Freshwater eels: A symbol of the effects of global change

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Freshwater eels: a symbol of the effects of global change

Running title: Freshwater eels and 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: (i) climate change affecting larval survival and drift, (ii) an increase in pollution leading to high levels of contamination exacerbated by their high lipid levels, (iii) increasing fragmentation and habitat loss that reduce dramatically the amount of available habitats and induce increased spawner mortality, (iv) the appearance of *Anguillicola crassus* a parasitic alien nematode that impairs spawning success and (v) 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, over-exploitation

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Table of contents

Introduction

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 XXth 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). More specifically, this example illustrates that cumulative effects of the different components of global change (Vitousek *et al.* 1997; Western 2001; Tylianakis *et al.* 2008; Jacoby *et al.* 2015; Miller *et al.* 2016) 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 *et al.* 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: (1) climate, (2) land use and land cover modifications that can result in habitat loss and fragmentation, (3) biogeochemical and hydrological cycles and pollution, (4) biotic mixing including biological invasions and (5) 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) though 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 (Menzel *et al.* 2006; Chevillot *et al.* 2017) and modification of distribution areas (Lassalle *et al.* 2009; Cheung *et al.* 2010; 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 *et al.* 2006; van Vliet *et al.* 2013).

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

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 (Collinge 1996; Fischer and Lindenmayer 2007; Brook *et al.* 2008). Habitat loss and ecosystem fragmentation are currently

considered major threats to biodiversity and represent one of the major challenges in ecosystem conservation and restoration (Tilman *et al.* 1994; Tischendorf and Fahrig 2000a,b; Sutherland *et al.* 2013), by impairing the ability of individuals to migrate to essential habitats (Gros and Prouzet 2014), isolating populations and reducing gene flow (Horreo *et al.* 2011; Haxton and Cano 2016), and by modifying species community structure (Perkin and Gido 2012). Fragmentation and habitat loss increase the risk of extinction cascades (Terborgh *et al.* 2001; Fischer and Lindenmayer 2007; Krauss *et al.* 2010; Junge *et al.* 2014; Haddad *et al.* 2015; van Leeuwen *et al.* 2016).

Biological invasion by alien species is our fourth component of global change (Vitousek *et al.* 1997; Occhipinti-Ambrogi and Savini 2003; Ricciardi 2007). Invasive species can affect native ones directly through predation, competition or parasitism, or indirectly by habitat modification or by spreading diseases (Lymbery *et al.* 2014). Arrival of alien species due to shifts in their distribution in response to climate change, uniformisation 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 and Cloern 1992; Cloern 1996; Grosholz 2002; Vilà *et al.* 2010). Currently, 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).

Finally, 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 (Turner *et al.* 1999; Christensen *et al.* 2003; Gascuel *et al.* 2011; Branch 2015; Drouineau *et al.* 2016b). Fisheries have also shaped the life histories of exploited fishes by acting as a permanent and continuous selection pressure (Jørgensen and Renöfält 2013; Heino *et al.* 2015).

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 i) a micro-evolutionary response, ii) phenotypic plasticity (Charmantier *et al.* 2008), or iii) 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 (Spurgeon 2000; Thomas *et al.* 2004; Steffen *et al.* 2005; Brook *et al.* 2008; Cahill *et al.* 2013; Urban 2015). The collapse of the three temperate anguillid eel populations is an excellent illustration of this phenomenon.

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 - from Norway to Morocco for the European eel (Tesch 2003), from Canada to Venezuela for American eel (Helfman *et al.* 1987), from Northern Philippines to Korea for Japanese eel (Tsukamoto 1990), which are reached after a long larval drift (larvae are called leptocephali) from distant marine spawning grounds (Sargasso Sea for *A. rostrata* and *A. anguilla* (Schmidt 1923; McCleave 1993) and west of Mariana Islands for *A. japonica* (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 colonise a large range of continental habitats from brackish to freshwater (Daverat *et al.* 2006; Arai and Chino 2012). 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 *et al.*

2015b; Chang *et al.* 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 (Han *et al.* 2010; Als *et al.* 2011; Côté *et al.* 2013; Pujolar 2013) and their long larval drift which limit 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 (Vélez-Espino and Koops 2009; Drouineau *et al.* 2014; Yokouchi *et al.* 2014). For example, sex ratio is generally female-biased in the northern parts of distribution areas (Vladykov 1966; Helfman *et al.* 1984; Vøllestad and Jonsson 1988; Vøllestad 1992) and in upstream parts of river catchments (Oliveira and McCleave 2000; Tesch 2003). Length-at-silvering (onset of sexual maturation) varies between between sexes and habitats. Males follow a time-minimising strategy, leaving continental waters as soon as they reach the minimal length to achieve the spawning migration, while females follow a size-maximising 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). Consequently, male length-at-silvering is rather set (Vøllestad 1992; Oliveira 1999), while females exhibit a wider range of sizes and are often larger in the northern parts of the distribution areas (Helfman *et al.* 1987; Davey and Jellyman 2005; Jessop 2010). These life history traits patterns 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 *et al.* 2014; Drouineau *et al.* 2014; Mateo *et al.* 2017a) but also of genetic polyphormism leading to spatially varying selection and/or genetically based habitat selection producing genetically distinct ecotypes (Gagnaire *et al.* 2012; Côté *et al.* 2014; Ulrik *et al.* 2014; Pavey *et al.* 2015; Mateo *et al.* 2017a).

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In addition to having similar life histories, the three anguillid species underwent a dramatic decline which started in the late 1970s (Dekker *et al.* 2003; Dekker and Casselman 2014). 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 to 99 % since the 80's (ICES 2015) while spawner abundance has also dropped (Dekker 2003a). 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 *et al.* 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 *A. anguilla* as critically endangered in 2008 (confirmed in 2010 and 2014) (Jacoby and Gollock 2014a) while *A. rostrata* and *A. japonica* have been classified as endangered since 2014 (Jacoby and Gollock 2014b; Jacoby *et al.* 2014). 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 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 *et al.* 1994b), over-fishing (Haro *et al.* 2000; Dekker 2003c; Tsukamoto *et al.* 2003), contamination (Belpaire *et al.* 2011, 2016), parasitism (Feunteun 2002; Kirk 2003) and blockage due to dams (Moriarty and

Dekker 1997; Kettle *et al.* 2011). These suspected causes match the above-mentioned components of global change: oceanic modifications resulting from global warming, over-fishing corresponds to over-harvesting 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. Finally, 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).

Component 1 - Global warming and ocean modification: impacts on eel migrations

Effect on leptocephalus drift and survival

The decline in eel populations is possibly linked to modifications of physical conditions in the oceans (Castonguay *et al.* 1994b; Knights *et al.* 1996; Bonhommeau *et al.* 2008a; 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 (Castonguay *et al.* 1994b; Bonhommeau *et al.* 2008a). 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 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 *et al.* 2009; Goberville *et al.* 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 (Desaunay and Guerault 1997; ICES 2001; Knights 2003; Kettle and Haines 2006; Friedland *et al.* 2007; Bonhommeau *et al.* 2008b, 2009; Munk *et al.* 2010), changes in oceanic currents modifying larval transport (Castonguay *et al.* 1994b; ICES 2001; Knights 2003; Friedland *et al.* 2007; 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 *et al.* 2001; Kimura and Tsukamoto 2006). In addition to statistical correlations, Lagrangian simulations of larval drift have also been carried out to explore some mechanisms (Kettle and Haines 2006; Kim *et al.* 2007; Bonhommeau *et al.* 2009, 2010; Zenimoto *et al.* 2009; Melià *et al.* 2013; Pacariz *et al.* 2014). 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 *et al*. (2008a) 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

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254 temperature due to climate change, led to a higher stratification of the Sargasso Sea and
255 consequently to a lower primary production, which could translate into lower food availability for
256 the leptocephali. Recently, Miller *et al*. (2016) proposed a more precise mechanism: the regime shift
257 resulted in a lower abundance of diatoms and a higher abundance of cyanobacteria, which may have
258 resulted in a lower production of carbohydrates which are crucial for the production of "marine
259 snow", the main food of eel larvae (Riemann *et al.* 2010).

260

261

262 **Effect on silver eel spawning migration**

263 Climate change can also affect the later stages of eel. Oceanic conditions and climate change can,
264 indirectly, influence river discharge (Arnell 1999; Milly *et al.* 2005) through modifications of
265 precipitation regimes (Kettle *et al.* 2011). The discharge regime is also modified by water extraction
266 for human use, agriculture and other industrial processes (Postel and Richter 2003; Verreault *et al.*
267 2012). River discharge and rainfall are important triggers (direct or indirect) of silver eel migration
268 (Boubée *et al.* 2001; Acou *et al.* 2008; Durif and Elie 2008; Bruijs and Durif 2009; Trancart *et al.*
269 2013; Reckordt *et al.* 2014; Drouineau *et al.* 2017). Higher river discharge increases migration
270 speed (Vøllestad *et al.* 1986; Tesch 2003). Reduced discharge delays migration and eels may even
271 be stopped until the following year if environmental conditions are not favourable (Durif *et al.*
272 2003; Drouineau *et al.* 2017). Finally, reduced discharge can lead to higher proportions of eels
273 going through turbines, since at low flow a higher proportion of water is guided through the
274 turbines, leading to higher mortalities (Jansen *et al.* 2007; Bau *et al.* 2013).

275

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 (Geeraerts and Belpaire 2009; Belpaire *et al.* 2011; ICES 2016). Contaminants that have been found in eels include: organic contaminants (Hodson *et al.* 1994; Ohji *et al.* 2006; Bilau *et al.* 2007; Blanchet-Letrouvé *et al.* 2014; Kammann *et al.* 2014; Guhl *et al.* 2014); heavy metals (Yang and Chen 1996; Maes *et al.* 2005; Pierron *et al.* 2008a,b; Nunes *et al.* 2014; Pannetier *et al.* 2016) and pesticides (Hodson *et al.* 1994; Gimeno *et al.* 1995; Couillard *et al.* 1997; Byer *et al.* 2013; Privitera *et al.* 2014).

Consequently, eels are sometimes used as bioindicators of contamination (Amiard-Triquet *et al.* 1987; Linde *et al.* 1996; Belpaire and Goemans 2007; McHugh *et al.* 2010). Contamination levels are often above human consumption standards (Bilau *et al.* 2007; Geeraerts and Belpaire 2009; Byer *et al.* 2013; 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 (Gilliers *et al.* 2006; Kerambrun *et al.* 2012; Fonseca *et al.* 2014) and the danger for human consumption have been demonstrated (Schuhmacher *et al.* 1994; Järup 2003; Halldorsson *et al.* 2007). While metallic contaminants have a long history in countries with extraction activities, organic contamination, pesticides, and nutrients loads are much more recent (Malmqvist and Rundle 2002; Morée *et al.* 2013). Many of them appeared in the second half of the XXth century in relation to agriculture intensification, urbanisation and industrial activities. During this period, fertiliser utilisation grew exponentially (Figure 6). PCBs and DDT production peaked around the 1960's (Harrad *et al.* 1994; Van Metre *et al.* 1998), i.e. 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*) 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 *et al.* 2011, 2012) and continued to increase until the mid-90s before declining in many rivers (Minaudo *et al.* 2015). Fertilisers 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 (PFOS), textile dyes, musk compounds, perfluorinated substances, organophosphorus flame retardants and plasticisers (ICES 2016).

There have been a few cases of direct eel mortalities due to contaminants (Dutil 1984; Dutil *et al.* 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 and Belpaire 2009). Contaminants may also be transferred to the offspring resulting in larval malformation (Robinet and Feunteun 2002; Byer *et al.* 2013; Rigaud *et al.* 2016; Foekema *et al.* 2016). As a fatty fish, eels are particularly sensitive to contamination. Most contaminants are highly concentrated in the lipid stores (Robinet and Feunteun 2002) and affect lipid metabolism (Fernández Vega *et al.* 1999; Corsi *et al.* 2005; 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 (van Ginneken and van den Thillart 2000; Van Den Thillart *et al.* 2004, 2007; Belpaire *et al.* 2009). For female eels, 67% of their fat store is spent on the spawning migration and oocyte maturation (Palstra and van den Thillart 2010). As lipids are mobilised 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 (Pierron *et al.* 2014; Baillon *et al.* 2015; ICES 2016), and also impairing migration success (Robinet and Feunteun 2002; Pierron *et al.* 2008a; Geeraerts and Belpaire 2009).

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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, i.e. the whole reproduction success.

Component 3 - Fragmentation and habitat loss: fragmentation by weirs and dams and consequences on upstream and downstream migration

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 and Drake 2007). Ranging is dedicated to the search of 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 and 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 *et al.* 1994a; Imbert *et al.* 2010; Fukuda *et al.* 2016). 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 (Daverat *et al.* 2005; Kaifu *et al.* 2010; Arai and

Chino 2012; Yokouchi *et al.* 2012; Béguer-Pon *et al.* 2015a), movements which correspond to station keeping and ranging.

The construction of dams accelerated worldwide during the 1950/60s (Dynesius and Nilsson 1994; Postel and Richter 2003; MacGregor *et al.* 2009) (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 XXth century in the St. Lawrence catchment caused a 40% habitat loss for the North American eel in this basin (Verreault *et al.* 2004). The situation is similar or worse in the United States (Busch *et al.* 1998), especially since most dams lack fishways (MacGregor *et al.* 2009). In Europe, 50-90% of habitats were lost by the end of XXth 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 *et al.* 2014).

Intensive dam constructions in Spain, Morocco and Portugal, have had drastic consequences on European eel distribution (Nicola *et al.* 1996; Lobon-Cervia 1999; Clavero and Hermoso 2015), possibly affecting the sex ratio since 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 (Postel and Richter 2003; Wolanski et al. 2011; Elliott and Whitfield 2011) that have led to river channelization, hydro-morphological 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 (Elliott and Hemingway 2002; Postel and Richter 2003; Basset et al. 2013). 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 and Prouzet 2014). In Japan, catch reduction rates in several rivers and lakes were positively correlated with the

372 rate of revetment along rivers and around lakes (Itakura *et al.* 2015b), also the condition factor of
373 eels and prey diversity were significantly lower in these modified habitats (Itakura *et al.* 2015a).

374

375 **Blockage during upstream migrations**

376 During their first year in continental waters, eels display an active migratory behaviour and then
377 shift to a resident behaviour (Imbert *et al.* 2010; Benchetrit *et al.* 2017). Resident behaviour does
378 not exclude habitat shifts (Daverat and Tomás 2006) though these types of movement correspond
379 more to ranging than strict migration (Dingle and Drake 2007). Upstream migration has a cost and
380 its evolutionary benefit is still unclear since eels can settle in a wide range of habitats (Tsukamoto *et*
381 *al.* 1998; Daverat *et al.* 2006; Yokouchi *et al.* 2012; Marohn *et al.* 2013). Glass eels with high
382 feeding rate and fast weight gain have a higher propensity to migrate (Bureau du Colombier *et al.*
383 2008). These glass eels also display a more gregarious and less aggressive behaviour (Geffroy and
384 Bardonnet 2012). Habitat selection could be a trade-off between growth (generally higher in
385 downstream habitats), survival (generally higher in upstream habitats), competition avoidance
386 (higher competition in downstream habitats) and energetic cost of migration (Mateo *et al.* 2017a;
387 Edeline 2007; Drouineau *et al.* 2014). Habitat selection is also partly related to genetic or epigenetic
388 polymorphism (Gagnaire *et al.* 2012; Côté *et al.* 2014; Pavey *et al.* 2015; Podgorniak *et al.* 2015b;
389 Mateo *et al.* 2017a). In such a scheme, habitat selection would be the result of a fitness optimisation
390 process in which fitness in a habitat would depend on habitat characteristics, competition in the
391 habitat, but also individual variability of growth rates due to the existence of genetically distinct
392 clusters of individuals (Côté *et al.* 2015; Mateo *et al.* 2017a).

393 Given this plasticity in habitat use, the consequences of obstacles on upstream migrations are
394 difficult to assess. Methods have been proposed to assess the passability of obstacles (Briand *et al.*
395 2005; Drouineau *et al.* 2015; Tremblay *et al.* 2016). Densities of eels are higher downstream of

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obstacles. This leads to (i) increased competition between individuals, which can subsequently result in lower survival (Vøllestad and Jonsson 1988; Bevacqua *et al.* 2011), (ii) increased susceptibility to predation (Drouineau *et al.* 2015; Larinier 2001; Garcia De Leaniz 2008; Agostinho *et al.* 2012), and overfishing (Dekker 2003c; Briand *et al.* 2005) and, (iii) possible modification to the sex ratio, since sex determination is density-dependent (Poole *et al.* 1990; De Leo and Gatto 1996; Roncarati *et al.* 1997; Tesch 2003; Davey and Jellyman 2005).

Finally, obstacles to upstream migration can act as a permanent selection pressure (Podgorniak *et al.* 2015a,b; Mateo *et al.* 2017b). 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 *et al.* 2017b).

Impaired downstream migrations

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

- Turbine characteristics: The mortality due to strikes by Kaplan turbines are generally greater than 15% and sometimes as high as 100% depending on fish length, wheel diameter, nominal discharge flow and speed of rotation (Gomes and Larinier 2008). For Francis turbines, Calles *et al*. (2010) estimated a mortality rate of 60% at a Swedish site while a

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mortality rate of about 16% was found at an American site (Richkus and Dixon 2003). Even if they survive passage through the turbines, eels can be wounded and have a reduced chance of reaching the spawning area.

- Site configuration can greatly influence the probability that a fish will pass through or by-pass the turbines. Since 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 *et al.* 2013, 2014), flow field manipulation (Piper *et al.* 2015), light (Patrick *et al.* 1982; Hadderingh *et al.* 1992) and infrasound barriers (Sand *et al.* 2000, 2001). The installation of bypasses is also a mitigation measure to prevent passages through turbines (Durif *et al.* 2003; Gosset *et al.* 2005; Haro *et al.* 2016).
- 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.
- Obstacle location within the catchment: since eels are not uniformly distributed within a river catchment (Ibbotson *et al.* 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, sub-lethal injuries can occur during obstacle passages because of impingements on hard structures

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(even in the absence of turbins), which can then impair spawning migration success (Bruijs and Durif 2009). Predation during downstream passage has also been recorded for many fish species (Williams *et al.* 2001; Muir *et al.* 2006; Garcia De Leaniz 2008). 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 and van den Thillart 2000). Delays induced by obstacles can impair escapement, especially when the environmental migration suitability window is limited (Verbiest *et al.* 2012; Drouineau *et al.* 2017). Finally, 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 *et al.* 2017b).

Component 4 - Alien species: effects of alien parasitoid *Anguillicola crassus*

Though 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), *Anguillicola crassus* is the alien species that has the most documented and widespread impact on eels, at least for European and American eels. *Anguillicola crassus* is a natural parasite of Japanese eel which was introduced into Europe in the mid 70's, early 80's, probably through the aquaculture trade (Koops and Hartmann 1989). It is now widespread in Europe (Kennedy and Fitch 1990; Evans and Matthews 1999; Lefebvre *et al.* 2002; Kirk 2003; Norton *et al.* 2005; Neto *et al.* 2010; Becerra-Jurado *et al.* 2014), and Northern Africa (Koops and Hartmann 1989; El Hilali *et al.* 1996; Maamouri *et al.* 1999; Hizem Habbechi *et al.* 2012; Dhaouadi *et al.* 2014). 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 and Oliveira 2009; Denny *et al.* 2013; Becerra-Jurado *et al.* 2014) 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 90's in Texas (Fries *et al.* 1996) and then in Chesapeake Bay and the Hudson River (Barse and Secor 1999). The invasion then quickly spread in the United States and in Canada (Machut and Limburg 2008; Aieta and Oliveira 2009; Rockwell *et al.* 2009; Denny *et al.* 2013; Hein *et al.* 2014). Though transmission is possible in brackish waters (Reimer *et al.* 1994; Kirk *et al.* 2000a,b; Lefebvre *et al.* 2002), the level of infection is lower than in freshwater (Kirk *et al.* 2000a,b; Kirk 2003).

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 *et al.* 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 *et al.* 2000b; Lefebvre *et al.* 2013) leading to necrosis in the most extreme cases (Molnár *et al.* 1994; Würtz and Taraschewski 2000). The alteration of the swimbladder has a direct impact on swimming capacity (Sprengel *et al.* 1991; Székely *et al.* 2009). It may imperil the transoceanic spawning migration (Palstra *et al.* 2007; Clevestam *et al.* 2011), especially because migrant eels display important diurnal vertical migrations (Chow *et al.* 2015; Béguer-Pon *et al.* 2015b; 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).

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493 **Component 5 - Exploitation of natural resources: an intensive exploitation of eels at all their**
494 **stages**

495 Eels are targeted by recreational and commercial fisheries at all continental life stages (glass eels,
496 yellow eels and silver eels) with a great variety of active and passive gears (Haro *et al.* 2000; Tesch
497 2003). Yellow and silver eels have been exploited for a long time as attested by representations of
498 eels in prehistoric pictographs (Citerne 1998, 2004). Eel was an important food resource for Native
499 Americans (MacGregor *et al.* 2009) and is a traditional food in Japan and East Asia (Tatsukawa
500 2003). The first official record of European eel fisheries dates back to 1086 (Dekker and Beaulaton
501 2016). In contrast to the situation for many commercial species, the culture of eel is not a closed
502 system in that it is still dependent on wild caught glass eels. Artificial reproduction and rearing of
503 glass eels has only been achieved for the Japanese eel (Tanaka *et al.* 2001, 2003; Kagawa *et al.*
504 2005) although these operations are still not commercially viable (Okamura *et al.* 2014). Artificial
505 reproduction has been achieved in European (Palstra and Thillart 2009) and American eels (Oliveira
506 and Hable 2010) but not rearing of glass eels.

507 The main shift in the traditional artisanal eel fisheries occurred as a result of the demand from on-
508 growing aquaculture (Moriarty and Dekker 1997; Haro *et al.* 2000). According to FAO statistics, eel
509 farming is now responsible for 90% of total eel production (versus wild-caught eels) and Japan is
510 thought to consume 70% of total freshwater eel production (Shiraishi and Crook 2015). While eel
511 aquaculture started in the late XIXth century and early XXth century in eastern Asia, it turned into a
512 stable industry after World War II (Ringuet *et al.* 2002). The high value of eel in Eastern Asia food
513 markets led to the development of highly competitive aquaculture farms (Liao 2001; Lee *et al.*
514 2003). The development of intensive farming explains why despite the decline in the wild
515 population, the production of *Anguilla spp*. increased nearly 20-fold between 1950 and 2007 (Crook
516 and Nakamura 2013). Since 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 lead aquaculture farms to import European and American glass eels (Moriarty and Dekker 1997; Haro *et al.* 2000; Ringuet *et al.* 2002; Lee *et al.* 2003), leading to an increase in fishing effort in Europe and a peak in landings in 1976 (Briand *et al.* 2008) and to the development of a large fishery targeting glass eels from North America (Meister and 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 (Prouzet 2002; Briand *et al.* 2005; Aranburu *et al.* 2016) since Spain and France recruit the highest proportion of European eel (Dekker 2000a). Similarly, high exploitation rates were observed in catchments on Canadian Atlantic seaboard (Jessop 2000; 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 *et al.* 2016a)). 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 2010). 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

541 also been implemented in China and Taiwan. In 2014, China, Japan, the Republic of Korea and
542 Taiwan agreed to restrict "initial input" into farms of glass eel of *A. japonica.*

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

554

555 **When forty years of global change has had a greater impact than the ice ages or continental**
556 **drift**

557 The genus *Anguilla* appeared more than 50 million years ago during the Eocene (Tsukamoto and
558 Aoyama 1998). *A. japonica* is thought to have appeared about 15 million years ago (Lin *et al.* 2001)
559 and *A. rostrata* and *A. anguilla* separated about 3 million years ago during the emergence of the isle
560 of Panama (Jacobsen *et al.* 2014). Those species have survived enormous changes: a succession of
561 ice ages (the last ice age maximum occurred approximately 22,000 years ago) and continental drift
562 that has progressively increased the distance between the spawning grounds and growth habitats
563 (Knights 2003). This demonstrates their evolutionary robustness (Knights 2003) and remarkable
564 adaptive capacity (Mateo *et al.* 2017a) based on adaptive phenotypic plasticity (Daverat *et al.* 2006;

Côté *et al.* 2014; Drouineau *et al.* 2014) and genetic polymorphism (Gagnaire *et al.* 2012; Pujolar *et al.* 2014; Ulrik *et al.* 2014; Pavey *et al.* 2015). 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 (Figures 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). Secondly, 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 do 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 XXth 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, i.e. approximately 1-3 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), world petroleum

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590 consumption which has increased by 3.5x since 1960, motor vehicles by a factor of16 since the
591 early 50s and increased water use for human consumption and agriculture (Figure 9). This
592 acceleration of human activity and consumption has been referred to as the "Great Acceleration"
593 (Steffen *et al.* 2005, 2015), and occurred about 20 years before the first signs of the decline in eel
594 populations, i.e. 1-2 eel generations. As mentioned earlier, river, estuaries and ecosystems have
595 suffered intense modifications over this period (Elliott and Hemingway 2002; Postel and Richter
596 2003; Basset *et al.* 2013, Postel and Richter 2003; Wolanski *et al.* 2011; Elliott and Whitfield 2011).
597 Eel populations are likely affected by global change as a whole, rather than by one specific
598 anthropogenic pressure, explaining why Castonguay *et al*. (1994a) could not identify a primary
599 cause for the decline of the American eel.

600

601 **The resilience of eels severely impaired by global change**

602 Several factors contribute to the resilience of eel populations. First, the presence of a brackish /
603 marine contingent (which skip the freshwater phase) can buffer the pressures specific to the
604 catadromous contingent such as dams, contamination, fishing or the parasite (ICES 2009).
605 Additionally, their very large diet spectrum (Sinha and Jones 1967; Tesch 2003), their resistance to
606 fluctuations in temperature, salinity, oxygen, food availability and temporary emersion (Brusle
607 1991; Tesch 2003) allow them to grow in a very large range of habitats. This plasticity in growth
608 habitat can generate a "storage effect" and a "portfolio effect" that mitigate against environmental
609 variability (ICES 2009). In a complex life cycle, a storage effect corresponds to a situation where a
610 specific stage of long duration and of limited sensitivity to environmental conditions, buffers the
611 effects of environmental conditions on other stages. For eels, the long duration of the continental
612 growth phase and its variability across habitats with generational overlaps allows the species to
613 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 resulted from the decline in silver eel abundance (Geffroy and Bardonnet 2015; Mateo et al. 2017b), 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 (Gagnaire *et al.* 2012; Côté *et al.* 2014; Pujolar *et al.* 2014; Ulrik *et al.* 2014; Pavey *et al.* 2015). 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 maximise 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), i.e. 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

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639 heterogeneity at both the distribution and catchment scale (Drouineau *et al.* 2014; Mateo *et al.*
640 2017a). In such a scheme, individuals are able to grow and survive in a wide range of habitats
641 thanks to phenotypic plasticity but some individuals are more adapted to some habitats than others
642 (ecotypes), and all individuals reproduce together (panmixia) ensuring that ecotypes are reshuffled
643 in each generation. The synergy of phenotypic plasticity and genetic polymorphism could explain
644 how a panmictic population can survive in such a wide and varied distribution area and be the basis
645 for the adaptive capacities of eels.

646 In this review, we have highlighted that not all pressures affect all habitats and individuals evenly.
647 Indeed, obstacles affect mostly individuals that settle preferentially in upstream habitats and habitat
648 loss mainly affects males located in the south-western part of the range of the European eel.
649 *Anguillicola crassus* has a greater impact on individuals that settle in freshwater habitats as opposed
650 to estuarine or marine (Kirk 2003). Finally, fisheries are not uniformly distributed, with European
651 silver eel fisheries mainly occurring at the edge of the distribution area, especially the northern
652 edge, though fisheries are also important along the Mediterranean coast (Castonguay *et al.* 1994a;
653 Moriarty and Dekker 1997; Dekker 2003b,c), and glass eel fisheries in the core (Dekker 2003c). By
654 affecting different habitats, anthropogenic pressures affect life history traits and ecotypes in
655 different ways (Figure 10). Climate change and glass eel fisheries probably affect all ecotypes:
656 climate change affects recruitment success. Glass eel fisheries, though not evenly distributed in the
657 distribution area, generally operate downstream of river catchments and consequently harvest
658 evenly all incoming glass eels. On the other hand, all the other anthropogenic pressures tend to
659 affect ecotypes corresponding to more upstream habitats. As such, these anthropogenic pressures
660 reduce the fitness of those individuals and can become an important selective pressure (Mateo *et al.*
661 2017). For example, half the American silver eels migrating down the St. Lawrence River, one of
662 the most productive areas for American eel (Casselman 2003), have been killed by hydropower
663 dams and fisheries (Verreault and 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.

Additionally, 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 porfolio 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 penalising some ecotypes more than others (Mateo *et al.* 2017b).

Other implications for eel management and research

The eel decline due to global change has several implications for management. First, global causes means 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 *et al.* 2003; Dekker and Casselman 2014) that called for immediate action and coordination at all scales. Though some progress has been made since the first declaration, there is clear need to improve management coordination among regional, national and

688 international authorities. Dekker (2016) pointed out the difficulties in the implementation of the Eel
689 Management Plan in Europe. International coordination has not yet started for the American eel
690 (MacGregor *et al.* 2008, 2009; Jacoby *et al.* 2014; Castonguay and Durif 2016). The East Asia Eel
691 Resource Consortium does not yet have any official support (Jacoby and Gollock 2014b), and the
692 first attempt at international coordination took place in 2014 between South Korea, China, Taiwan
693 and Japan with an agreement on the amount of glass eel that can be used for aquaculture.

694 Second, though it is difficult to disentangle the relative effects of various anthropogenic pressures
695 implicated in the decline, it is important to develop tools and methods to monitor and quantify their
696 effects in the future. Eels grow in very small and almost independent units corresponding to river
697 catchments (Dekker 2000b) with specific anthropogenic pressures, within which eels have different
698 life history traits. Consequently, it is difficult to assess the stock and extrapolate the overall effect of
699 anthropogenic pressure at the population scale, from observations collected at the river catchment
700 scale (Dekker 2000a). However, the improvement in data quality and the recent development of a
701 generic model that can be used at a larger geographic scale is a first step. For example, the GEREM
702 model provides estimates of glass eel recruitment that can be used to assess glass eel fishery
703 exploitation rates (Drouineau *et al.* 2016a; Bornarel *et al.* 2018). The models EDA (Briand *et al.*
704 2015) or SMEP (Aprahamian *et al.* 2007) can be used to assess the abundance of yellow eels in
705 river catchments. These can then be coupled with other models to assess spawner escapement and
706 the effect of different anthropogenic pressures such as hydropower production or fisheries (Jouanin
707 *et al.* 2012). Stock assessment models have also been proposed to support management (Dekker
708 2000a; Bevacqua and De Leo 2006; Oeberst and Fladung 2012; Bevacqua *et al.* 2015). However,
709 few tools are currently available to assess the impact of contaminants on eel populations. Similarly,
710 there is a lack of tools to quantify the effect of lost habitats on population dynamics, though some
711 methodologies are available which can quantify the amount of habitat lost due to fragmentation.
712 Though it is not possible to quantify the historical effects of anthropogenic pressures, quantifying

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and predicting pressures in the future would provide valuable information to prioritise management actions. Quantification is even more important since (1) 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), (2) management practices cannot mitigate anthropogenic pressures at similar temporal scales: reduction in fishing efforts are recent but are thought to operate quickly, whereas effort to mitigate contamination or fragmentation are older but are 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 (McDowall 1999; Limburg and Waldman 2009; Mota *et al.* 2015). The effects of fragmentation (Larinier 2001; Limburg and Waldman 2009; Haxton and Cano 2016), global warming (Friedland 1998; Friedland *et al.* 2000; Lassalle *et al.* 2008, 2009; Jonsson and Jonsson 2009; Elliott and Elliott 2010; Rougier *et al.* 2014), fisheries and pollution (McDowall 1999; Limburg and Waldman 2009) have been documented for most of these species. More generally, most migratory animals regardless of taxa have undergone similar declines (Sanderson *et al.* 2006; Berger *et al.* 2008; Wilcove and 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 has 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 XXth century, was too fast for the adaptive capacity of the eel, especially since 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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1971
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1973

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1974 **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 *et al.* 2008b)	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	Oscillations biological production in the Sargasso Sea

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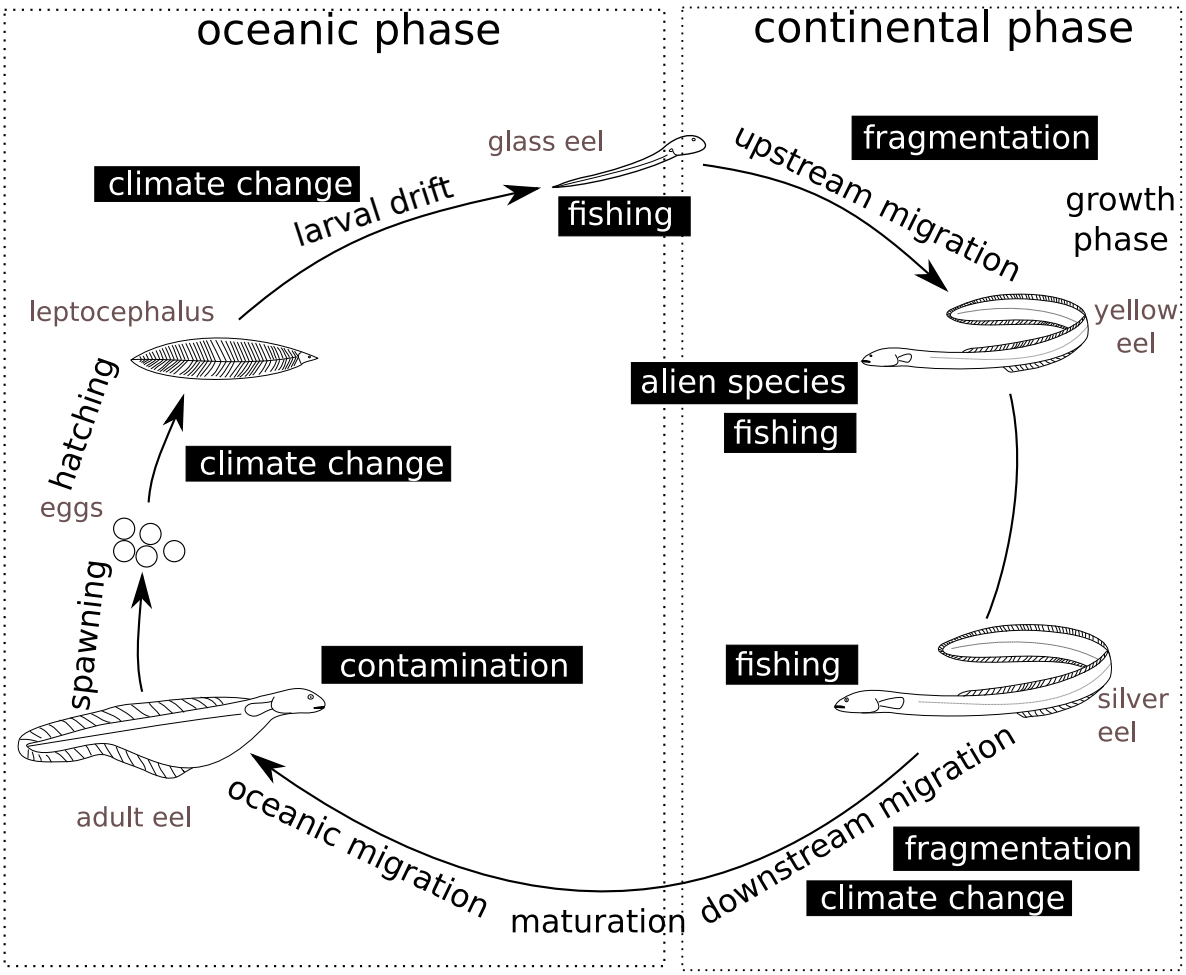
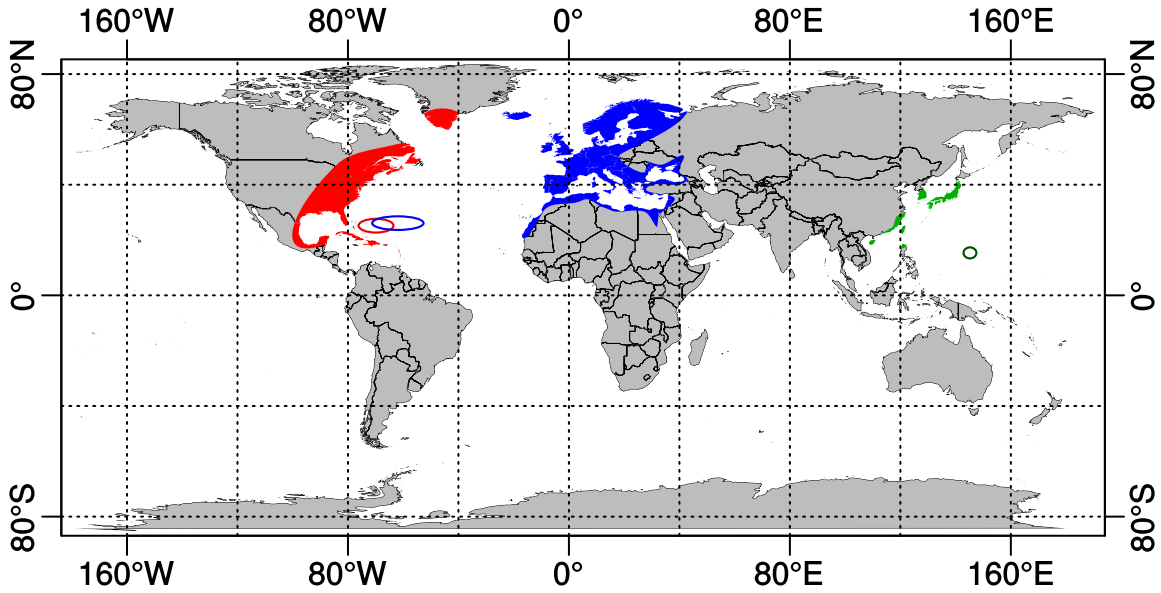
		Gulf Stream Index	
(Zenimoto *et al.* 2009)	Japanese eel	Lagrangian circulation model	Success of larval transport due to oscillation of the North Equatorial Current
(Munk *et al.* 2010)	European eel and presumably American eel	Field observations of oceanic fronts in the Sargasso Sea	Oscillations of fronts that alter the efficiency of retention on feeding grounds
(Durif *et al.* 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 Amercial eels	Field measurement of diatoms and cyanobacterial abundances in the Sargasso Sea	Lower availability of food after oceanic regime shift

1975



1977 **Figure 1** Lifecyle of the 3 *Anguilla* species and effects of global change components.



1979 **Figure 2** Spawning grounds (Tsukamoto *et al.* 2011; Miller *et al.* 2015) (open circles) and

1980 continental distribution of yellow eels (filled shapes) (Jacoby *et al.* 2015) for *A. rostrata* (red), *A.*

1981 *anguilla* (blue) and *A. japonica* (green).

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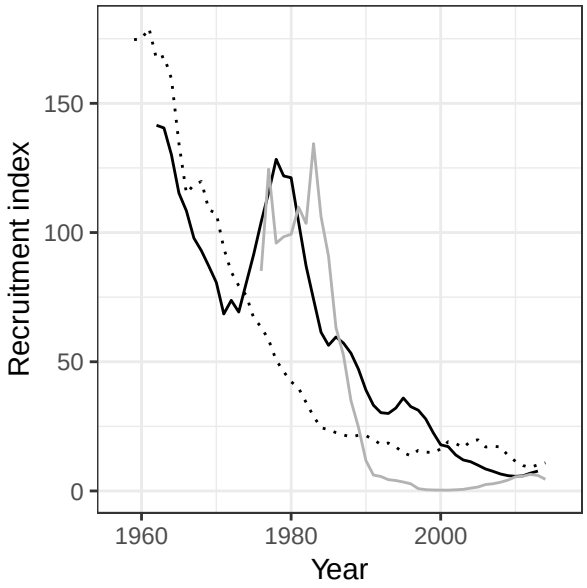
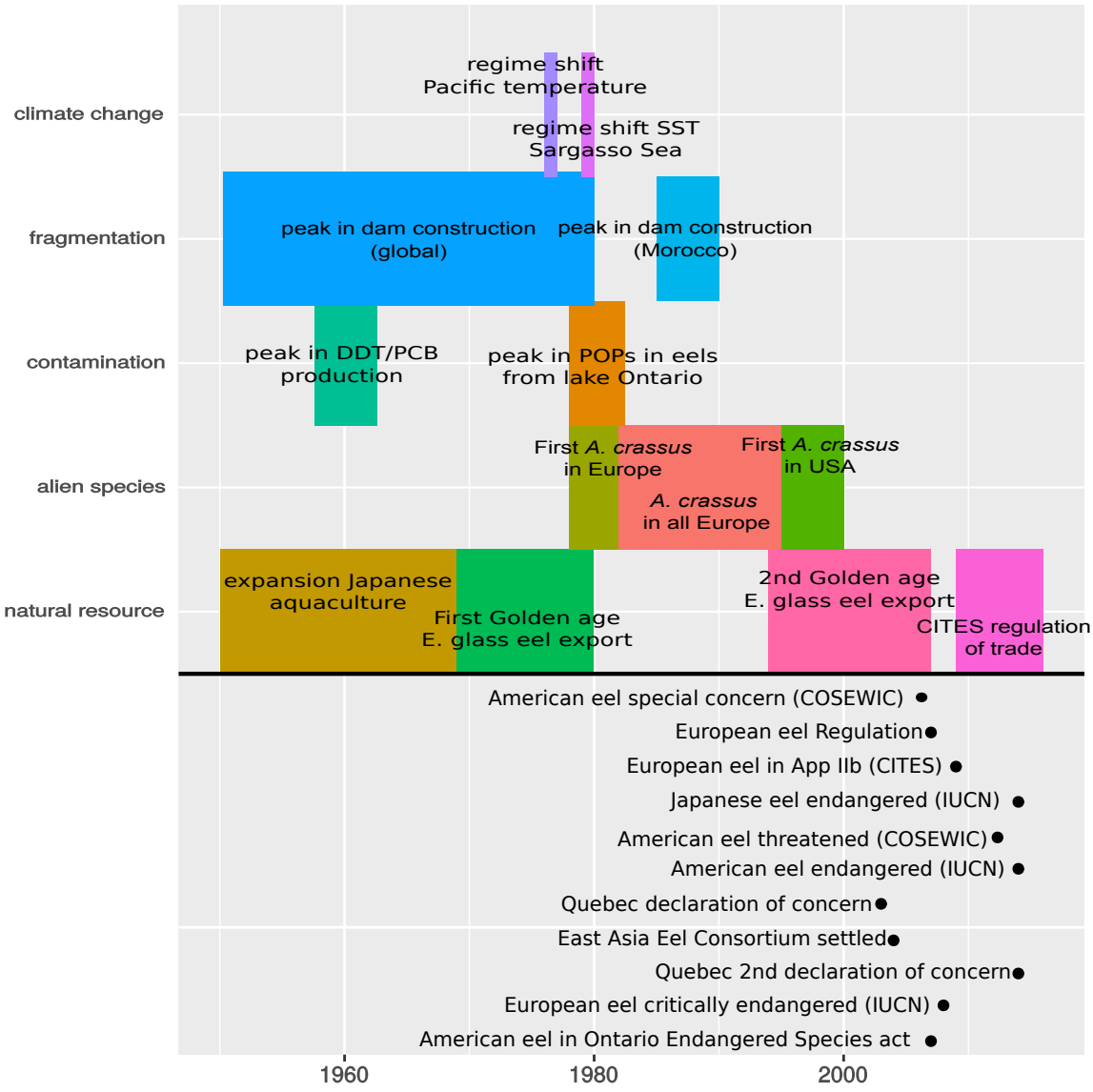


Figure 3 Recruitment series for the three temperate eel species. European eel series (black solid line) corresponds to the Elsewhere Europe index provided by ICES (2015a). American eel recruitment (grey solid line) corresponds to the recruitment in Lake Ontario through monitoring of eel passage at Moses 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 years moving geometric mean and expressed as a percentage of 1960s-1970s geometric mean.



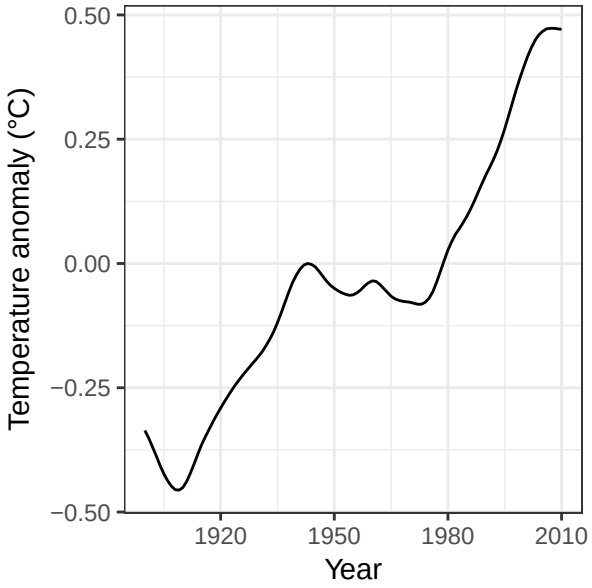
1992

1993 **Figure 4** Timelines of main events with respect to the five global change components and

1994 management of eel populations. Committee on the Status of Endangered Wildlife in

1995 Canada(COSEWIC) is a committee of experts that assesses and designates which wildlife species

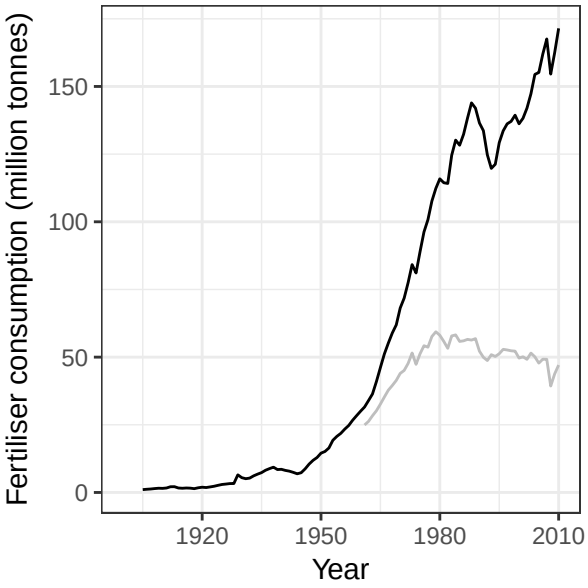
1996 are in some danger of disappearing from Canada



1997

1998 **Figure 5** Ocean temperature anomalies (left panel). Source (Morice *et al.* 2012; Steffen *et al.* 2015)

1999



2000

2001 **Figure 6** Global fertiliser consumption in OECD countries (grey) and in the world (black). Source

2002 (Steffen *et al*. 2015, International Fertilizer Industry Association Database)

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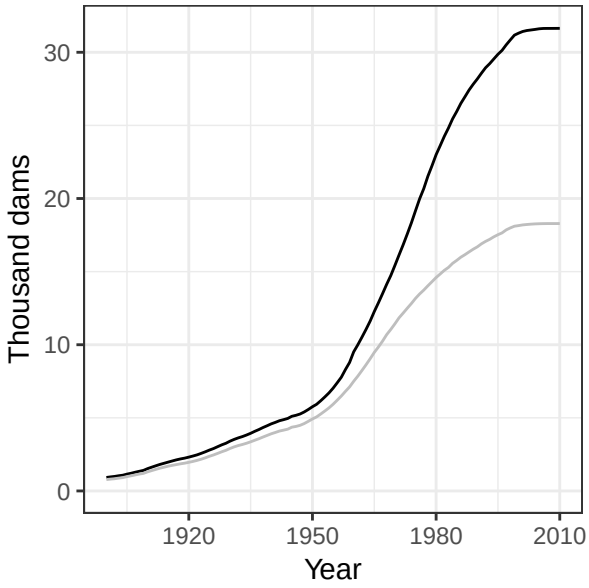

2003

2004 **Figure 7** Accumulative number of large dams in OECD countries (grey) and in the world (black).

2005 Source (World Commission on Dams 2000; Steffen *et al*. 2015)

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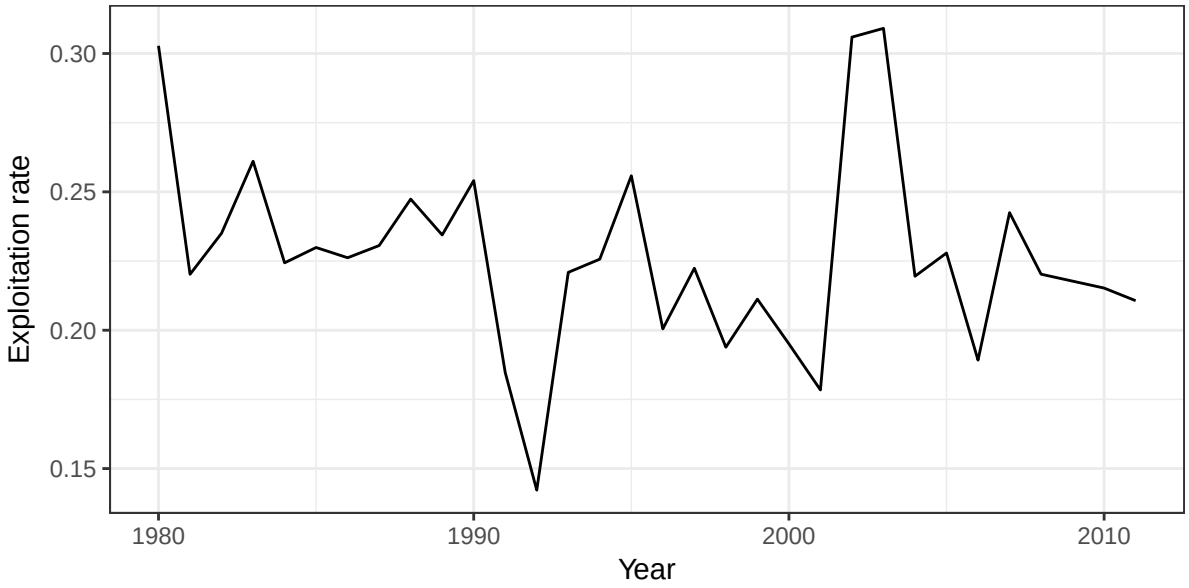

Figure **8** French glass eel exploitation rates expressed as the ratio of catch (tonnes) to recruitment (tonnes). Catches corresponds to an appraisal of historical catches based upon market and fishery data (Briand *et al.* 2008) while recruitments was estimated using the model GEREM (Drouineau *et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

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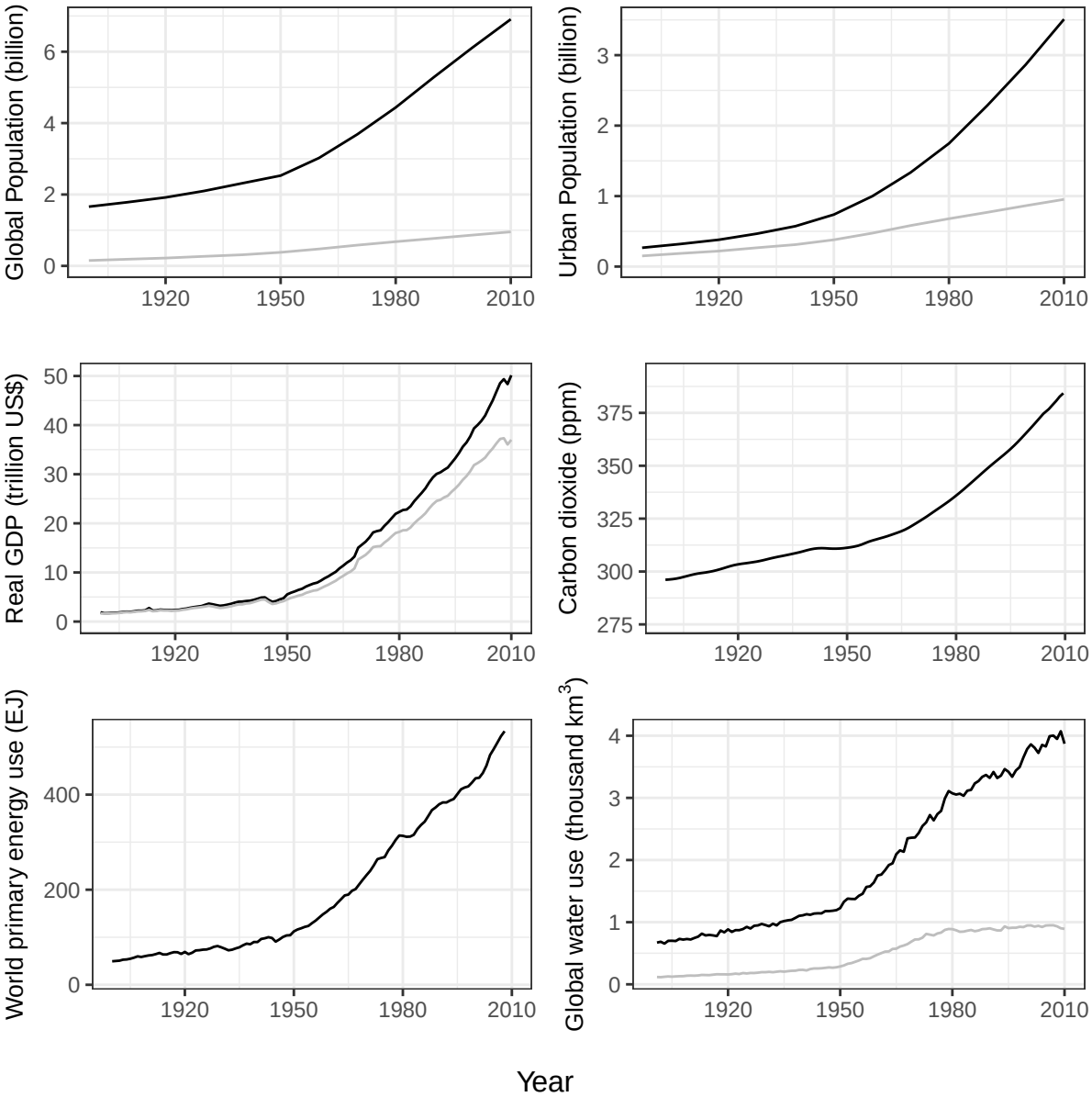
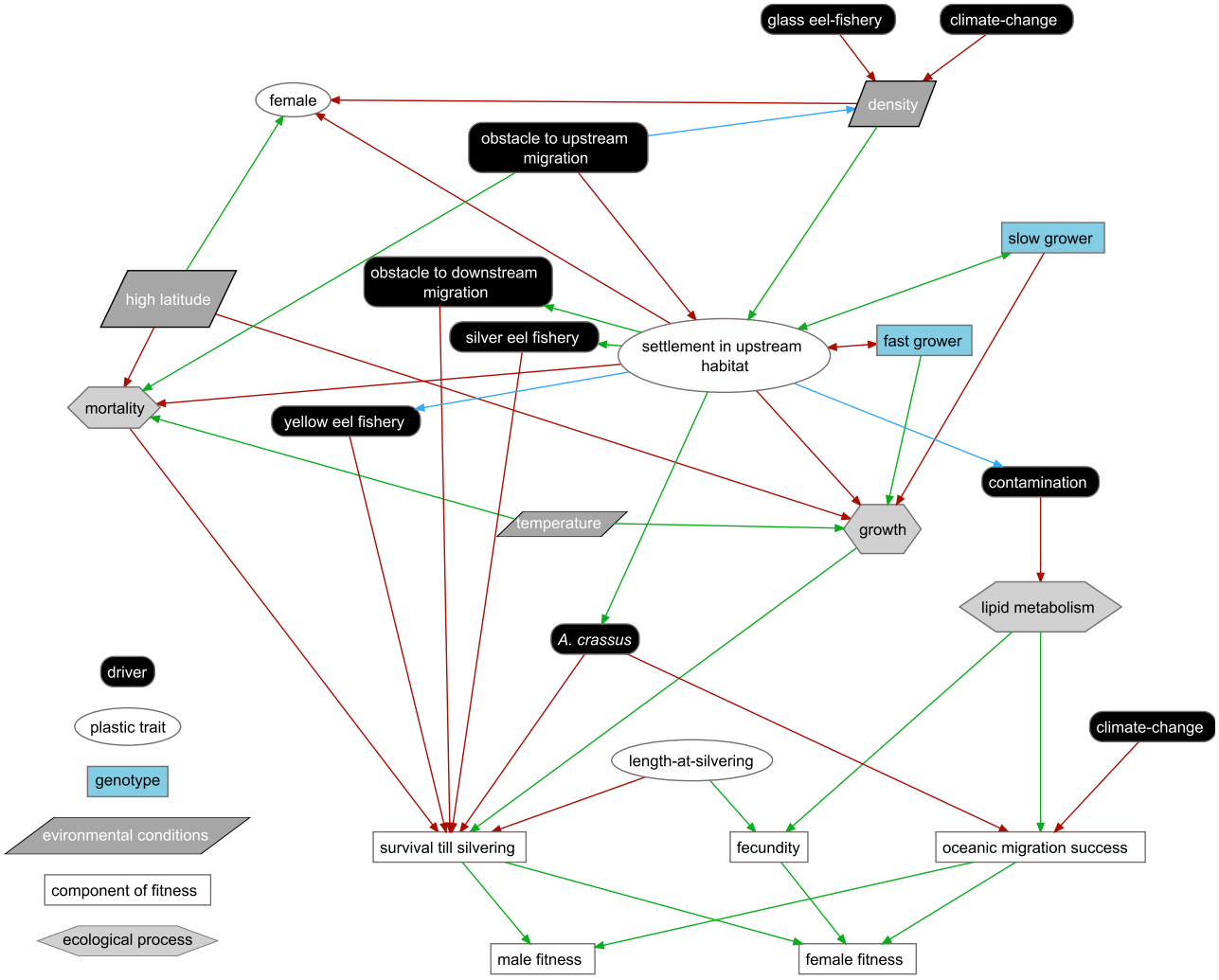


Figure 9 Various indicators of the Great Acceleration for OECD countries (grey) or the entire world (black). GDP=gross domestic product. Carbon dioxide from firn and ice core records (Law Dome, Antarctica) and Cape Grim, Australia (deseasonalised flask and instrumental records). Sources (Steffen *et al.* 2005), population (Goldewijk *et al.* 2010), CO2 (Etheridge *et al.* 1996; MacFarling Meure 2004; MacFarling Meure *et al.* 2006; Langenfelds *et al.* 2011), water use (Alcamo *et al.* 2003; aus der Beek *et al.* 2010; Flörke *et al.* 2013), energy use (GEA Writing Team 2012), GDP (World Bank indicators)



2019

2020 **Figure 10** Adaptation mechanisms to environmental heterogeneity as proposed in (Mateo *et al.*
2021 2017a;b ; Gagnaire *et al.* 2012; Côté *et al.* 2014; Drouineau *et al.* 2014; Boivin *et al.* 2015). A red
2022 arrow stands for "unfavourable", a green arrow stands for "favourable". A blue arrow stands for a
2023 relationship which is either favourable" or "unfavourable" depending on situations. There is a
2024 double arrow between genotypes and "settlement in upstream habitats" because it represents
2025 "spatially varying selection" and "genetic-dependent habitat selection". Regarding phenotypes,
2026 female is considered as opposite to male and "settlement in upstream habitats" as opposite to
2027 "settlement in downstream habitats".

2028