

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

Cinzia Podda,^{*1} Francesco Palmas,¹ Antonio Pusceddu,¹ Andrea Sabatini¹

¹Department of Life and Environmental Sciences, University of Cagliari, Via Fiorelli 1, 09126 Cagliari, Italy

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 salmon (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.

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 Gueraud, 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 cre-

ates 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 popula-

tion (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). Alter-

native approaches to the capture and the transfer of adult eels downstream of a barrier are also used worldwide (ICES, 2016; Jellyman and Unwin, 2017; Béguyer-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 Bardonnnet, 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, diseases), 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 (Lafaille *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.

Corresponding author: cpodda@unica.it

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REFERENCES

- Aalto E, Capoccioni F, Terradez Mas J, Schiavina M, Leone C, De Leo G, Ciccotti E, 2016. Quantifying 60 years of declining European eel (*Anguilla anguilla* L., 1758) fishery yields in Mediterranean coastal lagoons. *ICES J. Mar. Sci.* 73:101-110.
- Aarestrup K, Økland F, Hansen MM, Righton D, Gargan P, Castonguay M, Bernatchez L, Howey P, Sparholt H, Pedersen MI, McKinley RS, 2009. Oceanic spawning migration of the European eel (*Anguilla anguilla*). *Science* 325:1660.
- Acou A, 2006. [Bases biologiques d'un modèle pour estimer la biomasse féconde de l'anguille européenne en fonction des recrues fluviales et du contexte de croissance: approche comparative à l'échelle de petits bassins versants, Ph.D. thesis.]. [Article in French]. France: University of Rennes 1: 315 pp. http://www.diadfish.org/francais/documents_f.htm.
- Adam G, Feunteun E, Prouzet P, Rigaud C, 2008. [L'anguille européenne: indicateurs d'abondance et de colonisation.]. [Article in French]. Coll. Savoir-faire, Editions Quae, Versailles: 400 pp.
- Alexander J, Wilson R, Green W, 2012. A brief history and summary of the effects of river engineering and dams on the Mississippi River system and delta. Circular 1; US. Geological Survey Circular 1375: Reston, Virginia: 43 pp.
- Amara R, Selleslagh J, Billon G, Minier C, 2009. Growth and condition of 0-group European flounder, *Platichthys flesus* as indicator of estuarine habitat quality. *Hydrobiologia* 627:87-98.

- Amilhat E, Aarestrup K, Faliex E, Simon G, Westerberg H, Righton D, 2016. First evidence of European eels exiting the Mediterranean Sea during spawning migration. *Sci. Rep.* 6:21817.
- Anderson MJ, 1991. A new method for non-parametric multivariate analysis of variance. *Austral. Ecol.* 26:32-46.
- Arai T, Aoyama J, Ishikawa S, Miller MJ, Otake T, Inagaki T, Tsukamoto K, 2001. Early life history of tropical *Anguilla* leptocephali in the western Pacific Ocean. *Mar. Biol.* 138:887-895.
- Arai T, Daniel L, Otake T, Tsukamoto K, 1999. Metamorphosis and inshore migration of tropical eels, *Anguilla* spp., in the Indo-Pacific. *Mar. Ecol. Prog. Ser.* 182:283-293.
- Arai T, Kotake A, Harrod C, Morrissey M, McCarthy TK, 2019. Ecological plasticity of the European eel *Anguilla anguilla* in a tidal Atlantic lake system in Ireland. *J. Mar. Biolog. Assoc. U.K.* 99:1189-1195.
- Arai T, Kotake A, McCarthy TK, 2006. Habitat use by the European eel *Anguilla anguilla* in Irish waters. *Estuar. Coast. Shelf Sci.* 67:569-578.
- Arai T, Miller MJ, Tsukamoto K, 2003. Larval duration of the tropical eel *Anguilla celebesensis* from Indonesian and Philippine coasts. *Mar. Ecol. Prog. Ser.* 251:255-261.
- Aranburu A, Estibaliz D, Briand C, 2015. Glass eel recruitment and exploitation in a South European estuary (Oria, Bay of Biscay). *ICES J. Mar. Sci.* 73:111-121.
- Arribas C, Fernández-Delgado C, Oliva-Paterna FJ, Drake P, 2012. Oceanic and local environmental conditions as forcing mechanisms of the glass eel recruitment to the southernmost European estuary. *Estuar. Coast. Shelf Sci.* 107:46-57.
- Atkinson S, Carlsson JEL, Ball B, Egan D, Kelly-Quinn M, Whelan K, Carlsson J, 2018. A quantitative PCR based environmental DNA assay for detecting Atlantic salmon (*Salmo salar* L.) *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 28:1238-1243.
- Atta KI, 2013. Morphological, anatomical and histological studies on the olfactory organs and eyes of teleost fish: *Anguilla anguilla* in relation to its feeding habits. *JOBAS* 66:101-108.
- Aubrun L, 1986. [Inventaire de l'exploitation de l'anguille sur le littoral de la Bretagne.][Article in French]. ENSAR, Rennes: 107 pp.
- Aubrun L, 1987. [Inventaire de l'exploitation de l'anguille sur le littoral sud Gascogne.][Article in French]. Laboratoire de Biologie Halieutique, ENSA Rennes: 150 pp.
- Baltazar-Soares M, Biastoch A, Harrod C, Hanel R, Marohn L, Prigge E, Evans D, Bodles K, Behrens E, W. Böning K, Eizaguirre C, 2014. Recruitment collapse and population structure of the European eel shaped by local ocean current dynamics. *Curr. Biol.* 24:104-108.
- Baltazar-Soares M, Eizaguirre C, 2017. Animal navigation: the eel's magnetic guide to the Gulf Stream. *Curr. Biol.* 27:604-606.
- Barry J, Newton M, Dodd JA, Hooker OE, Boylan P, Lucas MC, Adams CE, 2015. Foraging specialisms influence space use and movement patterns of the European eel *Anguilla anguilla*. *Hydrobiologia* 766:333-348.
- Beaulaton L, Castelnau G, 2005. The efficiency of selective tidal stream transport in glass eel entering the Gironde (France). *Bull. fr. pêche piscic.* 5:378-379.
- Beaulaton L, Drouineau, H, 2018. Modelling the recruitment of European eel (*Anguilla anguilla*) throughout its European range. *ICES J. of Mar. Sci.* 75:541-552.
- Béguet-Pon M, Castonguay M, Shan S, Benchetrit J, Dodson JJ, 2015. Direct observations of American eels migrating across the continental shelf to the Sargasso Sea. *Nat. Commun.* 6:8705.
- Béguet-Pon M, Dodson JJ, Castonguay M, Jellyman D, Aarestrup K, Tsukamoto K, 2018. Tracking anguillid eels: five decades of telemetry-based research. *Mar. Freshw. Res.* 69:199.
- Béguet-Pon M, Ohashi K, Sheng J, Castonguay M, Dodson JJ, 2016. Modeling the migration of the American eel in the Gulf of St. Lawrence. *Mar. Ecol. Prog. Ser.* 549:183-198.
- Behrmann-Godel J, Eckmann R, 2003. A preliminary telemetry study of the migration of silver European eel (*Anguilla anguilla* L.) in the River Mosel, Germany *Ecol. Freshw. Fish* 12:196-202.
- Belpaire C, Goemans G, 2007. The European eel *Anguilla anguilla*, a rapporteur of the chemical status for the Water Framework Directive? *Vie et milieu - life and environment.* 57: 235-252.
- Benchetrit J, Béguet-Pon M, Sirois P, Castonguay M, Fitzsimons J, Dodson JJ, 2017. Using otolith microchemistry to reconstruct habitat use of American eels *Anguilla rostrata* in the St. Lawrence river-lake Ontario system. *Ecol. Freshw. Fish* 26:19-33.
- Benson T, de Bie J, Gaskell J, Vezza P, Kerr JR, Lumbroso D, Owen MR, Kemp PS, 2021. Agent-based modelling of juvenile eel migration via selective tidal stream transport. *Ecological Modelling* 443:109448.
- Bertin L, 1956. Eels, a biological study. Cleaver-Hume Press Ltd, London.
- Besson ML, Trancart T, Acou A, Charrier F, Mazel V, Legault A, Feunteun E, 2016. Disrupted downstream migration behaviour of European silver eels (*Anguilla anguilla*, L.) in an obstructed river. *Environ. Biol. Fishes* 99:779-791.
- Bevacqua D, Melià P, Gatto M, De Leo GA, 2015. A global viability assessment of the European eel. *Glob. Chang. Biol.* 21:3323-3335.
- Bevacqua D, Melià P, Schiavina M, Crivelli AJ, De Leo GA, Gatto M, 2019. A demographic model for the conservation and management of the European eel: an application to a Mediterranean coastal lagoon. *ICES J. Mar. Sci.* 76: 2164-2178.
- Birnie-Gauvin K, Tummers JS, Lucas MC, Aarestrup K, 2017. Adaptivemanagement in the context of barriers in European freshwater ecosystems. *J. Environ. Manag.* 204:436-441.
- Bisgaard J, Pedersen MI, 1991. Mortality and growth of wild and introduced cultured eels (*Anguilla anguilla* (L)) in a Danish stream, with special reference to a new tagging technique. *Dana* 9:57-69.
- Boëtius J, Harding EF, 1985. A re-examination of Johannes Schmidt's Atlantic eel investigations. *Dana* 4:129-162.
- Bonhommeau S, Castonguay M, Rivot E, Sabatié R, Le Pape O, 2010. The duration of migration of Atlantic *Anguilla* larvae. *Fish Fish.* 11:289-306.
- Bonhommeau S, Chassot E, Rivot E, 2008. Fluctuations in European eel (*Anguilla anguilla*) recruitment resulting from environmental changes in the Sargasso Sea. *Fish. Oceanogr.* 17:32-44.

- Bornarel V, Lambert P, Briand C, Antunes C, Belpaire C, Ciccotti E, Diaz E, Diserud O, Doherty D, Domingos I, Evans D, de Graaf M, O'Leary C, Pedersen M, Poole R, Walker A, Wickström H, Bouvet J, Prouzet P, Bru N, de Casamajor M, Lissardy M, Sanchez F, 2006. [Quantification de la biomasse saisonnière de civelles (*Anguilla anguilla*) dans l'estuaire de l'Adour et estimation du taux d'exploitationsaisonnier de la pêche professionnelle au tamis poussé.]. [Article in French]. Technical report, Ifremer. <http://www.ifremer.fr/indicang/sites-thematiques/pdf/flux-saison.pdf>.
- Boubee JA, Mitchell CP, Chisnall BL, West DW, Bowman EJ, Haro A, 2001. Factors regulating the downstream migration of mature eels (*Anguilla* spp.) at Aniwhenua Dam, Bay of Plenty, N. Z. J. Mar. Freshwater Res. 35:121-134.
- Bourillon B, Acou A, Trancart T, Belpaire C, Covaci A, Bustamante P, Faliex E, Amilhat E, Malarvannan G, Virag L, Aarestrup K, Bervoets L, Boisneau C, Boulenger C, Gargan P, Becerra-Jurado G, Lobón-Cerviá J, Maes GE, Pedersen MI, Poole R, Sjöberg N, Wickström H, Walker A, Righton D, Feunteun E, 2020. Assessment of the quality of European silver eels and tentative approach to trace the origin of contaminants - a European overview. Sci. Total Environ. 743:140675.
- Bradford RG, Carr JW, Page FH, Whoriskey F, 2009. Migration of silver American eels through a macrotidal estuary and bay, p.275-292. In: Challenges for diadromous fishes in a dynamic global environment. Haro A, Smith KL, Rulifson RA, Moffitt CM, Klauda RJ, Dadswell MJ, Cunjak RA, Cooper JE, Beal KL, Avery TS (eds.). American Fisheries Society Symposium, Bethesda, Md.
- Bracken FSA, Rooney SM, Kelly-Quinn M, King JJ, Carlsson J, 2019. Identifying spawning sites and other critical habitat in lotic systems using eDNA "snapshots": a case study using the sea lamprey *Petromyzon marinus* L. Ecol. Evol. 9:553-567.
- Breukelaar AW, Ingendahl D, Vriese FT, de Laak G, Staas S, Klein Breteler JGP, 2009. Route choices, migration speeds and daily migration activity of European silver eels *Anguilla anguilla* in the River Rhine, north-west Europe. J. Fish. Biol. 74:2139-2157.
- Brink K, Gough P, Royte J, Schollema PP, Wannigen H, 2018. 'From sea to source 2.0. Protection and restoration of fish migration in rivers worldwide.' (World Fish Migration Foundation: Groningen, Netherlands.): 364 pp.
- Bru N, Prouzet P, Lejeune M, 2009. Daily and seasonal estimates of the recruitment and biomass of glass eels runs (*Anguilla anguilla*) and exploitation rates in the Adour open estuary (Southwestern France). Aquatic Living Resources 22:509-523.
- Brujns M, Durif C, 2009. Silver eel migration and behaviour, p.65-95. In: Thillart G, Dufour S, Rankin JC (eds.), Spawning migration of the European eel.
- Bunn SE, Arthington AH, 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environ. Manage. 30:492-507.
- Bureau Du Colombier S, Bolliet V, Lambert P, Bardonnet A, 2007. Energy and migratory behaviour in glass eels (*Anguilla Anguilla*). Physiol. Behav. 92:684-690.
- Burkhead NM, 2012. Extinction rates in North American freshwater fishes, 1900–2010. Bioscience 62:798-808.
- Byrne D, Beckett, B, 2012. Wicklow Bridges Project. Assessment of the risk of barriers to migration of fish species in County Wicklow. Retrieved from. http://www.countywicklowheritage.org/documents/Wicklow_Bridges_Project_Fish_Passage_report.pdf.
- Calles O, Olsson IC, Comoglio C, Kemp PS, Blunden L, Schmitz M, Greenberg LA, 2010. Size-dependent mortality of migratory silver eels at a hydropower plant, and implications for escapement to the sea. Freshw. Biol. 55:2167-2180.
- Capoccioni F, Leone C, Belpaire C, Malarvannan G, Poma G, De Matteis G, Tancioni L, Contò M, Failla S, Covaci A, Ciccotti E, 2020. Quality assessment of escaping silver eel (*Anguilla anguilla* L.) to support management and conservation strategies in Mediterranean coastal lagoons. Environ. Monit. Assess. 192:570.
- Carlsson J, Aarestrup K, Nordwall F, Näslund I, Eriksson T, Carlsson JEL, 2004. Migration of landlocked brown trout in two Scandinavian streams as revealed from trap data. Ecol. Freshw. Fish 13:161-167.
- Carvajal-Quintero, JD, Januchowski-Hartley SR, Maldonado-Ocampo JA, Jézéquel C, Delgado J, Tedesco PA, 2017. Damming fragments species ranges and heightens extinction risk. Conserv. Lett. 10:708-716.
- Castonguay M, Dutil JD, Audet C, Miller R, 1990. Locomotor activity and concentration of thyroid hormones in migratory and sedentary juvenile American eels. T. AM. FISH. SOC. 6:946-956.
- Chapman BB, Skov C, Hulthen K, Brodersen J, Nilsson PA, Hansson LA, Brönmark C, 2012. Partial migration in fishes: definitions, methodologies and taxonomic distribution. J. Fish. Biol. 81:479-499.
- Chasco BE, Kaplan IC, Thomas AC, Acevedo-Gutiérrez A, Noren DP, Ford MJ, Bradley Hanson M, Scordino JJ, Jeffries SJ, Marshall KN, Shelton AO, Matkin C, Burke BJ, Ward EJ, 2017. Competing tradeoffs between increasing marine mammal predation and fisheries harvest of Chinook salmon. Sci. Rep. 7:15439.
- Cheng PW, Tzeng WN, 1996. Timing of metamorphosis and estuarine arrival across the dispersal range of the Japanese eel *Anguilla japonica*. Mar. Ecol. Progr. Ser. 131:87-96.
- Ciccotti E, 2005. Interactions between capture fisheries and aquaculture: the case of the eel (*Anguilla anguilla* L., 1758). In: S. Cataudella, D. Crosetti, & F. Massa (eds.), Interactions between capture fisheries and aquaculture: a methodological perspective. Rome: GFCM Studies and Reviews 78:190-203.
- Ciccotti E, Busilacchi S, Cataudella S, 2000. Eel, *Anguilla anguilla* (L.), in Italy: recruitment, fisheries and aquaculture. Dana 12:7-15.
- CITES (2020a). Conservation status of *Anguilla anguilla*. https://www.speciesplus.net/#/taxon_conce pts/3973/legal.
- CITES (2020b). Convention of Migratory Species (CMS) listing of *Anguilla anguilla*. https://www.speciesplus.net/#/taxon_conce pts/66526/legal.
- Clavero M, Hermoso V, 2010. Reservoirs promote the taxonomic homogenization of fish communities within river basins. Biodivers. Conserv. 20:41-57.
- Clément M, Chiasson AG, Veinott G, Cairns DK, 2014. What otolith microchemistry and stable isotope analysis reveal and conceal about anguillid eel movements across salinity boundaries. Oecologia 175:1143-1153.

- Close DA, Fitzpatrick MS, Li HW, 2002. The ecological and cultural importance of a species at risk of extinction, Pacific lamprey. *Fisheries* 27:19-25.
- Collas FP, Buijse AD, van den Heuvel L, van Kessel N, Schoor MM, Eerden H, Leuven RS, 2018. Longitudinal training dams mitigate effects of shipping on environmental conditions and fish density in the littoral zones of the river Rhine. *Sci. Total Environ.* 619-620:1183-1193.
- Comte L, Huguény B, Grenouillet G, 2016. Climate interacts with anthropogenic drivers to determine extirpation dynamics. *Ecography* 39:1008-1016.
- Cooke SJ, Midwood JD, Thiem JD, Klimley P, Lucas MC, Thorstad EB, Eiler J, Holbrook C, Ebner BC, 2013. Tracking animals in freshwater with electronic tags: past, present and future. *Anim. Biotelemetry* 1:5-19.
- Costa-Dias S, Sousa R, Lobón-Cerviá J, Laffaille P, 2009. The decline of diadromous fish in Western Europe inland waters: mains causes and consequence, p.67-92. In: *Fisheries: Management, economics and perspectives*. Nova Science Publishers.
- Cresci A, 2020. A comprehensive hypothesis on the migration of European glass eels (*Anguilla anguilla*). *Biol. Rev.* 95:1273-1286.
- Cresci A, Durif CM, Paris CB, Shema SD, Skiftesvik AB, Browman HI, 2019b. Glass eels (*Anguilla anguilla*) imprint the magnetic direction of tidal currents from their juvenile estuaries. *Commun. Biol.* 2:366.
- Cresci A, Paris CB, Durif CM, Shema S, Bjelland RM, AB Skiftesvik, Browman HI, 2017. Glass eels (*Anguilla anguilla*) have a magnetic compass linked to the tidal cycle. *Sci. Adv.* 3:e1602007.
- Cresci A, Paris CB, Foretich MA, Durif CM, Shema SD, O'Brien CE, Vikebø FB, Skiftesvik AB, Browman HI, 2019a. Atlantic haddock (*Melanogrammus aeglefinus*) larvae have a magnetic compass that guides their orientation. *iScience* 19:1173-1178.
- Crivelli A, Auphan N, Chauvelon P, Sanzoz A, Menella J, Poizat G, 2008. Glass eel recruitment, *Anguilla anguilla* (L.), in a Mediterranean lagoon assessed by a glass eel trap: factors explaining the catches. *Hydrobiologia* 602:79-86.
- Crnjar R, Sclalera G, Bigiani A, Tomassini Barbarossa I, Magherini PC, Pietra P, 1992. Olfactory sensitivity to amino acids in the juvenile stages of the European eel *Anguilla Anguilla* (L.). *J. Fish Biol.* 40:567-576.
- Culurgioni J, Figus V, Cabiddu S, De Murtas R, Cau A, Sabatini A, 2015. Larval Helminth parasites of fishes and shellfishes from Santa Gilla Lagoon (Sardinia, Western Mediterranean), and their use as bioecological indicators. *Estuaries Coasts* 38:1505-1519.
- Culurgioni J, Sabatini A, De Murtas R, Mattiucci S, Figus V, 2014. Helminth parasites of fish and shellfish from the Santa Gilla Lagoon in southern Sardinia, Italy. *J. Helminthol* 88:489-498.
- Cushing DH, 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.* 26:249-293.
- Cullen P, McCarthy TK, 2003. Hydrometric and meteorological factors affecting the seaward migration of silver eels (*Anguilla anguilla*, L.) in the lower River Shannon. *Environ. Biol. Fishes* 67:349-357.
- De Casamajor MN, Bru N, Prouzet P, 1999. [Influence de la luminosité nocturne et de la turbidité sur le comportement vertical de migration de la civelle d'anguille (*Anguilla anguilla* L.) dans l'estuaire de l'Adour.]. [Article in French] *Bull. fr. pêche piscic.* 355:327-347.
- De Leo GA, Melià Paco, Gatto M, Crivelli AJ, 2009. Eel population modeling and its application to conservation management. In: Casselman JM and Cairns DK (eds.), *Eels at the edge: science, status, and conservation concerns*. Proceedings of the 2003 international eel symposium. *Am. Fish Soc. Symp.* 58:327-345.
- Deiner K, Walser JC, Mächler E, Altermatt F, 2015. Choice of capture and extraction methods affect detection of freshwater biodiversity from environmental DNA. *Biol. Conserv.* 183:53-63.
- Dejean T, Valentini A, Duparc A, Pellier-Cuit S, Pompanon F, Taberlet P, Miaud C, 2011. Persistence of environmental DNA in freshwater ecosystems. *PLoS One* 6:8-11.
- Delpech C, Courrat A, Pasquaud S, Lobry J, Le Pape O, Nicolas D, Boët P, Girardin M, Lepage M, 2010. Development of a fish-based index to assess the ecological quality of transitional waters: the case of French estuaries. *Mar. Pollut. Bull.* 60:908-918.
- Dekker W, 1998. Long-term trends in the glass eels immigrating at Den Oever, The Netherlands. *Bull. fr. pêche piscic.* 349:199-214.
- Dekker W, 2000. The fractal geometry of the European eel stock. *ICES J. Mar. Sci.* 57:109-121.
- Dekker W, 2003a. Did lack of spawners cause the collapse of the European eel, *Anguilla anguilla*? *Fish. Manag. Ecol.* 10:365-376.
- Dekker W, 2003b. Status of the European eel stock and fisheries, p.237-254. In: Aida K., Tsukamoto K., Yamauchi K. (eds), *Eel Biology*. Springer, Tokyo.
- Dekker W, 2004. Slipping through our hands – population dynamics of the European eel. (PhD thesis). Amsterdam, the Netherlands: University of Amsterdam: 186 pp. http://www.diadfish.org/doc/these_2004/dekker_thesis_eel.pdf. Dekker W, Casselman JM, 2014.
- Dekker W, 2016. Management of the eel is slipping through our hands! Distribute control and orchestrate national protection. *ICES J. Mar. Sci.* 73:2442-2452.
- Dekker W, 2019. The history of commercial fisheries for European eel commenced only a century ago. *Fish. Manag. Ecol.* 6:6-19.
- Dekker W, Beaulaton L, 2016a. Climbing back up what slippery slope? Dynamics of the European eel stock and its management in historical perspective. *ICES J. Mar. Sci.* 73:5-13.
- Dekker W, Beaulaton L, 2016b. Faire mieux que la nature - the history of eel restocking in Europe. *Environ. Hist.* 22: 255-300.
- Dekker W, Casselman JM, 2014. The 2003 Québec Declaration of concern about eel declines - 11 years later: are eels climbing back up the slippery slope? *Fisheries* 39:613-614.
- Dekker W, Casselman JM, Cairns DK, Tsukamoto K, Jellyman D, Lickers H, 2003. Worldwide decline of eel resources necessitates immediate action: Québec Declaration of Concern. *Fisheries* 28:28-30.
- Desaunay Y, Guerauld D, 1997. Seasonal and long-term changes in biometrics of eel larvae: a possible relationship between

- recruitment variation and North Atlantic ecosystem productivity. *J. Fish Biol.* 51:317-339.
- Delrez N, Zhang H, Liefgrig F, Mélard C, Farnir F, Boutier M, Donohoe O, Vanderplasschen A, 2021. European eel restocking programs based on wild-caught glass eels: feasibility of quarantine stage compatible with implementation of prophylactic measures prior to scheduled reintroduction to the wild. *J. Nat. Conserv.* 59:125933.
- Desprez M, Crivelli AJ, Lebel I, Massez G, Gimenez O, 2013. Demographic assessment of a stocking experiment in European Eels. *Ecol. Freshw. Fish* 22:412-420
- Dias MS, Tedesco PA, Huguény B, Jézéquel C, Beauchard O, Brosse S, Oberdorff T, 2017. Anthropogenic stressors and riverine fish extinctions. *Ecol. Indic.* 79:37-46.
- Domingos I, 1992. Fluctuation of glass eel migration in the Mondego estuary (Portugal) in 1988 and 1989. *Irish Fisheries Investigations: Series A (Freshwater) (Ireland)* 36:1-4.
- Dorow M, Schulz S, Frankowski J, Ubl C, 2019. Using a telemetry study to assess the boundary net efficiency of an enclosure system used for yellow eel density monitoring. *Fish. Manag. Ecol.* 26:70-75.
- Drouineau H, Bau F, Alric A, Deligne N, Gomes P, Sagnes P, 2017. Silver eel downstream migration in fragmented rivers: use of a bayesian model to track movements triggering and duration. *Aquat. Living Resour.* 30:1-9.
- Drouineau H, Briand C, Lambert P, Beaulaton P, 2018. GEREM (Glass Eel Recruitment Estimation Model): A model to estimate glass eel recruitment at different spatial scales. *Fish Res.* 174:68-80.
- Drouineau H, Carter C, Rambonilaza M, Beaufaron G, Bouleau G, Gassiat A, Lambert P, le Floch S, Tétard S, de Oliveira E, 2018b. River continuity restoration and diadromous fishes: much more than an ecological issue. *Environ. Manage.* 61:671-686.
- Drouineau H, Durif C, Castonguay M, Mateo M, Rochard E, Verreault G, Yokouchi K, Lambert P, 2018a. Freshwater eels: a symbol of the effects of global change. *Fish Fish.* 19:903-930.
- Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard AH, Soto D, Stiassny MLJ, Sullivan CA, 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* 81:163-182.
- Durant JM, Hjermmann DO, Ottersen G, Stenseth NC, 2007. Climate and the match or mismatch between predator requirements and resource availability. *Clim. Res.* 33:271-283.
- Durif CMF, 2003. [La migration d'avalaison de l'anguille européenne *Anguilla anguilla*: Caractérisation des fractions dévalantes, phénomène de migration et franchissement d'obstacles.][Article in French]. Thèse de doctorat, Université Paul Sabatier, Toulouse: 350 pp.
- Durif CMF, Elie P, 2008. Predicting downstream migration of silver eels in a large river catchment based on commercial fishery data. *Fish Manag. Ecol.* 15:127-137.
- Durif CMF, Gjosaeter J, Vollestad LA, 2011. Influence of oceanic factors on *Anguilla anguilla* (L.) over the twentieth century in coastal habitats of the Skagerrak, Southern Norway. *Proc. R. Soc. Lond. Series B* 278:464-473.
- Edeline E, Beaulaton L, Le Barh R, Elie P, 2007. Dispersal in metamorphosing *Anguilla anguilla* juvenile eel. *Mar. Ecol. Prog. Ser.* 344:213-218.
- Edeline E, Dufour S, Briand C, Fatin D, Elie P, 2004. Thyroid status is related to migratory behavior in *Anguilla anguilla* glass eels. *Mar. Ecol. Prog. Ser.* 282:161-270.
- Edeline E, Dufour S, Elie P, 2005. Role of glass eel salinity preference in the control of habitat selection and growth plasticity in *Anguilla Anguilla*. *Mar. Ecol. Prog. Ser.* 304:191-199.
- Edeline E, Dufour S, Elie P (2009) Proximate and ultimate control of eel continental dispersal. In: Van Den Thillart G, Dufour S, Rankin JC (eds.) Spawning migration of the european eel: reproduction index, a useful tool for conservation management. *Fish fish. ser.* 30:433-461.
- Eldrogi N, Luthon F, Larroque B, Alqaddafi S, Bolliet V, 2018. Motion estimation of glass eels by differential methods. *ISTJ*: pp.299-315.
- Elie P, Rochard E, 1994. [Migration des civelles d'anguilles (*Anguilla anguilla* L.) dans les estuaires, modalités du phénomène et caractéristiques des individus.][Article in French]. *Bull. fr. pêche piscic.* 335:81-98.
- Elliott M, Whitfield AK, Potter IC, Blaber SJM, Cyrus DP, Nordlie FG, Harrison TD, 2007. The guild approach to categorizing estuarine fish assemblages: a global review. *Fish Fish.* 8:241-268.
- Enbody ED, Pettersson ME, Sprehn CG, Palm S, Wickströmb H, Andersson L, 2021. Ecological adaptation in European eels is based on phenotypic plasticity. *PNAS* 118:e2022620118.
- EU (2007). Council Regulation (EC) No. 1100/2007 of 18 September 2007, establishing measures for the recovery of the stock of European eel. *Official Journal of the European Union L.* 248:17-23.
- Evans NT, Li Y, Renshaw MA, Olds BP, Deiner K, Turner CR, Jerde CR, Lodge DM, Lamberti GA, Pfrender ME, 2016. Fish community assessment with eDNA metabarcoding: effects of sampling design and bioinformatic filtering. *Can. J. Fish. Aquat. Sci.* 74:1362-1374.
- FAO, 2003. *Inland Fisheries*.
- FAO, 2007. Report of the second FAO *Ad Hoc* Expert Advisory Panel for the Assessment of Proposals to Amend Appendices I and II of CITES Concerning Commercially Exploited Aquatic Species. Rome, 26–30 March 2007. *FAO Fisheries Report. No. 833. Rome: 133 pp.*
- Feunteun E, 2002. Management and restoration of the European eel population (*Anguilla anguilla*): An impossible bargain? *Ecol. Eng.* 18:575-591.
- Feunteun E, Acou A, Laffaille P, Legault A, 2000. European eel (*Anguilla anguilla*): prediction of spawner escapement from continental population parameters. *Can. J. Fish. Aquat. Sci.* 57:1627-1635.
- Feunteun E, Laffaille P, 2011. Commercially important catadromous fish. *Encyclopedia of Life Support Systems (EOLSS): 27 pp.*
- Feunteun E, Laffaille P, Robinet T, Briand C, Baisez A, Olivier JM, Acou A, 2003. A review of upstream migration and movements in inland waters by anguillid eels: towards a general theory, p.181-190. In: Aida K, Tsukamoto K, Yamauchi K (eds.) *Eel biology*. Springer, Tokyo.
- Fischer ES, Blackburn SE, Liss SA, Hughes JS, Li H, Deng ZD, 2019. How small can we go? Evaluating survival, tag retention, and growth of juvenile Chinook salmon im-

- planted with a new acoustic microtag. *N. Am. J. Fish. Manag.* 39:1329-1336.
- Friedland KD, Miller MJ, Knights B, 2007. Oceanic changes in the Sargasso Sea and declines in recruitment of the European eel. *ICES J. Mar. Sci.* 64:519-530.
- Forward RB, Tankersley RA, 2001. Selective tidal-stream transport of marine animals *Oceanogr. Mar. Biol.: Ann. Rev.* 39:201-213.
- Galbraith HS, Blakeslee CJ, Schmucker AK, Johnson NS, Hansen MJ, Li W, 2017. Donor life stage influences juvenile American eel *Anguilla rostrata* attraction to conspecific chemical cues. *J. Fish Biol.* 90:384-395.
- Gandolfi G, Pesaro M, Tongiorgi P, 1984. Environmental factors affecting the ascent of elvers, *Anguilla anguilla* (L.), into the Arno River. *Oebalia* 126:17-35.
- Geffroy B, Bardonnat A, 2015. Sex differentiation and sex determination in eels: consequences for management. *Fish Fish.* 17:375-398.
- Garcia de Leániz, C, 2008. Weir removal in salmonid streams: implications, challenges and practicalities. *Hydrobiologia* 609:83-96.
- Garibaldi A, Turner N, 2004. Cultural keystone species: implications for ecological conservation and restoration. *Ecol. Soc.* 9:1.
- Garman GC, 1992. Fate and potential significance of postspawning anadromous fish carcasses in an Atlantic coastal river. *Trans. Am. Fish. Soc.* 121:390-394.
- Gascuel D, Feunteun E, Fontenelle G, 1995. Seasonal dynamics of estuarine migration in glass eels (*Anguilla anguilla*). *Aquat. Living Resour.* 8:123-133.
- Grill G, Lehner B, Thieme M, Geenen B, Tickner D, Antonelli F, Babu S, Borrelli P, Cheng L, Crochetiere H, Ehalt Macedo H, Filgueiras R, Goichot M, Higgins J, Hogan Z, Lip B, McClain ME, Meng J, Mulligan M, Nilsson C, Olden jd, Opperman JJ, Petry P, Reidy Liermann C, Saénz L, Salinas-Rodriguez S, Schelle P, Schmitt RJP, Snider J, Tan F, Tockner K, Valdujo PH, van Soesbergen, Zarfl C, 2019. Mapping the world's free-flowing rivers. *Nature.* 569:215-221.
- Guarniero I, Cariani A, Ferrari A, Sulliotti V, Emmanuele P, Casalini A, Tinti F, Mordenti O, 2020. Sexual behaviour and reproductive performance of the endangered European eel *Anguilla anguilla* (Linnaeus, 1758) based on direct observations and paternity assignment in semi-natural conditions. *Aquac. Rep.* 16:100258.
- Gutiérrez-Estrada JC, Pulido-Calvo I, 2015. Is the Atlantic surface temperature a good proxy for forecasting the recruitment of European eel in the Guadalquivir estuary? *Prog. Oceanogr.* 130:112-124.
- Han YS, Hsiung KM, Zhang H, Chow LY, Tzeng WN, Shinoda A, Yoshinaga T, Hur SP, Hwang SD, Iizuka Y, Kimura S, 2019. Dispersal characteristics and pathways of Japanese glass eel in the East Asian continental shelf. *Sustainability* 11:2572.
- Han YS, Lin YF, Wu CR, Iizuka Y, Castillo TR, Yambot IU, Malmalangkap MD, Yambot AV, 2016. Biogeographic distribution of the eel *Anguilla luzonensis*: dependence upon larval duration and oceanic currents. *Mar. Ecol. Prog. Ser.* 551:227-238.
- Hanel R, Briand C, Diaz E, Döring R, Sapounidis A, Warmerdam W, Andrés M, Freese M, Marcellis A, Marohn L, Pohlmann JD, van Scharrenburg M, Waidmann N, Walstra J, Werkman M, de Wilde J, Wysujack K, 2019. Research for PECH Committee – environmental, social and economic sustainability of European eel management. European Parliament, Policy Department for Structural and Cohesion Policies, Brussel: 192 pp.
- Hanel R, Stepputtis D, Bonhommeau S, Castonguay M., Schaber M., Wysujack K, Vobach M, Miller MJ, 2014. Low larval abundance in the Sargasso Sea: new evidence about reduced recruitment of the Atlantic eels. *Naturwissenschaften* 101:1041-1054.
- Harrison AJ, Walker AM, Pinder AC, Briand C, Aprahamian MW, 2014. A review of glass eel migratory behaviour, sampling techniques and abundance estimates in estuaries: implications for assessing recruitment, local production and exploitation. *Rev. Fish Biol. Fish.* 24:967-983.
- Hewavitharane CA, Pickering TD, Rico C, Mochioka N, 2020. Early life history of tropical freshwater eels (*Anguilla* spp.) recruiting to Viti Levu, Fiji Islands, in the western South Pacific. *Mar. Freshw. Res.* 71:452-460.
- Higuchi T, Watanabe S, Manabe R, Kaku T, Okamura A, Yamada Y, Miller MJ, Tsukamoto K, 2018. Tracking *Anguilla japonica* silver eels along the West Marina Ridge using pop-up archival transmitting tags. *Zool. Stud.* 57:24.
- Huertas M, Canário AVM, Hubbard PC, 2008. Chemical communication in the genus *Anguilla*: a minireview. *Behaviour* 145:1389-1407.
- ICES, 2011. Report of the 2011 session of the joint EIFAAC/ICES working group on eels (WGEEL), 5-9 September 2011, Lisbon, Portugal: 244 pp.
- ICES, 2016. Report of the Working Group on Eels (WGEEL), 15-22 September 2016, Cordoba, Spain. (ICES CM 2016/ACOM: 19). http://ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2016/WGEEL/wgeel_2016.pdf.
- ICES, 2018. Report of the Joint EIFAAC/ICES/GFCM Working Group on Eels (WGEEL), 5-12 September 2018, Gdańsk, Poland. ICES CM 2018/ACOM:15, 152 pp.
- ICES. 2019. Report of the Joint EIFAAC/ICES/GFCM Working Group on Eels (WGEEL), ICES Scientific Reports. 1:50, 177 pp.
- ICES, 2020. Report of the Joint EIFAAC/ICES/GFCM Working Group on Eels (WGEEL). ICES Scientific Reports. 2:85, 223 pp.
- Imbert H, Labonne J, Rigaud C, Lambert P, 2010. Resident and migratory tactics in freshwater European eels are sizedependent. *Freshw. Biol.* 55:1483-1493.
- IUCN, 2014. The IUCN Red List of Threatened Species: *Anguilla anguilla*. <http://www.iucnredlist.org>.
- IUCN, 2019. The IUCN Red List of Threatened Species. <http://www.iucnredlist.org>.
- Jacoby DMP, Casselman JM, Crook V, DeLucia MB, Ahn H, Kaifu K, Kurwie T, Sasal P, Silfvergrip AMC, Smith KG, Uchida K, Walker AM, Gollock MJ, 2015. Synergistic patterns of threat and the challenges facing global anguillid eel conservation. *GECCO* 4:321-333.
- Januchowski-Hartley SR, McIntyre PB, Diebel M, Doran PJ, Infante DM, Joseph C, Allan JD, 2013. Restoring aquatic ecosystem connectivity requires expanding inventories of

- both dams and road crossings. *Front. Ecol. Environ.* 11:211-217.
- Jegstrup IM, Rosenkilde P, Regulation of post-larval development in the European eel: thyroid hormone level, progress of pigmentation and changes in behaviour. *J. Fish Biol.* 63:168-175.
- Jellyman DJ, Arai T, 2016. Juvenile eels: upstream migration and habitat use, p.171-191. In: Arai T, (ed.), *Biology and ecology of anguillid eels.*
- Jellyman DJ, Glova GJ, Todd PR, 1996. Movements of short-finned eels, *Anguilla australis*, in Lake Ellesmere, New Zealand: results from mark-recapture studies and sonic tracking. *N.Z. J. Mar. Freshw. Res.* 30:371-381.
- Jellyman DJ, Lambert PW, 2003. Factors affecting recruitment of glass eels into the Grey River, New Zealand. *Fish Biol.* 63:1067-1079.
- Jellyman DJ, Tsukamoto K, 2002. First use of archival transmitters to track migrating freshwater eels *Anguilla dieffenbachii* at sea. *Mar. Ecol. Prog. Ser.* 233:207-215.
- Jones J, Börger L, Tummers J, Jones P, Lucas M, Kerr J, Kemp P, Bizzi S, Consuegra S, Marcello L, Vowles A, Belletti B, Verspoor E, Bund de Gough, P, Garcia de Leániz C, 2019. A comprehensive assessment of stream fragmentation in Great Britain. *Sci. Total Environ.* 673:756-762.
- Katz J, Moyle PB, Quinous RM, Israel J, Purdy S, 2013. Impending extinction of salmon, steelhead, and trout (Salmonidae) in California. *Environ. Biol. Fish.* 96:1169-1186.
- Kemp PS, O'Hanley JR, 2010. Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. *Fish. Manag. Ecol.* 17:297-322.
- Kettle AJ, Bakker DCE, Haines K, 2008. Impact of the North Atlantic Oscillation on the trans-Atlantic migrations of the European eel (*Anguilla anguilla*). *J. Geophys. Res.* 113:26.
- Kettle AJ, Haines K, 2006. How does the European eel (*Anguilla anguilla*) retain its population structure during its larval migration across the North Atlantic Ocean? *Can. J. Fish. Aquat. Sci.* 63:90-106.
- Kettle AJ, Vøllestad LA, Wibig J, 2011. Where once the eel and the elephant were together: decline of the European eel because of changing hydrology in southwest Europe and north-west Africa? *Fish Fish.* 12:380-411.
- Kirk RS, 2003. The impact of *Anguillicola crassus* on European eels. *Fish. Manag. Ecol.* 10:385-394.
- Knights B, 2003. A review of the possible impacts of long-term oceanic and climate changes and fishing mortality on recruitment of anguillid eels of the Northern Hemisphere. *Sci. Total Environ.* 310:237-244.
- Knudsen SW, Ebert RB, Hesselsøe M, Kuntke F, Hassingboe J, Bondgaard Mortensen P, Thomsen PF, Sigsgaard EE, Klitgaard Hansen B, Nielsen EEG, Møller PR, 2019. Species-specific detection and quantification of environmental DNA from marine fishes in the Baltic Sea. *J. Exp. Mar. Biol. Ecol.* 510:31-45.
- Kroon FJ, Phillips S, 2016. Identification of human-made physical barriers to fish passage in the Wet Tropics region, Australia. *Mar. Freshw. Res.* 67:677-681.
- Kullmann B, Adamek M, Steinhagen D, Thiel R, 2017. Anthropogenic spreading of anguillid herpesvirus 1 by stocking of infected farmed European eels, *Anguilla anguilla* (L.), in the Schlei fjord in northern Germany. *J. Fish Dis.* 40:1695-1706.
- Kullmann B, Thiel R, 2018. Bigger is better in eel stocking measures? Comparison of growth performance, body condition, and benefit-cost ratio of simultaneously stocked glass and farmed eels in a brackish fjord. *Fish. Res.* 205:132-140.
- Laffaille P, Baisez A, Rigaud C, Feunteun E, 2004. Habitat preferences of different European eel size classes in a reclaimed marsh: a contribution to species and ecosystem conservation. *Wetlands* 24:642-651.
- Laffaille P, Caraguel JM, Legault A, 2007. Temporal patterns in the upstream migration of European glass eels (*Anguilla anguilla*) at the Couesnon estuarine dam. *Estuar. Coast. Shelf Sci.* 73:81-90.
- Laffaille P, Feunteun E, Baisez A, Robinet T, Acou T, Legault A, Lek S, 2003. Spatial organisation of European eel (*Anguilla anguilla* L.) in a small catchment. *Ecol. Freshw. Fish* 12:254-264.
- Laffaille P, Rigaud C, 2008. [Indicateurs de colonisation et de sédentarisation, p.230-275.][Article in French]. In: Adam G, Feunteun E, Prouzet P, Rigaud C (eds.), *L'anguille européenne, Indicateurs d'abondance et de colonisation*, QUAE, Paris.
- Lagarde R, Peyre J, Amilhat E, Bourrin F, Prellwitz F, Simon G, Faliex E, 2021. Movements of non-migrant European eels in an urbanised channel linking a Mediterranean lagoon to the sea. *Water* 13:839.
- Lambert P, Lassalle G, Acolas ML, Bau F, Castelnaud G, Daverat F, Jatteau P, Rigaud C, Rochard E, Roqueplo C, de Jouvenel F, 2019. A foresight analysis in fisheries science: the case study of migratory fish research. *Futures* 111:90-103.
- Larinier M, 2000. Dams in fish migration, p.1-23. In: Berkamp McCartney M, Dugan P, McNeely J, Acreman MG (eds.). *Dams, Ecosystem Functions and Environmental Restoration*. Cape Town.
- Larinier M, 2001. Environmental issues, dams and fish migration, p.45-90. In: Marmulla, G. (ed.), *Dams, Fish and Fisheries. Opportunities, challenges and conflict resolution*. FAO Fisheries Technical Paper. No. 419. FAO, Rome.
- Larinier, M., 2002. Location of fishways. *Bull. fr. pêche piscic.* 364:39-53
- Larinier M, Travade F, 2002. Downstream migration: problems and facilities. *Bull. fr. pêche piscic.* 364:181-207.
- Lasne E, Laffaille P, 2009. Assessing the freshwater distribution of yellow eel. *Knowl. Manag. Aquatic Ecosyst.* 04:390-391.
- Lassalle G, Rochard E, 2009. Impact of twenty-first century climate change on diadromous fish spread over Europe, North Africa and the Middle East. *Glob. Chang. Biol.* 15:1072-1089.
- Lecomte-Finiger R, 1992. Growth history and age at recruitment of European glass eels (*Anguilla anguilla*) as revealed by otolith microstructure. *Mar. Biol.* 114:205-210.
- Lin YJ, Lozys L, Shiao JC, Lizukaand Y, Tzeng WN, 2007. Growth differences between naturally recruited and stocked European eel *Anguilla anguilla* from different habitats in Lithuania. *J. Fish Biol.* 71:1773-1787.
- Lin YJ, Yalçın-Özdilek S, Iizuka Y, Gümüş A, Tzeng WN, 2011. Migratory life history of European eel *Anguilla anguilla* from freshwater regions of the River Asi, southern Turkey and their high otolith Sr:Ca ratios. *J. Fish Biol.* 78:860-868.
- Liss SA, Znotinas KR, Blackburn SE, Fischer ES, Hughes JS, Harnish RA, Li H, Deng ZD, 2021. From 95 to 59 millime-

- tres: a new active acoustic tag size guideline for salmon. *Can. J. Fish. Aquat. Sci.* 78:943-957.
- Lucas MC, Baras E, 2001. Migration of freshwater fishes. Blackwell Science Ltd, Oxford: 412 pp.
- Maitland PS, 2003. Ecology of the river, brook and sea lamprey. *Conserving Natura 2000. Rivers Ecology Series No. 5.* English Nature, Peterborough: 54 pp.
- Maes GE, Raeymaekers JAM, Pampoulie C, Scynaeve A, Goemans G, Belpaire C, Volckaert FAM, 2005. The catadromous European eel *Anguilla anguilla* (L.) as a model for freshwater evolutionary ecotoxicology: relationship between heavy metal bioaccumulation, condition and genetic variability. *Aquat. Toxicol.* 73:99-114.
- Manabe R, Aoyama J, Watanabe K, Kawai M, Miller MJ, Tsukamoto K, 2011. First observations of the oceanic migration of Japanese eel, from pop-up archival transmitting tags. *Mar. Ecol. Prog. Ser.* 437:229-240.
- Marui M, Arai T, Miller MJ, Jellyman DJ, Tsukamoto K, 2001. Comparison of early life history between New Zealand temperate eels and Pacific tropical eels revealed by otolith microstructure and microchemistry. *Mar. Ecol. Prog. Ser.* 213:273-284.
- Matondo NB, Benitez JP, Dierckx A, Rollin X, Ovidio M, 2020. An evaluation of restocking practice and demographic stock assessment methods for cryptic juvenile European eel in upland rivers. *Sustainability* 12:1124.
- Matondo NB, Séleck E, Dierckx A, Benitez JP, Rollin X, Ovidio M, 2019. What happens to glass eels after restocking in upland rivers? A long-term study on their dispersal and behavioural traits. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 29:374-388.
- McCleave JD, 2001. Fish: eels, p.800-809. In: Steele J. and McNeil C. (eds.). *Encyclopedia of Ocean Sciences.* Academic Press, London.
- McCleave JD, Kleckner RC, 1985. Oceanic migrations of Atlantic eels (*Anguilla* spp.): adults and their offspring. *Contr. Mar. Sci.* 27:316-337.
- McDowall RM, 1988. Diadromy in fishes: migration between freshwater and marine environments. Croom Helm, London: 308 pp.
- McDowall RM, 1992. Diadromy-origins and definitions of terminology. *Copeia*: 248-251.
- McIntyre PB, Reidy Liermann C, Childress E, Hamann EJ, Hogan JD, Januchowski-Hartley SR, Koning AA, Neeson TM, Oele DL, Pracheil BM, 2016. Conservation of migratory fishes in freshwater ecosystems, p.324-360. In: *Conservation of Freshwater Fishes*, Closs GP, Krkosek M, Olden JD (eds). Cambridge University Press: Cambridge.
- Meybeck M, 2003. Global analysis of river systems: From Earth system controls to Anthropocene syndromes. *Philos. Trans. R. Soc., Series B, Biological Sciences* 358:1935-1955.
- Milardi M, Lanzoni M, Gavioli A, Fano EA, Castaldelli G, 2018. Tides and moon drive fish movements in a brackish lagoon. *Estuar. Coast. Shelf Sci.* 215:207-214.
- Miller MJ, Bonhommeau S, Munk P, Castonguay M, Hanel R, McCleave JD, 2015. A century of research on the larval distributions of the Atlantic eels: a re-examination of the data. *Biol. Rev.* 90:1035-1064.
- Miller MJ, Feunteun E, Tsukamoto K, 2016. Did a “perfect storm” of oceanic changes and continental anthropogenic impacts cause northern hemisphere anguillid recruitment reductions? *ICES J. Mar. Sci.* 73:43-56.
- Miller MJ, Kimura S, Friedland KD, Knights B, Kim H, Jellyman DJ, Tsukamoto K, 2009. Review of ocean-atmospheric factors in the Atlantic and Pacific Oceans influencing spawning and recruitment of anguillid eels. *Am. Fish. Soc. Symp.* 69:231-249.
- Miller MJ, Westerberg H, Sparholt H, Wysujack K, Sørensen SR, Marohn L, Jacobsen MW, Freese M, Ayala DJ, Pohlmann JD, Svendsen JC, Watanabe S, Andersen L, Møller PR, Tsukamoto K, Munk P, Hane R, 2019. Spawning by the European eel across 2000 km of the Sargasso Sea. *Biol. Lett.* 15:20180835.
- Moccia D, Salvadori L, Ferrari S, Carucci A, Pusceddu A, 2020. Implementation of the EU ecological flow policy in Italy with a focus on Sardinia. *Adv. Oceanogr. Limnol.* 2020:11
- Montgomery DR, 2003. King of fish: the thousand-year run of salmon. Westview Press. Boulder, Colo., USA: 304 pp.
- Moore KA, Jarvis JC, 2008. Environmental factors affecting recent summertime eelgrass diebacks in the lower Chesapeake Bay: implications for long-term persistence. *J. Coast. Res. Spl. Issue* 55:135e147.
- Morais P, Daverat F, 2016. An introduction to fish migration. Boca Raton, Florida (USA): CRC Press: 315 pp.
- Moriarty C, Dekker W, 1997. Management of the European eel. *Fish. Bull.* 15:1-110.
- Moriarty C, McCarthy D, 1982. Eel, p.3-6. In: EIFAC Technical Paper No. 42 European Inland Fisheries Advisory Commission (ed.), Report of the Symposium on Stock Enhancement in the Management of Freshwater Fisheries.
- Mueller R, Liss S, Deng ZD, 2019. Implantation of a new micro acoustic tag in juvenile Pacific lamprey and American eel. *J. Vis. Exp.* 145:e59274.
- Myers GA, 1949. Usage of anadromous, catadromous and allied terms for migratory fishes. *Copeia* 1949:89-97.
- Naisbett-Jones LC, Putman NF, Stephenson JF, Ladak S, Young KA, 2017. A magnetic map leads juvenile European eels to the Gulf Stream. *Curr. Biol.* 27:1236-1240.
- Naismith IA, Knights B, 1990. Studies of sampling methods and of techniques for estimating populations of eels, *Anguilla anguilla* L. *Aquac. Fish. Manag.* 21:357-367.
- Nunn, A.D., Cowx, I.G., 2012. Restoring river connectivity: prioritizing passage improvements for diadromous fishes and lampreys. *Ambio* 41:402-409.
- NOAA. 2017. Fisheries economics of the United States: 169 pp. <https://www.fisheries.noaa.gov/feature-story/fisheries-economics-united-states-2015>.
- Oliveira K, 1997. Movements and growth rates of yellow-phase American eels in the Annaquatucket River, Rhode Island. *Trans. Amer. Fish. Soc.* 126:638-646.
- OSPAR. 2010. Background Document for European eel *Anguilla anguilla*. OSPAR Commission: 29 pp.
- Ovidio M, Serebinski AL, Philippart JC, Matondo BN, 2013. A bit of quiet between the migrations: the resting life of the European eel during their freshwater growth phase in a small stream. *Aquat. Ecol.* 47:291-301.
- Ovidio M, Tarrago-Bès F, Matondo BN, 2015. Short-term responses of glass eels transported from UK to small Belgian streams. *Ann. Limnol. Int. J. Limnol.* 51:219-226.
- Pacariz S, Westerberg H, Björk G, 2014. Climate change and

- passive transport of European eel larvae. *Ecol. Freshw. Fish* 23:86–94.
- Padgett TE, Thomas RE, Borman DJ, Mould DC, 2020. Individual-based model of juvenile eel movement parametrized with computational fluid dynamics-derived flow fields informs improved fish pass design. *R. Soc. Open Sci.* 7:191505.
- Palm S, Dannewitz J, Prestegard T, Wickstrom H, 2009. Panmixia in European eel revisited: no genetic difference between maturing adults from southern and northern Europe. *Heredity* 103:82–89.
- Pedersen MI, 1998. Recapture rate, growth and sex of stocked cultured eels *Anguilla anguilla* (L.). *Bull. français pêche piscic.* 349:153–162.
- Pedersen MI, 2000. Long-term survival and growth of stocked eel, *Anguilla anguilla* (L.), in a small eutrophic lake. *Dana* 12:71–76.
- Pedersen MI, 2009. Does stocking of Danish lowland streams with elvers increase European eel populations? *Am. Fish. Soc. Symp.* 58:149–156.
- Pedersen MI, Rasmussen GH, 2016. Yield per recruit from stocking two different sizes of eel (*Anguilla anguilla*) in the brackish Roskilde Fjord. *ICES J. Mar. Sci.* 73:158–164.
- Perkin JS, Gido KB, 2012. Fragmentation alters stream fish community structure in dendritic ecological networks. *Ecol. Appl.* 22:2176–2187.
- Pike C, Crook V, Gollock M, 2020. *Anguilla anguilla*. In: The IUCN Red List of Threatened Species: e.T60344A 152845178.
- Piper AT, Svendsen JC, Wright RM, Kemp PS, 2017. Movement patterns of seaward migrating European eel (*Anguilla anguilla*) at a complex of riverine barriers: implications for conservation. *Ecol. Freshwater Fish* 26:87–98.
- Piper AT, Whitec PR, Wright RM, Leightonc TG, Kempa PS, 2019. Response of seaward-migrating European eel (*Anguilla anguilla*) to an infrasound deterrent. *Ecol. Eng.* 127:480–486.
- Piper AT, Wright RM, Walker AM, Kemp PS, 2013. Escapement, route choice, barrier passage and entrainment of seaward migrating European eel, *Anguilla anguilla*, within a highly regulated lowland river. *Ecol. Eng.* 57:88–96.
- Podda C, Palmas F, Frau G, Chessa G, Culurgioni J, Diciotti R, Fois N, Sabatini A, 2020. Environmental influences on the recruitment dynamics of juvenile European eels, *Anguilla anguilla*, in a small estuary of the Tyrrhenian Sea, Sardinia, Italy. *Aquatic Conserv.: Mar. Freshw. Ecosyst.* 30:1638–1648.
- Podgorniak T, Blanchet S, De Oliveira E, Daverat F, Pierron F, 2016. To boldly climb: behavioural and cognitive differences in migrating European glass eels. *R. Soc. open sci.* 3:150665.
- Polyakov IV, Bhatt US, Simmons HL, Walsh D, Walsh JE, Zhang X, 2005. Multidecadal variability of North Atlantic temperature and salinity during the twentieth century. *J. Clim.* 18:4562–4581.
- Prigge E, Marohn L, Hanel R, 2013. Tracking the migratory success of stocked European eels *Anguilla anguilla* in the Baltic Sea. *J. of Fish Biol.* 82:686–699.
- Prouzet P, 2002. Historique des captures de civelles, intensité actuelle de leur exploitation, variation de leur capturabilité par la pêche professionnelle maritime et indices de colonisation sur le bassin versant de l'Adour. Technical report, Ifremer. <http://www.ifremer.fr/indicang/boite-bassins-versants/pdf/historique-capture-civelle.pdf>.
- Psuty I, Draganik B, 2008. The effectiveness of glass eel stocking in the Vistula lagoon, Poland. *AIeP* 2:103–111.
- Radinger J, Hölker F, Horky P, Slavik O, Dendoncker N, Wolter C, 2016. Synergistic and antagonistic interactions of future land use and climate change on river fish assemblages. *Glob. Change Biol.* 22:1505–1522.
- Raeymaekers JA, Maes GE, Geldof S, Hontis I, Nackaerts K, Volckaert FA, 2008. Modeling genetic connectivity in sticklebacks as a guideline for river restoration. *Evol. Appl.* 1:475–488.
- Réveillac É, Feunteun E, Berrebi P, Gagnaire PA, Lecomte-Finiger R, Bosc P, Robinet T, 2008. *Anguilla marmorata* larval migration plasticity as revealed by otolith microstructural analysis. *Can. J. Fish. Aquat. Sci.* 65:2127–2137.
- Réveillac É, Robinet T, Rabenevanana MW, Valade P, Feunteun E, 2009. Clues to the location of the spawning area and larval migration characteristics of *Anguilla mossambica* as inferred from otolith microstructural analyses. *J. Fish. Biol.* 74:1866–1877.
- Righton D, Westerberg H, Feunteun E, Okland F, Gargan P, Amilhat E, Metcalfe J, Lobon-Cervia J, Sjo Berg N, Simon J, Acou A, Vedor M, Walker A, Trancart T, Brämick U, Aarestrup K, 2016. Empirical observations of the spawning migration of European eels: the long and dangerous road to the Sargasso Sea. *Sci. Adv.* 2:e1501694.
- Ringuet S, Muto F, Raymakers C, 2002. Eels: Their Harvest and Trade in Europe and Asia. *TRAFFIC Bulletin* 19:2–27.
- Robinet T, Lecomte-Finiger R, Escoubeyrou K, Feunteun E, 2003. Tropical eels *Anguilla* spp. recruiting to Réunion Island in the Indian Ocean: taxonomy, patterns of recruitment and early life histories. *Mar. Ecol. Prog. Ser.* 259:263–272.
- Robinet T, Réveillac E, Kuroki M, Aoyama J, Tsukamoto K, Rabenevanana MW, Valade P, Gagnaire PA, Berrebi P, Feunteun E, 2008. New clues for freshwater eels (*Anguilla* spp.) migration routes to eastern Madagascar and surrounding islands. *Mar. Biol.* 154:453–463.
- Rochard E, Pellegrini P, Marchal J, Béguer M, Ombredane D, Lassalle G, Menvielle E, Baglinière JL, 2009. Identification of diadromous fish species on which to focus river restoration: an example using an eco-anthropological approach (the Seine basin, France). *Challenges for diadromous fishes in a dynamic global environment. Am. Fish. Soc. Symp.* 69:691–711.
- Rosell R, Evans D, Allen M, 2005. The eel fishery in Lough Neagh, Northern Ireland - an example of sustainable management? *Fish. Manag. Ecol.* 12:377–385.
- Rossier O, 1997. Comparison of gillnet sampling and night visual census of fish communities in the littoral zone of Lake Geneva, Switzerland. *Arch. Hydrobiol.* 139:223–233.
- Sanderson FJ, Donald PF, Pain DJ, Burfield IJ, van Bommel FPJ, 2006. Long-term population declines in Afro-Paleartic migrant birds. *Biol. Conserv.* 131:93–105.
- Sandlund OT, Diserud Poole OH, Bergesen K, Dillane M, Rogan G, Durif C, Thorstad EB, Vøllestad LA, 2017. Timing and pattern of annual silver eel migration in two European watersheds are determined by similar cues. *Ecol. Evol.* 7:5956–5966.
- Schabetsberger R, Økland F, Aarestrup K, Kalfatak D,

- Sichrowsky U, Tambets M, Dall'Oimo G, Kaiser R, Miller P, 2013. Oceanic migration behaviour of tropical Pacific eels from Vanuatu. *Mar. Ecol. Prog. Ser.* 475:177-190.
- Schabetsberger R, Okland F, Kalfatak D, Sichrowsky U, Meelis T, Aarestrup K, Gubili C, Sarginson J, Boufana B, Jehle R, Dall'Olmo G, Miller MJ, Scheck A, Kaiser R, Quartly G, 2015. Genetic and migratory evidence for sympatric spawning of tropical Pacific eels from Vanuatu. *Mar. Ecol. Prog. Ser.* 521:171-187.
- Schabetsberger R, Scheck A, Kaiser R, Leana R, Gubili C, Økland F, 2019. Oceanic migration behaviour of Pacific eels from Samoa. *Fish. Manag. Ecol.* 26:53-56.
- Schiavina M, Bevacqua D, Melià P, Crivelli AJ, Gatto M, De Leo GA, 2015. A user-friendly tool to assess management plans for European eel fishery and conservation. *Environ. Model. Softw.* 64:9-17.
- Schmidt J, 1922. The breeding places of the eel. *Philos. Trans. R. Soc.* 211:179-208.
- Schmucker AK, Johnson NS, Galbraith HS, Li W, 2016. Glass-eel-stage American eels respond to conspecific odor as a function of concentration. *T. AM. FISH. SOC.* 145:712-722.
- Schulze T, Kahl U, Radke RJ, Benndorf J, 2004. Consumption, abundance and habitat use of *Anguilla anguilla* in a mesotrophic reservoir. *J. Fish Biol.* 65:1543-1562.
- Secor DH, 2015. *Migration ecology of fishes*. Baltimore, USA: John Hopkins University Press: 304 pp.
- Shiao JC, Ložys L, Iizuka Y and Tzeng WN, 2006. Migratory patterns and contribution of stocking to the population of European eel in Lithuanian waters as indicated by otolith Sr:Ca ratios. *J. Fish Biol.* 69:749-769.
- Shields FD, Knight SS, Cooper M, 1995. Incised stream physical habitat restoration with stone weirs. *Regul. Rivers Res. Manag.* 10:181-198.
- Sjöberg NB, Wickström H, Asp A, Petersson E, 2017. Migration of eels tagged in the Baltic Sea and Lake Mälaren in the context of the stocking question. *Ecol. Freshw. Fish* 26:517-532.
- Simon J, Dörner H, 2014. Survival and growth of European eels stocked as glass- and farm-sourced eels in five lakes in the first years after stocking. *Ecol. Freshw. Fish* 23:40-48.
- Simon J, Dörner H, Scott RD, Schreckenbach K, Knösche R, 2013. Comparison of growth and condition of European eels stocked as glass and farm sourced eels in lakes in the first four years after stocking. *J. Appl. Ichthyol.* 29:323-330.
- Smith KM, Byron CJ, Sulikowski JA, 2016. Modeling predator-prey linkages of diadromous fishes in an estuarine food web. *Mar. Coast. Fish.* 8:476-491.
- Sola C, 1995. Chemoattraction of upstream migrating glass eels *Anguilla Anguilla* to earthy and green odorants. *Env. Biol. Fishes* 43:179-185.
- Sola C, Tongiorgi P, 1996. The effects of salinity on the chemotaxis of glass eels, *Anguilla Anguilla*, to organic earthy and green odorants. *Env. Biol. Fishes* 47:213-218.
- Sorensen PW, 1986. Origins of the freshwater attractant(s) of migrating elvers of the American eel, *Anguilla rostrata*. *Env. Biol. Fishes* 17:185-200.
- Stacey JA, Pratt TC, Verreault G, Fox MG, 2015. A caution for conservation stocking as an approach for recovering Atlantic eels. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 25:569-580.
- Taberlet P, Coissac E, Pompanon F, Brochmann C, Willerslev E, 2012. Towards next-generation biodiversity assessment using DNA metabarcoding. *Mol. Ecol.* 21:2045-2050.
- Teichert N, Tetard S, Trancart T, Feunteun E, Acou A, de Oliveira E, 2020. Resolving the trade-off between silver eel escapement and hydropower generation with simple decision rules for turbine shutdown. *J. Env. Manag.* 261:110212.
- Tesch FW, 1977. *The eel. Biology and management of anguillid eels*. Chapman & Hall, London: 370 pp.
- Tesch FW, 2003. *The eel*. Blackwell Science: 408 pp.
- Thorstad EB, Rikardsen AH, Alp A, Økland F, 2013. The use of electronic tags in fish research – an Overview of Fish Telemetry Methods. *Turkish J. Fish. Aquat. Sci.* 13:881-896.
- Tosi L, Sola C, 1993. Role of geosmin, a typical inland water odour, in guiding glass eel *Anguilla anguilla* (L.) Migration. *Ethology* 95:177-185.
- Tosi L, Spampanato A, Sola C, Tongiorgi P, 1989. Relation of water odour, salinity and temperature to ascent of glass-eels, *Anguilla anguilla* (L.): a laboratory study. *J. Fish Biol.* 36:327-340.
- Trancart T, Acou A, De Oliveira E, Feunteun E, 2013. Forecasting animal migration using SARIMAX: an efficient means of reducing silver eel mortality caused by turbines. *Endanger. Species Res.* 21:181-190.
- Trancart T, Carpentier A, Acou A, Charrier F, Mazel V, Danet V, Feunteun E, 2020. When “safe” dams kill: analyzing combination of impacts of overflow dams on the migration of silver eels. *Ecol. Eng.* 145:105741.
- Trancart T, Lambert P, Daverat F, Rochard E, 2014. From selective tidal transport to counter-current swimming during watershed colonisation: An impossible step for young-of-the-year catadromous fish? *Knowl. Manag. Aquat. Ecosyst.* 2014:412.
- Trancart T, Tétard S, Acou A, Feunteun E, Schaeffer F, de Oliveira E, 2018. Silver eel downstream migration in the River Rhine, route choice, and its impacts on escapement: A 6-year telemetry study in a highly anthropized system. *Ecol. Eng.* 123:202-211.
- Tsukamoto K, 1990. Recruitment mechanism of the eel, *Anguilla japonica*, to the Japanese coast. *J. Fish. Biol.* 36:659-671.
- Tsukamoto K, Aoyama J, 1998. Evolution of the freshwater eels of the genus *Anguilla*: a probable scenario. *Environ. Biol. Fish.* 52:139-148.
- Van Ginneken VJT, Maes GE, 2005. The European eel (*Anguilla anguilla*, Linnaeus), its lifecycle, evolution and reproduction: a literature review. *Rev. Fish. Biol. Fish* 15:367-398.
- Van Puijbroek PJTM, Buijse AD, Kraak MHS, Verdonschot PFM, 2019. Species and river specific effects of river fragmentation on European anadromous fish species. *River Res. Appl.* 35:68-77.
- Verreault G, Mingelbier M, Dumont P, 2012. Spawning migration of American eel *Anguilla rostrata* from pristine (1843–1872) to contemporary (1963–1990) periods in the St Lawrence Estuary, Canada. *J. Fish. Biol.* 81:387-407.
- Vörösmarty CJ, McIntyre PB, Gessner MO, Dudgeon D, Prusevich A, Green P, Glidden S, Bunn SE, Sullivan CA, Reidy Liermann C, Davies PM, 2010. Global threats to human water security and river biodiversity. *Nature* 467:555-561.
- Walker AM, Andonegi E, Apostolaki P, Aprahamian M, Beaulaton L, Bevacqua D, Bevacqua P, Briand C, Cannas A, De Eyto E, Dekker W, De Leo G, Diaz E, Doering-Arjes P, Fladung E, Jouanin C, Lambert P, Poole R, Oeberst R, Schi-

- avina M, 2013. Lot 2: Pilot project to estimate potential and actual escapement of silver eel. Final project report, service contract S12.539598, Studies and pilot projects for carrying out the common fisheries policy. Brussels, European Commission, Directorate - General for Maritime Affairs and Fisheries (DG Mare): 358 pp.
- Wang CH, Tzeng WN, 2000. The timing of metamorphosis and growth rates of American and European eel *leptocephali*: a mechanism of larval segregative migration. *Fish. Res.* 46:191-205.
- Weber M, 1986. Fishing method and seasonal occurrence of glass eels (*Anguilla anguilla*, L.) in the Rio Minho, west coast of the Iberian peninsula. *Vie Milieu* 366:243-250.
- Westerberg H, Miller MJ, Wysujack K, Marohn L, Freese M, Pohlmann JD, Watanabe S, Tsukaoto K, Hanel R, 2018. Larval abundance across the European eel spawning area: an analysis of recent and historic data. *Fish Fish.* 19:890-902.
- Westerberg H, Sjöberg N, Lagenfelt I, Aarestrup K, Righton D, 2014. Behaviour of stocked and naturally recruited European eels during migration. *Mar. Ecol. Progr. Ser.* 496:145-157.
- Westerberg IK, Wagener T, Coxon G, McMillan HK, Castellarin A, Montanari A, Freer J, 2016. Uncertainty in hydrological signatures for gauged and ungauged catchments, *Water Resour. Res.* 52:1847-1865.
- Westin L, 1998. The spawning migration of European silver eel (*Anguilla anguilla* L.) with particular reference to stocked eel in the Baltic. *Fish. Res.* 38:257-270.
- Westin L, 2003. Migration failure in stocked eels *Anguilla anguilla*. *Mar. Ecol. Pr. Ser.* 254:307-311.
- Wickström H, Sjöberg NH, 2014. Traceability of stocked eels—the Swedish approach. *Ecol. Freshw. Fish* 23:33-39.
- Wickström H, Westin L, Clevestam P, 1996. The biological and economic yield from a long-term eel-stocking experiment. *Ecol. Freshw. Fish* 5:140-147.
- Wilcove DS, Wikelski M, 2008. Going, going, gone: is animal migration disappearing. *PLoS Biol.* 6:e188.
- Wilkes MA, Mckenzie M, Webb JA, 2018. Fish passage design for sustainable hydropower in the temperate Southern Hemisphere: an evidence review. *Rev. Fish Biol. Fish.* 28:117-135.
- Winter H, Jansen H, Bruijs M, 2006. Assessing the impact of hydropower and fisheries on downstream migrating silver eel, *Anguilla anguilla*, by telemetry in the River Meuse. *Ecol. Freshw. Fish* 15:221-228.
- Wofford JE, Gresswell RE, Banks MA, 2005. Influence of barriers to movement on within-watershed genetic variation of coastal cutthroat trout. *Ecol. Appl.* 15:628-637.
- Wolter C, 2015. Historic catches, abundance, and decline of Atlantic salmon *Salmo salar* in the River Elbe. *Aquat. Sci.* 77:367-380.
- Wysujack K, Westerberg H, Aarestrup K, Trautner J, Kurwie T, Nagel F, Hanel R, 2015. The migration behaviour of European silver eels (*Anguilla anguilla*) released in open ocean conditions. *Mar. Freshw. Res.* 66:145-157.
- Zarfl C, Lumsdon AE, Berlekamp J, Tydecks L, Tockner K, 2015. A global boom in hydropower dam construction. *Aquat. Sci.* 77:161-170.
- Zompola S, Katselis G, Koutsikopoulos C, Cladas Y, 2008. Temporal patterns of glass eel migration (*Anguilla anguilla* L. 1758) in relation to environmental factors in the Western Greek inland waters. *Estuar. Coast. Shelf Sci.* 80:330-338.