



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



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ABSTRACT

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

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

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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-

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