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Freshwater eels: A symbol of the effects of global change

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Abstract

Temperate eels *Anguilla anguilla* (European eel), *A. rostrata* (American eel) and *A. japonica* (Japanese eel) are three catadromous species which have been declining since the 1970s/1980s despite their remarkable adaptive capacity. Because of their specific life cycles, which share distant oceanic spawning grounds and continental growth stage, eels are affected by five components of the global change: (a) climate change affecting larval survival and drift, (b) an increase in pollution leading to high levels of contamination exacerbated by their high lipid levels, (c) increasing fragmentation and habitat loss that reduce dramatically the amount of available habitats and induce increased spawner mortality, (d) the appearance of *Anguillicola crassus* a parasitic alien nematode that impairs spawning success, and (e) the impact of commercial and recreational fisheries for all life stages of eel. In this context, the rapid increases of pressures during the "Great Acceleration" have surpassed the adaptive capacity of eels. This illustrates that cumulative effects of global change can lead to the collapse of species, even in species that have amazingly high adaptive capacities.

KEYWORDS
adaptation, *Anguilla* spp., climate change, contamination, ecosystem fragmentation, overexploitation

1 | INTRODUCTION

1.1 | Global change: Five components that threaten biodiversity

In 2005, the Millennium Ecosystem Assessment (2005a) pointed out that, despite an increase in human welfare during the twentieth century, anthropogenic actions threaten the ability of ecosystems to sustainably provide important goods and services, especially for future generations. Such human-caused environmental changes are generally referred to as global change (Steffen et al., 2005). In this paper, we illustrate how the rate at which global change is happening can endanger even highly adaptive species such as temperate eels *Anguilla anguilla* (European eel), *A. rostrata* (American eel) and *A. japonica* (Japanese eel). In a more specific manner, this example illustrates that cumulative effects of the different components of global change (Jacoby et al., 2015; Miller, Feunteun, & Tsukamoto, 2016; Tylianakis, Didham, Bascompte, & Wardle, 2008; Vitousek, D'antonio, Loope, Rejmanek, & Westbrooks, 1997; Western, 2001) can produce rates of change that exceed a species' adaptive capacity, a central question in the debate on the effects of climate and global change (Donner, Skirving, Little, Oppenheimer, & Hoegh-Guldberg, 2005; Visser, 2008).

Soulé (1991) proposed a list of the main threats to biodiversity that include six components: habitat loss, habitat fragmentation, overexploitation, exotic species, pollution and climate change. Later, the United States National Research Council (2000) proposed a very similar list of ongoing changes: (a) climate, (b) land use and land cover modifications that can result in habitat loss and fragmentation, (c) biogeochemical and hydrological cycles and pollution, (d) biotic mixing including biological invasions, and (e) overexploitation of natural resources especially in oceanic ecosystems. The main difference with Soulé's proposal is that habitat loss and habitat fragmentation were merged into a single component. This latter listing was then endorsed by many authors, including IPCC (2001), the Millennium Ecosystem Assessment (2005b), Simberloff (2012) and Pe'er et al. (2013), although Pe'er et al. (2013) did not mention pollution. The IGPB (Steffen et al., 2005; executive summary) and the Global Change Program of the Royal Society of Canada (1992) provided more detailed lists of components of global change (IGBP: oil harvest, transformation of land surface, nitrogen waste, use of freshwater, greenhouse gas, marine habitat destruction, overexploitation of fisheries, extinction rates of species—GCPRSC: climate change, energy and resource consumption, air and water pollution, ozone depletion, population increase, extinction events, land and soil degradation). These components can be merged into the five more general components from IPCC (except perhaps "population increase" which can be shared by various components).

Among these components of global change, the best documented is global warming, which is due to increased greenhouse gas emission by human activities (IPCC, 2015), affecting the biosphere at all scales (Gattuso et al., 2015). Global warming already has visible impacts on the ecology of living organisms (Hughes, 2000; Walther et al., 2002) with impacts on their phenology (Chevillot et al., 2017; Menzel et al., 2006) and modification of distribution areas (Cheung et al., 2010; Lassalle, Crouzet, & Rochard, 2009; Nicolas et al., 2011; Rougier et al., 2015). Global warming alters biogeochemical cycles such as the water cycle. For example, the seasonality of river discharge (amplitude between low and high discharge) is expected to increase, while average discharges will increase in some regions and decrease in others (Nohara, Kitoh, Hosaka, & Oki, 2006; van Vliet et al., 2013).

The second component is increasing nutrient, contaminant and pesticide loads in the ecosystem due to industries, agriculture and urbanization (Verhoeven, Arheimer, Yin, & Hefting, 2006). These increased loads destabilize nutrient cycles and can have direct consequences, such as eutrophication (Rabalais, Turner, Díaz, & Justić, 2009; Tilman et al., 2001). At the individual scale, contaminants and pesticides can have a large range of deleterious effects, such as altered metabolism, immunotoxicity, endocrine disruption or neurotoxicity (ICES, 2016; Köhler & Triebskorn, 2013). Moreover, many contaminants are ecologically harmful because persistent biomagnifying chemicals can accumulate in food webs at high trophic levels (Köhler & Triebskorn, 2013; Van Oostdam et al., 2005).

Another component is the modification of habitats due to anthropogenic land use, which can lead to fragmentation of aquatic and terrestrial ecosystems or even habitat loss (Brook, Sodhi, & Bradshaw, 2008; Collinge, 1996; Fischer & Lindenmayer, 2007). Habitat loss and ecosystem fragmentation are currently considered major threats to biodiversity and represent one of the major challenges in ecosystem conservation and restoration (Sutherland et al., 2013; Tilman, May, Lehman, & Nowak, 1994; Tischendorf & Fahrig, 2000a, 2000b), by impairing the ability of individuals to migrate to essential habitats (Gros & Prouzet, 2014), by isolating populations and reducing gene flow (Haxton & Cano, 2016; Horreo et al., 2011), and by modifying species community structure (Perkin & Gido, 2012). Fragmentation and habitat loss increase the risk of extinction cascades (Fischer & Lindenmayer, 2007; Haddad et al., 2015; Junge, Museth, Hindar, Kraabøl, & Vøllestad, 2014; Krauss et al., 2010; van Leeuwen, Museth, Sandlund, Qvenild, & Vøllestad, 2016; Terborgh et al., 2001).

Biological invasion by alien species is our fourth component of global change (Occhipinti-Ambrogi & Savini, 2003; Ricciardi, 2007; Vitousek et al., 1997). Invasive species can affect native ones directly through predation, competition or parasitism, or indirectly by habitat modification or by spreading diseases (Lymbery, Morine, Kanani, Beatty, & Morgan, 2014). Arrival of alien species due to shifts in their distribution in response to climate change, uniformization of habitat or transport by humans can profoundly reshape species interactions and has consequences at the species, community and ecosystem levels but also on the provision of ecosystem services (Alpine & Cloern, 1992; Cloern, 1996; Grosholz, 2002; Vilà et al., 2010). Now, there are about 10,000 alien species registered in Europe, while ecological impacts have been documented for 11% of them and economic impacts for 13% (Vilà et al., 2010).

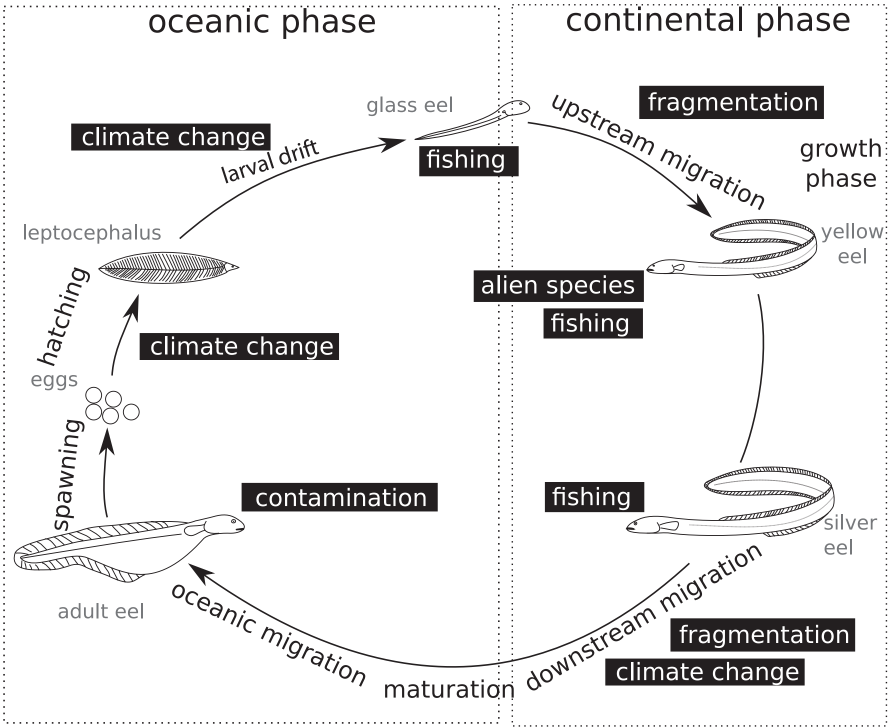

FIGURE 1 Life cycle of the three *Anguilla* species and effects of global change components

At last, the last component is the overexploitation of natural resources (Brook et al., 2008). For example, fisheries have had major impacts on marine ecosystems, depleting stocks with potential impacts on fishing food webs, and impacts on habitats because of destructive fishing gear (Branch, 2015; Christensen et al., 2003; Drouineau, Lobry, et al., 2016; Gascuel et al., 2011; Turner, Thrush, Hewitt, Cummings, & Funnell, 1999). Fisheries have also shaped the life histories of exploited fishes by acting as a permanent and continuous selection pressure (Heino, Pauli, & Dieckmann, 2015; Jørgensen & Renöfält, 2013).

Through the combined impacts of these five components, global change leads to an extremely rapid modification of ecosystems. Species can display different kinds of adaptive response to address this threat, such as local adaptation through (a) a micro-evolutionary response, (b) phenotypic plasticity (Charmantier et al., 2008) or (c) modification of their distribution area (Hughes, 2000). However, adaptation is not always possible, especially in cases of synergies among components which can lead to rates of change outpacing a species adaptive capacity (Brook et al., 2008). In this context, global change threatens extinction for many species (Brook et al., 2008; Cahill et al., 2013; Spurgeon, 2000; Steffen et al., 2005; Thomas et al., 2004; Urban, 2015). The collapse of the three temperate anguillid eel populations is an excellent illustration of this phenomenon.

1.2 | Temperate eels: Endangered species impacted by diverse anthropogenic pressures

European eel, American eel and Japanese eel are three temperate catadromous species that share many remarkable ecological features (Figure 1). They have a large distribution area in continental waters

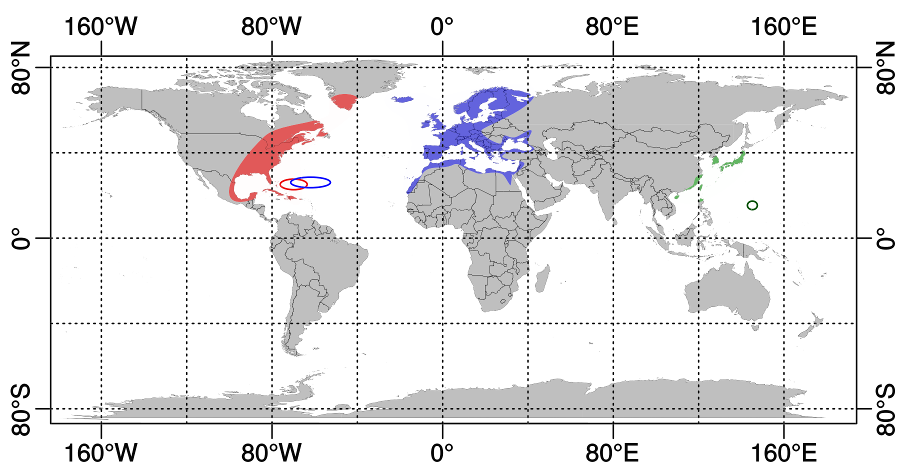

FIGURE 2 Spawning grounds (Miller et al., 2015; Tsukamoto et al., 2011) (open circles) and continental distribution of yellow eels (filled shapes) (Jacoby et al., 2015) for American (red), European (blue) and Japanese (green) eels

(Figure 2; Tesch, 2003), from Canada to Venezuela for American eel (Helfman, Facey, Stanton Hales, & Bozeman, 1987), from Northern Philippines to Korea for Japanese eel (Tsukamoto, which are reached after a long larval drift (larvae are called leptocephali) from distant marine spawning grounds (McCleave, 1993; Schmidt, 1923) and west of Mariana Islands for Japanese eel (Tsukamoto, 1992)). After this migration, the larvae metamorphose into glass eels upon reaching the continental shelf (Tesch, 2003). They subsequently penetrate continental waters, turning into pigmented yellow eels, where they colonize a large range of continental habitats from brackish to freshwater (Arai & Chino, 2012; Daverat et al., 2006). After a growth phase lasting from 3 to over 30 years, yellow eels metamorphose into silver eels and migrate back to their spawning grounds (Béguer-Pon, Castonguay, Shan, Benchetrit, & Dodson, 2015; Chang, Miyazawa, & Béguer-Pon, 2016; Righton et al., 2016). The eels mature en route and presumably die following spawning.

Eels have successfully adapted to very heterogeneous growth environments at both the distribution area and catchment scale. Eels are panmictic (Als et al., 2011; Côté et al., 2013; Han, Hung, Liao, & Tzeng, 2010; Pujolar, 2013), and their long larval drift limits the possibility of local genetic adaptation. However, there are correlations between environmental gradients and spatial patterns in life history traits throughout the distribution area and within river catchments (Drouineau, Rigaud, Daverat, & Lambert, 2014; Vélez-Espino & Koops, 2009; Yokouchi et al., 2014). For example, sex ratio is generally female-biased in the northern parts of distribution areas (Helfman, Bozeman, & Brothers, 1984; Vladykov, 1966; Vøllestad, 1992; Vøllestad & Jonsson, 1988) and in upstream parts of river catchments (Oliveira & McCleave, 2000; Tesch, 2003). Length-at-silvering (onset of sexual maturation) varies between sexes and habitats. Males follow a time-minimizing strategy, leaving continental waters as soon as they reach the minimal length to achieve the spawning migration, while females follow a size-maximizing strategy, adapting their length-at-silvering to local growth and mortality conditions finding a trade-off between survival and fecundity (Helfman et al., 1987; Vøllestad, 1992). Therefore, male length-at-silvering is rather set (Oliveira, 1999; Vøllestad, 1992), while females exhibit a wider range of sizes and are often larger in the northern parts of the distribution areas (Davey & Jellyman, 2005; Helfman et al., 1987; Jessop, 2010). These patterns of life history traits are thought to be the result of adaptive phenotypic plasticity that allows individuals to adapt their life history traits to a wide range of environmental conditions (Côté, Castonguay, McWilliam, Gordon, & Bernatchez, 2014; Drouineau et al., 2014; Mateo, Lambert, Tétard, Castonguay, et al., 2017) but also of genetic polymorphism leading to spatially varying selection and/or genetically based habitat selection producing genetically distinct ecotypes (Côté et al., 2014; Gagnaire, Normandeau, Côté, Hansen, & Bernatchez, 2012; Mateo, Lambert, Tétard, Castonguay, et al., 2017; Pavey et al., 2015; Ulrik et al., 2014).

In addition to having similar life histories, the three anguillid species underwent a dramatic decline which started in the late 1970s (Dekker & Casselman, 2014; Dekker et al., 2003). The collapse became evident through the analyses of the recruitment indices of the three species (Figure 3). Recruitment series of glass eels are the most reliable indices to estimate trends in eel populations throughout their range, because they are less influenced by local conditions than indices using older stages. In Europe, recruitment has decreased by 90%–99% since the 1980s (ICES, 2015). Concerning the American eel, the recruitment in the upper Saint Lawrence River and Lake Ontario has nearly ceased in one of the most productive areas (Casselman, 2003) and commercial silver eel CPUE dropped by at least 50% in 40 years in the Saint Lawrence River (de Lafontaine, Gagnon, & Côté, 2009). Recruitment of Japanese eel has followed a very similar decline, corresponding to 80% in the last decades (Dekker et al., 2003; Tanaka, 2014). As a result, IUCN classified European eel as critically endangered in 2008 (confirmed in 2010 and 2014) (Jacoby & Gollock, 2014a) while American and Japanese eels have been classified as endangered since 2014 (Jacoby, Casselman, DeLucia, Hammerson, & Gollock, 2014; Jacoby & Gollock, 2014b). Meanwhile, conservation regulations have flourished for the three species (Figure 4). The European Commission implemented a regulation in 2007 (Council Regulation [EC] No 1100/2007) establishing measures for the recovery of the stock of European eel and calling for a reduction in anthropogenic mortalities. The North American eel is "endangered" since 2008 as under Ontario's Endangered Species Act, which prohibits their fishing and trading. The Canadian

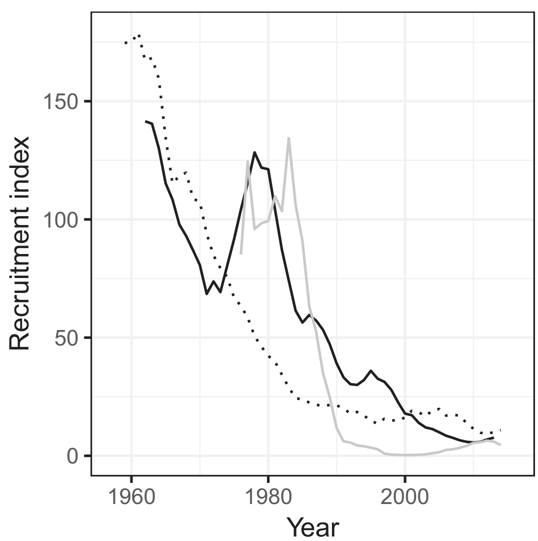

FIGURE 3 Recruitment series for the three temperate eel species. European eel series (black solid line) corresponds to the Elsewhere Europe index provided by ICES (2015). American eel recruitment (grey solid line) corresponds to the recruitment in Lake Ontario through monitoring of eel passage at Moses Saunders hydroelectric dam (A. Mathers, Ontario Ministry of Natural Resources, personal communication). Japanese eel recruitment (black dotted line) corresponds to Japanese catch statistics (data may include young yellow eels larger than glass eels during 1957–1977—provided by Statistics Department, Ministry of Agriculture, Forestry and Fisheries, Japan, till 2002 and from Fisheries Agency, Japan since 2003). Data were smoothed using a 5-year moving geometric mean and expressed as a percentage of the 1960s–1970s geometric mean

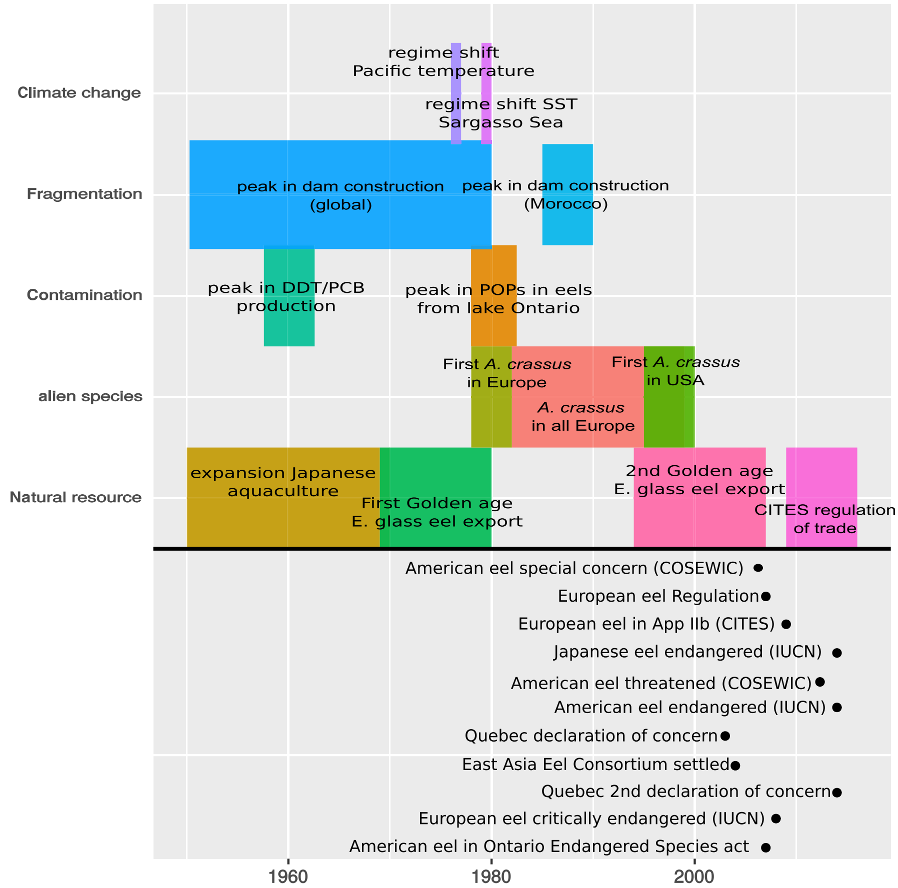

FIGURE 4 Timelines of main events with respect to the five global change components and management of eel populations. Committee on the Status of Endangered Wildlife in Canada (COSEWIC) is a committee of experts that assesses and designates which wildlife species are in some danger of disappearing from Canada [Colour figure can be viewed at wileyonlinelibrary.com]

federal Government is currently considering whether the American eel should be listed as "Threatened" under the federal Species at Risk Act. The Japanese eel is "endangered" on the Japanese Red List published by the Ministry of Environment, Japan in 2013.

The eel population declines possibly result from oceanic changes (Castonguay, Hodson, Moriarty, Drinkwater, & Jessop, 1994), overfishing (Dekker, 2003c; Haro et al., 2000; Tsukamoto, Aoyama, & Miller, 2003), contamination (Belpaire, Geeraerts, Evans, Ciccotti, & Poole, 2011; Belpaire, Pujolar, Geeraerts, & Maes, 2016), parasitism (Feunteun, 2002; Kirk, 2003) and blockage due to dams (Kettle, Asbjørn Vøllestad, & Wibig, 2011; Moriarty & Dekker, 1997). These suspected causes match the above-mentioned components of global change: oceanic modifications resulting from global warming, overfishing corresponds to overharvesting of natural resources, the eel swimbladder parasite is an alien species, blockage due to dams is an example of habitat loss due to land use, and contamination is the direct result of the increased pollutant load. The respective effects of anthropogenic pressures are difficult to disentangle and probably acted synergistically in the declines of eel populations (Jacoby et al., 2015; Miller et al., 2016). Here, we focus on the timelines of events and on the spatial dimension to show how some anthropogenic pressures have had a greater impact on certain habitats (and consequently eels in these habitats) than others. At last, we discuss why the overall decline may be interpreted as the result of the combined effect of the global change components and how the cumulative pressures have had a more drastic impact, than 50 million years of evolution, by radically reducing adaptive capacities of eels. Even though there are growing concerns about the situation of tropical eels and many similarities with temperate eels (Jacoby et al., 2015), we restricted our analysis to temperate eels of the genus *Anguilla* because they are in the worst situation according to IUCN criteria, and are the three most commercially important species (Jacoby et al., 2015).

2 | COMPONENT 1—GLOBAL WARMING AND OCEAN MODIFICATION: IMPACTS ON EEL MIGRATIONS

2.1 | Effect on leptocephalus drift and survival

The decline in eel populations is possibly linked to modifications of physical conditions in the oceans (Bonhommeau, Chassot, Planque, et al., 2008; Castonguay, Hodson, Moriarty, et al., 1994; Knights, White, & Naismith, 1996; Miller et al., 2009, 2016). The synchronous declines of the three eel species may indicate the involvement of large-scale drivers, such as changes in oceanic conditions that affect hatching and subsequent survival of larvae (Bonhommeau, Chassot, Planque, et al., 2008; Castonguay, Hodson, Moriarty, et al., 1994). Global warming has had a measurable impact on sea surface temperatures (Figure 5) and on different oceanic features (North Atlantic Oscillation, El Niño Southern Oscillation and North Equatorial Current) influencing recruitment success of temperate eels. Global

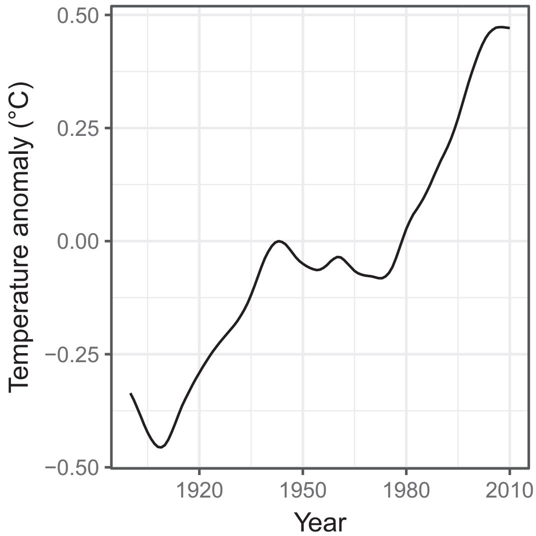

FIGURE 5 Ocean temperature anomalies (left panel). Source (Morice, Kennedy, Rayner, & Jones, 2012; Steffen et al., 2015)

warming has also had visible impacts on planktonic communities: important shifts in the diversity, abundance and spatial distribution of planktonic species in the Atlantic Ocean, where plankton is crucial for eel larval growth and survival (Beaugrand, 2004; Beaugrand, Luczak, & Edwards, 2009; Goberville, Beaugrand, & Edwards, 2014).

Indeed, there are correlations between glass eel recruitment and different oceanic indicators, such as the North Oscillation Index (NAO) and sea surface temperatures (Table 1). Because most studies computed statistical correlations, the underlying mechanisms are speculative. Three main mechanisms have been proposed: a limitation in trophic conditions (Bonhommeau, Chassot, & Rivot, 2008; Bonhommeau et al., 2009; Desaunay & Guerault, 1997; Friedland, Miller, & Knights, 2007; ICES, 2001; Kettle & Haines, 2006; Knights, 2003; Munk et al., 2010), changes in oceanic currents modifying larval transport (Castonguay, Hodson, Moriarty, et al., 1994; Friedland et al., 2007; ICES, 2001; Knights, 2003; Zenimoto et al., 2009), and/or spatial oscillations of a salinity front used by adult eels to detect the spawning grounds which then lead to oscillations in the success of larval transport (Kimura, Inoue, & Sugimoto, 2001; Kimura & Tsukamoto, 2006). In addition to statistical correlations, Lagrangian simulations of larval drift have also been carried out to explore some mechanisms (Bonhommeau, Castonguay, Rivot, Sabatié, & Le Pape, 2010; Bonhommeau et al., 2009; Kettle & Haines, 2006; Kim et al., 2007; Melià et al., 2013; Pacariz, Westerberg, & Björk, 2014; Zenimoto et al., 2009). These simulations suggested that, while for European eel the correlation between NAO and recruitment more likely reflects an indirect effect of trophic conditions in the Sargasso Sea (Bonhommeau et al., 2009; Pacariz et al., 2014), changes in oceanic currents directly affect Japanese eel larval drift (Kim et al., 2007; Zenimoto et al., 2009).

Analysing simultaneously the declines of the three species, Bonhommeau, Chassot, Planque, et al. (2008) highlighted the synchrony between regime shifts in the Atlantic and Pacific sea surface temperature, primary production and recruitment of the three species. They postulated that an increase in sea surface temperature due to climate change led to a higher stratification of the Sargasso Sea and consequently to a lower primary production, which could translate into lower food availability for the leptocephali. In recent times, Miller et al. (2016) proposed a more precise mechanism: The regime shift resulted in a lower abundance of diatoms and a higher abundance of cyanobacteria, which may have resulted in a lower production of carbohydrates which are crucial for the production of "marine snow," the main food of eel larvae (Riemann et al., 2010).

2.2 | Effect on silver eel spawning migration

Climate change can also affect the later stages of eel. Oceanic conditions and climate change can, indirectly, influence river discharge (Arnell, 1999; Milly, Dunne, & Vecchia, 2005) through modifications of precipitation regimes (Kettle et al., 2011). The discharge regime is also modified by water extraction for human use, agriculture and other industrial processes (Postel & Richter, 2003; Verreault, Mingelbier, & Dumont, 2012). River discharge and rainfall are important triggers (direct or indirect) of silver eel migration (Acou, Laffaille, Legault, & Feunteun, 2008; Boubée et al., 2001; Bruijs & Durif, 2009; Drouineau et al., 2017; Durif & Elie, 2008; Reckordt, Ubl, Wagner, Frankowski, & Dorow, 2014; Trancart, Acou, Oliveira, & Feunteun, 2013). Higher river discharge increases migration speed (Tesch, 2003; Vøllestad et al., 1986). Reduced discharge delays migration, and eels may even be stopped until the following year if environmental conditions are not favourable (Drouineau et al., 2017; Durif, Elie, Gosset, Rives, & Travade, 2003). At last, reduced discharge can lead to higher proportions of eels going through turbines, since at low flow a higher proportion of water is guided through the turbines, leading to higher mortalities (Bau et al., 2013; Jansen, Winter, Bruijs, & Polman, 2007).

3 | COMPONENT 2—INCREASED CONTAMINATION LOAD: CONTAMINATION OF EELS AND CONSEQUENCES ON ITS PHYSIOLOGY

Eels are vulnerable to contamination because of their high trophic level and high level of lipid storage (Belpaire et al., 2011; Geeraerts & Belpaire, 2009; ICES, 2016). Contaminants that have been found in eels include the following: organic contaminants (Bilau et al., 2007; Blanchet-Letrouvé et al., 2014; Guhl, Stürenberg, & Santora, 2014; Hodson et al., 1994; Kammann et al., 2014; Ohji, Harino, & Arai, 2006), heavy metals (Maes et al., 2005; Nunes et al., 2014; Pannetier et al., 2016; Pierron, Baudrimont, Dufour, et al., 2008; Pierron, Baudrimont, Lucia et al., 2008; Yang & Chen, 1996) and pesticides (Byer et al., 2013; Couillard, Hodson, & Castonguay, 1997; Gimeno, Ferrando, Sanchez, Gimeno, & Andreu, 1995; Hodson et al., 1994; Privitera, Aarestrup, & Moore, 2014).

TABLE 1 Main references exploring the impact of oceanic conditions on recruitment

Reference	Species	Oceanic index	Proposed mechanisms
Desaunay and Guerault (1997)	European eel	Oceanic temperature	Food availability
Kimura et al. (2001)	Japanese eel	Southern Oscillation Index El Niño/Southern Oscillation	Oscillations of the salinity front that affects larvae growth and survival during their migration
ICES (2001)	American and European eels	North Atlantic Oscillation Index	Changes of transport due to modification of Gulf Stream path Trophic limitations due to oscillation in plankton abundance
Knights (2003)	American and European eels	North Atlantic Oscillation Index Sea surface temperature	Changes of transport due to modification of Gulf Stream path Trophic limitations due to oscillation in plankton abundance
Kettle and Haines (2006)	European eel	Lagrangian circulation model	Food availability
Kimura and Tsukamoto (2006)	Japanese eel	Field observation on salinity front	Oscillations of spawning location due to movements of salinity front induced by El Niño
Friedland et al. (2007)	European eel and presumably American eel	North Atlantic Oscillation	Food availability in the Sargasso Sea larval drift
Kim et al. (2007)	Japanese eel	Lagrangian circulation model	Success of larval transport due to oscillation of the North Equatorial Current
Bonhommeau, Chassot, and Rivot (2008)	European eel	Sea surface temperature in the Sargasso Sea	Food availability
Bonhommeau et al. (2009)	European eel	Lagrangian circulation model North Atlantic Oscillation Index Transport Index Gulf Stream Index	Oscillations biological production in the Sargasso Sea
Zenimoto et al. (2009)	Japanese eel	Lagrangian circulation model	Success of larval transport due to oscillation of the North Equatorial Current
Munk et al. (2010)	European eel and presumably American eel	Field observations of oceanic fronts in the Sargasso Sea	Oscillations of fronts that alter the efficiency of retention on feeding grounds
Durif, Gjøsæter, and Vøllestad (2011)	European eel	Analysis of a 100-year old time series of eel abundance	Relationship to NAO and temperature conditions in the Sargasso Sea
Pacariz et al. (2014)	European eel	Lagrangian circulation model	Decline of success of larval transport due to current modifications (rejected)
Miller et al. (2016)	European, Japanese and American eels	Field measurement of diatoms and cyanobacterial abundances in the Sargasso Sea	Lower availability of food after oceanic regime shift

Therefore, eels are sometimes used as bioindicators of contamination (Amiard-Triquet, Amiard, Andersen, Elie, & Metayer, 1987; Belpaire & Goemans, 2007; Linde, Arribas, Sanchez-Galan, & Garcia-Vazquez, 1996; McHugh et al., 2010). Contamination levels are often above human consumption standards (Bilau et al., 2007; Byer et al., 2013; Geeraerts & Belpaire, 2009; ICES, 2014, 2016) and have led to fishing prohibitions in various sites in European countries (Germany, Belgium, Netherlands, France, Italy) (Belpaire et al., 2016).

These contaminants are widely found in freshwater fishes (Streit, 1998), and their effects on fish biology (Fonseca et al., 2014; Gilliers et al., 2006; Kerambrun et al., 2012) and the danger for human consumption have been demonstrated (Halldorsson, Meltzer, Thorsdottir, Knudsen, & Olsen, 2007; Järup, 2003; Schuhmacher, Batiste, Bosque, Domingo, & Corbella, 1994). While metallic contaminants have a long history in countries with extraction activities, organic contamination, pesticides and nutrients loads are much more recent (Malmqvist & Rundle, 2002; Morée, Beusen, Bouwman, & Willems, 2013). Many of them appeared in the second half of the twentieth century in relation to agriculture intensification, urbanization and industrial activities. During this period, fertilizer utilization grew exponentially (Figure 6). PCBs and DDT production peaked around the 1960s (Harrad et al., 1994; Van Metre, Wilson, Callender, & Fuller, 1998); that is, about 20 years before eels started to decline, and concentrations remain high in river sediments explaining why levels are still high in eels (ICES, 2016). Persistent organic pollutants (POPs) had a dramatic effect on lake trout (*Salvelinus namaycush*)

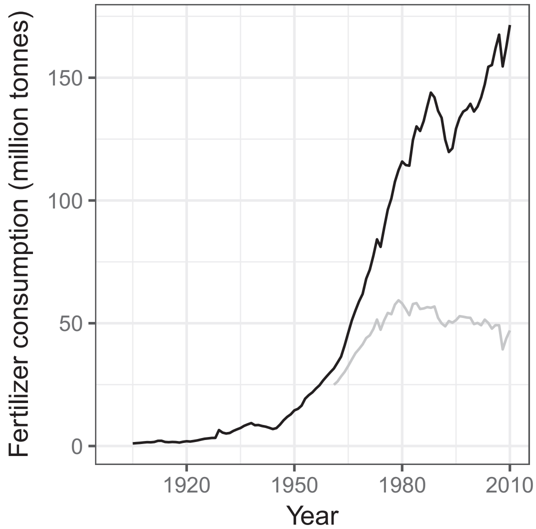

FIGURE 6 Global fertilizer consumption in OECD countries (grey) and in the world (black). Source (Steffen et al., 2015, International Fertilizer Industry Association Database)

in Lake Ontario (Cook et al., 2003) and concentrations peaked in American eel in Lake Ontario in the late 1960s, about 20 years before the American eel recruitment collapse (Byer et al., 2015). The increased nutrient load to water bodies has caused detrimental impacts on humans and aquatic ecosystem health (Grizzetti, Bouraoui, & Aloe, 2012; Grizzetti et al., 2011) and continued to increase until the mid-1990s before declining in many rivers (Minaudo, Meybeck, Moatar, Gassama, & Curie, 2015). Fertilizers are still used at a very high level (Figure 6). Moreover, new contaminants are appearing in the water and in eels, such as perfluorooctanesulfonic acid, textile dyes, musk compounds, perfluorinated substances, organophosphorus flame retardants and plasticizers (ICES, 2016).

There have been a few cases of direct eel mortalities due to contaminants (Dutil, 1984; Dutil, Besner, & McCormick, 1987), but in the majority of cases, the impact is at the sublethal level ranging from tissue damage, stress, effects on osmoregulation, behaviour alteration, hormonal perturbation and genotoxic effects (Couillard et al., 1997; Geeraerts & Belpaire, 2009). Contaminants may also be transferred to the offspring resulting in larval malformation (Byer et al., 2013; Foekema, Kotterman, de Vries, & Murk, 2016; Rigaud et al., 2016; Robinet & Feunteun, 2002). As a fatty fish, eels are particularly sensitive to contamination. Most contaminants are highly concentrated in the lipid stores (Robinet & Feunteun, 2002) and affect lipid metabolism (Corsi et al., 2005; Fernández-Vega, Sancho, Ferrando, & Andreu-Moliner, 1999; Pierron et al., 2007). This is especially critical at the silver eel stage when lipid levels are highest (over 13%) to achieve their transoceanic migration to the spawning grounds (Belpaire et al., 2009; Van Den Thillart, Palstra, & Van Ginneken, 2007; Van Den Thillart et al., 2004; van Ginneken & van den Thillart, 2000). For female eels, 67% of their fat store is spent on the spawning migration and oocyte maturation (Palstra & van den Thillart, 2010). As lipids are mobilized during spawning migration, contaminants are more likely to be released into the blood at high concentrations, thus negatively affecting gonad maturation and oocyte production, as they do in other fish species (Baillon et al., 2015; ICES, 2016; Pierron et al., 2014), and also impairing migration success (Geeraerts & Belpaire, 2009; Pierron, Baudrimont, Dufour, et al., 2008; Robinet & Feunteun, 2002). As a summary, contaminants can act as a classical stressor during the continental stage of eel, but then have the potential to dramatically impair maturation and migration success, that is the whole reproduction success.

4 | COMPONENT 3—FRAGMENTATION AND HABITAT LOSS: FRAGMENTATION BY WEIRS AND DAMS AND CONSEQUENCES ON UPSTREAM AND DOWNSTREAM MIGRATION

4.1 | Movements, habitats and fragmentation

Movement is a key feature of living organisms to find food, mates and avoid predation (Nathan et al., 2008). Several types of movements can be distinguished. The first type, called "station keeping" (Dingle, 1996), takes place within the home range of the animal and corresponds to simple movements for foraging and predation avoidance. The two other types of movement, ranging and migration, occur outside the home range (Dingle & Drake, 2007). Ranging is dedicated to the search for a specific resource (mate, food, etc.) and stops when the resource is found (Jeltsch et al., 2013). Migration is generally triggered by physiological and environmental cues and not by the search for a specific resource such as food or mates. It affects most individuals in the population, occurs over a long timescale, requires orientation and suggests a return journey (Dingle, 1996; Dingle & Drake, 2007).

Diadromous fish, such as eels, undergo two long migrations (Tesch, 2003): The first migration, from the spawning grounds to their growth habitat, includes a phase of active upstream migration in river catchments during the early years of their continental life-stage (Castonguay, Hodson, Couillard, et al., 1994; Fukuda, Aoyama, Yokouchi, & Tsukamoto, 2016; Imbert, Labonne, Rigaud, & Lambert, 2010). During the second migration, eels return to the oceanic spawning grounds from their growth habitats in rivers or coastal waters. Eels may also move between different habitats during their continental stage (Arai & Chino, 2012; Béguer-Pon, Castonguay, Benchetrit, et al., 2015; Daverat, Tomas, Lahaye, Palmer, & Elie, 2005; Kaifu, Tamura, Aoyama, & Tsukamoto, 2010; Yokouchi et al., 2012), movements which correspond to station keeping and ranging.

The construction of dams accelerated worldwide during the 1950/1960s (Dynesius & Nilsson, 1994; MacGregor et al., 2009; Postel & Richter, 2003) (Figure 7), about 20 years before the eel population declined. This massive construction of dams has restrained eel movements and available habitats. The construction of hydropower dams during the twentieth century in the St. Lawrence catchment caused a 40% habitat loss for the North American eel in this basin (Verreault, Dumont, & Mailhot, 2004). The situation is similar

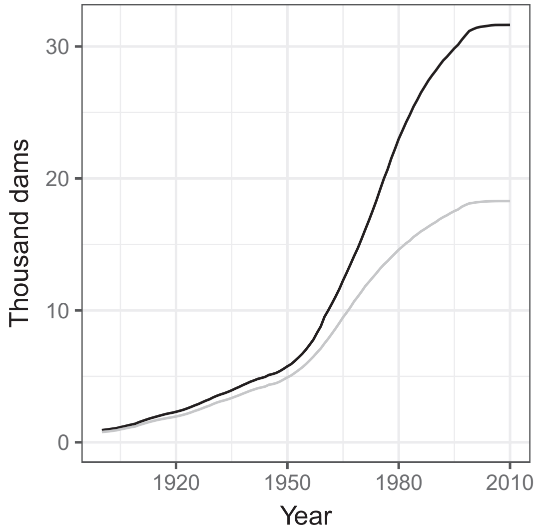

FIGURE 7 Accumulative number of large dams in OECD countries (grey) and in the world (black). Source (Steffen et al., 2015; World Commission on Dams, 2000)

or worse in the United States (Busch, Lary, Castilione, & McDonald, 1998), especially because most dams lack fishways (MacGregor et al., 2009). In Europe, 50%–90% of habitats were lost by the end of the twentieth century (Feunteun, 2002). For the Japanese eel, approximately 75% of effective habitats were lost between 1970 and 2010 in Japan, Korea, Taiwan and China, with a maximum in China (>80%) and Taiwan (~50%) (Chen, Huang, & Han, 2014).

Intensive dam constructions in Spain, Morocco and Portugal, have had drastic consequences on European eel distribution (Clavero & Hermoso, 2015; Lobon-Cervia, 1999; Nicola, Elvira, & Almodóvar, 1996), possibly affecting the sex ratio as this area yields mainly male eels and is closest to the spawning area (Kettle et al., 2011).

Dams and weirs are not the only factors affecting eel habitats: Rivers provide multiple goods and services to society (Elliott & Whitfield, 2011; Postel & Richter, 2003; Wolanski, McLusky, van den Belt, & Costanza, 2011) that have led to river channelization, hydromorphological modifications, drying out of lateral wetland, wetland drainage, water extraction, modification of land use in the floodplain that can lead to higher erosion and sedimentation (Basset et al., 2013; Elliott & Hemingway, 2002; Postel & Richter, 2003). As an example, typical eel habitats, such as estuarine marshes and intertidal zones, have been lost because of flood protection walls, agriculture activities and navigation (Gros & Prouzet, 2014). In Japan, catch reduction rates in several rivers and lakes were positively correlated with the rate of revetment along rivers and around lakes (Itakura, Kitagawa, Miller, & Kimura, 2015), and also, the condition factor of eels and prey diversity were significantly lower in these modified habitats (Itakura, Kaino, Miyake, Kitagawa, & Kimura, 2015).

4.2 | Blockage during upstream migrations

During their first year in continental waters, eels display an active migratory behaviour and then shift to a resident behaviour (Benchetrit et al., 2017; Imbert et al., 2010). Resident behaviour does not exclude habitat shifts (Daverat & Tomás, 2006) although these types of movement correspond more to ranging than strict migration (Dingle & Drake, 2007). Upstream migration has a cost and its evolutionary benefit is still unclear as eels can settle in a wide range of habitats (Daverat et al., 2006; Marohn, Jakob, & Hanel, 2013; Tsukamoto, Nakai, & Tesch, 1998; Yokouchi et al., 2012). Glass eels with high feeding rate and fast weight gain have a higher propensity to migrate (Bureau du Colombier, Lambert, & Bardonnet, 2008). These glass eels also display a more gregarious and less aggressive behaviour (Geffroy & Bardonnet, 2012). Habitat selection could be a trade-off between growth (generally higher in downstream habitats), survival (generally higher in upstream habitats), competition avoidance (higher competition in downstream habitats) and energetic cost of migration (Drouineau et al., 2014; Edeline, 2007; Mateo, Lambert, Tétard, Castonguay, et al., 2017). Habitat selection is also partly related to genetic or epigenetic polymorphism (Côté et al., 2014; Gagnaire et al., 2012; Mateo, Lambert, Tétard, Castonguay, et al., 2017; Pavey et al., 2015; Podgorniak, Milan, et al., 2015). In such a scheme, habitat selection would be the result of a fitness optimization process in which fitness in a habitat would depend on habitat characteristics, competition in the habitat, but also individual variability of growth rates due to the existence of genetically distinct clusters of individuals (Côté et al., 2015; Mateo, Lambert, Tétard, Castonguay, et al., 2017).

Given this plasticity in habitat use, the consequences of obstacles on upstream migrations are difficult to assess. Methods have been proposed to assess the passability of obstacles (Briand, Fatin, Feunteun, & Fontenelle, 2005; Drouineau et al., 2015; Tremblay, Cossette, Dutil, Verreault, & Dumont, 2016). Densities of eels are higher downstream of obstacles. This leads to (a) increased competition between individuals, which can subsequently result in lower survival (Bevacqua, Melià, de Leo, & Gatto, 2011; Vøllestad & Jonsson, 1988), (b) increased susceptibility to predation (Agostinho, Agostinho, Pelicice, & Marques, 2012; Drouineau et al., 2015; Garcia De Leaniz, 2008; Larinier, 2001) and overfishing (Briand et al., 2005; Dekker, 2003c), and (c) possible modification to the sex ratio, as sex determination is density-dependent (Davey & Jellyman, 2005; De Leo & Gatto, 1996; Poole, Reynolds, & Moriarty, 1990; Roncarati, Melotti, Mordenti, & Gennari, 1997; Tesch, 2003).

At last, obstacles to upstream migration can act as a permanent selection pressure (Mateo, Lambert, Tétard, & Drouineau, 2017; Podgorniak, Angelini, et al., 2015; Podgorniak, Milan, et al., 2015). Côté et al. (2014) demonstrated the existence of two clusters of individual eels with differing genetic basis: a cluster of slow growers and a cluster of fast growers, while Pavey et al. (2015) demonstrated the existence of genetically distinct ecotypes, with different growth rates and different sex ratios. By impairing migration within catchments, obstacles can decrease the fitness of some types of individuals; those individuals who genetically belong to the “freshwater habitat” may not be able to reach suitable habitats or will suffer damage during their downstream migration (Mateo, Lambert, Tétard, & Drouineau, 2017).

4.3 | Impaired downstream migrations

Most studies dealing with downstream migration have focused on mortality due to passage through hydropower turbines (Boubée & Williams, 2006; Calles et al., 2010; Carr & Whoriskey, 2008; Coutant & Whitney, 2000; Gosset, Travade, Durif, Rives, & Elie, 2005; Pedersen et al., 2012; Winter, Jansen, & Bruijs, 2006). Several factors influence the mortality induced by hydropower plants:

1. Turbine characteristics: The mortality due to strikes by Kaplan turbines is generally greater than 15% and sometimes as high as 100% depending on fish length, wheel diameter, nominal discharge flow and speed of rotation (Gomes & Larinier, 2008). For Francis turbines, Calles et al. (2010) estimated a mortality rate of 60% at a Swedish site while a mortality rate of about 16% was found at an American site (Richkus & Dixon, 2003). Even if they survive passage through the turbines, eels can be wounded and have a reduced chance of reaching the spawning area.
2. Site configuration can greatly influence the probability that a fish will pass through or by-pass the turbines. As silver eels follow the main flow (Jansen et al., 2007), the orientation of the water intake with respect to the main channel influences the probability of turbine passage (Bau et al., 2013). Different types of barriers have been proposed to divert eels from turbine passage, such as fish-friendly trashracks (Raynal, Chatellier, Courret, Larinier, & David, 2014; Raynal, Courret, Chatellier, Larinier, & David, 2013), flow field manipulation (Piper et al., 2015), light (Hadderingh, Van Der Stoep, & Hagraken, 1992; Patrick, Sheehan, & Sim, 1982) and infrasound barriers (Sand, Enger, Karlsen, Knudsen, & Kvernstuen, 2000; Sand et al., 2001). The installation of bypasses is also a mitigation measure to prevent passages through turbines (Durif et al., 2003; Gosset et al., 2005; Haro, Watten, & Noreika, 2016).
3. Environmental conditions: In a period of low discharge, when the flow through the turbine is high compared to the flow over weir, more eels will pass through the turbines than at high discharge, when the turbine flow is small compared to the weir flow.
4. Obstacle location within the catchment: As eels are not uniformly distributed within a river catchment (Ibbotson, Smith, Scarlett, & Aprhamian, 2002), the number of eels impacted by a given facility depends on the number of eels that settle upstream the facility. Therefore, it is necessary to estimate the distribution of fish within catchments to assess the effect of hydropower plants at the catchment scale. In the SEAHOPE model, the total mortality induced by hydropower plants in a given catchment was estimated by coupling a model that predicts the proportion of fish killed when passing each individual plant with a model that predicts the spatial distribution of eels within the catchment (Jouanin et al., 2012).

However, direct mortality is not the only impact obstacles can have on downstream migrants. First, sublethal injuries can occur during obstacle passages because of impingements on hard structures (even in the absence of turbines), which can then impair spawning migration success (Bruijs & Durif, 2009). Predation during downstream passage has also been recorded for many fish species (Garcia De Leaniz, 2008; Muir, Marsh, Sandford, Smith, & Williams, 2006; Williams, Smith, & Muir, 2001). Moreover, increased energy costs induced by obstacle passage may have a delayed impact on migration success and fecundity: Silver eels stop feeding during the spawning migration, and their lipid stores are crucial to achieve the oceanic migration and produce oocytes (Van Ginneken & van den Thillart, 2000). Delays induced by obstacles can impair escapement, especially when the environmental migration suitability window is limited (Drouineau et al., 2017; Verbiest, Breukelaar, Ovidio, Philippart, & Belpaire, 2012). At last, similarly to obstacles to upstream migration, obstacles to downstream migration affect specific types of individual: individuals that settle upstream of the obstacle (i.e. individuals that settle in upstream habitats and individuals that were able to pass the obstacle), as such, obstacles may have the potential to exert a selection pressure on the population (Mateo, Lambert, Tétard, & Drouineau, 2017).

5 | COMPONENT 4—ALIEN SPECIES: EFFECTS OF ALIEN PARASITOID *ANGUILLICOLA CRASSUS*

Although competition is possible with some alien species such as the European catfish (Bevacqua et al., 2011), or even with introduced American (Han et al., 2002) and European eels in East Asia (Aoyama et al., 2000), *A. crassus* is the alien species that has the most documented and widespread impact on eels, at least for European and American eels. *A. crassus* is a natural parasite of Japanese eel which was introduced into Europe in the mid-1970s, early 1980s, probably through the aquaculture trade (Koops & Hartmann, 1989). It is now widespread in Europe (Becerra-Jurado et al., 2014; Evans & Matthews, 1999; Kennedy & Fitch, 1990; Kirk, 2003; Lefebvre, Contournet, Priour, Soulas, & Crivelli, 2002; Neto, Costa, Costa, & Domingos, 2010; Norton, Rollinson, & Lewis, 2005) and Northern Africa (Dhaouadi et al., 2014; El Hilali, Yahyaoui, Sadak, Maachi, & Taghy, 1996; Hizem Habbechi, Kraiem, & Elie, 2012; Koops & Hartmann, 1989; Maamouri, Gargouri, Ould Daddah, & Bouix, 1999). Systematic monitoring of eel diseases is still limited to a few countries, impairing our ability to assess the overall prevalence (ICES, 2015). However, many studies have reported a significant prevalence at sites in both North America and Europe (Aieta & Oliveira, 2009; Becerra-Jurado et al., 2014; Denny, Denny, & Paul, 2013) and an analysis of the European Eel Quality Database confirmed the prevalence of the infection in Europe (Belpaire et al., 2011).

The invasion in North America started for the same reason, a few years after its introduction into Europe. The first record occurred in the second half of the 1990s in Texas (Fries, Williams, & Johnson, 1996) and then in Chesapeake Bay and the Hudson River (Barse & Secor, 1999). The invasion then quickly spread in the United States and in Canada (Aieta & Oliveira, 2009; Denny et al., 2013; Hein, Arnott, Roumillat, Allen, & de Buron, 2014; Machut & Limburg, 2008; Rockwell, Jones, & Cone, 2009). Although transmission is possible in brackish waters (Kirk, Kennedy, & Lewis, 2000; Kirk, Lewis, & Kennedy, 2000; Lefebvre et al., 2002; Reimer, Hildebrand, Scharberth, & Walter, 1994), the level of infection is lower than in freshwater (Kirk, 2003; Kirk, Kennedy, et al., 2000; Kirk, Lewis, et al., 2000).

This swimbladder parasite has multiple impacts on its host. The parasite causes inflammation of the swimbladder leading to multiple bacterial infections, stress and loss of appetite (Kirk, 2003; Lefebvre, Fazio, Mounaix, & Crivelli, 2013). However, the most serious damage is on the swimbladder itself. The infection may alter the gas composition of the swimbladder, block the pneumatic duct, impairing the organ's function (Kirk, Lewis, et al., 2000; Lefebvre et al., 2013) leading to necrosis in the most extreme cases (Molnár, Székely, & Perényi, 1994; Würtz & Taraschewski, 2000). The alteration of the swimbladder has a direct impact on swimming capacity (Sprengel & Lüchtenberg, 1991; Székely, Palstra, Molnár, & van den Thillart, 2009). It may imperil the transoceanic spawning migration (Clevestam, Ogonowski, Sjoberg, & Wickstrom, 2011; Palstra, Heppener, Van Ginneken, Székely, & Van den Thillart, 2007), especially because migrant eels display important diurnal vertical migrations (Béguer-Pon, Castonguay, Shan, et al., 2015; Chow et al., 2015; Righton et al., 2016) that require buoyancy control. This higher energetic cost of migration, due to a malfunctioning swimbladder, will affect individuals which may already have reduced lipid storage available, due to the infection (Marohn et al., 2013).

6 | COMPONENT 5—EXPLOITATION OF NATURAL RESOURCES: AN INTENSIVE EXPLOITATION OF EELS AT ALL THEIR STAGES

Eels are targeted by recreational and commercial fisheries at all continental life stages (glass eels, yellow eels and silver eels) with a great variety of active and passive gears (Haro et al., 2000; Tesch, 2003). Yellow and silver eels have been exploited for a long time as attested by representations of eels in prehistoric pictographs (Citerne, 1998, 2004). Eel was an important food resource for Native Americans (MacGregor et al., 2009) and is a traditional food in Japan and East Asia (Tatsukawa, 2003). The first official record of European eel fisheries dates back to 1086 (Dekker & Beaulaton, 2016). In contrast to the situation for many commercial species, the culture of eel is not a closed system in that it is still dependent on wild-caught glass eels. Artificial reproduction and rearing of glass eels have only been achieved for the Japanese eel (Kagawa, Tanaka, Ohta, Unuma, & Nomura, 2005; Tanaka, Kagawa, & Ohta, 2001; Tanaka, Kagawa, Ohta, Unuma, & Nomura, 2003) although these operations are still not commercially viable (Okamura, Horie, Mikawa, Yamada, & Tsukamoto, 2014). Artificial reproduction has been achieved in European (Palstra & van den Thillart, 2009) and American eels (Oliveira & Hable, 2010) but not rearing of glass eels.

The main shift in the traditional artisanal eel fisheries occurred as a result of the demand from on-growing aquaculture (Haro et al., 2000; Moriarty & Dekker, 1997). According to FAO statistics, eel farming is now responsible for 90% of total eel production (vs wild-caught eels) and Japan is thought to consume 70% of total freshwater eel production (Shiraishi & Crook, 2015). While eel aquaculture started in the late nineteenth century and early twentieth century in eastern Asia, it turned into a stable industry after World War II (Ringuet, Muto, & Raymakers, 2002). The high value of eel in Eastern Asia food markets led to the development of highly competitive aquaculture farms (Lee, Chen, Lee, & Liao, 2003; Liao, 2001). The development of intensive farming explains why despite the decline in the wild population, the production of *Anguilla* spp. increased nearly 20-fold between 1950 and 2007 (Crook & Nakamura, 2013). As these farms depend on wild-caught animals, the demand for glass eel increased considerably and prices climbed to very high levels, completely transforming the industry. The shortage of Japanese glass eels since the early 1970s leads aquaculture farms to import European and American glass eels (Haro et al., 2000; Lee et al., 2003; Moriarty & Dekker, 1997; Ringuet et al., 2002), leading to an increase in fishing effort in Europe and a peak in landings in 1976 (Briand, Bonhommeau, Castelnaud, & Beaulaton, 2008) and to the development of a large fishery targeting glass eels from North America (Meister & Flagg, 1997). After a period of less favourable market conditions, the prices soared again during the early 1990s (Briand et al., 2008). A threefold increase in prices of European glass eel was observed between 1993 and 1997 (Ringuet et al., 2002), resulting in a "gold rush" for entry into the North American fishery (Haro et al., 2000). Because of these incredibly high prices, eel became the most valuable species landed in France in the early 2000s (Castelnaud, 2000) and Europe exported half of its production to Asia in the mid-2000s (Briand et al., 2008). The increase in fishing effort led to very high exploitation rates in certain French and Spanish catchments (Aranburu, Diaz, & Briand, 2016; Briand et al., 2005; Prouzet, 2002) as Spain and France recruit the highest proportion of European eel (Dekker, 2000a). In a similar manner, high exploitation rates were observed in catchments on Canadian Atlantic seaboard (Jessop, 2000) or in Taiwan (Tzeng, 1984). In France, about 25% of the arriving glass eels were harvested by commercial fisheries, and this estimate did not include the catch from illegal fisheries (Figure 8; Drouineau, Beaulaton, Lambert, & Briand, 2016). In Japan, these proportions rose from about 25% in the early 1950s to approximately 40% in the 1980s (Tanaka, 2014). The Eel European Regulation has limited the fishing effort and required that 60% of caught eels be dedicated for restocking. Moreover, European eel exports have been restricted after its inclusion on Appendix II of the Convention on Trade of Endangered Species in 2009 and a ban of all imports and exports from and to the European Union implemented in 2010 (Nijman, 2015). In Japan, glass eel fisheries are forbidden and a special licence is required to capture seed for aquaculture and research. Specific permission is now required for aquaculture, and restrictions have also been implemented in China and Taiwan. In 2014, China, Japan,

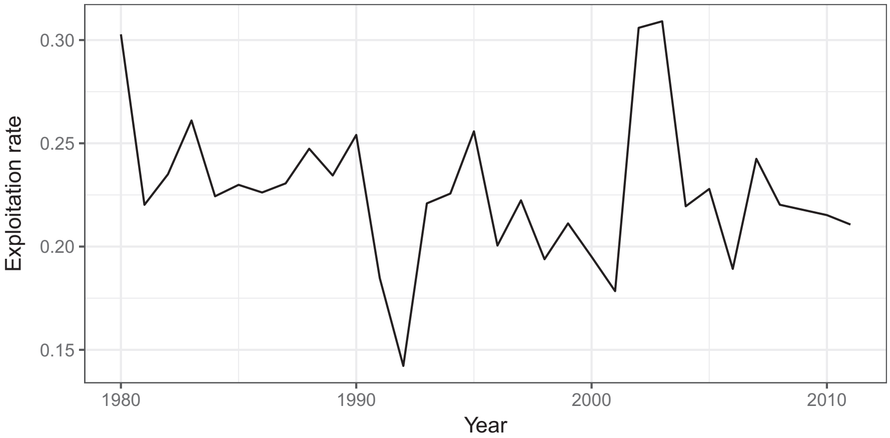

FIGURE 8 French glass eel exploitation rates expressed as the ratio of catch (tonnes) to recruitment (tonnes). Catches correspond to an appraisal of historical catches based upon market and fishery data (Briand et al., 2008) while recruitments were estimated using the model GEREM (Drouineau, Beaulaton, et al., 2016)

the Republic of Korea and Taiwan agreed to restrict "initial input" into farms of glass eel of Japanese eel.

The catch of silver eels has decreased throughout the world (Cairns et al., 2014; Dekker, 2003a; Tatsukawa, 2003; Tsukamoto, Aoyama, & Miller, 2009) because of a reduction in abundance of the stock and because of a decrease in fishing effort, accelerated by recent management measures. Silver eel fisheries have, for example, completely disappeared in Taiwan (Tzeng, 2016) and are restricted in 11 prefectures in Japan (Jacoby & Gollock, 2014b). In Europe, the decline in the silver eel catches has preceded the decline in recruitment (Dekker, 2003a). Silver eel fisheries used to predominate at the northern edge of their distribution area and in the western Mediterranean (Aalto et al., 2016; Amilhat, Farrugio, Lecomte-Finiger, Simon, & Sasal, 2008; Dekker, 2003b, 2003c), and in some catchments, exploitation rates can still be high. Regarding the American eel, silver eel landings used to be dominated by-catches in the Saint Lawrence River (Castonguay, Hodson, Couillard, et al., 1994), but they have also severely declined and a large-scale licence buyout in Quebec has recently accelerated this trend (Cairns et al., 2014).

7 | WHEN FORTY YEARS OF GLOBAL CHANGE HAS HAD A GREATER IMPACT THAN THE ICE AGES OR CONTINENTAL DRIFT

The genus *Anguilla* appeared more than 50 million years ago during the Eocene (Tsukamoto & Aoyama, 1998). Japanese eel is thought to have appeared about 15 million years ago (Lin, Poh, & Tzeng, 2001), and American and European eels separated about 3 million years ago during the emergence of the Isle of Panama (Jacobsen et al., 2014). Those species have survived enormous changes: a succession of ice ages (the last ice age maximum occurred approximately 22,000 years ago) and continental drift that has progressively increased the distance between the spawning grounds and growth habitats (Knights, 2003). This demonstrates their evolutionary robustness (Knights, 2003) and remarkable adaptive capacity (Mateo, Lambert, Tétard, Castonguay, et al., 2017) based on adaptive phenotypic plasticity (Côté et al., 2014; Daverat et al., 2006; Drouineau et al., 2014) and genetic polymorphism (Gagnaire et al., 2012; Pavey et al., 2015; Pujolar et al., 2014; Ulrik et al., 2014). Despite millions of years of adaptation, these three eel species have undergone a dramatic decline in only a few decades.

Identifying the main drivers of the eel decline is still in debate. The main arguments to support the importance of specific stressors are based on the synchrony between the time of the collapse in eel and the stressor. However, many factors impair our ability to disentangle their respective effects. First, the simultaneous decline of the three species strongly suggests the influence of large-scale factors and therefore of a possible oceanic influence. However, other stressors display very similar increasing trends at the global scale before the beginning of the decline (4; 6; 7). Moreover, the beginning of the eel decline is very difficult to identify because of the complex life cycles of the species (Figure 2) and their long life expectancy (up to 30 years). It would be interesting to compare with tropical species that also show signs of decline but comparative data with Southern hemisphere tropical species are scarce (Jacoby et al., 2015; Jellyman, 2016). Second, robust quantitative historical data on eel and the anthropogenic pressures are lacking for this period. Third, where these data do exist they mainly come from specific river catchments and it is not possible to extrapolate these data to the whole distribution area because the anthropogenic pressure does not have the same effect everywhere and eels display a great diversity in life history traits. Each stressor probably played a role in the collapse and the combination of stressors in the second half of the twentieth century probably had a cumulative effect that heightened the overall effect of the individual stressors (Jacoby et al., 2015; Miller et al., 2016). The decline occurred about 30 years after the Second World War, that is approximately one to three eel generations. This period corresponds to a period of high economic development "Les Trentes Glorieuses," in which agricultural production process, industrial process and energy consumption quickly increased. This can be seen through the acceleration of many indicators since the 1950s/1960s listed in the study of Steffen et al. (2005), for example world population, gross domestic product (increased by a factor of 15 since 1950),

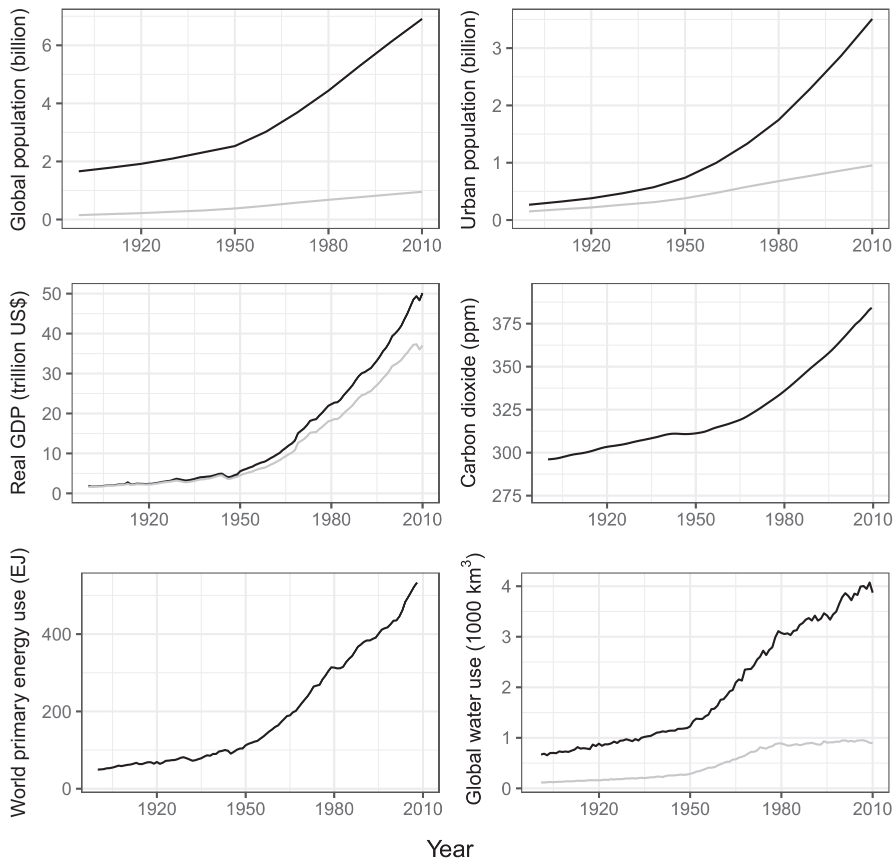

FIGURE 9 Various indicators of the Great Acceleration for OECD countries (grey) or the entire world (black). GDP: gross domestic product. Carbon dioxide from firn and ice core records (Law Dome, Antarctica) and Cape Grim, Australia (deseasonalized flask and instrumental records). Sources (Steffen et al., 2005), population (Goldewijk, Beusen, & Janssen, 2010), CO_2 (Etheridge et al., 1996; Langenfelds et al., 2011; MacFarling Meure, 2004; MacFarling Meure et al., 2006), water use (Alcamo et al., 2003; aus der Beek et al., 2010; Flörke et al., 2013), energy use (GEA Writing Team, 2012), and GDP (World Bank indicators)

world petroleum consumption which has increased by 3.5× since 1960, motor vehicles by a factor of 16 since the early 1950s and increased water use for human consumption and agriculture (Figure 9). This acceleration of human activity and consumption has been referred to as the "Great Acceleration" (Steffen, Broadgate, Deutsch, Gaffney, & Ludwig, 2015; Steffen et al., 2005), and occurred about 20 years before the first signs of the decline in eel populations, that is one to two eel generations. As mentioned earlier, river, estuaries and ecosystems have suffered intense modifications over this period (Basset et al., 2013; Elliott & Hemingway, 2002; Elliott & Whitfield, 2011; Postel & Richter, 2003, 2003; Wolanski et al., 2011). Eel populations are likely affected by global change as a whole, rather than by one specific anthropogenic pressure, explaining why Castonguay, Hodson, Couillard, et al. (1994) could not identify a primary cause for the decline of the American eel.

8 | THE RESILIENCE OF EELS SEVERELY IMPAIRED BY GLOBAL CHANGE

Several factors contribute to the resilience of eel populations. First, the presence of a brackish/marine contingent (which skip the freshwater phase) can buffer the pressures specific to the catadromous contingent such as dams, contamination, fishing or the parasite (ICES, 2009). In addition, their very large diet spectrum (Sinha & Jones, 1967; Tesch, 2003), their resistance to fluctuations in temperature, salinity, oxygen, food availability and temporary emersion (Brusle, 1991; Tesch, 2003) allow them to grow in a very large range of habitats. This plasticity in growth habitat can generate a "storage effect" and a "portfolio effect" that mitigate against environmental variability (ICES, 2009). In a complex life cycle, a storage effect corresponds to a situation where a specific stage of long duration and of limited sensitivity to environmental conditions, buffers the effects of environmental conditions on other stages. For eels, the long duration of the continental growth phase and its variability across habitats with generational overlaps allows the species to buffer the faster cyclic variations of oceanic conditions affecting recruitment (even in a single cohort, some individuals are likely to face unfavourable oceanic conditions while others will face more favourable oceanic conditions during their spawning migration, reproduction and larval drift of their offspring) (Secor, 2015a). A portfolio effect corresponds to the expression "don't put all your eggs in the same basket." For eels, their large adaptive capacity allows them to settle in a wide range of habitats, smoothing out environmental fluctuations in each habitat: If one habitat is temporarily unsuitable, it is compensated by other habitats that remain suitable (Secor, 2015a). More generally, the large diversity of tactics during the continental phase and presumably during the spawning migration may correspond to remarkable bet-hedging well suited to address environmental variability (Daverat et al., 2006; Righton et al., 2016). The environmental sex determination may also be a compensatory mechanism: The higher production of females in a context of depleted population may mitigate the reduction in eggs production that would result from the decline in silver eel abundance (Geffroy & Bardonnet, 2016; Mateo, Lambert, Tétard, & Drouineau, 2017), especially since eels have a high fecundity.

Then, how might have global change led to such a fast collapse despite eel adaptive capacities and those compensatory mechanisms? Eels are panmictic and thus have long been considered genetically homogeneous; however, recently a genetic polymorphism in eel populations was found to be correlated with environmental gradients (Côté et al., 2014; Gagnaire et al., 2012; Pavey et al., 2015; Pujolar et al., 2014; Ulrik et al., 2014). These correlations are thought to result from spatially variable selection (some individuals are genetically more adapted than others to survive in some habitats) or of genetically based habitat selection (some types of individuals tend to settle preferentially in some habitats to maximize their fitness). The existence of genetically distinct types of individuals which are more or less adapted to the different types of habitats available within their distribution area (northern vs southern habitats, marine vs brackish vs freshwater habitats), that is ecotypes (Pavey et al., 2015), combined with a large phenotypic plasticity are assumed to play the main role in eel adaptive capacity, enabling the species to address the wide environmental heterogeneity at both the distribution and catchment scale (Drouineau et al., 2014; Mateo, Lambert, Tétard, Castonguay, et al., 2017). In such a scheme, individuals are able to grow and survive in a wide range of habitats thanks to phenotypic plasticity but some individuals are more adapted to some habitats than others (ecotypes), and all individuals reproduce together (panmixia) ensuring that ecotypes are reshuffled in each generation. The synergy of phenotypic plasticity and genetic polymorphism could explain how a panmictic population can survive in such a wide and varied distribution area and be the basis for the adaptive capacities of eels.

In this review, we have highlighted that not all pressures affect all habitats and individuals evenly. Indeed, obstacles affect mostly individuals that settle preferentially in upstream habitats and habitat loss mainly affects males located in the south-western part of the range of the European eel. *Anguillicola crassus* has a greater impact on individuals that settle in freshwater habitats as opposed to estuarine or marine (Kirk, 2003). At last, fisheries are not uniformly distributed, with European silver eel fisheries mainly occurring at the edge of the distribution area, especially the northern edge, although fisheries are also important along the Mediterranean coast (Castonguay, Hodson, Couillard, et al., 1994; Dekker, 2003b, 2003c; Moriarty & Dekker, 1997), and glass eel fisheries in the core (Dekker, 2003c). By affecting different habitats, anthropogenic pressures affect life history traits and ecotypes in different ways (Figure 10). Climate change and glass eel fisheries probably affect all ecotypes: Climate change affects recruitment success. Glass eel fisheries, though not evenly distributed in the distribution area, generally operate downstream of river catchments and consequently harvest evenly all incoming glass eels. On the other hand, all the other anthropogenic pressures tend to affect ecotypes corresponding to more upstream habitats. As such, these anthropogenic pressures reduce the fitness of those individuals and can become an important selective pressure (Mateo, Lambert, Tétard, Castonguay, et al., 2017; Mateo, Lambert, Tétard, & Drouineau, 2017). For example, half the American silver eels migrating down the St. Lawrence River, one of the most productive areas for American eel (Casselman, 2003), have been killed by hydropower dams and fisheries (Verreault & Dumont, 2003). Such selection pressure over 30 years or more (one to two eel generations) may have reduced the prevalence of individuals adapted to such types of habitats (northernmost area, longest migration from spawning grounds) in the panmictic eel population and explain why recruitment to the St. Lawrence River has been so much more reduced than elsewhere in their distribution range. Reducing this genetic polymorphism as a result of anthropogenic-induced selection may irrevocably alter the species capacity to adapt and modify its sex ratio.

In addition, by decreasing the diversity of ecotypes and consequently, decreasing the capacity of eels to live in a wide range of habitats, anthropogenic pressures may have reduced the portfolio and storage effects which, as we said before, are crucial to address environmental variability and to improve resilience. In view of this, diversity is crucial for temperate eels (Secor, 2015b) and management should preserve this diversity to ensure population resilience. Moreover, it is crucial to improve our knowledge of the mechanisms involved in eel adaptation and of the effects of anthropogenic pressures on their capacity to adapt to the global change. A recent analysis outlines that even pressures that do not kill any eels can have impacts on eel populations by penalizing some ecotypes more than others (Mateo, Lambert, Tétard, & Drouineau, 2017).

9 | OTHER IMPLICATIONS FOR EEL MANAGEMENT AND RESEARCH

The eel decline due to global change has several implications for management. First, global causes mean global solutions are warranted. By global solutions, we do not mean that there should be a unique set of management measures across all distribution areas, but rather coordinated international management acting on each source of anthropogenic pressure. This was proposed in the Quebec declaration of concern (Dekker & Casselman, 2014; Dekker et al., 2003) that called for immediate action and coordination at all scales. Although some progress has been made since the first declaration, there is clear need to improve management coordination among regional, national and international authorities. Dekker (2016) pointed out the difficulties in the implementation of the Eel Management Plan in Europe. International coordination has not yet started for the American eel (Castonguay & Durif, 2016; Jacoby et al., 2014; MacGregor et al., 2008, 2009). The East Asia Eel Resource Consortium does not yet have any official support (Jacoby & Gollock, 2014b), and the first attempt at international coordination took place in 2014 between South Korea, China, Taiwan and Japan with an agreement on the amount of glass eel that can be used for aquaculture.

Second, although it is difficult to disentangle the relative effects of various anthropogenic pressures implicated in the decline, it is

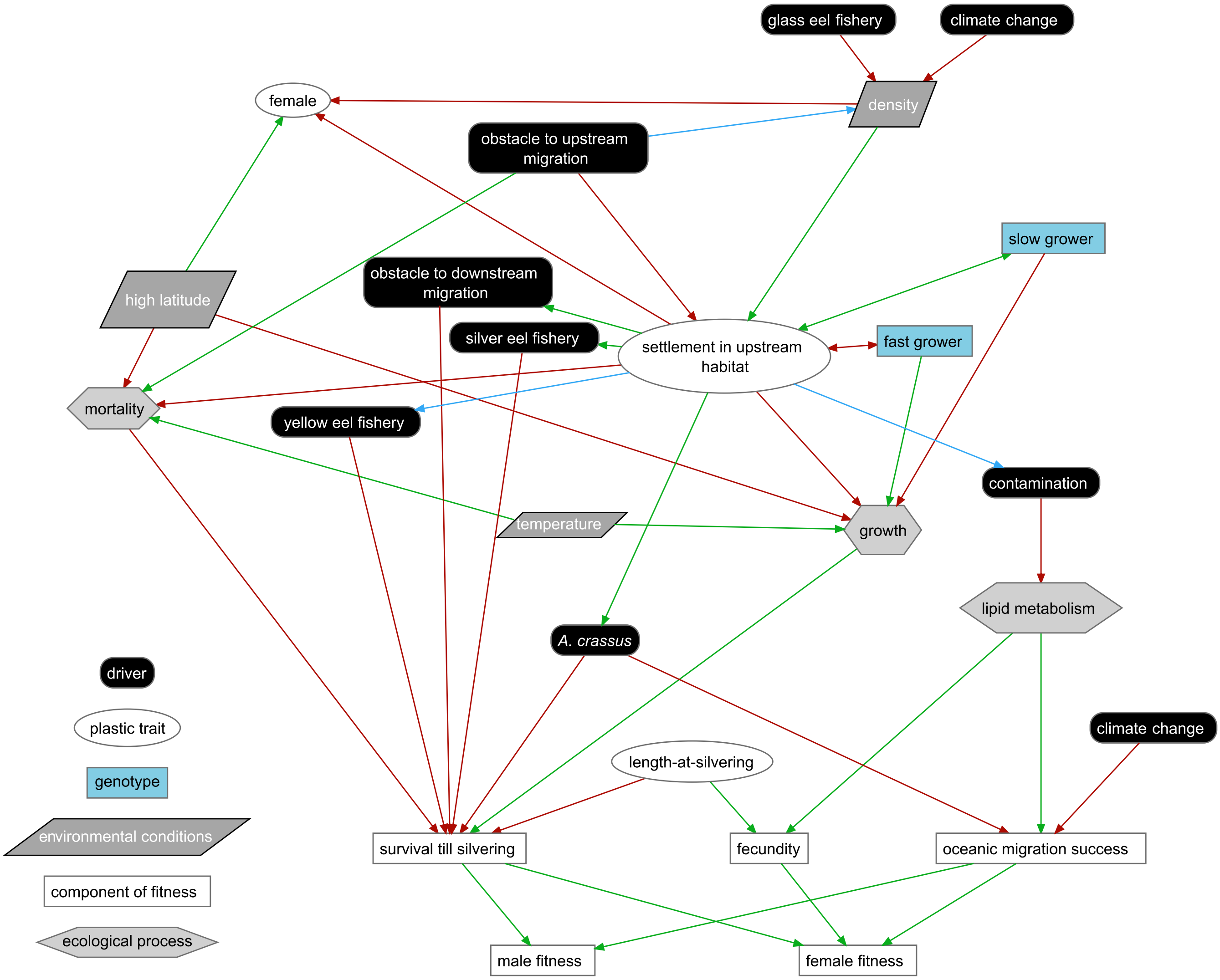

FIGURE 10 Adaptation mechanisms to environmental heterogeneity as proposed in Mateo, Lambert, Tétard, Castonguay, et al. (2017), Mateo, Lambert, Tétard, and Drouineau (2017), Gagnaire et al. (2012), Côté et al. (2014), Drouineau et al. (2014) and Boivin et al. (2015). A red arrow stands for "unfavourable," a green arrow stands for "favourable." A blue arrow stands for a relationship which is either favourable" or "unfavourable" depending on situations. There is a double arrow between genotypes and "settlement in upstream habitats" because it represents "spatially varying selection" and "genetic-dependent habitat selection." Regarding phenotypes, female is considered as opposite to male and "settlement in upstream habitats" as opposite to "settlement in downstream habitats"

important to develop tools and methods to monitor and quantify their effects in the future. Eels grow in very small and almost independent units corresponding to river catchments (Dekker, 2000b) with specific anthropogenic pressures, within which eels have different life history traits. Therefore, it is difficult to assess the stock and extrapolate the overall effect of anthropogenic pressure at the population scale, from observations collected at the river catchment scale (Dekker, 2000a). However, the improvement in data quality and the recent development of a generic model that can be used at a larger geographic scale is a first step. For example, the GEREM model provides estimates of glass eel recruitment that can be used to assess glass eel fishery exploitation rates (Bornarel et al., 2018; Drouineau, Beaulaton, et al., 2016). The models EDA (Briand, Beaulaton, Chapon, Drouineau, & Lambert, 2015) or SMEP (Aprahamian, Walker, Williams, Bark, & Knights, 2007) can be used to assess the abundance of yellow eels in river catchments. These can then be coupled with other models to assess spawner escapement and the effect of different anthropogenic pressures such as hydropower production or fisheries (Jouanin et al., 2012). Stock assessment models have also been proposed to support management (Bevacqua & De Leo, 2006; Bevacqua, Melià, Gatto, & De Leo, 2015; Dekker, 2000a; Oeberst & Fladung, 2012). However, few tools are currently available to assess the impact of contaminants on eel populations. In a similar manner, there is a lack of tools to quantify the effect of lost habitats on population dynamics, although some methodologies are available which can quantify the amount of habitat lost due to fragmentation. Although it is not possible to quantify the historical effects of anthropogenic pressures, quantifying and predicting pressures in the future would provide valuable information to prioritize management actions. Quantification is even more important as (a) it is not possible to mitigate some of the pressures affecting eels (parasitism, climate change), so it is necessary to compensate their effects with mitigation measures on the other pressures (fishery, fragmentation, contamination); (b) management practices cannot mitigate anthropogenic pressures at similar temporal scales: Reduction in fishing efforts is recent but is thought to operate quickly, whereas effort to mitigate contamination or fragmentation is older but is much more complex and longer to implement.

Of course, temperate eels are not the only species endangered by global change and most diadromous fishes have undergone severe declines (Limburg & Waldman, 2009; McDowall, 1999; Mota et al., 2015). The effects of fragmentation (Haxton & Cano, 2016; Larinier, 2001; Limburg & Waldman, 2009), global warming (Elliott & Elliott, 2010; Friedland, 1998; Friedland, Hansen, Dunkley, & MacLean, 2000; Jonsson & Jonsson, 2009; Lassalle, Béguer, Beaulaton, & Rochard, 2008; Lassalle et al., 2009; Rougier et al., 2014), fisheries and pollution (Limburg & Waldman, 2009; McDowall, 1999) have been documented for most of these species. More generally, most migratory animals regardless of taxa have undergone similar declines (Berger, Young, & Berger, 2008; Sanderson, Donald, Pain, Burfield, & van Bommel, 2006; Wilcove & Wikelski, 2008) raising the question of sustainability of migratory tactics in the face of global change. In this context, why should eels be considered as a symbol of the effect of global change? Because the original life cycle of eels make them vulnerable to all five components of global change, and the cumulated impacts of those five components have outpaced the adaptive capacities of these species acquired through million years of evolution. The rate of change during the Great Acceleration in the second half of the twentieth century was too fast for the adaptive capacity of the eel, especially because the five components of global change acted simultaneously. It explains how a species that was considered a vermin species in French salmonid rivers until the 1980s has become critically endangered in only 25 years, after millions of years of existence.

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