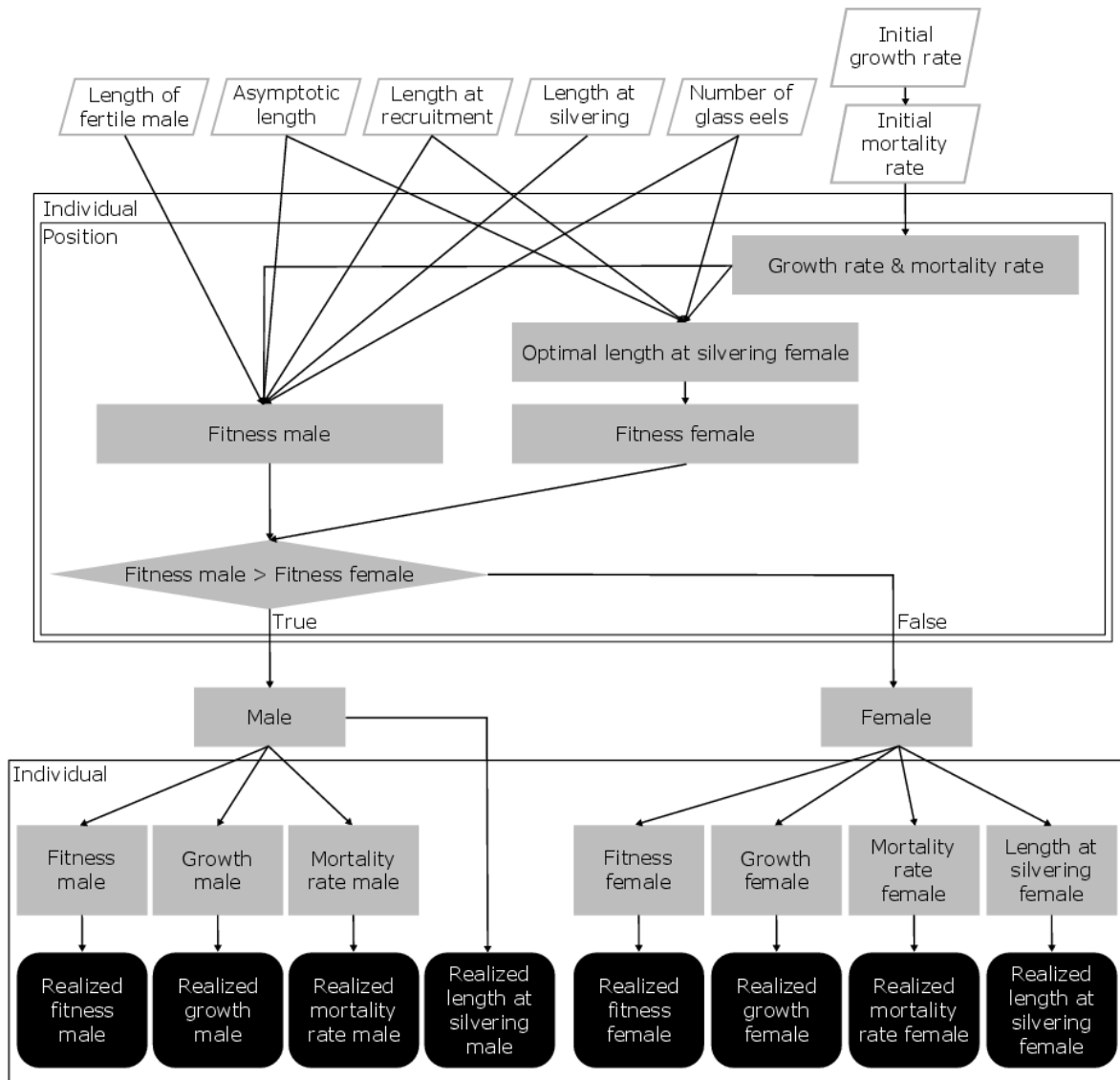


846

847 **Fig. 1.** Flow chart representing the fish biological pathway.

848

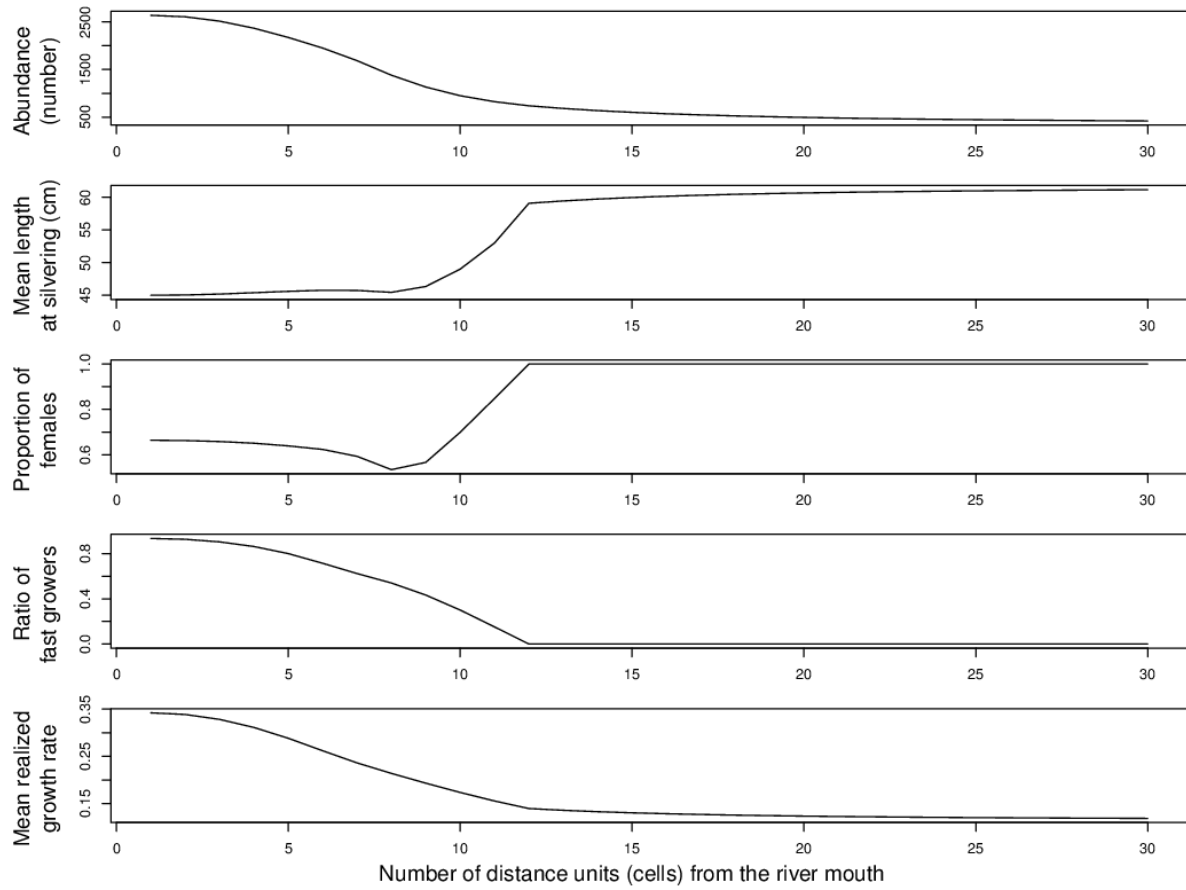




849

850 **Fig. 2.** Algorithm of the model GenEveel.

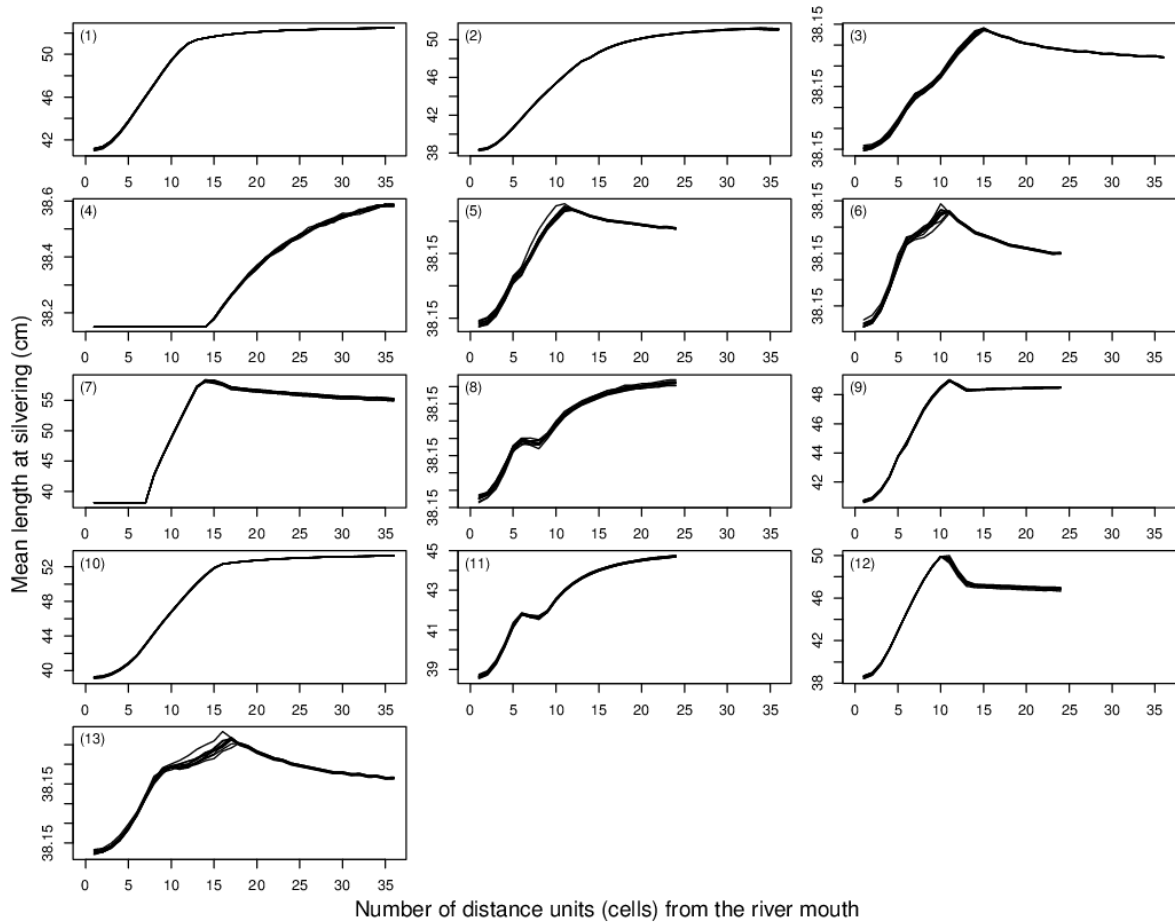
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852

853 **Fig. 3.** Output values for the five spatial patterns resulting from the reference simulation.

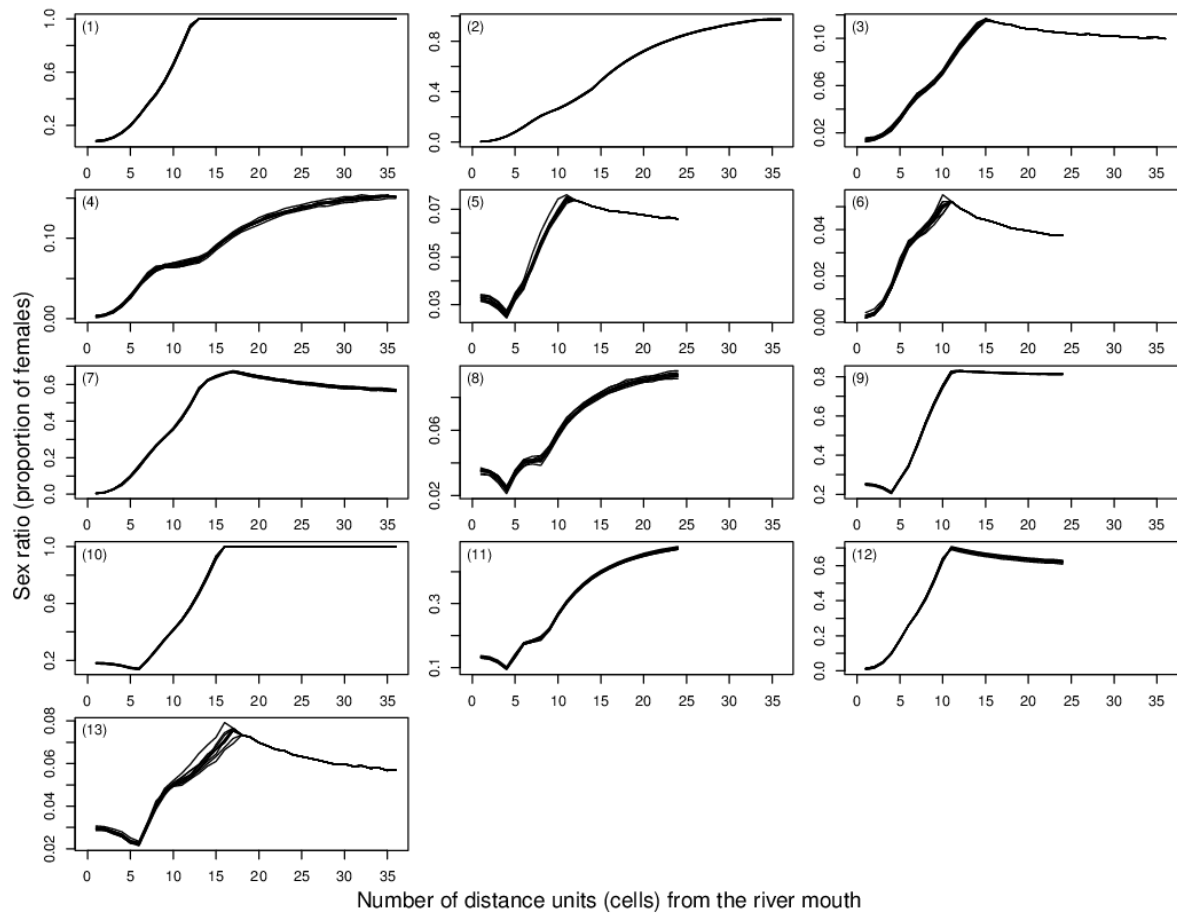
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855

856 **Fig. 4.** Simulated mean length at silvering patterns in the 13 combinations of parameters that  
857 consistently mimic the pattern described in the literature. These 13 combinations correspond to the  
858 13 combinations that generate consistent patterns for all the five spatial patterns. Each plot stands  
859 for a combination (the number is an identifier of the combination that can be found in table 4) and  
860 each line stands for a replicate.

861



862

863 **Fig. 5.** Simulated sex ratio (proportions of females) patterns in the 13 combinations of parameters  
 864 that consistently mimic the pattern described in the literature. These 13 combinations correspond to  
 865 the 13 combinations that generate consistent patterns for all the five spatial patterns. Each plot  
 866 stands for a combination (the number is an identifier of the combination that can be found in table  
 867 4) and each line stands for a replicate.

868 **Supplemental Information**

869 **Table S1.** Results of the 256 combinations. The signs +/- refer to the modalities of the parameters  
870 groups . The last five columns represent the spatial patterns. An ascendant arrows stands for positive  
871 Mann-Kendall tau value (increasing trend from downstream to upstream). Conversely, a descendant  
872 arrow stands for a negative Mann-Kendall tau value.