REVIEW

Hard times for catadromous fish: the case of the European eel *Anguilla anguilla* (L. 1758)

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ABSTRACT

Catadromous fish species can be defined important organisms for their ecological, economical, and cultural value. Because of a complex life cycle, catadromous fish species are exhibited to the cumulative effect of multiple anthropogenic threats that resulted in worldwide decline since the beginning of the 20th century. Among the most iconic catadromous species, the European eel *Anguilla anguilla* has aroused considerable interest, and to date, many aspects of its life cycle remain relatively unknown. Although conspicuous efforts by the research to ensure the perpetuation of the species were conducted, the identification of the best tools to reduce the threats that affect eels remains challenging. In this narrative review, the state of the knowledge and main threats about the life cycle, the habitat occupancy, the recruitment, and migration patterns of the European eel have been reported.

INTRODUCTION

The term diadromy describes migrations between freshwater and marine environments (Myers, 1949; McDowall, 1988; McDowall, 1992). Diadromous species include less than 3% of the world fish fauna (Eschmeyer and Fong, 2016), among which several ones are economically and culturally important, such as freshwater anguillid eels and salmons (Chapman *et al*., 2012).

Catadromous fish are characterized by a complex life cycle where fish breed in the ocean and growth in continental coastal and/or inland waters (McCleave, 2001), as seen in anguillids (Tesch, 2003; Elliot *et al*., 2007). Main ecological services provided by catadromous fish consist for example in the provision of food, and in the regulation of ecosystem functions by transporting nutrients and linking different biomes (Druineau *et al*., 2018a). Globally, these animals have been appreciated for human consumption showing a relevant economic interest (Costa-Dias *et al.,* 2009; Feunteun and Laffaille, 2011). Catadromous fish can be also used as indicators of environmental quality and functionality (Smith *et al*., 2016). For instance, they are also commonly used as a metric in the assessment of water bodies ecological status in the European Water Framework Directive (Delpech *et al*., 2010) or as bio-indicators of water quality (Amara *et al*., 2009), reflecting both habitat longitudinal connectivity and habitat quality. In this context, an exiguous number of catadromous fish species are identified as 'umbrella species' in order to ensure the protection of these species and their habitats (Rochard *et al*., 2009). They are also magnified by many cultures, foster a belonging sense, and support million-dollar fishing (Garman, 1992; Close *et al*., 2002; Montgomery, 2003; Chasco *et al*. 2017; NOAA, 2017). Because of this general interest, catadromous fish are object of studies in all their dimensions (Drouineau *et al*., 2018b) and strongly linked to research questions associated with animal migration (Secor, 2015; Morais and Daverat, 2016).

Catadromous fish use along their migration pathways a variety of habitats and face many diverse environmental threats (McIntyre *et al*., 2016). In Europe, as observed for most migratory animals (Sanderson *et al*., 2006; Wilcove and Wikelski, 2008), a worldwide decline of migratory fish has been recorded at least since the beginning of the 20th century (Béguer *et al*., 2007; Wolter, 2015; Lambert *et al*., 2019). The causes are numerous and likely cumulative (*e.g.*, obstacles to migration, deterioration in essential habitat and water quality, unsustainable fisheries, parasite introductions), although quantitative evidence has been rarely demonstrated (Dekker and Casselman, 2014). As a result, many catadromous species are now classified as rare, endangered, or extinct, in the IUCN Red List (IUCN, 2019). There is, therefore, an urgent need to develop approaches that provide reliable quantification of the specific impacts of the different anthropogenic pressures acting on catadromous species. This would help support the implementation of effective mitigation measures and provide adequate tools for national and international regulation around the world. Among the most iconic catadromous species, the European eel *Anguilla anguilla* (Linnaeus, 1758) has been the focus of many studies (*e.g.*, Dekker, 2003a; Bonhommeau *et al*., 2008; Kettle *et al*., 2011; Baltazar-Soares *et al.*, 2014; Schiavina *et al*., 2015; Aalto *et al*., 2016; Righton *et al*., 2016; Bornarel *et* al., 2018; Bevacqua *et al*., 2019; Dekker, 2019). The life cycle of the European eel *A. anguilla* has stimulated great curiosity and interest since at least the 4th century BC, where already some important Greek philosophers like Aristotle hypothesized on the origin of this species, which remained enshrouded in mystery for millennia. The recent interest increase in eel biology is primarily linked to conservation issues. Therefore, to implement our knowledge about the main natural and anthropogenic threats to its survivorship and identify possible solutions to preserve it, there is an urgent need to gain further insights into *A. anguilla* life-history.

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In this narrative review, we present the state of the knowledge about the life cycle, habitat occupancy, recruitment, and migration patterns of the European eel and about the major threats most likely have contributed to the decline of eels.

LIFE CYCLE, HABITAT OCCUPANCY AND MIGRATION PATTERNS OF

The life cycle of the genus *Anguilla*: common features

Eels of the genus *Anguilla* (Schrank, 1798) are the only genus of Anguilliformes with a catadromous life cycle (McDowall, 1988). The life cycle of anguillid eels involves five developmental stages: leptocephalus (larvae), glass eel (transparent juvenile stage), elver (pigmented juvenile stage), yellow eel (immature adult) and silver eel (partially mature adult) (Bertin, 1956; Tesch, 1977; Cresci, 2020). The larval stage duration varies in different regions worldwide and can last from several months to some years, according to the species and biogeographic region (Tsukamoto, 1990; Lecomte-Finiger, 1992; Cheng and Tzeng, 1996; Arai *et al*., 1999; 2001; 2003; Wang and Tzeng, 2000; Marui *et al*., 2001; Robinet *et al*., 2003; Robinet *et al*., 2008; Reveillac *et al*., 2008; 2009; Bonhommeau *et al*., 2010; Han *et al*., 2016; 2019; Hewavitharane *et al*., 2020). The larval phase suffers high mortality thereby influencing recruitment success (Cushing, 1990; Durant *et al*., 2007). After metamorphosis into glass eels, juveniles leave oceanic waters, starting the upstream migration crossing coastal waters (Tesch, 2003; Cresci, 2020). Glass eels represent the recruitment phase to continental waters (ICES, 2011) and constitute the natural source of supply of the species because its artificial reproduction is not yet possible (Pedersen and Ramussen, 2016). Glass eels develop into elvers and settle as yellow eels for many years (about 5-25 years) in coastal and inland water habitats (*e.g*., estuaries, rivers, streams, ponds, and lakes) (Tesch, 2003; Cresci, 2020). After this trophic phase, eels start the downstream migration during the silver eel stage (Tesch, 2003) that is initiated by endogenous and exogenous signals that coincide with optimal conditions for successful migration (Sandlund *et al*., 2017). The migration peaks in rivers properly occur during rainfall events associated with flow pulses, affecting water velocity, turbidity, and conductivity (Cullen and McCarthy, 2003; Durif *et al*., 2008; Drouineau *et al*., 2017). Once gonad maturation starts, eels run downstream mainly at night, during rising river flow phases (Behrmann-Godel and Eckmann, 2003), which also provide protection against predation and reduce the swimming energy cost to return to the offshore spawning area (Tesch, 2003; Sandlund *et al*., 2017; Cresci, 2020).

Habitat occupancy

The European eel *A. anguilla* is a panmictic species (Palm *et al*., 2009; Enbody *et al*., 2021) distributed across most of the coastal countries in Europe and North Africa and spanning the entire Mediterranean basin (ICES, 2018). Because the complex life cycle, the cryptic behavior, and body shape features of eels, results hard to find appropriate and standardized sampling technique for the monitoring of the European eel in several aquatic environments (Naismith and Knight, 1990; Lasne and Laffaille, 2009). Furthermore, many aspects of the resident stage of eels in freshwaters during their growth phase are still insufficiently understood such as ecology in terms of space and time use (Feunteun *et al*., 2003; Imbert *et al.*, 2010).

The habitats occupancy can be investigated through the otolith microchemistry used to determine the type of habitat of individuals throughout their life, primarily using the strontium (Sr) to calcium (Ca) ratio to distinguish freshwater phases from brackish and seawater phases (Tsukamoto and Aoyama, 1998; Arai *et al.*, 2006; Shiao *et al*., 2006; Lin *et al*., 2011 Arai *et al*., 2019). More recently, other elements, such as barium (Ba) and manganese (Mn), have been used to assess finer-scale movement patterns (Benchetrit *et al*., 2017). This technique constitutes a reliable tool for the assessment of habitat use and growth throughout the entire life span between freshwater and saline waters (Clément *et al*., 2014).

Experimental electrofishing has been recognized an efficient sampling method to catch eel in freshwaters despite some limits (*e.g.*, deep waters) (Laffaille and Rigaud, 2008), while fishery-based time-series are usually utilized to assess eels' temporal trends (ICES, 2020). Glass eel fisheries are carried out in the estuaries, or under dams, to study the natural abundance of glass eels in time and space (Dekker *et al*., 2003b). Several dipnet types are applied, on foot or using boats (Aubrun, 1986), trawls (Aubrun, 1987), stow nets (Weber, 1986), and fyke nets (Ciccotti *et al*., 2000). Fisheries for yellow and silver eels foresee a wide range of gears that include nets, spears, pots, hooks, in coastal areas, lagoons, rivers, lakes, and streams (Dekker *et al*., 2003b).

Several studies used telemetry to investigate individual movement patterns, site fidelity, habitat use and home range exploitation in relation to seasonal and environmental factors (*e.g.*, Ovidio *et al*., 2013; Barry *et al*., 2015; Piper *et al*., 2017; Trancart *et al*., 2018; Dorow *et al*., 2019; Piper *et al*., 2019; Teichert *et al*., 2020).

Furthermore, diel, and seasonal phenology and the effect of environmental drivers on non-migrant eel movements were investigated using acoustic camera to evaluate the presence of eels swimming toward the inland waters (Lagarde *et al*., 2021). Studies on the presence of eels' population were conducted also with visual observation in inland waters (*e.g.*, lakes and reservoirs) (Rossier, 1997; Schulze *et al*., 2004).

Another tool that could support to understand the eels' habitat occupancy is represented by the environmental DNA (eDNA) analysis (Knudsen *et al*., 2019). eDNA assays for target species and eDNA metabarcoding are both promising techniques for establishing species presence from environmental samples (Taberlet *et al*., 2012; Evans *et al*., 2016; Deiner *et al*., 2017). These indirect methods are cheap to implement at a large scale and can be used to quickly establish the spatial distribution of a target species (Atkinson *et al*., 2018; Bracken *et al*., 2019). Instead, when it is difficult to assess the presence of a species because the species couldn't simply be present, direct methods (fish tagging) or physical survey assessments may be more appropriate (Kemp and O'Hanley, 2010).

Juveniles' migration and orientation

Migration mechanisms, including orientation, behavior and route architecture throughout the entire life of anguillid eels have been revealed by means of the recent advanced technologies like agent-based model, ABM, particle tracking model of upstream migrating juvenile eels (Padgett *et al*., 2020; Benson *et al*., 2021), motion analysis of glass eels (Eldrogi *et al*., 2018), tiny acoustic transmitters (Fischer *et al*., 2019; Mueller *et* al., 2019; Liss *et al*., 2021), satellite tracking for migrant adults (*e.g.*, Aarestrup *et al*., 2009; Westerberg *et al*., 2014; Wysujack *et al*., 2015; Amilhat *et al.*, 2016; Righton *et al*., 2016 for the European eel; Manabe *et al*., 2011; Higuchi *et al*., 2018 for the Japanese eel *Anguilla japonica*; Schabetsberger *et al*., 2013; 2015; 2019 for Pacific eels *A. marmorata* and *A. megastoma*; Beguer-Pon *et al*., 2015 for the American eel *Anguilla rostrata*).

To reduce migration energy costs (Forward and Tankersley, 2001; Bureau du Colombier *et al*., 2007; Edeline, 2007), juveniles catadromous species are transported in continental waters by entering the water column during floodtides and descending to the bottom during ebbtides using flood tide transport (FTT) to migrate through estuaries and thus colonize catchments (Forward and Tankersley, 2001). But in absence of this condition, an alternative migratory tactic to undertake upstream migration reckon on an active swimming running after salinity gradient (Cresci, 2020), and using earthy and green odors as attractant (Sola and Tongiorgi, 1996). For instance, several authors showed that chemical cues (*e.g.*, green odors, amino acids, and bile salts) such as freshwater plumes and salinity gradients transporting inland odors into estuaries can guide estuarine juveniles' migration (Tosi *et al*., 1988; Tosi *et al.*, 1989; Crnjar *et al*., 1992; Tosi and Sola, 1993; Sola, 1995; Atta *et al*., 2013). Indeed, eels possess one of the most sensitive olfactory systems among fish, and olfaction plays a central role in their life (Huertas *et al.*, 2008). Glass eels, for example, are attracted by inland odors, derived from the decomposition of detritus associated with the flora and microfauna in freshwater (Sorensen, 1986). Among inland odors, geosmin (trans-1,10-dimethyltrans- 9-decalol) play a role in attracting glass eels (Tosi and Sola, 1993; Sola, 1995). In addition, it would seem that geosmin operates as an attractant in freshwater and as a repellent in sea water (Tosi and Sola, 1993). Moreover, glass eels' migratory behavior may be also affected by physiological changes, alterations of locomotor activity, and decreasing of body condition (Edeline *et al.*, 2007). Social interactions represent a selective element for the migration and timing of glass eels' settlement linked to specific habitat survival and growth (Edeline *et al*., 2009).

Some studies provided evidence that thyroid hormones are involved in glass eel migration (Edeline *et al*., 2004; 2005). Decreasing levels of thyroid hormones in juvenile eels might explain the decreasing rate of development and the decreasing propensity to migrate during the transition from the leptocephalus larval to the elver stage (Jegstrup and Rosenkilde 2003). This hypothesis is corroborated in subadults of the American eel *A. rostrata*, in which elevated T4 plasma levels are correlated with increased locomotion activity (Castonguay *et al*., 1990). Furthermore, European glass eels' river colonizers exhibit increased thyroid hormone concentrations when compared to estuarine migrants (Castonguay *et al*. 1990; Edeline *et al*., 2004) suggesting a switch from a high migrating to settling behavior strongly linked to thyroid hormones production.

The migration of catadromous fish can also be explained with the 'pheromone hypothesis', according to which fish can release particular odors into the water (pheromones, likely amino acids; Crnjar *et al*., 1992) functioning as attractants for conspecifics (Schmucker *et al*., 2016). The attractive power of these cues is stage dependent in the eels, it is more accentuated on glass eels and gradually disappears in pigmented glass eels and elvers likely due to physiological and behavioral changes, alternative cues possibly become main attractants (Schmucker *et al*., 2016; Galbraith *et al*., 2017).

Mechanisms regulating glass eels' orientation are most likely innate and involve geomagnetic-based compass mechanisms based on the inclination and intensity of the magnetic field (Naisbett-Jones *et al*., 2017). However, leptocephali stage present in the Sargasso Sea may not possess that same magnetic sensing ability as the glass eels because substantial body rearrangements and related physiological changes (Tesch, 2003; Baltazar-Soares and Eizaguirre, 2017).

More recent studies confirmed that glass eels can orient their migration using the Earth's magnetic field (Cresci *et al*., 2017, Cresci *et al*., 2019a) and lunar cues (Cresci *et* *al*., 2019b), as a reference to imprint a memory of tidal currents in estuaries and to facilitate position holding and upstream migration (Cresci *et al*., 2019b). However, although many individual pieces of the complex puzzle of glass eels' orientation and migratory behavior have been elucidated, a holistic mechanism to discriminate how they migrate from the continental slope to estuaries and whether this path is memorized until returning to the sea in the adult stages is still far from being identified.

Adult migration behavior

The spawning migration patterns of the European eel in the Atlantic Ocean have been studied due to their long distances (about 2000–8000 km) (Schmidt, 1922; Miller *et al*., 2019). The long migration paths are notable because the amplitude of their scale and the excellent ability to trace the birth location using an unrevealed combination of sensory cues (McCleave and Kleckner, 1985).

Mark–recapture studies have been used to evaluate eels' home range, habitat preferences, diel and seasonal movements (Jellyman *et al*. 1996; Oliveira, 1997; Laffaille *et al*., 2003).

Direct observations of the migratory behavior of yellow and silver eels were made using electronic tags (*e.g.*, Amilhat *et al*., 2016; Righton *et al*., 2016; Béguer-Pon *et al*., 2018; Dorow *et al*., 2019; Teichert *et al*., 2020; Trancart *et al*., 2020). Telemetry represents a reliable method to study the spatial ecology of eels, providing the opportunity to track fish in real time or from archived data to remote receivers, enabling data to be retrieved without recapturing the tag (Torstad *et al*., 2013). The development and miniaturization of pop-up satellite archival tags have allowed the tracking of silver eels at sea, unravelling part of the mystery surrounding the oceanic migration of anguillid eels (Jellyman and Tsukamoto 2002; Aarestrup *et al*. 2009; Béguer-Pon *et al*. 2015, Amilhat *et* al., 2016). Fundamental telemetry studies on silver eels investigated their migration from freshwaters to oceanic spawning areas, including survival, progression rate and behavioral and external physical factors associated with migration. To date, no telemetry studies on eels have been used with other available physiologically oriented sensors, such as electrocardiography or electromyography (Cooke *et al*. 2013), or any other environmental sensors, such as conductivity or oxygen, while tracking eels in the wild.

Recently, some studies have shed light on the possible effects of global change in eels' migration patterns: climate change and warming related thermal and hydrological modifications of aquatic ecosystems could delay or bring forward silver eels (Verreault *et al*.,2012) and alter patterns of glass eels' migration (Moore and Jarvis, 2008). Migratory phenology and habitat change as affected by current climate change should therefore be a priority of future studies.

EELS' RECRUITMENT DYNAMICS

Success and extent of eels' recruitment depends both on global (Knights, 2003; Kettle and Haines, 2006; Bonhommeau *et al*., 2008; Pacariz *et al*., 2014; Gutierrez-Estrada and Pulido-Calvo, 2015; Bornarel *et al*., 2018) and local factors, whose interaction modulate spatial and temporal dynamics of recruits entering brackish environments and freshwaters (Gascuel *et al*.,1995; Arribas *et al*., 2012; Harrison *et al*., 2014; Trancart *et al*., 2014; Aranburu *et al*., 2015). Recruitment dynamics at the local scale can vary daily, seasonally, and annually (Bru *et al*., 2009; Laffaille *et al*., 2007; Zompola *et al*., 2008; Arribas *et al.*, 2012, Podda *et al*., 2020), are well known for Atlantic estuaries and rivers of Europe (Beaulaton and Castelnaud, 2005; Harrison *et al*., 2014), and relatively less known for the estuaries located in the southernmost distribution area (Arribas *et al*., 2012).

Although only one cohort recruits each year (Desaunay and Guerault, 1997), glass eels arrive in different waves from different routes (Boëtius and Harding, 1985). The preference of glass eels for freshwater or brackish water varies with the body condition and the timing of arrival to the continental shelf (Edeline *et al*., 2005). Reconstructions of exact hatching site and migration routes of the larvae and glass eel, based on mere analyses of recruitment and sampling data (Dekker, 1998; Lecomte-Finger, 1992), have been carried out since the early 20th century (Boëtius and Harding, 1985; Van Ginneken and Maes, 2005; Westerberg *et al*., 2018).

Most of the available multi-year temporal series on glass eels' recruitment to European estuaries is based on fishery and/or scientific surveys, however pluriannual fishery independent studies are very scarce. Fishery data-based glass eels' recruitment estimates generally suffer from sampling (methods and protocols) and temporal biases (fishing season). For example, in Europe, most surveys to estimate recruitment rates have been conducted in rivers or estuaries, where the eels' dispersion is influenced by the riverbed or river mouth width, allowing easier glass eel samplings (Adam *et al*., 2008; Bru *et al*., 2009; Zompola *et al*., 2008).

Models like the glass eel recruitment estimation model one (GEREM)(Drouineau *et al*. 2016) estimated the annual glass eel recruitment at different spatial scales, providing a recruitment index to robustly compare spatial variation trends, with large biases for specific regions where data are scarce or not existent (*e.g.*, North Africa, Eastern Mediterranean, and the Baltic Sea).

Moreover, it must be noticed that an accurate knowledge of the physical-chemical characteristics of the surveyed environments is also needed to properly assess movement and distribution of eels in both the biomes hosting their life cycle (Adam *et al*., 2008). This need creates a significant challenge: precise information on eels' numbers entering inland waters and moving through the biomes would be collected to understand recruitment dynamics, but, yet it is hard to be obtained because of the complex, often unpredictable, environmental variability of shallow water ecosystems that can mask natural patterns at the relevant spatial scales. Implementing standardized data collection programmes of glass eels' abundance should be therefore a major investment of future research and stock assessment protocols.

THREATS TO *A. ANGUILLA*

The global status of the eel is primarily a consequence of a prolonged decline of its recruitment across the entire distribution area (Moriarty and Dekker, 1997; ICES, 2020 and author therein). Many factors have been identified as recruitment short- or medium-term drivers but, so far, it has been difficult to reach clear conclusions about what are the primary drivers of its decline. Multiple environmental factors (*e.g.*, river flow, changes in the North Atlantic Oscillation, warming of sea surface temperature, currents) probably affected the documented decline (*e.g.*, Gandolfi *et al*., 1984; Domingos, 1992; Elie and Rochard, 1994; de Casamajor *et al*., 1999; Prouzet, 2002; Jellyman and Lambert, 2003; Knights, 2003; Polyakov *et al*., 2005; Bouvet *et al*., 2006; Bureau Du Colombier *et al*., 2007; Friedland *et al*., 2007; Laffaille *et al*., 2007; Adam *et al*., 2008; Bonhommeau *et al*., 2008; Crivelli *et al*., 2008; Kettle *et al*., 2008; Zompola *et al*., 2008; Miller *et al*., 2009; Durif *et al*., 2011; Kettle *et al*., 2011; Arribas *et al*., 2012; Baltazar-Soares *et al*., 2014; Hanel *et al*., 2014; Milardi *et al*., 2018; Podda *et al*., 2020).

While eels are still a common species throughout Europe, their stocks have been declining rapidly during the last 40-50 years (Dekker, 2016). The decline of the eel global stock affects indeed its entire geographical range, also concerning the southern part of its distribution area, as documented by a concurrent decline in glass eels' recruitment, as well as by contracting local stocks in the Mediterranean Region (Ciccotti, 2005; Aalto *et al*., 2016; Amilhat *et al*., 2016). Silver eels' abundance decreased by as much as 90% between 1975 and 2010 (Bevacqua *et al*., 2015) with human mediated activities being a contributing factor to this decline (Calles *et al*., 2010; Feunteun, 2002; Piper *et al*., 2013). It is known that a combination of natural causes and anthropogenic pressures has been impacting both the eel stock and its habitats (Jacoby *et al*., 2015; Miller *et al*., 2016; Drouineau *et al*., 2018b). The European eel is subjected to fishing activities at all continental life stages (from juveniles to adults) and high fishing mortality estimated over the entire life cycle suggests that overfishing represents one of the main threats for the survival of the entire eel population (FAO, 2007). Furthermore, all commercial production of *A. anguilla* (intensive and extensive farming, commercial and recreational fishing) depends on the exploitation of wild stocks (juveniles to supply farms, adults for fishing) (OSPAR, 2010). To deal with this problem there are various regional management measures currently undertaken to regulate European eel fisheries. Principal conservation measures in place for glass, yellow and silver eels include a ban on commercial fishing of glass eels, gear regulations, quotas, closed seasons, licenses for fishing, size limits, free gaps in weirs and requirements for elver passes (Ringuet *et al*., 2002). Other pressures play an important role in the decline of the European eel, and include also habitat loss, water pollution, parasitism, and migration obstacles (dams, weirs, pumping stations) (*e.g.*, Baltazar-Soares *et al.*, 2014; Culurgioni et al., 2014; 2015; Bevacqua *et al.*, 2015; Aalto *et al.*, 2016; Dekker and Beaulaton, 2016). These factors affect European eels most in the continental phase of their life cycle, while environmental factors, such as climate change, mostly influence their oceanic phase (Drouineau *et al*., 2018b). However, as eels can spend most of their life in freshwater (Tesch, 2003) the environmental stressors affecting their life in this biome needs to be studied thoroughly.

In 2007, the European Commission developed a specific legislation (Council Regulation (EC) No. 1100/2007) to protect eels (European Commission, 2007). European eel has been listed also in Appendix II of the Convention on International Trade in Endangered Species (CITES, 2020) and in Appendix II of Convention for the Conservation of Migratory Species (CMS) (CITES, 2020). Most recently, the International Union for Conservation of Nature (IUCN) has recently classified the European eel as Critically Endangered (IUCN, 2014; Pike *et al.*, 2020).

The stock of the European eel is currently at its historical minimum. For more than half a century, stock abundance and fishing yield have declined by about 5% per year, to less than 10% of its historical level (Dekker, 2003a; 2004; ICES, 2019). From 1980 to 2010 recruitment of young eel (glass eel) from the ocean towards the continent dropped consistently by approximately 15% per year, to 1%-10% of its former levels (Dekker, 2000; ICES, 2020). The causes of these downward trends are not clear, and, consequently, efficient remedies and mitigation measures are hard to design (Dekker, 2016). Hence, the dynamics of the population are only marginally known (Dekker, 2004) in the current relatively well-documented years, and even more so for the decades during which the stock declined (Dekker, 2016). To fill these gaps of knowledge, monitoring programmes have been established, and models of stock dynamics also developed (De Leo *et al*., 2009; Walker *et al*., 2013).

Many discoveries were made in the 20th century about the behavior and movement ecology of this species. Extensive sampling programs were conducted in the Atlantic Ocean to understand the horizontal and vertical movement of eel leptocephali (Hanel *et al*., 2014; Miller *et al*., 2015), and direct observations of the migratory behavior of yellow and silver eels were made using telemetry (Amilhat *et al*., 2016; Righton *et al*., 2016; Béguer-Pon *et al*., 2018). However, less is known about the migratory behavior of glass eels during their complex journey from the continental slope to estuaries.

General threats to the survivorship of *A. anguilla* span across their entire home range including either freshwater, marine coastal, and oceanic habitats. Threats to reproducing stocks in freshwater are, obviously, conceivably more of concern. Freshwater ecosystems are threatened habitats by multiple human disturbances (Vörösmarty *et al*., 2010), which are expected to affect future species ranges (Comte *et al*., 2016; Radinger *et al*., 2016). From a legislative perspective, the presence of obstacles to river flow is important for determining the hydromorphological status of a river in terms of hydrological regime, continuity, morphological condition, and ecological flows (EU Water Framework Directive (WFD) 2000/60/EC; Moccia *et al*., 2020). Indeed, in recent years, there has been a growing interest about ecological consequences of river fragmentation by physical obstacles (Garcia de Leániz, 2008; Januchowski-Hartley *et al*., 2013; Kroon and Phillips, 2016; Birnie-Gauvin *et al*., 2017; Jones *et al*., 2019). Recent estimates of fragmentation suggest that 63% of rivers worldwide are no longer free-flowing and that half of all rivers reaches have diminished connectivity (Grill *et al*., 2019). Rivers' flows have been regulated for the purposes of flood protection, navigation, and agricultural development, as well as for electricity production and other human uses. However, these regulations have overall degraded river geomorphological and hydrological conditions (*e.g.*, by the fragmentation of river networks and generating a deficit of sediment transport) (Alexander *et al*., 2012; Grill *et al*., 2019). In river ecosystems, fragmentation due to dam building and changes to river flows due to drought may affect river continuity and can be considered a key driver of the Anthropocene biodiversity crisis (Meybeck, 2003; Dudgeon *et al*., 2006; Zarfl *et al*., 2015). River connectivity interruption threatens ecosystems' structure and functioning by hindering movements of migratory species, the exchange of individuals and of genetic information between populations (Wofford *et al*., 2005; Raeymaekers *et al*., 2008;), altering aquatic habitats, flow, and sediment transport regimes (Bunn and Arthington, 2002).

Disruption of natural movements can affect the extent, viability, and persistence of native aquatic species, and has caused a decline in the distribution and abundance of many fish populations, including eels (Feunteun, 2002; Burkhead, 2012; Katz *et al*., 2013). In this regard, we stress here that catadromous fish are declining worldwide, also because of direct and indirect effects generated by dams building (Shields *et al*., 2005; Collas *et al*., 2018.

In particular dams mediated river fragmentation limits fish dispersal and likely increases their extinction risk (Carvajal-Quintero *et al*., 2017; Dias *et al*., 2017). For example, hydroelectric dams can cause injury, direct mortality, delays in migration times, and inhibit downstream migration in *A. anguilla* (Behrmann-Godel and Eckmann, 2003; Durif *et al*., 2003; Winter *et al*., 2006; Bruijs and Durif, 2009). Downstream passage at non-powered dams (*i.e*., dams not equipped with turbines) can have minor impacts, as the passage of fish through them is usually safe (Besson et al., 2016), but anyway can delay migration (Larinier, 2000; Larinier and Travade, 2002; Besson *et al*., 2016) and result in lower (20%) annual migration rates when compared to equivalent non-obstructed rivers (Feunteun *et al*., 2000; Acou, 2006).

A high level of connectivity between habitats in a river system and between a river and the sea is vital for sustaining healthy stream fish populations and assemblages that migrate among several habitats, for suitable feeding, spawning, and refuge conditions (Lucas and Baras, 2001; Maitland, 2003; Carlsson *et al*., 2004; Perkin and Gido, 2012; van Puijenbroek *et al*., 2019): this holds conceivably true particularly for the survivorship of catadromous fish that migrate across different aquatic biomes.

Eels can climb along waterfalls and weirs of hydropowers (Byrne and Beckett, 2012). Nevertheless, most counteracting methods applied to mitigate negative effects of dams on fish migration, do not grant success for all migratory fish upstream, and even if they do, successful catadromous fish species can encounter unfavorable habitat conditions in reached reservoirs (Larinier, 2001; van Puijenbroek *et al*., 2019). Upstream migration in presence of dams may be also delayed given the required time to obtain further fish passages (Larinier, 2001; Lucas and Baras, 2001; Brink *et al*., 2018). Moreover, because general upstream effects of dams increase with the size of the dam and reservoir (Birnie-Gauvin *et al*., 2017; Brink *et al*., 2018), large dams, usually, tend to be more harmful than smaller barriers. Downstream migration in presence of dams can enhance mortality due to predation in reservoirs and passage in hydropower turbines or spillway (Larinier, 2001; Wilkes *et al*., 2018). Hence, independently of the movement direction and of the presence of fish transposition devices, dams can severely impair catadromous fish movement and, thus, are partly responsible for the decline of catadromous species and, in particular, of eels (Calles *et al*., 2010; Feunteun, 2002; Piper *et al*., 2013). Widespread eel ladders could aid upstream migration, although to date, few efficiency assessments of their efficiency exist (Jellyman and Arai, 2016). Alternative approaches to the capture and the transfer of adult eels downstream of a barrier are also used worldwide (ICES, 2016; Jellyman and Unwin, 2017; Béguer-Pon *et al*., 2018). A management of the water regimes alterations of the dams during the fish migratory peaks could be also an effective measure (Boubee *et al*., 2001; Trancart *et al*., 2013), but they can be complicated if they are not predicted to limit the economic loss (Teichert *et al*., 2020).

SUCCESS AND LIMITS OF EELS RESTOCKING PRACTICES

Restocking practices are used for conservation, protection, or recovery purposes of endangered species and to increase the productivity of fish stocks (FAO, 2003). Among the actions undertaken to recovery the European eel population, restocking practices in continental systems where natural recruitment is low or absent are still underdeveloped (Moriarty and McCarthy, 1982; Andersson *et al*., 1991; Wickström *et al*., 1996; Pedersen, 1998; Simon and Dörner, 2014; Ovidio et al., 2015; Hanel *et al*., 2019). Eels' restocking initiated in Europe before to the 20th century and has been done for decades across the entire continent (Wickström *et al*., 1996; Moriarty and Dekker, 1997; Psuty and Draganik, 2008; Dekker and Beaulaton, 2016).

The release of glass eels in closed catchments can efficiently support local eels' production and as well as promote local employment (Wickström *et al*., 1996; Pedersen, 2000; Rosell *et al*., 2005; Psuty and Draganik, 2008). Moreover, among the conservation measures conceived for inland waters that are distant from the sea, restocking is the only solution that enhances the local stocks Simon *et* al., 2013; Ovidio *et* al., 2015; Matondo *et al*., 2019). Considering that a proportion of stocked eels needs to escape as silver eels, contrasting for example hydropower-induced mortality during the downstream migration (Winter *et al*., 2006), restocking is probably the best long-term plan to meet the silver eels' escapement target in the Eel Recovery Plan of the European Union.

To date, the success of eels' artificial reproduction in captivity has not yet been totally obtained, therefore, domestication and aquaculture may represent an effective tool to satisfy purchaser requests and to preserve natural stocks (Guarniero *et al*., 2020). However, this species represents a true challenge for breeding and production (*e.g.*, egg quality, fertilization rate, and larval survival are the main challenges). Wild-caught glass eels and elvers represent the only supply of restocking, that can be translocated from estuaries to rivers with low or without natural immigration (Pedersen *et* al., 2000; Matondo *et al*., 2019). In their new freshwater environments, restocked young eels can survive, grow, and mature into silver eels that, ultimately, display a seaward migration behavior that is similar to the one exhibited by naturally recruited wild eels (*e.g.*, Shiao *et* al., 2006; Ovidio *et* al., 2015; Kullmann and Thiel, 2018; Matondo *et al*., 2019; Felix *et al*., 2020). Nevertheless, it is yet to be demonstrated whether restocking is an efficient measure to restore the eels' stocks and also to produce new mature individuals that could successfully contribute to the successive spawning stocks (Westin, 1998; 2003; Prigge *et al*., 2013; Westerberg *et al*., 2014). Moreover, further studies are also needed to assess the impact of restocking practices on the future sexual differentiation of the restocked individuals (Geffroy and Bardonnet, 2015; Ovidio *et al*., 2015). Restocked eels' long-term survival is also still debated (Westin, 1998; 2003; Prigge *et al*., 2013; Westerberg *et al*., 2014).

The size and stage of restocking material (glass eel *vs*. yellow eel), their origin (cultured *vs*. wild eels), their health status (*e.g.*, parasites, infections, deseases), and the trophic status of the water body may altogether influence the restocking yield (Prigge *et al*., 2013; Pedersen *et al*., 2016; Ovidio *et al*., 2015). The annual growth in length and the survival rates of restocked eels vary strongly among different recipient environments, and depend upon the characteristics of rearing location, the wild origin of reared eels, and the stage used (juvenile *vs*. adult eels) (Bisgaard and Pedersen, 1991; Pedersen, 1998; Lin *et al*., 2007; Simon *et al*., 2013; Simon and Dörner, 2014). Recent studies reported that natural mortality of restocked populations decreases with increasing individual body mass and, thus, restocking carried out with larger eels resulted in a better survival rate and, consequently, in a higher yield (Pedersen *et al*., 2016). More recent experiments showed that restocked eels have an initial delay of their downstream migration, and those recaptured eels have lower body length and weight, likely attributable to their allochthonous origin (Prigge *et al.*, 2013). Interestingly, however, both restocked and farmed eels show similar migratory behaviors and routes during spawning migrations in the open ocean (Westerberg *et al*., 2014; Chen *et al*., 2018). Information about the effects of restocked eels' density on the restocking yield are much less, and densities used for restocking are, typically, site specific and established based on the natural recruitment and yield per recruit estimates (Moriarty and Dekker, 1997). Moreover, as few studies have contextually investigated survival, growth, dispersal, and movement of the restocked eels (Shiao *et al.*, 2006; Pedersen et al., 2009; Desprez et al., 2013; Wickström *et al.*, 2014; Ovidio *et al.*, 2015; Sjöberg *et al*., 2017), little is known about the best procedure for implementing restocking with maximum survival rates in riverine ecosystems and, even, about how to accurately assess the level of restocking success (Pedersen 2000; Pedersen, 2009; Deprez *et al*., 2013; Matondo *et al*., 2019).

Based on the above cues and considering the still large gaps of knowledge about the best protocol to restock efficiently depaupered eels' populations (Wickström and Sjöberg, 2014; Stacey *et al*., 2015), we claim the need of new and science-based assessments of restocking protocols in different scenarios, possibly coping with the expected habitat quality modifications caused by climate change and unintentionally to the anthropogenic emergence and spread of pathogens (*e.g.*, *Anguillicola crassus* Kirk, 2003; Wickström *et al*., 2014, and Anguillid Herpesvirus 1, AngHV-1, Kullmann *et al.*, 2017) (Delrez *et al*., 2021).

THE WAY FORWARD

Despite the research effort to date, identification of the best technologies to reduce the threats that impair *A. anguilla* remains challenging. Data about the distribution range of the European eel are still spatially and temporally fragmented, and the available ones are still affected by a large heterogeneity in the sampling methods and in analysis protocols. These gaps of knowledge represent altogether major biases for any possible generalization about the life cycle of eels. Thus, the put in place of standardized monitoring programmes represents a priority to increase our knowledge of the eels' life cycle and their migration patterns. Only when these gaps of knowledge will be filled, restoration of environmental connectivity, particularly when rivers' flow is interrupted by artificial obstacles like dams, will contribute to enhance eels' stocks and their ability to fuel future generations. In this regard, we anticipate that the removal or mitigation of migration barriers, by promoting fish passage and habitat restoration, could represent a key step to enhance the yield of any eventual restocking practice without prejudice to the risk that restoring connectivity could facilitate the dispersion of alien fish species in a catchment (Clavero and Hermoso, 2010). Better understand habitat-eel relationships is probably one of the most promising ways that may contribute to habitat restoration for restoring inland eel stocks (Laffaille *et al*., 2004). Using eels to study water contamination based on an integrated approach (ecotoxicological, parasitological, pollution topics) is crucial for the evaluation of environmental health, and chemical status of water bodies, and will directly be beneficial for restoration of eels' stocks and consequently for ensuring water quality and habitat conservation (Maes *et* al., 2005; Belpaire and Goemans, 2007; Bourillon *et al*., 2020; Capoccioni *et al.*, 2020). With this in mind, we contend that identifying river basins and the minimum proportion of river stretches that could serve as "eel reserves" is also needed, along with collaborative research approach between researchers and stakeholders, with the final aim of establishing protocols of eels' exploitation that respond to the principles of a sustainable use of resources and development.

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