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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

3 Maria Mateo¹, Patrick Lambert¹, Stéphane Tétard², and Hilaire Drouineau¹

4
5 ¹ Irstea, UR EABX Ecosystèmes aquatiques et changements globaux, HYNES Irstea-EDF R&D, 50
6 avenue de Verdun, 33612 Cestas, France

7 ² EDF R&D, HYNES Irstea-EDF R&D, Laboratoire National d'Hydraulique et Environnement
8 quai Watier, 78401 Chatou, France

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

28 Corresponding author: Maria Mateo

29 Phone number: +33 (0)5 57 89 09 98

30 Email: maria.mateo@irstea.fr

1. Introduction

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

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

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

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

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

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

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

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

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

2. Materials and methods

2.1. GenEveel

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

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

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

2.2. Impacts of anthropogenic pressures

2.2.1. Glass eel fishery

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

2.2.2. Obstacles to upstream migration

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

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

2.2.3. Turbine mortality

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

2.2.4. Silver eel fishery

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

2.3. Model sequence

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

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

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

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

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

2.4. Numerical exploration of the model and results analysis

2.4.1. Experimental design

Our objective was to compare the intensity of effects of anthropogenic pressures rather than locations. Therefore, we chose a set of parameters that were similar among pressures. For locations, 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 explore the effect of pressure intensity, we used Latin hypercube sampling (LHS) (Iman and Conover, 1980; McKay, 1988; McKay et al., 2000). LHS is classical tool used to carry out global

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

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

2.4.2. Results analysis

For each output Y , we fitted a generalized additive model on the 10,000 simulations using Y as a 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 variables:

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

with $s()$ as a smoother function.

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

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

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

3. Results

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

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

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

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

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

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

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

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

4. Discussion

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

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

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

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

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

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

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

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

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

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

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

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

4.5. Anthropogenic pressures as selective pressures

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

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

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

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

4.6. Conclusion

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

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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_{0.66}*: silver eel fishery located near
712 the river source, *s_{0.1}*: silver eel fishery located near the river mouth, *t_{0.66}*: turbine located near the river source,
713 *t_{0.1}*: turbine located near the river mouth, *b_{0.66}*: obstacle to upstream migration, *b_{0.1}*: 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_{0.1}</i>	0.77	-0.75	-0.57	-0.01	0.88
<i>b_{0.66}</i>	0.02	0	0.01	0.01	0.02
<i>s_{0.1}</i>	-0.39	-0.33	-0.14	-0.42	-0.35
<i>s_{0.66}</i>	-0.02	0	0.01	-0.01	-0.03
<i>t_{0.1}</i>	-0.39	-0.33	-0.12	-0.4	-0.35
<i>t_{0.66}</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

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

Supplementary data

Table A1. Summary of the GAM model. edf corresponds to the estimated degrees of freedom for each model parameter. F corresponds to the Fisher statistics when the Gaussian family is used and Chis.sq to the χ^2 statistics when the binomial family is used. P-values are not presented (although all are smaller than 0.05) because significance tests are not recommended when analyzing simulation model results (White et al., 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_{0.1})</i>	5.0	266.2	3.3	451.8	8.8	56266.4	1.0	3906.1	8.7	52527.1
<i>s(s_{0.66})</i>	1.0	7.7	2.2	1.6	8.8	485.7	6.8	2.1	8.1	592.6
<i>s(b_{0.1})</i>	3.4	3066.9	5.2	3311.3	9.0	2598861.4	4.0	194.8	8.7	1001753.5
<i>s(b_{0.66})</i>	1.0	5.3	1.0	0.3	8.7	515.9	1.0	4.3	8.9	783.7
<i>s(t_{0.1})</i>	2.5	545.4	2.9	497.5	8.9	56169.5	1.0	3727.6	8.9	54605.7
<i>s(t_{0.66})</i>	1.0	1.3	2.0	2.0	8.9	541.1	2.5	3.3	8.0	357.9