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1 Impacts that cause the highest direct mortality of individuals do not necessarily have the greatest  
2 influence on temperate eel escapement

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## 9 **Abstract**

10 Temperate eels are three panmictic catadromous species with a long period of oceanic passive larval  
11 drift and large distribution areas in contrasting environments. Spatial patterns of life history traits  
12 have been observed, and are correlated with environmental gradients, and may arise from both  
13 adaptive phenotypic plasticity and genetic polymorphism. This raises the question of the effect of  
14 spatially heterogeneous anthropogenic pressures on these populations. In this context, we used  
15 Geneveel, an individual-based optimization model that includes both phenotypic plasticity and  
16 genetic polymorphism, to explore the effects of different kinds of anthropogenic pressures: glass eel  
17 and silver eel fisheries, obstacles to upstream migration, and turbine mortality. More specifically,  
18 we analyzed the effects of these pressures on five output variables: the number of escapees, the  
19 proportion of females, the proportion of slow growers, the mean length-at-silvering and the  
20 resulting egg production. Our results suggest that phenotypic plasticity could act as a compensatory  
21 mechanism that mitigates the effects of some pressures (glass eel fishery and obstacles to upstream  
22 migration) and could be a source of resilience for the population, while other pressures did not show  
23 any compensatory effect (silver eel fishery and turbine mortality). Therefore, global impacts are  
24 very hard to assess, and the pressure that kills the most individuals does not necessarily have the  
25 biggest impact on the spawning biomass.

## 26 **Keywords:**

27 Temperate eels; anthropogenic pressures; adaptive mechanisms; life history traits; modeling

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## 31 **1. Introduction**

32 Temperate eels (*Anguilla rostrata*, *A. anguilla*, *A. japonica*) are three catadromous species that  
33 reproduce at sea and grow in continental waters. They display remarkable similarities in life history  
34 traits (Daverat et al., 2006; Edeline, 2007). The three populations are panmictic (Als et al., 2011;  
35 Han et al., 2010; Pujolar, 2013). Reproduction occurs in the Sargasso Sea for *A. anguilla* and *A.*  
36 *rostrata* (McCleave, 1993; Schmidt, 1923) and west of the Mariana Islands for *A. japonica*  
37 (Tsukamoto, 1992). Larvae (known as leptocephali) are subject to a long and passive trans-oceanic  
38 drift. When arriving on the continental shelves, leptocephali metamorphose into young and  
39 transparent eels, called glass eels (Tesch, 2003), and enter continental waters, where they become  
40 pigmented yellow eels, the immature adult stage. After a variable period, generally lasting from  
41 three to 15 years, yellow eels metamorphose again into silver eels (this metamorphosis is generally  
42 called “silvering”), the seaward migration stage. They achieve their sexual maturation while  
43 migrating back to spawning grounds. Because of the long larval drift, their distribution area is very  
44 large, and the growth phase can occur in very heterogeneous river basins, from Morocco to Norway  
45 (Tesch, 2003) for the European eel, from Venezuela to Greenland for *A. rostrata* (Helfman et al.,  
46 1987), and from the northern Philippines to Korea for *A. japonica* (Tsukamoto, 1992).

47 Concomitantly to this environmental heterogeneity, temperate eels display remarkable life  
48 history trait patterns at both distribution and river catchment scales (Vélez-Espino and Koops,  
49 2009). Among them, the sex ratio is highly variable at different spatial scales: female-biased sex  
50 ratios are generally observed in the northern part of the distribution area, while male-biased sex  
51 ratios are observed in the southern part (Kettle et al., 2011). At the catchment scale, sex ratios are  
52 male biased in downstream habitats (Oliveira and McCleave, 2000; Tesch, 2003). This question of  
53 sex ratio is relevant since eel sex is not genetically determined, but depends on environmental  
54 conditions (Davey and Jellyman, 2005; Geffroy, 2012; Geffroy and Bardonnet, 2015), and males  
55 and females display very different life history tactics (Helfman et al., 1987). Males are assumed to  
56 have a time-minimizing strategy; since their reproductive success does not depend on their size,  
57 they are assumed to leave continental waters as soon as they reach the minimal size required to  
58 successfully migrate back to spawning grounds (Oliveira, 1999; Van Den Thillart et al., 2007;  
59 Vollestad, 1992). On the other hand, female reproductive success is assumed to be a trade-off  
60 between size at maturity (known as length-at-silvering) and survival, called a size-maximizing  
61 strategy. This size-maximizing strategy assumption is supported by the observation of larger  
62 females in the northern part of the distribution area (slow growth but lower mortality) than in the  
63 southern part (Davey and Jellyman, 2005; Helfman et al., 1984).

64 Indeed, eels display a large range of tactics in terms of habitat use for growth, with some  
65 settling in estuarine waters, while others moving far upstream in river catchments (Arai and Chino,  
66 2012; Daverat et al., 2006; Tsukamoto et al., 1998). Higher densities are observed in downstream  
67 habitats, which are the most accessible and the most favorable in terms of growth rates (Daverat et  
68 al., 2012; Helfman et al., 1984; Melià et al., 2006). However, other eels also settle in the upper parts  
69 of river catchments. Edeline (2007) proposed that more limited intraspecific competition may  
70 overcome migratory energy costs, such as loss in growth rate. This assumption was challenged by  
71 Cairns et al. (2009), who did not observe a decrease in natural mortality in upstream habitats that  
72 would outweigh the cost of migration and the decrease in growth rate.

73 Few studies have explored whether the observed spatial phenotypic patterns are the result of  
74 adaptive mechanisms to environmental variability, and they therefore remain poorly understood.  
75 The panmixia and long and passive larval drifts impair the possibility of local adaptation.  
76 Phenotypic plasticity has been proposed as an adaptive response to environment variability for  
77 many species (Gotthard and Nylin, 1995; Levins, 1963; Pigliucci, 2005), and Ernande and  
78 Dieckmann (2004) demonstrated that density dependence favors the selection of plastic phenotypes.  
79 In this context, assuming that phenotypic plasticity is an adaptive response to environmental  
80 variability, Drouineau et al. (2014) developed an optimization model that was able to mimic most of

81 the observed patterns at both the distribution area and river catchment scales. The existence of  
82 correlations between genotypic patterns and environmental conditions have been observed (Boivin  
83 et al., 2015; Côté et al., 2015, 2014, 2009; Gagnaire et al., 2012; Pujolar et al., 2014; Ulrik et al.,  
84 2014). Côté et al. (2014, 2009) and Boivin et al. (2015) observed differences in growth rates  
85 depending on eel origin that were preserved after several months in common garden experiments.  
86 Pujolar et al. (2014), Gagnaire et al. (2012) and Ulrik et al. (2014) observed patterns in single-  
87 nucleotide polymorphisms correlated with environmental conditions. They assumed that individual  
88 genetic differences contribute to the emergence of phenotypic spatial patterns because of differential  
89 selection by the environment, but that these differences are reshuffled in each generation because of  
90 panmixia. In this context, Mateo et al. (in press) developed a new model, called GenEveel, that was  
91 able to mimic all observed patterns assuming the existence of genetic polymorphism in growth rate  
92 and adaptive phenotypic plasticity. It suggested that the genetic polymorphism and phenotypic  
93 plasticity may have been selected by natural selection as an adaptation to environmental  
94 heterogeneity and density dependence. In this context, selection of growth habitats, length-at-  
95 silvering and sex determination would be plastic traits that enable individuals to optimize their  
96 fitness in a wide range of environments.

97 This issue of adaptation to environmental variability is presently crucial because temperate eels  
98 have suffered dramatic collapses (Dekker, 2009; Dekker and Casselman, 2014; Jacoby et al., 2015),  
99 and *A. anguilla* is classified as critically endangered by the IUCN (Jacoby and Gollock, 2014a),  
100 while *A. rostrata* and *A. japonica* are classified as endangered (Jacoby et al., 2014; Jacoby and  
101 Gollock, 2014b). Several factors have been proposed to explain these declines (Jacoby et al., 2015),  
102 including changes in oceanic conditions (Castonguay et al., 1994), contamination and habitat  
103 degradation (Belpaire et al., 2016; Byer et al., 2015), parasitism (Feunteun, 2002; Kirk, 2003),  
104 fishing pressure (Dekker, 2003a), fragmentation including massive habitat loss (Kettle et al., 2011),  
105 and hydroelectricity-induced mortality (Castonguay et al., 1994). In view of this situation, the  
106 European Commission introduced European Regulation N° 1100/2007, imposing a new set of  
107 measures designed to reverse the decline. Since eel management is under the responsibility of  
108 member states, each member state was required to implement Eel Management Plans, enforcing  
109 management measures to decrease all sources of anthropogenic mortalities. Because of the  
110 heterogeneity in anthropogenic pressures, these measures are quite heterogeneous, targeting  
111 different types of pressures among countries and regions. The impact of anthropogenic pressures is  
112 indeed generally assessed by quantifying the induced mortality rates. Indeed, the European  
113 Regulation uses the biomass of escapees as a management target (the Regulation required that  
114 management measures should be implemented to ensure that silver eel escapement is at least 40%  
115 of the escapement in pristine conditions). However, in the presence of genetic polymorphism and  
116 phenotypic plasticity, anthropogenic pressures can have a wide range of effects in terms of life  
117 history traits. They can be a selective pressure advantaging fast or slow growers or have  
118 consequences in terms of the sex ratio, length-at-silvering or spatial distribution by affecting plastic  
119 traits.

120 In view of this, we decided to use GenEveel (Mateo et al., in press) to assess the impact of  
121 anthropogenic pressures on silver eel escapement, not only by quantifying the number of escapees,  
122 but also by assessing their effect on the sex ratio, the proportions of slow and fast growers, the  
123 length-at-silvering and the resulting egg production after a generation in continental waters exposed  
124 to different kinds of anthropogenic pressures. We chose to focus on four kinds of anthropogenic  
125 pressures: (i) the glass eel fishery, (ii) obstacles to upstream migration, (iii) turbine mortality during  
126 downstream migration, and (iv) the silver eel fishery. (i) Glass eel fishing is a widespread activity in  
127 France, the UK, Spain, Portugal and Italy (ICES, 2016), in some North American rivers (Cairns et  
128 al., 2008; Dutil et al., 2009; Jessop, 1998) and in Asian waters (Tatsukawa, 2003). In the Bay of  
129 Biscay, the glass eel fishery used to be the most important fishery in France in terms of turnover  
130 (Castelnaud, 2000), and the Bay of Biscay is assumed to receive the main part of the total

131 recruitment (Dekker, 2000). These fisheries harvest young, sexually undetermined individuals  
132 entering continental waters. In some river basins, the glass eel fishery can catch nearly all  
133 individuals entering the basins, such as in the Vilaine River, where the recruitment rate is less than  
134 5% some years (Briand et al., 2005). (ii) Fragmentation by human-induced obstacles can impact  
135 upstream migration (Drouineau et al., 2015; Tremblay et al., 2016). By blocking individuals during  
136 their upstream migration, they confine them into restricted parts of river basins (Kettle et al., 2011).  
137 (iii) During downstream migration, they can impair migration to the sea (Drouineau et al., 2017;  
138 Tremblay et al., 2016), especially because of mortality induced by passage through hydropower  
139 facilities (Pedersen et al., 2012; Winter et al., 2006). (iv) Finally, silver eel fishing is a widespread  
140 activity (Aalto et al., 2016; Amilhat et al., 2008; Bernotas et al., 2016; Verreault et al., 2012;  
141 Westerberg and Wickström, 2016) that targets large silvers when they migrate back to sea.

142 We adapted the GenEveel model and developed five output indicators (number of escapees,  
143 proportion of females, egg production, length-at-silvering, and proportion of slow growers) to  
144 consider the impact of anthropogenic pressures on population dynamics. We carried out a numerical  
145 exploration of the model and fitted statistical models to assess the effects of the anthropogenic  
146 pressures on the outputs. This enables us to quantify the impact of pressures on the different  
147 components and to discuss the implications.

## 148 2. Materials and methods

### 149 2.1. GenEveel

150 GenEveel is an individual-based model. It postulates that the population is composed of two  
151 types of individuals (slow and fast growing) based on a genetic polymorphism and that individuals  
152 determine their sex and select their growth habitat and length-at-silvering to optimize their fitness.  
153 Assuming that males follow a time-minimizing strategy, their fitness is assumed to be proportional  
154 to their survival rate until a constant length-at-silvering is reached. On the other hand, females are  
155 assumed to follow a size-maximizing strategy, and their fitness is constrained by a trade-off  
156 between fecundity at length-at-silvering and the survival rate to this length, with the length-at-  
157 silvering selected to optimize this trade-off. Growth is assumed to be a combination of intrinsic  
158 growth rates (slow and fast growers) modulated by environmental effects, with faster growth rates  
159 in downstream habitats. Survival is a product of environmental effects and density dependence.

160 The environment, a single river catchment, is represented by 30 contiguous cells (growth  
161 habitat) with prespecified effects on individual growth and mortality rates. One by one, individuals  
162 determine their sex and select their growth habitat and length-at-silvering based on the combination  
163 that maximizes fitness.

164 A complete description of the model can be found in Mateo et al. (in press). We parameterized  
165 the model as in the reference simulation in Mateo et al. (in press) for this study, which consisted of  
166 the best set of values found in the literature for the European eel. Seventeen parameters were used  
167 in the model to characterize the environment (as cells in the river catchment) and individuals  
168 (demographic, growth and fitness parameters).

### 169 2.2. Impacts of anthropogenic pressures

#### 170 2.2.1. Glass eel fishery

171 The glass eel fishery was characterized by the catch rate,  $g$ , i.e., the proportion of individuals  
172 caught by the fishery. The glass eel fishery was assumed to harvest individuals before sex  
173 determination and habitat selection. Consequently, if  $N$  eels entered the catchment, glass eel catches  
174 were assumed to follow a binomial distribution,  $\text{binomial}(N, g)$ , and the number of survivors was  
175 the complement.

#### 176 2.2.2. Obstacles to upstream migration

177 We used two obstacles (0.66 and 0.1, respectively, according to the relative distance along the  
178 river and referring to the 20<sup>th</sup> and 3<sup>th</sup> cells of the 30 that represent the river catchment) characterized

179 by their blockage rates ( $b_{0.66}$  and  $b_{0.1}$ , respectively) and locations ( $po_{0.66}$  and  $po_{0.1}$ , respectively,  
180 which represent cells of the catchments). For each individual, we restricted the possible  
181 combinations of growth habitat, length-at-silvering and sex to cells near the river mouth,  $po_{0.1}$ , with  
182 a probability  $b_{0.1}$  and to cells near the river source,  $po_{0.66}$ , with probability  $(1-b_{0.1}) \cdot (1-b_{0.66})$ .

### 183 2.2.3. Turbine mortality

184 The two obstacles also had turbine mortality rates ( $t_{0.66}$  and  $t_{0.1}$ , respectively). Each individual  
185 located upstream of the obstacle and that survived until length-at-silvering were killed by turbines,  
186 with a probability corresponding to the mortality rates.

### 187 2.2.4. Silver eel fishery

188 The silver eel fishery was assumed to affect eels in a similar way to the mortality due to  
189 turbines. We assumed that two successive silver eel fisheries occur, one located near the river source  
190 at position  $ps_{0.66}$  and one near the river mouth at position  $ps_{0.1}$ . These fisheries were characterized  
191 by catch rates of  $s_{0.66}$  and  $s_{0.1}$ , respectively. Each individual located upstream of the obstacle and  
192 that survived until length-at-silvering were caught by silver eel fisheries with a probability  
193 corresponding to the catch rates.

## 194 2.3. Model sequence

195 The glass eel fishery occurred first, as it is the first source of mortality encountered by young  
196 eels. Then, GenEveel was used to position individuals in the catchment with restrictions due to  
197 obstacles to determine their sex, length-at-silvering and survival probability to length-at-silvering.  
198 The survivors that reached maturity in the upper parts of the river migrated downstream and were  
199 impacted by the silver eel fishery and the turbine located near the river source. The remaining fish  
200 were then impacted by the silver eel fishery and the turbine located near the river mouth.

201 Fig. 1 represents the model sequence. A proportion,  $g$ , of recruits was first harvested by the glass  
202 eel fishery. Among the  $1-g$  individuals that escaped the glass eel fishery, a proportion,  $b_{0.1}$ , was  
203 constrained to settle downstream of the first obstacle, and only  $(1-b_{0.1}) \cdot (1-b_{0.66})$  were free to settle  
204 in the whole catchment. After sex determination and habitat selection (the combination that  
205 maximized the expected fitness), individuals underwent downstream migration and were harvested  
206 with a given probability if they passed a silver eel fishery or a turbine.

207 We computed five indicators based on the survivors (escapees):

- 208 1. number of escapees ( $N_s$ );
- 209 2. mean length-at-silvering ( $L_s$ );
- 210 3. proportion of females (sex ratio) ( $SR$ );
- 211 4. egg production (sum of female fecundity among survivors) ( $E$ ); and
- 212 5. proportion of slow growers ( $SI$ )

213 The first indicator is the traditional indicator for quantifying mortality and is generally used as a  
214 proxy of the spawning biomass, although not accounting for trait modifications. The next two  
215 indicators aim to measure the effect of anthropogenic pressures on two plastic traits. The fourth  
216 indicator quantifies the total effects of pressures on egg production and is a more direct proxy than  
217 the number of escapees because it combines both induced mortality and trait modifications. The last  
218 indicator is used to quantify the selective pressure induced by each anthropogenic pressure.

## 219 2.4. Numerical exploration of the model and results analysis

### 220 2.4.1. Experimental design

221 Our objective was to compare the intensity of effects of anthropogenic pressures rather than  
222 locations. Therefore, we chose a set of parameters that were similar among pressures. For locations,  
223 pressure positions were set at the same cells in the catchment:  $ps_{0.66}=po_{0.66}=20$  and  $ps_{0.1}=po_{0.1}=3$ . To  
224 explore the effect of pressure intensity, we used Latin hypercube sampling (LHS) (Iman and  
225 Conover, 1980; McKay, 1988; McKay et al., 2000). LHS is classical tool used to carry out global

226 sensitivity analysis of models (Blower and Dowlatabadi, 1994; Helton et al., 2005; Helton and  
227 Davis, 2003; Manache and Melching, 2004). It allows an efficient exploration of the input  
228 parameter space; estimation of output statistics, such as sensitivity indices; and variance  
229 decomposition. It subdivides each parameter into  $X$  intervals and then samples those intervals with  
230 probability  $1/X$  (random sampling within intervals), ensuring that each parameter interval is  
231 sampled only once and that two parameters are not sampled in the same interval in the same  
232 experiment. By doing this, LHS ensures a random association of parameter values and allows their  
233 respective effects to be disentangled.

234 In our LHS, the resulting design matrix is made up of all anthropogenic pressures ( $g$ ,  $b_{0.66}$ ,  $b_{0.1}$ ,  
235  $s_{0.66}$ ,  $s_{0.1}$ ,  $t_{0.66}$ ,  $t_{0.1}$ ) in columns, defined at an interval of 0 (no pressure) to 1 (impact all individuals).  
236 Intervals were then subdivided into 100 subintervals, corresponding to simulations in rows. We built  
237 100 independent LHSs to account for model stochasticity, resulting in 10,000 simulations.

#### 238 2.4.2. Results analysis

239 For each output  $Y$ , we fitted a generalized additive model on the 10,000 simulations using  $Y$  as a  
240 dependent variable and the anthropogenic pressures ( $g$ ,  $b_{0.66}$ ,  $b_{0.1}$ ,  $s_{0.66}$ ,  $s_{0.1}$ ,  $t_{0.66}$ ,  $t_{0.1}$ ) as explanatory  
241 variables:

$$242 \quad Y \sim s(g) + s(s_{0.1}) + s(s_{0.66}) + s(b_{0.1}) + s(b_{0.66}) + s(t_{0.1}) + s(t_{0.66})$$

243 with  $s()$  as a smoother function.

244 The Gaussian family was used for the number of escapees ( $Ns$ ), length-at-silvering ( $Ls$ ) and egg  
245 production ( $E$ ) (a log transformation was used for  $Ns$  and  $E$  to normalize the distribution), while the  
246 binomial family was used for the proportion of females ( $SR$ ) and slow growers ( $Sl$ ).

247 Generalized additive models (GAMs) were fitted using the package `mgcv` (Wood, 2011) in R (R  
248 Development Core Team, 2011). Plots of marginal effects were used to explore the relations  
249 between pressures and outputs. The signs of the regression coefficients indicated whether the  
250 pressure has a positive or negative impact on the indicator. The proportion of explained variance  
251 was used to compare the strength of the effects of anthropogenic pressures.

252 We computed the partial rank correlation coefficients (PRCC) (Saltelli et al., 2000) to assess the  
253 global effects of pressures on each output variable using the package `sensitivity` (Pujol et al., 2016).  
254 These coefficients assessed the degree of association between an output variable and a predictor  
255 after removing the effects of other predictors.

### 256 3. Results

257 The PRCC are summarized in Table 1. The glass eel fishery had the most important influence; it  
258 had negative effects on the number of escapees and positive effects on the length-at-silvering and  
259 the proportion of females. Its influence was more limited on egg production (negative effects) and  
260 the proportion of slow growers (positive effects). Regarding egg production, the silver eel fishery  
261 and turbine located near the river mouth had negative effects that were similar to that of the glass  
262 eel fishery. Unsurprisingly, they also had important negative effects on the proportion of slow  
263 growers, the mean length-at-silvering and the number of escapees. Obstacles located near the river  
264 mouth had a great influence on all indicators except egg production; they had negative effects on  
265 the length-at-silvering and the proportion of females and positive effects on the number of escapees  
266 and the proportion of slow growers. The turbine and silver eel fishery located near the river source  
267 had lesser influences on the model outputs than the rest of the pressures.

268 The GAM summaries are presented in Table A1. All pressures had a negative impact on the  
269 number of escapees ( $Ns$ ) except for obstacles located near the river mouth ( $b_{0.1}$ ), which had a  
270 positive impact (Table 1 - Fig. 2). Indeed, they blocked individuals in a zone with faster growth  
271 rates, decreasing the time to length-at-silvering and increasing the survival until escapement.  
272 Interestingly, the slope of the glass eel fishery effect was more moderate for small intensities than  
273 for strong intensities (Fig. 2). At low intensities, fisheries led to a decrease in density and therefore

274 to lower density-dependent mortality and a higher survival rate of the remaining individuals, which  
275 balanced the effect of the fishery.

276 Regarding the proportion of females (Fig. 2 - Table 1), the glass eel fishery had the greatest  
277 impact by removing individuals. It drastically decreased the density and consequently the density-  
278 dependent mortality, favoring females, especially at high intensity (Fig. 2). The patterns were less  
279 obvious for the other pressures, except for obstacles located near the river mouth ( $b_{0,1}$ ); after a given  
280 level, an increasing blockage rate increased the density in downstream habitats, increasing the  
281 density-dependent mortality and favoring males (Fig. 2).

282 The effects of other pressures (turbines and the silver eel fishery) was not due to density  
283 dependence, but rather the distribution of individuals in the river catchment; there was a female-  
284 biased sex ratio in the upstream habitat, and females were consequently more impacted by  
285 mortalities directed toward downstream migrants.

286 Regarding the length-at-silvering (Table 1 - Fig. 2), the results were very similar to the  
287 proportion of females since males have a constant and low length-at-silvering, while females have a  
288 variable and larger length-at-silvering. However, the effects of the silver eel fishery and the turbine  
289 located near the river mouth ( $s_{0,1}$  and  $t_{0,1}$ , respectively) were much more obvious.

290 Although obstacles located near the river mouth and the glass eel fishery ( $b_{0,1}$  and  $g$ ,  
291 respectively) were the pressures most impacting the three first indicators, the silver eel fishery and  
292 the turbine located near the river mouth ( $s_{0,1}$  and  $t_{0,1}$ , respectively) had similar influences on egg  
293 production, and they were more important than the glass eel fishery ( $g$ ) (Table 1). Indeed, the effect  
294 of  $g$  on the number of escapees was mitigated by the lower competition and the production of  
295 females in downstream zones of the catchment, explaining the flat effects observed for low  $g$  (Fig.  
296 2). For obstacles located near the river mouth ( $b_{0,1}$ ), the increase in the number of escapees  
297 explained an increase in egg production when blockage was low. However, for high blockage rates,  
298 the increase in escapees (Fig. 2) was outweighed by a higher proportion of males (Fig. 2), leading to  
299 a decrease in egg production (Fig. 2). For the silver eel fishery and the turbine located near the river  
300 mouth ( $s_{0,1}$  and  $t_{0,1}$ , respectively), their impacts on both the proportion of females and the number of  
301 escapees were negative, decreasing the effect on egg production.

302 Finally, the silver eel fishery and the turbine located near the river mouth decreased the  
303 proportion of slow growers because those individuals tended to settle in upstream habitats and were  
304 consequently more impacted than fast growers (Table 1 - Fig. 2). On the other hand, obstacles  
305 located near the river mouth tended to increase the proportion of slow growers; those individuals  
306 were blocked in downstream habitats where growth was faster, resulting in a better survival until  
307 length-at-silvering (as observed in the number of escapees ( $N_s$ ), Fig. 2). However, blocked  
308 individuals were “constrained” to remain in downstream habitats, resulting in a decrease in their  
309 fitness and to strong competition with fast growers. Interestingly, the glass eel fishery, which  
310 harvested slow and fast growers equally, tended to favor fast growers at low intensities and slow  
311 growers at high intensities (Fig. 2; at high intensities, the very low density-dependent mortality  
312 strongly benefited slow growers by removing fast growers, which were dominant competitors).

## 313 4. Discussion

### 314 4.1. Assessing the impact of anthropogenic pressures: why consider other indicators than only the 315 number of escapees?

316 The collapse in temperate eel populations required immediate actions (Dekker, 2009) to  
317 decrease all sources of anthropogenic pressures. This is the spirit of the European Regulation on the  
318 European eel and of subsequent eel management plans in European Union Member States.  
319 Logically, the first criteria used to assess the impact of anthropogenic pressures are mortality rates  
320 and escapement. However, given the large phenotypic variability observed at the distribution scale  
321 (Vélez-Espino and Koops, 2009), likely due to both phenotypic plasticity (Drouineau et al., 2014;  
322 Mateo et al., in press) and the consideration of genetic polymorphism (Côté et al., 2015), the



323 number of escapees may not be sufficient, and it is worthwhile to explore the effects of  
324 anthropogenic pressures on other components. Thus, the aim of this study was to use the GenEveel  
325 model to explore the effects of different types of anthropogenic pressures on the number of escapees  
326 as well as other indicators accounting for life history traits and genetic polymorphism.

#### 327 *4.2. Using a theoretical model to explore the possible consequences of anthropogenic pressures*

328 GenEveel is a theoretical model, but is parameterized with the best biological information  
329 available in the literature. Regarding the intensity, high levels have been observed for each type of  
330 pressure. For example, the exploitation rates of glass eels were found to be very high in some  
331 catchments: 13-30% in the Adour River (France) (Prouzet, 2002), 6.2-48.7% in the Oria River  
332 (Spain) (Aranburu et al., 2016), 30.8-51.8% in Nova Scotia (Jessop, 2000), 44.1-75% in Shang-Chi  
333 (Taiwan) (Tzeng, 1984) and even 78.1-99.7% in the Vilaine River (France) (Briand et al., 2005).  
334 The passability for upstream migration was estimated to range between 19.8 and 49.1% for an  
335 obstacle in the Canal des Etangs (France) (Drouineau et al., 2015). A similar result was obtained by  
336 Briand et al. (2005), who calculated an efficiency of the trapping ladder as 30% in the Vilaine  
337 catchment (France). Passability is probably even lower for obstacles not equipped with an eel  
338 ladder. Turbine impacts appear to vary considerably depending on study sites. On the Meuse River,  
339 Winter et al. (2007) estimated that the two hydropower plants induced an overall mortality of  
340 approximately 20-30%. In a Swedish river, Calles et al. (2010) found mortality rates of 40% and  
341 60% induced by two plants. At a Polish site, Dębowski et al. (2016) estimated a mortality rate of  
342 55%. Mortality due to silver eel fisheries also varies from 22-26% in the Meuse River (Netherlands)  
343 (Winter et al., 2006) to 82% mortality in the Gudena River and Randers Fjord (Denmark)  
344 (Aarestrup et al., 2008) and can reach even higher levels in some Mediterranean lagoons (Amilhat  
345 et al., 2008).

346 Given the large variability in the pressure intensities, and the fact that they vary at the  
347 distribution area scale, we used a Latin hypercube sampling design to carry out the global  
348 exploration of their effects in a theoretical catchment in GenEveel. Consequently, the exercise is  
349 clearly theoretical, and our raw results should not be used to classify the effects of anthropogenic  
350 pressures. However, they provide valuable insights on the type of effects induced by the different  
351 pressures and indicate that the significance of these effects greatly depends on the considered output  
352 indicator.

353 We did not consider the effects of yellow eel fisheries in this exercise for various reasons. First,  
354 the GenEveel model did not describe the growth phase precisely, so it is difficult to incorporate such  
355 mortalities. Moreover, most of the pressures occur in specific parts of the catchments (the estuary  
356 for glass eel fisheries, obstacles one after another) and at a specific times (migration), while yellow  
357 eel fisheries are more widespread and occur all along the growth phase, so comparisons of these  
358 pressures would be more uncertain.

#### 359 *4.3. The effect of anthropogenic pressures depends on their location within the catchment*

360 Among the most obvious results, the impacts of anthropogenic pressures clearly depend on their  
361 location in the river catchment, and pressures located in the very upper parts of the catchment,  
362 where densities are low, have limited impacts. Although this result is obvious, its consequence at the  
363 population scale is less obvious because anthropogenic activities are not uniformly distributed  
364 across the distribution area. For example, in Europe, some hydropower facilities can be found in  
365 downstream areas of river catchments, similar to in Scandinavia, while they are located upstream in  
366 France. Silver eel fisheries are mainly located in Scandinavia and the Mediterranean Sea (Dekker,  
367 2003b), while glass eel fisheries are dominant in France and Spain. Since life history patterns and  
368 differences in densities are also observed at the distribution area scale, it is very difficult to draw up  
369 an overall picture of the effect of each individual pressure at the population scale.

#### 370 *4.4. Effect of pressures on escapement: existence of compensatory mechanisms*

371 Another important message is that the number of escapees and the resulting egg production are  
372 not necessarily correlated. In our simulations, glass eel fisheries and migratory obstacles had the  
373 greatest influence on the number of escapees, the sex ratio and the length-at-silvering (although the  
374 effects were different depending on pressures). Nevertheless, the silver eel fishery and turbine  
375 mortality had similar negative impacts on egg production, which were greater than that of the glass  
376 eel fishery and were more significant than those of obstacles. This is explained by compensatory  
377 mechanisms that mitigate the negative effects of glass eel fisheries and obstacles to upstream  
378 migration, while there are no such mechanisms for those of silver eel fisheries and turbine mortality.  
379 For example, the decrease in escapement induced by the glass eel fishery can be compensated by  
380 the higher production of females. For obstacles to upstream migration, the decrease in female  
381 production is compensated by the better survival of individuals and consequently an increase in  
382 escapement. In other words, the pressure inducing the highest direct mortality does not necessarily  
383 have the greatest influence on silver eel escapement. Even pressures that do not induce any direct  
384 mortality, such as migratory obstacles, can influence some demographic attributes of escapees, such  
385 as the proportion of females or length-at-silvering. For example, obstacles close to the river mouth  
386 blocked individuals during their upstream migration in downstream habitats. As a consequence,  
387 slow growers that usually tend to settle in upstream habitats are forced to settle in downstream  
388 habitats with a faster growth rate and higher mortality due to competition. In these conditions, slow  
389 growers become males with a time-minimizing strategy, while they would have turned into females  
390 with a size-maximizing strategy in upstream habitats; this is why the proportion of females  
391 decreased. Since growth is fast in downstream habitats and those individuals mature very early (at  
392 male length-at-silvering), they have a higher survival rate until silvering than they would have  
393 known in upstream habitats, leading to an increase in the proportion of slow growers. However,  
394 they would have had higher fitness as a female in upstream habitats since the loss in survival would  
395 have been compensated by high fecundity.

396 Interestingly, by decreasing the number of individuals that enter the river catchment, a  
397 simulation with a glass eel fishery “mimics” a simulation with a depleted population. It is  
398 interesting to note that in such a situation, a decrease in competition enables individuals to settle in  
399 downstream habitats, where growth is faster. More females are also produced because of these  
400 lower densities. As a result, egg production is less impacted than the number of escapees. As such,  
401 the phenotypic plasticity of eels can be considered as a resilience factor in a depleted population.

#### 402 *4.5. Anthropogenic pressures as selective pressures*

403 The final output of the model is the impact of anthropogenic pressures on slow and fast growers.  
404 Most pressures, except for the glass eel fishery, tend to favor fast growers over slow growers, and as  
405 such, anthropogenic pressures can be selective pressures. The selective pressure induced by  
406 obstacles on elver migration has already been observed at the gene expression level (Podgorniak et  
407 al., 2015a, 2015b, 2016). If most anthropogenic activities act as several pressures favoring fast  
408 growers, we can wonder how slow growers were preserved by natural selection. A possible  
409 explanation may be due to gender differences. Males are predominantly fast growers, while females  
410 are both slow and fast growers (Côté et al., 2015; Mateo et al., in press), but slow-growing females  
411 have a larger length-at-silvering and greater fecundity than fast-growing females (Mateo et al., in  
412 press). In a high-abundance context, we can assume that males are fast growers, females are  
413 predominantly slow growers, and the two types are necessary. In a collapsed population,  
414 anthropogenic pressures tend to favor males and fast growers (Table 1), and egg production can  
415 become limiting. Consequently, the few remaining slow-growing females (which are less impacted  
416 by competition and can settle in downstream habitats) can become even more important, explaining  
417 their preservation to some extent. To validate this assumption, it would be interesting to carry out a  
418 similar simulation exercise at the population scale and with multiple generations to explore the  
419 impacts of anthropogenic pressures on the two types of individuals. Moreover, this would allow us

420 to explore the assumption of spatially varying selection proposed by Gagnaire et al. (2012) and Côté  
421 et al. (2014) by simulating the arrival of slow and fast growers in random and contrasting river  
422 catchments, where they would suffer different mortalities and would consequently be more or less  
423 adapted.

424 Selective pressure due to fishing activities on exploited marine stocks has been demonstrated for  
425 many fish stocks (Law, 2000; Pinsky and Palumbi, 2014). A major collapse in abundance is required  
426 to reduce the overall genetic diversity. Since current recruitment is now less than 5% of historical  
427 recruitment and, for the American eel, recruitment has ceased in Lake Ontario and Upper Saint-  
428 Lawrence (Casselman, 2003), a loss of genetic diversity is not impossible This question of diversity  
429 at the individual level is crucial for eel conservation since it may contribute to population resilience  
430 through a storage and portfolio effect (Secor, 2015).

431 The misunderstanding of the effects of anthropogenic pressures also means that we poorly  
432 understand the effects of some mitigating measures. Stocking programs have been widely used  
433 (Couillard et al., 2014) and are still widely used by European countries (Brämick et al., 2016; Josset  
434 et al., 2016; Simon et al., 2013). However, by modifying densities and moving slow or fast growers  
435 into habitats where they are not adapted, such measures can have unexpected effects on escapement.  
436 Such observations were made in Canada, where eels were stocked in the Great Lakes, and the  
437 escapees produced were more similar to escapees from their original sites than to native silver eels  
438 from the Great Lakes (Couillard et al., 2014; Stacey et al., 2015). Exploring this issue with  
439 GenEeel by artificially “moving” individuals after their sex and growth habitat have been  
440 determined will bring new insights into the ways stocking programs can affect the whole  
441 population.

#### 442 4.6. Conclusion

443 Our theoretical exercise provided new insights on the impact of anthropogenic pressures, both direct  
444 and indirect. Since this simulation exercise is purely theoretical and because of the spatial  
445 heterogeneity in both anthropogenic pressures and eel life history traits, it is impossible to promote  
446 any specific management measures, which should be chosen according to the local conditions.  
447 However, our results imply that managers and scientists should not only assess the quantity of  
448 escapees but also their quality. Quantifying human-induced mortalities and the effects of  
449 anthropogenic pressures on the number of escapees is a main priority, given the dramatic situation  
450 of the three temperate eel populations. However, further research to investigate the possible impacts  
451 of anthropogenic pressures on phenotypic changes in life history traits and consequently the  
452 reproductive output of the spawning stock will be required to achieve sustainable management of  
453 the species.

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458

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709 **Tables**

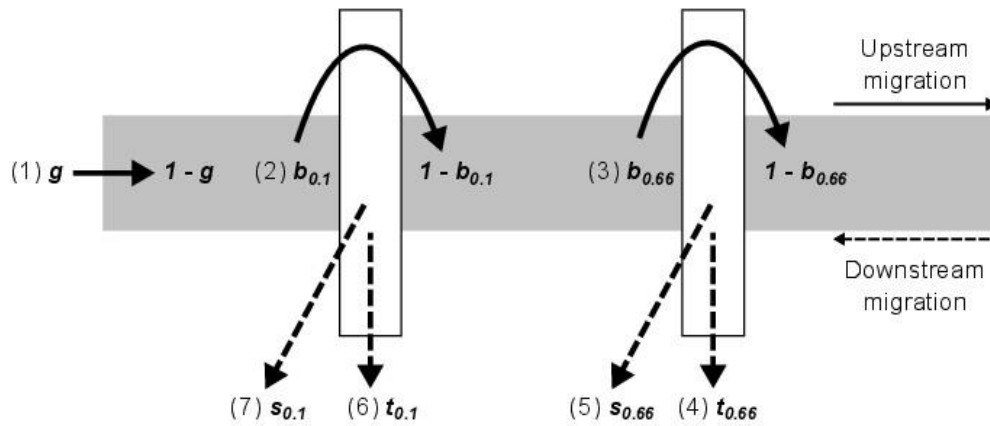
710 **Table 1.** Partial rank correlation coefficients between output variables (columns) and pressures (rows). A  
711 positive coefficient indicates a positive correlation. *g*: glass eel fishery, *s<sub>0.66</sub>*: silver eel fishery located near  
712 the river source, *s<sub>0.1</sub>*: silver eel fishery located near the river mouth, *t<sub>0.66</sub>*: turbine located near the river source,  
713 *t<sub>0.1</sub>*: turbine located near the river mouth, *b<sub>0.66</sub>*: obstacle to upstream migration, *b<sub>0.1</sub>*: obstacle to downstream  
714 migration.

	<i>Ns</i>	<i>Ls</i>	<i>SR</i>	<i>E</i>	<i>SI</i>
<i>g</i>	-0.95	0.94	0.95	-0.49	0.22
<i>b<sub>0.1</sub></i>	0.77	-0.75	-0.57	-0.01	0.88
<i>b<sub>0.66</sub></i>	0.02	0	0.01	0.01	0.02
<i>s<sub>0.1</sub></i>	-0.39	-0.33	-0.14	-0.42	-0.35
<i>s<sub>0.66</sub></i>	-0.02	0	0.01	-0.01	-0.03
<i>t<sub>0.1</sub></i>	-0.39	-0.33	-0.12	-0.4	-0.35
<i>t<sub>0.66</sub></i>	-0.01	-0.02	-0.01	-0.01	-0.01

715

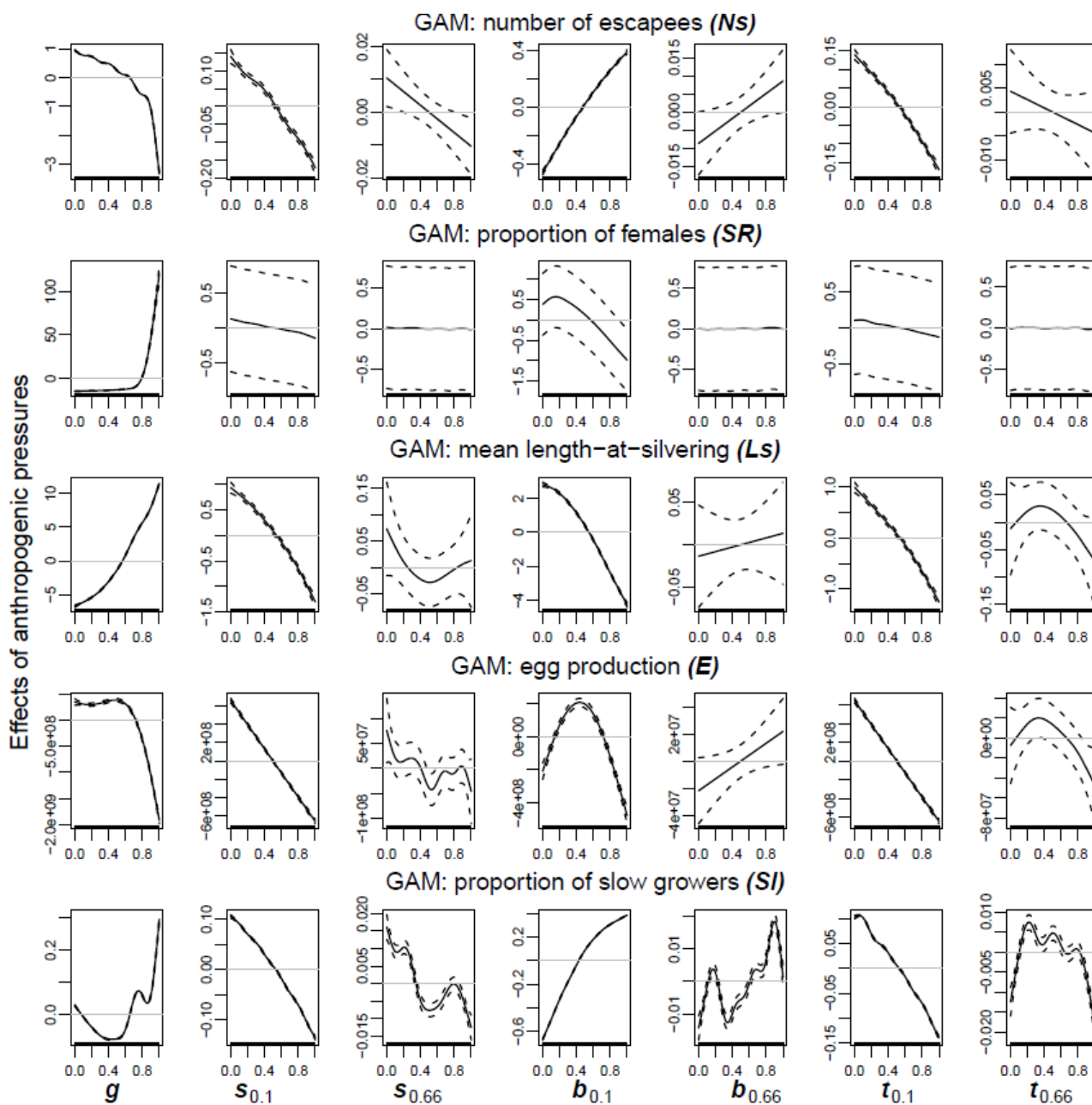
716

717 **Figures**



718

719 **Figure 1.** Conceptual representation of the catchment, indicating the seven anthropogenic pressures  
720 considered in the study: 1)  $g$ : catch rate by the glass eel fishery, 2)  $b_{0.66}$  and 3)  $b_{0.1}$ : blockage rates (located  
721 near the river source and the river mouth, respectively), 4)  $t_{0.66}$  and 6)  $t_{0.1}$ : turbine mortality rates (located  
722 near the river source and the river mouth, respectively), 5)  $s_{0.66}$  and 7)  $s_{0.1}$ : catch rates by the silver eel  
723 fisheries (located near the river source and the river mouth, respectively).  
724



725

726 **Figure 2.** Effects of the pressures on the five indicators estimated by the GAMs.  $g$ : glass eel fishery,  $s_{0.66}$  and  
 727  $s_{0.1}$ : silver eel fisheries located near the river source and the river mouth, respectively,  $t_{0.66}$  and  $t_{0.1}$ : turbines  
 728 located near the river source and the river mouth, respectively,  $b_{0.66}$  and  $b_{0.1}$ : obstacles located near the river  
 729 source and the river mouth, respectively.

730

731 **Supplementary data**

732 **Table A1.** Summary of the GAM model. edf corresponds to the estimated degrees of freedom for each model  
 733 parameter. F corresponds to the Fisher statistics when the Gaussian family is used and Chis.sq to the  $\chi^2$   
 734 statistics when the binomial family is used. P-values are not presented (although all are smaller than 0.05)  
 735 because significance tests are not recommended when analyzing simulation model results (White et al.,  
 736 2014).

	<i>Ns</i>		<i>Ls</i>		<i>SR</i>		<i>E</i>		<i>Sl</i>	
	edf	F	edf	F	edf	Chi.sq	edf	F	edf	Chi.sq
<i>s(g)</i>	9	18517.8	8.6	14036.4	9.0	3849436.9	6.6	1257.1	9.0	23175.6
<i>s(s<sub>0.1</sub>)</i>	5.0	266.2	3.3	451.8	8.8	56266.4	1.0	3906.1	8.7	52527.1
<i>s(s<sub>0.66</sub>)</i>	1.0	7.7	2.2	1.6	8.8	485.7	6.8	2.1	8.1	592.6
<i>s(b<sub>0.1</sub>)</i>	3.4	3066.9	5.2	3311.3	9.0	2598861.4	4.0	194.8	8.7	1001753.5
<i>s(b<sub>0.66</sub>)</i>	1.0	5.3	1.0	0.3	8.7	515.9	1.0	4.3	8.9	783.7
<i>s(t<sub>0.1</sub>)</i>	2.5	545.4	2.9	497.5	8.9	56169.5	1.0	3727.6	8.9	54605.7
<i>s(t<sub>0.66</sub>)</i>	1.0	1.3	2.0	2.0	8.9	541.1	2.5	3.3	8.0	357.9

737