Chapter 1

General introduction

1.1 Connectivity and migration

Living in an anthropogenic world with an estimated population increase to 9 billion by 2050, consequences for all ecosystems on Earth are obvious (Vitousek et al., 1997). It is now widely accepted that global change results in the rapid decline or even extinction of various species on the one hand and in the (human-induced) expansion of others (Brook et al., 2008; Pimm et al., 2006). Consequently, maintaining the diversity of species and functioning of ecosystems will increasingly require human intervention. An important aspect to be addressed related to global change, diversity conservation and consequently ecosystem functioning, is habitat connectivity, allowing animal movement over convenient distances (Council, 2000). Knowledge about movement patterns is crucial for our understanding of the ecology, life history, behaviour and conservation of animals. Animal movement is the general term for an organism's displacement, motivated by an inherent mechanism such as feeding, resting or reproduction. Depending on that goal, animal movement can be classified in three general groups:

1. **Station keeping** is the movement of an organism within a home range towards or away from a specific location for foraging and predator avoidance (i.e. homing location such as a den or nest) (Dingle, 1996).
2. **Ranging** is the permanent movement of an organism from one home range to another (Dingle and Drake, 2007).
3. **Migration** is a persistent and unidirectional movement, characterised by the temporal inhibition of stationary responses (Kennedy, 1985).

The most extensive animal movements relate to migration, present throughout the entire animal kingdom. During the last century, many migrating animals have disappeared or declined in numbers substantially due to various anthropogenic causes with the most prominent being overexploitation, climate change, habitat destruction and migration barriers (Wilcove and Wikelski, 2008). One of the best known examples of migratory animal extinction is that of passenger pigeons (*Ectopistes migratorius* L.), a migratory bird gone extinct in 1914. The passenger pigeon was one of the most abundant endemic bird species to North-America, but due to hunting and trapping, their number declined below a sustainable population, driving them to extinction (Bucher, 1992; Halliday, 1980). A similar story holds true for the American bison (*Bison bison* L.) (Taylor, 2011): the North American population of ca. 30

million bisons was decimated to nearly 100 specimens by the late 19th century to fulfill the industrial leather demand.

Further, climate change is already impacting species distributions as their niche is shifting over latitude, likely leading to alterations in community interactions (Perry et al., 2005). However, redistribution as a response to climate change of species with slow dispersal capacities, low fecundity and fragmented ranges will likely fail due to the fast pace of climate change (Aitken et al., 2008; Pearson, 2006; Thomas et al., 2004).

Finally, urbanization, roads and artificial waterways lead to habitat destruction, migration barriers and consequently a patchy habitat distribution. For example, the common toad (*Bufo bufo* L.) is the amphibian with the highest road mortality rate in Europe, attributed to its reproduction migration from wintering sites to nearby located ponds (Santos et al., 2007). Also many fish species suffer from migration barriers such as weirs, dams, pumps and hydropower stations which prevent them from successfully completing their life cycle, by impairing movement between, for instance, spawning and foraging habitats (see further) (Larinier, 2001). However, in some occasions migration barriers can act beneficial, for instance towards species rehabilitation. Specifically, migration barriers can prevent mixing of locally adapted subpopulations with introduced specimens of subpopulations from other regions or even escaped cultivated species. Especially for fish, a lot of historical stocking has been conducted for angling and rehabilitation purposes. Yet, the stocked fish often come from catchments different than the rehabilitated population. Despite sometimes impressive restocking numbers, rarely do the fish contribute to the rehabilitation process (Koskinen et al., 2002; Poteaux et al., 1998). This is likely explained by stocked species' different genetic lineage and consequently they are not fully adapted to the local conditions, causing them being outcompeted by the local population (Fleming et al., 2000; Hansen et al., 2000). As such, Van Houdt et al. (2005) found evidence of genetic pure lineages in brown trout (*Salmo trutta* L.) in the Meuse catchment in Belgium, likely attributed to migration barriers preventing mixing with stocked specimens down river. Specimens with a pure genetic lineage can aid restoration of populations elsewhere in the river catchment. Also, migration barriers prevent the spread of invasive species. In southern California, for instance, the invasive red swamp crayfish (*Procambarus clarkii* Girard) was almost absent upstream of large barriers, while capture-recapture indicated they moved frequently between pools downstream of the barriers, illustrating their high mobility (Kerby et al., 2005).

Declining numbers of migratory species can have important consequences for ecosystems. Specifically, migrating animals play an important role in nutrient distribution. Many salmon and trout species grow to adulthood in marine environments and migrate up rivers for spawning to subsequently die. This results in a nutrient flux of marine nutrients into inland ecosystems (Wilcove and Wikelski, 2008). Due to migration barriers, salmon and trout populations in the Pacific have declined tremendously, leading to a depletion in marine nitrogen and phosphorous reception of over 90% in Northwest Pacific rivers (Gresh et al., 2000). Spring migration of song birds from Central America to Northern America had a substantial impact on insect abundance, eating over 10 tons of insects per day (Wilcove and Wikelski, 2008). Not only does this illustrate pest control, but the birds may have an important impact on nutrient distribution as well. However, nutrient distribution attributed to migration is not always positive. Large numbers of Lesser Snow Geese (*Chen caerulescens*

caerulescens L.) and Ross' Geese (*Chen rossii* Cassin) forage in nutrient rich agricultural areas, but roost in wetlands, causing a substantial nitrogen and phosphorous load in the water (Post et al., 1998). This problem arises especially due to wetlands becoming more scarcer, resulting in overcrowded space use by the geese.

Another important aspect to address related to migration, is disease spread. Many migrating animals carry zoonotic diseases (Altizer et al., 2011; Webster et al., 2002) and due to human population expansion, we interfere more frequently with those animals, leading to a higher chance of getting infected (e.g. the paramyxoviruses 'Nipah' and 'Hendra' in flying foxes (Daszak et al., 2006; Philbey et al., 1998; Plowright et al., 2008), Lyme and West-Nile virus in birds (Alekseev et al., 2001; Rappole et al., 2000) and SARS (Severe Acute Respiratory Syndrome) in carnivores (Bell et al., 2004)). Even more, by restricting animal movement, they are forced in smaller habitats and consequently occur in larger densities, which makes them more prone to diseases (Altizer et al., 2011). Salmon farms for example are susceptible to sea lice (*Lepeophtheirus salmonis* Krøyer) infections and by placing them along migration corridors, the parasite can rapidly spread across the wild population (Krkošek et al., 2007).

Despite our anthropogenic world hampers animal movement, migration in particular, a paradox exists: never before has the distribution of alien species be so prominent as during the last decades. Especially the increase of international trade, accompanied with the construction of (rail)roads and canals during the Industrial Revolution in the 1800s enhanced biological invasions (Hulme, 2009). Alien species that become invasive can pose serious economic and ecological consequences (Andersen et al., 2004; Kolar and Lodge, 2001).

They can cause shifts in ecological communities (Andersen et al., 2004; McKinney and Lockwood, 1999), thereby affecting ecosystem structure and functioning. By competing with native species, they can severely affect the density of different species within a certain ecosystem, resulting in environmental and economic costs (Pimentel et al., 2005).

1.2 Regulated water ways throughout the world and their impact on fish populations

Among the most anthropogenically altered ecosystems, are aquatic environments: worldwide, water levels of freshwater systems are controlled by structures such as pumping and hydropower stations, weirs, dams, shipping locks and sluices (Arlinghaus et al., 2002; Baumgartner et al., 2009; Bowen et al., 2003; Buysse et al., 2014; Lassalle et al., 2009). Due to global change (e.g. population increase with accompanied consumption) and climate change in particular, hydrology will be affected in the future. It has already been shown that timing of water runoff in large European catchments (e.g. Rhine, Rhône and Danube) will change by an intensifying winter and reduced summer runoff. Obviously, this will affect our hydrological management, such as navigation and hydropower developments (Schröter et al., 2005).

The above mentioned structures for water regulation, so called movement barriers, hamper the movement of aquatic organisms, especially fish (Baumgartner et al., 2009; Crook et al., 2009; Lassalle et al., 2009; Sutherland et al., 2013; Thompson et al., 2011). Fish are a crucial link in ecosystems as they influence substantial types of ecosystem services such as regulating food web dynamics, nutrient and carbon fluxes, ecosystem resilience, sediment transport (Holmlund and Hammer, 1999). Not only are fish a crucial link in ecosystems, they are an economically important group of animals as well. Due to the growing human population, sufficient protein sources are crucial and the demand for fish is ever increasing (FAO, 2016). Consequently, fish are one of the most traded food items in the world and it is of utmost importance to manage their populations sustainably. This can be achieved by understanding their lifecycle and behaviour. To fulfil their lifecycle, many fish species move between different habitats, such as feeding habitat, spawning habitat and nurseries, encompassing extensive migrations in doing so. Regarding fish migration, distinctions can be made depending if species use solely freshwater environments, marine environments or move between the two:

- **Potamodromous**: fish spawn in the upper reaches of rivers and grow in the lower reaches (e.g. brown trout (*Salmo trutta fario* L.), European chub (*Squalius cephalus* L.))
- **Oceanodromous**: both spawning and growing phase occur in the marine environment (e.g. Bluefin tuna (*Thunnus thynnus* L.), Atlantic goliath grouper (*Epinephelus itajara* Lichtenstein)).
- **Diadromous**:
  - Catadromous: fish spawn in marine habitat and reach adulthood in freshwater habitats (e.g. European eel (*Anguilla anguilla* L.), Giant mottled eel (*Anguilla marmorata* Quoy & Gaimard))
  - Anadromous: fish spawn in freshwater habitat and reach adulthood in marine habitat (e.g. Atlantic salmon (*Salmo salar* L.), Atlantic sturgeon (*Acipenser sturio* L.)

- Amphidromous: fish spawn in freshwater habitat, larvae drift into marine habitats and migrate back into freshwater habitat to reach adulthood (Dolly Varden (*Salvelinus malma* Walbaum), mountain mullet (*Dajaus monticola* Bancroft)).

Being highly mobile animals, fish suffer when connectivity is constrained (Larinier, 2001; Drouineau et al., 2018a; Limburg and Waldman, 2009). Movement barriers can impact fish, and diadromous and potamodromous fish in particular, both on a transversal (i.e. influencing up- and downstream movement; e.g. by weirs, dams, pumping stations, shipping locks and sluices) as a lateral level (i.e. affecting fish movement from the river to flood plains and vice versa; e.g. by dykes) (Aarts et al., 2004; Drouineau et al., 2018a). Another aspect is mortality caused by hydropower plants, pumping stations and turbine stations (Buysse et al., 2014; Winter et al., 2006). Despite the development of fish-friendly pump adaptations and fish passages to reduce mortality (Buysse et al., 2015; Clay, 1994), the efficacy of many presumably fish-friendly adaptations remains to be established (Boggs et al., 2004; Gowans et al., 1999; Keefer et al., 2004; Marmulla, 2001; Roscoe and Hinch, 2010). Next to mortality effects, pumping stations may also affect migration behaviour, resulting in delays or even migration stops. Consequently, delays or migration stops may result in a higher predation risk or reduced fitness and therefore contribute to the decline of a species (Marmulla, 2001; Silva et al., 2018).

Polders are one particular ecosystem type where the role of barriers is crucial. A polder is an anthropogenic system where water is maintained at a lower level than outside the polder by pumping stations and weirs, which are two types of barriers that can negatively influence migration of both diadromous and potamodromous fish species (Buysse et al., 2014; Falke and Gido, 2006). Due to climate change, the associated rising sea level and a growing human population, pressure on dewatering systems is likely to intensify in the future, resulting in the development of more polders with their accompanying movement barriers (Beatty et al., 2014; Hannah et al., 2007; Hermoso and Clavero, 2011; Maceda-Veiga, 2013).

Another widely distributed anthropogenic altered water body, are shipping canals for navigation and irrigation (Vitousek et al., 1997). Their number is likely to increase in the future due to climate change and a growing human population (Hannah et al., 2007). Canals are commonly characterised by a low structural variability (e.g. concrete embankments without riparian vegetation) with shipping locks, weirs and turbine stations, resulting in a regulated water flow. In addition to navigation, canals support industrial water management by facilitating water withdrawals and waste water disposal. It has already been shown that shipping canals may have a negative effect on local freshwater fish communities (Arlinghaus et al., 2002; Wolter and Arlinghaus, 2003). Such negative effects can be direct (e.g. shear stress, ship waves, dewatering and backwash...) or indirect (e.g. habitat fragmentation and simplification, loss of spawning and nursery habitats...) (see Wolter and Arlinghaus (2003) for an extensive review). Although the impact of shipping canals on non-migratory fish species has been extensively studied (Arlinghaus et al., 2002; Wolter, 2001; Wolter and Arlinghaus, 2003), knowledge on their effects on diadromous fish species remains poorly understood. Shipping canals generate threats for diadromous fish species: structures such as shipping locks, weirs and turbine stations, as well as the regulated water flow, may hamper migration behaviour (e.g. by disorientation). However, shipping canals may also provide alternative opportunities such as new migration routes, by connecting river basins or creating shorter migration routes to the sea. Depending on the impact of these canals on fish migration, proposed management measures could for instance include adjusted flow regulation or mitigation measures at turbine stations and shipping locks.

Providing numerous goods and services and playing a crucial role in fish life cycles, there is an urgent need to effectively restore aquatic ecosystems (Elliott and Whitfield, 2011; Postel and Richter, 2012).

1.3 Anguillid life cycle

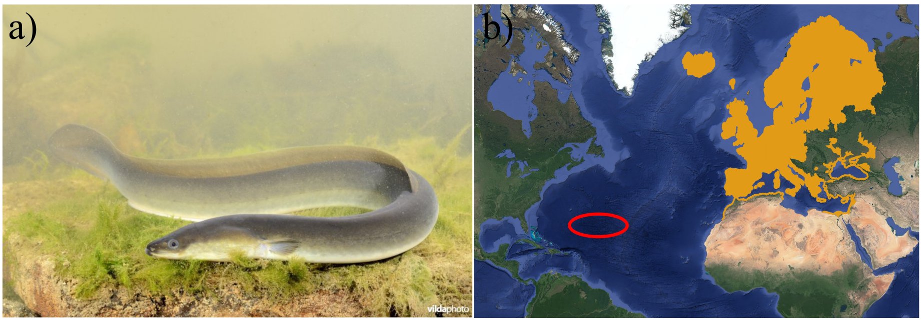
A particular group of diadromous fish are the catadromous eels of the genus *Anguilla*, family Anguillidae, within the order Anguilliformes. They are of high interest for water management due to their role as flagship species. Specifically, since eels have a complex life cycle, they are sensitive to the five components of global change, i.e. climate change, habitat loss and fragmentation, pollution, introduced parasites and overexploitation (Drouineau et al., 2018b). As they can withstand a variety of environmental conditions, a density decline in a local catchment often indicates a substantial deterioration of the ecosystem functioning (Drouineau et al., 2018b). Consequently, when management takes actions to improve densities, other aquatic life will likely benefit from it as well (Feunteun, 2002; Simberloff, 1998). Also, since eels easily accumulate pollutants (Section 1.4.3), they are reliable bio-indicators for water pollution. They are, for instance, used to conclude on the chemical status of water basins within the Water Framework Directive (Belpaire and Goemans, 2008; Belpaire et al., 2008).

Anguillid eels evolved between 70 million and 40 million years ago from a tropical deep sea ancestor (Aoyama et al., 2001; Inoue et al., 2010; Tsukamoto et al., 2002). Nowadays, the genus consists of 16 species of which three are further divided into two subspecies (Ege, 1939; Watanabe, 2003; Watanabe et al., 2004, 2005, 2009, 2014). They are found in both temperate, tropical and subtropical regions and all undertake excessive spawning migrations ranging between a couple of hundred to several thousands of kilometers (Arai, 2016). Despite the fact that spawning occurs in the ocean, Anguillid eels occur in both freshwater and marine systems, a trait likely evolved to exploit the relatively risk-free and productive freshwater habitats available in the tropics (Tsukamoto et al., 2002). Although being classified as catadromous, Tsukamoto and Nakai (1998) found that a part of the European and Japanese eel (*A. japonica* Temminck and Schlegel, 1846) do not swim up freshwater systems and therefore, both species can be considered facultative catadromous. The authors hypothesized that sea residency may be more common for temperate eel species due to the less productive fresh water systems, but further research is needed to confirm this hypothesis.

Spawning of anguillid eels is very similar among the different species and starts in a tropical sea. Since the European eel is the focus of this PhD dissertation, we will therefore explain the anguillid lifecycle of this species (Fig. 1.1). The distribution of the panmictic European eel population ranges from Northern Europe in Iceland and Norway over the Mediterranean to Northern Africa (Als et al., 2011; Dekker, 2003). Although nor spawning eels nor eggs have been observed in the wild, it is assumed that the European eel spawns in the Sargasso Sea. The Sargasso Sea is located in the North Atlantic Ocean covering a relatively large area over one million square miles (ca 20–30°N, 48–79°W).

This assumption is made, since in the early 1900s a Danish scientist called Johannes Schmidt went on a campaign, fishing against the incoming waves of willow-shaped eel larvae, i.e. leptocephalus larvae (Fig. 1.2a) (Schmidt, 1922). It was in the Sargasso Sea that the smallest stadium (7 mm) of these larvae was found. The larvae drift with the eastward flow of the Gulf Stream, followed by the North Atlantic Drift towards the European continent and North Africa. It is near the continental slope that the leptocephalus larvae transform into glass eels, small eels lacking pigmentation (Fig. 1.2b) (Antunes and Tesch, 1997). Although it is unknown how long this trans-Atlantic migration takes, it is estimated to range between seven months and over two years, depending on the used method (Bonhommeau et al., 2010). Some glass eels will stay in coastal areas and estuaries (Tsukamoto and Nakai, 1998), while others will migrate upstream in rivers (Tesch, 2003). Due to their small size and accompanied weak swimming ability, it is unlikely they can migrate against the tides and river current for a very long time (Feunteun et al., 2008). Therefore, the glass eels make use of selective tidal stream transport (STST) to migrate upstream: they ascend into the water column during the appropriate tide and descend to the bottom during the reverse tide (Creutzberg, 1961; Trancart et al., 2012; Walker et al., 1978).

a) b)



c)

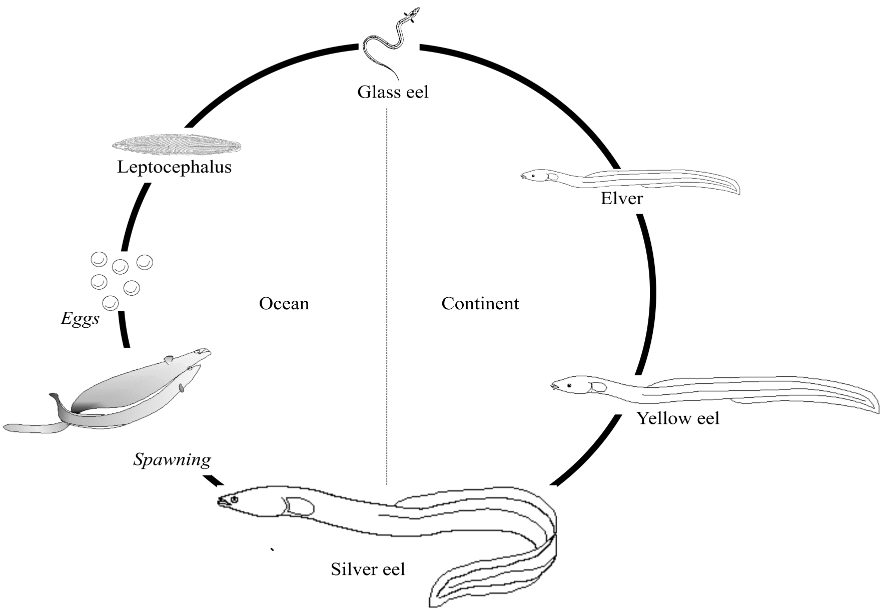


Figure 1.1: a) The European eel (photo credit: Rollin Verlinde) b) is distributed throughout Europe (orange-filled shape) and presumably spawns somewhere in the Sargasso Sea (red ellipse) (distribution data are obtained by IUCN and the spawning location is based on Miller et al. (2015)). c) The eel has a complex lifecycle with leptochepalus larvae drifting to continental Europe and North-Africa where they subsequently metamorphose in glass, yellow and silver eels to migrate back to the spawning location (source: Dekker (2008)).

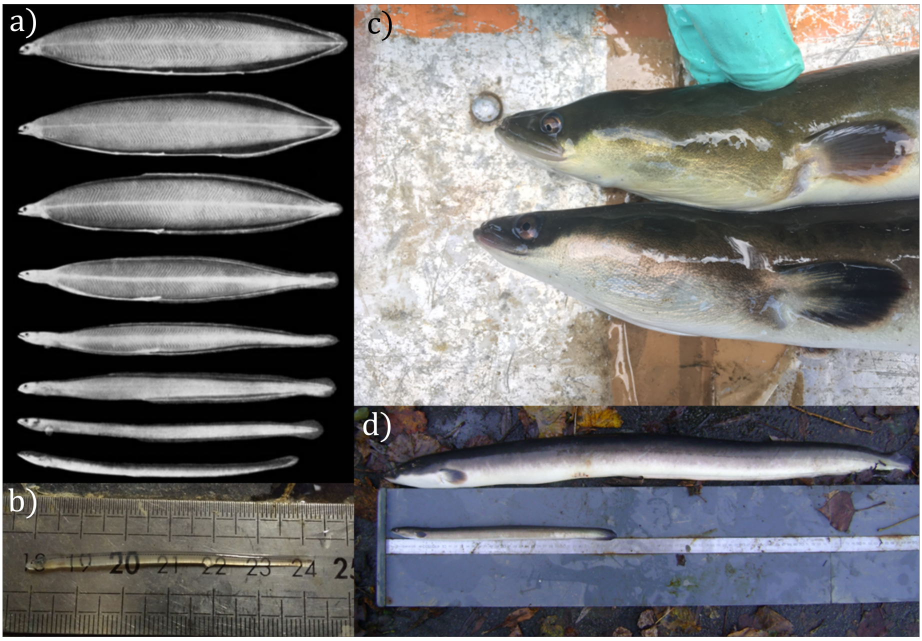


Figure 1.2: a) Gradual transition from a full grown leptocephalus larva to glass eels (figure adopted from Schmidt (1909)). b) A glass eel. c) The head region of a yellow (upper) and a silver eel (lower). Yellow eels have a yellowish colour, while silver eels are characterised by a grey back and white belly. Notice the enlarged eyes and pectoral fins of the silver eel. d) Eels show sexual dimorphism, with female silver eels (upper a 93 cm long female) growing much larger than males (lower a 38 cm male), which do not exceed 45 cm total length (Durif et al., 2005).

During the following stage, the glass eels start to pigment and develop into elvers, which in their turn grow as yellow eels (Fig. 1.2c). Yellow eels are rather sedentary with a limited home range and strong site fidelity (Baras et al., 1998; McGovern and McCarthy, 1992; Walker et al., 2014). Yellow eels (but also the other life stages) are primarily nocturnal, hiding near the bottom in crevices and under branches during daytime, but diurnal movement during overcast weather has been reported (Baras et al., 1998; McGovern and McCarthy, 1992). During the growing stage, eel adopt an opportunistic feeding pattern, preying on insects and their larvae, molluscs, annelids, macroinvertebrates and fish (Lammens et al., 1985; Schulze et al., 2004; Sinha and Jones, 1967; Van Liefferinge et al., 2012). Based on what they eat, eels' head shape can differ, with narrow headed eels feeding on small/soft prey and broad headed eels on large/hard prey (De Meyer et al., 2016; Lammens and Visser, 1989; Proman and Reynolds, 2000). The morphological difference is attributed to the development of larger jaw closing muscles in broad headed eels (De Meyer et al., 2016). However, recent research indicated a genetic link with head shape as well (De Meyer et al., 2017b). Yellow eels grow for three to over 20 years in continental waters to accumulate fat before migrating back as silver eels to the spawning area (Boëtius and Boëtius, 1985; Tesch, 2003; Vøllestad, 1992). Silver eels are characterized by the silver white belly, dark grey back and enlarged eyes and pectoral fin (Durif et al., 2005). These morphological changes are an adaptation to the pelagic phase of this life stage. Notably, sexual dimorphism between male and female silver eels exists, with males not growing larger than 45 cm (Fig. 1.2d) (Dekker et al., 1998; Durif et al., 2005; Lobón-Cerviá et al., 1995). This can be explained by their different life strategy: females adopt a size-maximizing strategy by growing older and larger, while males adopt a time-minimizing strategy (Helfman et al., 1987; Vøllestad, 1992). The consensus is that silver eels migrate to the sea in autumn, although spring migration has been observed as well (Aarestrup et al., 2008; Sandlund et al., 2017; Verbiest et al., 2012). Different environmental cues may trigger migration, such as water temperature, precipitation and discharge (Sandlund et al., 2017; Travade et al., 2010; Vøllestad et al., 1986). Migrating during a peak discharge enables the eels to save as much energy as possible for spawning itself, an important feature for a semelparous species. Especially since silver eels stop feeding during migration and even parts of their skeleton is resorbed to fulfill nutrient needs (Chow et al., 2010; Rolvien et al., 2016; Tesch, 2003). Once in the ocean, eels start to show a diel vertical migration pattern: at night they migrate higher in the water column and during daytime, they descend to deeper layers, a mechanism attributed to predator avoidance or thermoregulation (Aarestrup et al., 2009; Righton et al., 2016; Westerberg et al., 2007, 2014). Despite a lot of research on the European eel life cycle, many knowledge gaps still exist, preventing proper management. And notwithstanding the numerous tracking studies at sea (Amilhat et al., 2016; Righton et al., 2016; Aarestrup et al., 2009; Huisman et al., 2016; Westerberg et al., 2014), until now, a silver eel has never been tracked into its spawning site.

1.4 The European eel problem

Reports on the European eel decline of the continental stages (i.e. yellow and silver eels) date back to the early 1800s (Anonymous, 1865, 1867; Dekker and Beaulaton, 2015). The exact causes are speculative, but articles from the late 1800s and early 1900s indicate that habitat fragmentation and migration barriers may have played an important role (Adickes, 1888; Walter, 1910). For instance, Benecke (1884) already mentioned the construction of glass eel ladders (see Section 1.5.3). It was, however, until the 1970s that a substantial decline in the glass eel recruitment was apparent, indicating a decline between 90% and 99% (Dekker and Casselman, 2014) (Fig. 1.3). This led to the species being listed as critically endangered in 2008 under the IUCN Red List (Jacoby and Gollock, 2014). Various causes likely contribute to this decline, among the most referred to in literature are movement barriers, habitat loss and deterioration, pollution, overexploitation, human-introduced parasites and changes in ocean climate (Clavero and Hermoso, 2015; Buysse et al., 2014; Feunteun, 2002; Køie, 1991; Miller and Tsukamoto, 2016; Moriarty and Dekker, 1997). It is hard to hierarchically order each cause of decline, especially since their impact can differ according to the geographical scale (habitats, countries and their water management...). Yet, a recent report indicates that fishing and non-fishing mortality may have a similar impact (ICES, 2016).

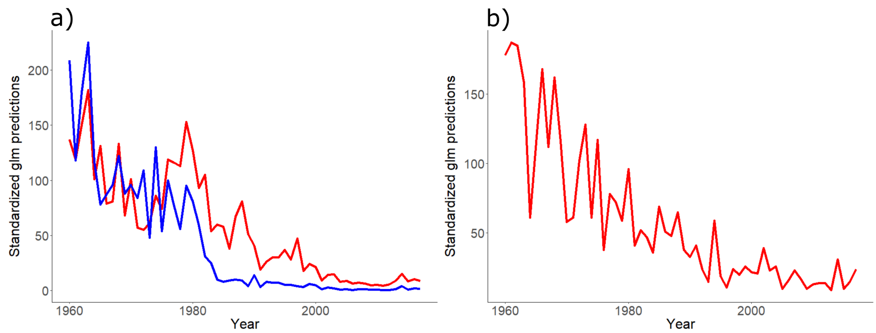


Figure 1.3: a) The recruitment decline of a) glass eels in the North Sea region (blue) and elsewhere in Europe (red), and of b) yellow eels in Europa. Recruitment values are geometric means from generalised linear model estimates. Data for the North Sea comprised data sets from Norway, Sweden, Germany, Denmark, The Netherlands and Belgium. Data from the UK, Ireland, France, Spain, Portugal, and Italy were used for elsewhere in Europe (ICES, 2018).

1.4.1 Movement barriers

Movement barriers pose an important threat to the European eel population on different levels such as inaccessibility of qualitative habitat, mortality, disorientation and delays (Feunteun, 2002; Moriarty and Dekker, 1997). The impact of each level varies with the eel's life stage, for instance, inaccessibility of qualitative habitat mainly poses a problem for glass eel colonisation and yellow eel ranging and migration behaviour, while barriers resulting in mortality, delays and disorientation mainly affect silver eel escapement.

Barriers hampering glass and silver eel migration are often referred to as migration barriers. Moriarty and Dekker (1997) summarized that of the 123,798 km^2 potential eel habitat in Europe (both marine and freshwater, artificial and natural), 36,463 km^2 (29%) is inaccessible. More specifically, 82% of the eel habitat in the Iberian peninsula has become inaccessible since the 19th century, resulting in eels mainly occupying coastal zones (Clavero and Hermoso, 2015). It is, however, unknown what the population dynamics and eel movements were in the absence of movement barriers. For instance, land reclamation accompanied by the construction of dykes and pumping stations resulted in the loss of qualitative estuarine habitat such as salt marshes and lagoons. Further, construction of movement barriers prevents upstream migration of glass eels, elvers and yellow eels (Clavero and Hermoso, 2015). This may force upstream migrating eels to settle in coastal regions, leading to an adaptive mismatch between genotype and the occupied habitat. Specifically, it has been observed that glass eels, which were caught in coastal areas, but restocked in upstream locations, had a faster annual growth rate and migrated at a smaller size back to the sea compared to natural recruits (Stacey et al., 2015). Additionally, it is unknown if migration barriers influenced population dynamics in coastal areas, since both historical and current data on eel abundance and distribution in those areas is scarce and in many regions absent.

Migration barriers also affect silver eel escapement back into the sea. Many studies indicated a high mortality of silver eels passing through pumping stations or hydropower plants (Berg, 1986; Buysse et al., 2014, 2015; Larinier and Travade, 2002; Winter et al., 2006, 2007). Mortality rates vary among the mechanism used: propeller pumps, for example, can kill up to 97% of migrating silver eels, while this is near 20% for Archimedes pumps and hydropower turbines (Buysse et al., 2014, 2015; Winter et al., 2007). Next to direct mortality, migration barriers and the accompanied regulated water flow may also lead to substantial delays (e.g. by disorientation), resulting in a higher predation risk or reduced fitness (Marmulla, 2001). However, the consequences of such delays on the eel's lifecycle are poorly understood and urgently require further research (Silva et al., 2018).

1.4.2 Habitat quality

It is beyond dispute that aquatic habitats have deteriorated since the Industrial Revolution. Not only limit connectivity constraints suitable habitat for eels (Larinier, 2001), deterioration is mainly caused by, for instance, land reclamation, canalization and dredging (Aarts et al., 2004; Feunteun, 2002). Canalization in particular results in a low structural variability (e.g. concrete embankments without riparian vegetation). The function of canals is diverse and includes amongst others navigation, support of industrial water management by facilitating water withdrawals and waste water disposal. It has already been shown that shipping canals may have a negative effect on local freshwater fish communities (Arlinghaus et al., 2002; Wolter and Arlinghaus, 2003). Such negative effects can be direct (e.g. shear stress, ship waves, dewatering and backwash...) or indirect (e.g. habitat fragmentation and simplification, loss of spawning and nursery habitats...) (see Wolter and Arlinghaus (2003) for an extensive review). Nonetheless, qualitative habitat characterized by a network of rivers, connected ponds and ditches, results in a high habitat diversity and thus many potential growth areas for yellow eels (Lasne et al., 2008). This could lead to higher growth rates, and larger eels have a higher survival rate (Boulenger et al., 2016). Even more, areas located close to the sea may, in the absence of migration barriers, be easily colonised by glass eels (Laffaille et al., 2004). Yet, little is known about the importance of qualitative habitat for eels, especially for the sedentary yellow eel stage (Laffaille et al., 2005).

1.4.3 Pollution

Related to habitat deterioration, are the high abundance and diversity of pollutants flushed yearly into marine and aquatic systems, where they especially bind to sediment particles (Cooper, 1993; Schwarzenbach et al., 2006; Weis, 2014). Being a benthic species and due to their high fat content, eels are prone to bioaccumulation of lipophilic pollutants (Belpaire, 2008; Belpaire et al., 2008). It is unlikely that eels die from pollutant bioaccumulation (except from spills or accidents, (Bálint et al., 1997; Christou, 2000; Knights, 1997)), yet, pollution can have sublethal effects. A lot of research has been conducted in this field and effects on various physiological systems have been indicated, a.o. immune, nervous, endocrine and reproduction system (see Geeraerts and Belpaire (2010) for an extensive review). Pollution may constrain successful spawning migration since they stop feeding during spawning migration and therefore rely on their fat reserve (Belpaire et al., 2016; Chow et al., 2010). Consequently, it has been suggested that as lipid deposits are depleted during migration, lipophilic contaminants are released into the blood and interfere with the eel's physiology, impacting vital organs and gonads among others (Larsson et al., 1991). Luckily, due to waste water treatment, water quality is improving (Thyssen, 2001), which has been reflected by the decrease in pollutant concentrations in eels (de Boer et al., 2010; Maes et al., 2008). Yet, it is unknown if current concentrations affect eel reproduction (Knights, 1997), especially since new pollutants are emerging.

1.4.4 Overexploitation

Eels are an important product for human consumption and their exploitation dates far back to 1086 (Dekker, 2018; Dekker and Beaulaton, 2015). It was not until the late 1800s that eel fisheries expanded substantially by modernisation and commercialisation, leading to larger catches with a peak of over 20,000 tonnes annually exploited eels in Europe during the 1960s (Dekker, 2018). Yet the yields have dropped substantially since the recruitment decline in the 1970s, being nowadays around 8,000 tonnes (Fig. 1.4) (FAO; http://www.fao.org/fishery/species/2203/en). Every continental phase of the European eel (i.e. glass, yellow and silver eels) is exploited and is often region specific. Glass eels, for instance, are fished in countries near the Bay of Biscay where their abundance still reaches the highest numbers, while yellow and silver eels are fished throughout the eel's distribution range (Dekker, 2016).

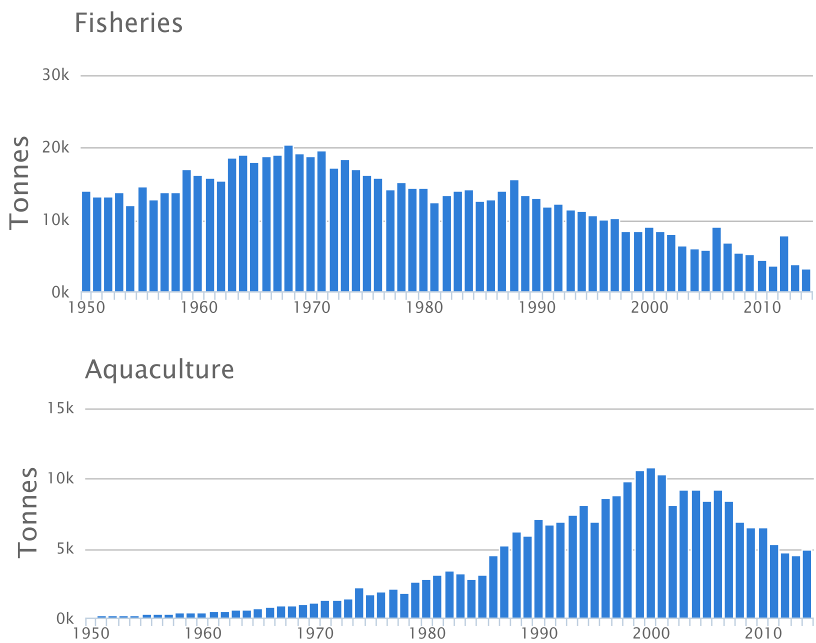


Figure 1.4: Global fisheries and aquaculture production of the European eel (figure adopted from http://www.fao.org/fishery/species/2203/en).

Glass eels are caught for both direct consumption (a delicacy called 'angulas' in Spain; in 2016s fishing season, the first 1.25 kg caught glass eels were sold for €5,500) and as seedlings for aquaculture facilities; the latter producing nowadays up to 5,000 tonnes of eels per year and therefore comprise the largest part of eel exploitation. Since it is not yet possible to breed European eels in captivity, the aquaculture sector still depends on the recruitment of the wild population for production, limiting its productivity. Due to the high Asian eel demand and the related decline of the Japanese eel stock, a lot of illegal trafficking exists of European glass eels to Asia. It is estimated that 10 tonnes of glass eels have been smuggled from Europe to Asia during the 2016-2017 fishing season (Anonymous, 2017a). Further, yellow and silver eels are both commercially caught with various fishing techniques (e.g. fyke nets, eel pots, stow nets...) to create eel products like jellied, smoked and fried eels (the latter with a green sauce based on seven green herbs is considered a delicacy in Flanders). Next to commercial fishing, in some European countries recreational fishing for eels exist by means of line fishing or bobbing. Although total yields from recreational eel fisheries are hard to quantify, an extraction of 30 tonnes per year was estimated based on a questionnaire in Flanders (Belgium) in 2016 (ICES, 2017). This in spite of a negative governmental advice due to high pollutant levels in eels. Obviously, exploitation has an impact on the eel population. Some studies have indicated that silver eel fisheries substantially impede the number of escaping silver eels (Aarestrup et al., 2010; Moriarty and Dekker, 1997).

1.4.5 Parasites

A possible biological contributor to the European eel decline, is the introduction of the Asian parasitic swim bladder nematode *Anguillicoloides crassus* (Kuwahara, Niimi and Itagaki, 1974) Moravec and Taraschewski, 1988. This species was introduced in Europe during the eighties likely with import of its native host, the Japanese eel, for consumption and restocking by foreign infected European eels (Belpaire et al., 1989). Once the eels consumed infected cyclopoid copepods, the intermediate host, *A. crassus* larvae move from the intestines into the swim bladder, where they feed on blood, grow till adulthood and reproduce (De Charleroy et al., 1990). *A. crassus* infection involves tissue scarring, leading to a lower swim bladder elasticity and an accompanied enlarged chance of rupture. Since eels apply extensive diel vertical migrations in the ocean spanning a vertical depth range over 500 m, infection may impair spawning migration (Aarestrup et al., 2009; Barry et al., 2014; Righton et al., 2016). Indeed, experiments by Palstra et al. (2007) suggested that infected eels show lower swim speeds and higher migration costs. Yet, a recent telemetry study in the North and Baltic Sea compared migration behaviour between an infected eel with three non-infected eels and indicated a minor impact on migration behaviour by the parasitic nematode (Simon et al., 2018).

1.4.6 Climate change

Human activities have a substantial impact on climate change, affecting marine ecosystems and influencing marine currents (Böning et al., 2008; Halpern et al., 2008). Ocean climate change likely plays an important role in the glass eel recruitment decline as well (Arribas et al., 2012; Bonhommeau et al., 2008; Feunteun, 2002; Knights, 2003; Miller and Tsukamoto, 2016). Warm winters, for instance, lead to a lower productivity in the Sargasso Sea (Bates, 2001), which may lead to starvation of leptocephalus larvae (Bonhommeau et al., 2008). Also, changes in currents, resulting in a prolonged migration phase, might make leptocephalus larvae more prone to diseases and predation, exacerbating eel recruitment (Kettle et al., 2008; Knights, 2003; Moriarty and Dekker, 1997). Notably, due to their opportunistic behaviour, eels are likely less influenced by continental climate change (Knights, 2003; Schulze et al., 2004; Van Liefferinge et al., 2012). Even more, Knights (1997) speculated that an increase in continental temperature may favour eel growth. He also speculated that a precipitation increase in Northern Europe may favour silver eels runs, yet, a dryer climate in the south may have the opposite effect.

1.5 The European Eel Regulation and current management

To aid conservation and recovery of the European eel population, the European Union adopted a Council Regulation (European Eel Regulation; EC no. 1100/2007) which imposes a management system that ensures 40% escapement of the spawning stock biomass, defined as the best estimate of the theoretical escapement rate if the stock were completely free of anthropogenic influences. To do so, the Regulation proposes actions at several levels of the nationally defined "eel river basins" (i.e. each EU Member State identifies natural habitat for the European eel within their national territories), resulting in national Eel Management Plans (EMPs): reducing commercial and recreational fisheries, restocking measures, improving aquatic connectivity and habitat quality, translocating silver eels to areas from where they can freely migrate into the marine environment, combatting predators, temporary switching off hydropower stations and aquaculture measures. Consequently, 20 countries developed EMPs (Belgium, Denmark, Estonia, Finland, France, Germany, Greece, Ireland, Italy, Latvia, Lithuania, The Netherlands, Norway, Poland, Portugal, Spain, Sweden, Tunisia, Turkey and the UK), which are under the international supervision of the ICES Eel Working Group (WGEEL).

1.5.1 Exploitation limitations

As mentioned above, eel fisheries target all life stages and exploitation pressure varies among geographical regions (Table 1.1). Considering glass eels and elvers, the EU Eel Regulation demands that 60% of the annual caught eels < 12 cm are traded for stocking purposes only. In addition, due to a continuing decline in eel recruitment, glass eel export outside of Europe became prohibited from 2010 onwards; especially Asia was an important consumer. Yet, the illegal trade of European glass eels to Asia hinders efficient management. Actions to reduce fishing mortality of yellow and silver eels include national eel quota, adapted fishing gear, restricted fishing periods and areas, and a minimum size; which all differ according to national measurements. Since it would be to exhaustive to delineate the fisheries policy of all 20 countries, we refer to the WGEEL report of 2017 for an extensive overview (Anonymous, 2017d). Nonetheless, we summarise the policies of four countries (Belgium, Ireland, The Netherlands and UK) to illustrate its diverseness.

- In Belgium, there is no commercial fishing for eels anymore and in Wallonia, the southern part of Belgium, recreational fishing for eels is prohibited. In Flanders it is allowed by hand line fishing and bobbing; fyke and eel pot fishing is prohibited and therefore considered as poaching. A fisherman is allowed to take maximum five eels of minimum 30 cm per fishing session.
- In Ireland, commercial eel fisheries were closed after the EU Eel Regulation implementation. Some recreational fishery exists, but its impact is considered low, especially since there is no eel culture in Ireland.

- In The Netherlands commercial fishing is allowed in specific areas (i.e. areas free from or with tolerable levels of pollution). Yet, it is prohibited from September till December to maximise silver eel escapement. The minimum landing size of an eels is 28 cm. Recreational eel fishing is prohibited in inland waters and when caught, eels have to be retrieved immediately into the water they were caught from.
- Apart from the glass eel fisheries in the UK, commercial yellow and silver eel fisheries exist by licensed fishermen, handling a minimum size of 30 cm and fishing from 1st April till the 15th of February. Recreational eel fishing is allowed, however, all eels have to be released alive in the water they came from.

Next to these national measurements, the Council of Europe recently agreed to close fisheries on European eel $>$ 12 cm in Union Waters of ICES areas for three consecutive months between 1 September 2018 and January 2019; the onset of those three months can be determined by each country independently (Anonymous, 2017b).

Being an exploited species, the Sustainable Eel Group (SEG) is working on a sustainable eel label, based on the MSC label: the SEG Standard (http://www.sustainableeelgroup.org/seg-standard/). The goal of the label is, as stated from their website, "To maximise the contribution of eel fishers, ranchers, aquaculturalists, traders and consumers of eel products to the restoration of healthy eel populations, distributed throughout their natural range, fulfilling their role in the aquatic environment and supporting sustainable use for the benefit of communities, local economies and traditions". Further, the Eel

Stewardship Fund (ESF) helps funding eel management practices (e.g. buying glass eels for restocking) or eel research with the profits from the trade of ESF labelled eels (e.g. €1 from the selling price of ESF labelled eels in the supermarket is used for eel conservation or research).

Table 1.1: Overview of the commercial and recreational fishing allowances for the 20 countries in the EU Eel Regulation after Anonymous (2015) and Anonymous (2017d). Note however, that some countries do not make a distinction between yellow and silver eel fisheries. Also, recreational eel fishing data is not always available. Therefore, it is considered permitted for consumption unless stated otherwise.

Country	Commercial fishing			Recreational fishing	
	Glass eel	Yellow eel	Silver eel	Catch & Release	Consumption
Belgium					x
Denmark		x	x		x
Estonia		x	x		x
Finland					x
France	x	x	x		x
Germany		x	x		x
Greece			x		
Ireland					x
Italy	x	x	x		x
Latvia		x	x		x
Lithuania		x	x		x
The Netherlands		x	x		
Norway		x			
Poland		x	x		x
Portugal	x	x			x
Spain	x	x	x		x
Sweden			x		x
Tunesia		x	x		x
Turkey		x	x		x
UK		x	x	x	

1.5.2 Restocking and redistribution

As already mentioned above, 60% of the commercially caught glass eels are destined for restocking purposes. In the 1980s, glass eel restocking reached a peak, followed by a decline until 2010 when the EU Eel Regulation was implemented (Anonymous, 2017c) (Fig. 1.5). The recent increase was due to lower market prices, leading to higher numbers within the fixed stocking budgets. In Belgium for instance, from 2008 till 2017, 117 - 540 kg glass eels have been stocked annually, equalling €59,670 – 83,945 (Anonymous, 2017d).

Despite the substantial restocking effort, its impact on European eel recovery is dubious. Dekker and Beaulaton (2016) extensively summarized and reviewed 175 years of glass eel restocking in Europe and concluded that the measure only moderately contributed to the fishing yield, partly compensated the recruitment decline and did not improve spatio-temporal distribution substantially. Although post-evaluation of glass eel restocking is scarce, Ovidio et al. (2015) observed that glass eels in Belgian tributaries had grown and dispersed substantially one year after restocking. In that respect at least a part of the restocked glass eels can manifest themselves. Nonetheless, only a fraction of elvers (n = 130) was caught the year after restocking (2.5 kg glass eels were stocked, with an estimated n = ± 10,387), which may be attributed to natural mortality by predation and disease, ranging outside the range of the study area and inefficiency of electrofishing for catching glass eels (Ovidio et al., 2015). Yet, failed short-term adaptation of glass eels into their new environment is not excluded. Although glass eel and elver survival rate was 100% after translocation from estuarine conditions in the wild to fresh, 50% and 100% salt water in an experimental design (Crean et al., 2005), Stacey et al. (2015) found that stocked American glass eels had a faster growth rate, led to a different sex ratio and matured at smaller sizes and earlier ages than their naturally recruited conspecifics. They hypothesized that, despite being a panmictic species, life-history traits are attributed to selection during ingress migration, i.e. the spatially varying selection hypothesis. Therefore, spawning contribution of stocked eels may be limited and questions stocking as an efficient management measure over large geographical areas. Stacey et al. (2015) suggests to apply restocking within the same catchment to overcome migration barriers.

Further, the orientation mechanisms of migrating silver eels are not fully understood and the hypothesis of an imprinted map during glass eel migration still exists. Translocating glass eels to areas thousands of kilometers from their capture location may therefore result in disorientation during migration and unsuccessful spawning. Westin (1990), for instance, found that silver eels developed from stocked glass eels missed the outlet of the Baltic during a tracking study. In contrast, Westerberg et al. (2014) observed no significant difference in migration behaviour between silver eels from stocked and naturally recruited glass eels.

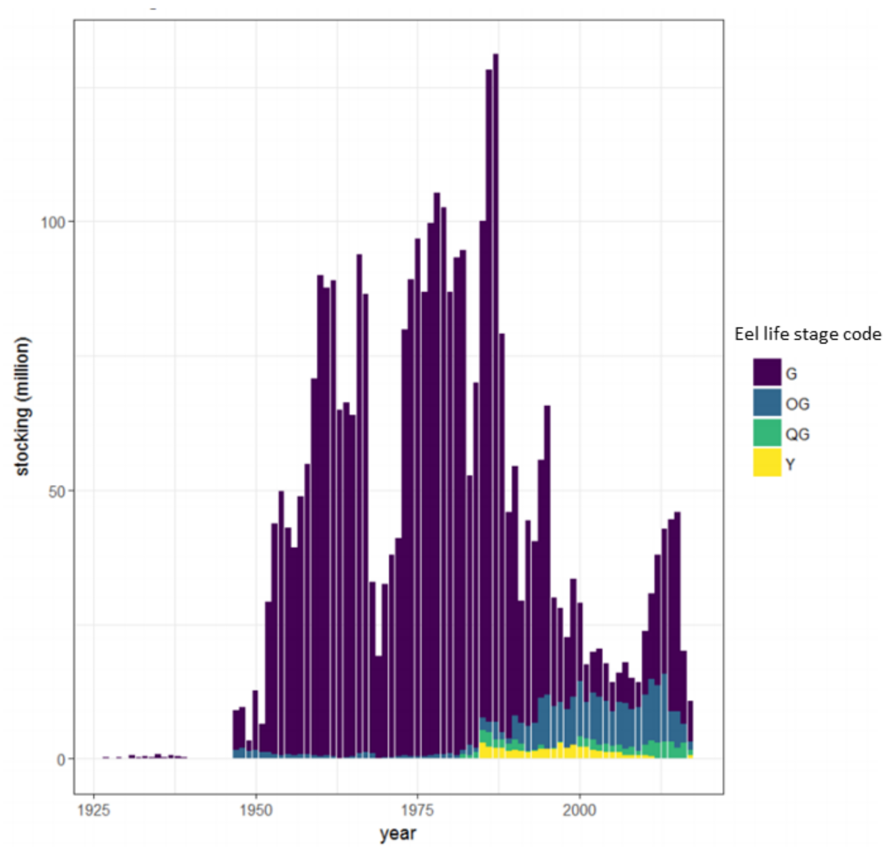


Figure 1.5: The number of eels stocked from 1925 till 2016 (G: glass eels; OG: ongrown eels; QG: quarantined eels; Y: wild caught yellow eels) (figure adopted from Anonymous (2017c)).

Another reason why glass eel restocking is not effective, is due to the various factors affecting eel survival (Section 1.4). Moving glass eels from coastal areas to tributaries overcome migration barriers during upstream migration of glass eels and elvers, but does not solve the problem for downstream migration in the silver eel stage. However, note that catching silver eels upstream of a migration barrier to transport them to a part of the river free of migration barriers is an applied management measure (i.e. "trap-and-truck") (McCarthy et al., 2008; Richkus and Dixon, 2002). Yet, this is very labour intensive and requires therefore substantial human interference, including stress during the catching and transportation process. Nonetheless, as long as there is no adequate solution implemented for all possible stressors, it will be hard for the eel population to recover (Drouineau et al., 2018b).

1.5.3 Improving connectivity

The eel's lifecycle encompasses two migration phases in freshwater: upstream migration as glass eels, elvers and yellow eels to colonize suitable growing habitats and downstream migration as silver eels to reach the sea for spawning (Nzau Matondo and Ovidio, 2016; Tesch, 2003). Consequently, solving migration barriers need to act on both phases.

The majority of the fish passes constructed for upstream migrating fish, target strong and fast swimmers such as anadromous salmonids and shads (Beach, 1984; Larinier and Marmulla, 2004). Several types exist, often accompanied with a strong current acting as a guiding cue: pool type, Denil or baffle type, De Wit and nature like fish passes (Larinier and Marmulla, 2004; Viaene et al., 2004). Due to their small size and accompanied weak swimming ability, it is unlikely that glass eels can migrate against the strong currents present in fish passes for a very long time (Feunteun et al., 2008). A popular construction to aid upstream glass eel migration, are eel ladders (Legault et al., 1990; Benecke, 1884). The construction consists of a slope, often under 15° - 45°, with specific substrate (e.g. nylon bristles or coconut mats) overrun by water (Legault, 1992; Solomon and Beach, 2003). The concept is that glass eels detect the flow, migrate/crawl up the slope and consequently overcome a migration barrier such as a dam, weir, pumping station or tidal sluice. Such a management measure often requires human interference by translocating the collected glass eels in a reservoir at the end of the ladder over the migration barrier. In addition, crawling up a slope may increase predation, disease or stress, resulting in a higher mortality. Another management action recently applied, is adjusted tidal barrier management (Mouton et al., 2011b). During the glass eel migration season, tidal barriers are opened ajar (e.g. 10 cm) during high tide to allow glass eel intrusion. The study of Mouton et al. (2011b) observed no conductivity increase upstream during implementation of the management measure.

Once reaching maturity, silver eels commence their downstream migration, encountering numerous migration barriers. As mentioned above (Section 1.4.1), pumping stations and hydropower turbines cause substantial mortalities and injuries in downstream migrating fish. Consequently, management measures are being developed. In a specific Belgian polder area, an Archimedes pumping station got fish-friendly 'de Wit' adaptions by applying curved edges on the first windings of the screws, which should lead to less blade strikes (Buysse et al., 2015). Yet, no significant difference in eel mortality was found before the measurement was taken (Buysse et al., 2014). Due to the high mortality caused by turbines, some hydropower plants are shut down during the silver eel migration season, sometimes accompanied by a MIGROMAT (i.e. silver eels held in a container to monitor their activity) (Adam, 2000). However, due to the accompanied substantial economic losses, this is not always feasible. Further, management measures are taken to prevent eels from migrating through pumps and turbines, for example by eel racks (Russon et al., 2010) and light deflection systems (Hadderingh et al., 1999, 1992). Nonetheless, when deflected, eels still need to overcome the barrier. Fish bypasses for upstream migration rarely work in the opposite direction, likely because downstream migrating fish follow the main flow instead of seeking for a specific cue, like the repellent current downstream from a fish pass. Consequently, research and development of efficient downstream fish passes is urgently needed (Feunteun, 2002; Larinier and Marmulla, 2004; Solomon and Beach, 2003). One applied practice to overcome migration barriers is catching silver eels and transporting them to an area from where they can freely migrate into the sea (i.e. trap and transport) (Moriarty and Dekker, 1997). Yet, this method is very labour intensive and may induce stress, negatively influencing the eel's fitness. A non-labour intensive approach was recently found by Egg et al. (2017), who pointed out that eels can safely pass hydropower plants via an undershot weir. Nonetheless, technical constraints may inhibit the construction of undershot weirs, consequently there is an urgent need for more and other effective cost-efficient solutions.

1.6 Research objectives and outline of the PhD thesis

Despite the establishment of the EU Eel Regulation in 2007, the European eel population reached a historical minimum and many knowledge gaps remain (Dekker, 2016). With the improving water quality resulting from the Water Framework Directive and eel management mainly focusing on overexploitation and restocking, an important bottleneck in eel management is movement behaviour related to suitable habitat (i.e. yellow eel movement behaviour) and migration barriers (i.e. silver eel migration behaviour). Adequate mitigation measures to improve the silver eel escapement rate require proper insight in both (1) yellow eel movement behaviour in nursery areas and (2) silver eel migration behaviour and how these are affected by current management practices.

The objective of this thesis is to investigate movement behaviour of large female eels, both in their yellow (i.e. sedentary) and silver (i.e. migratory) stage. Namely, to investigate movement behaviour, eels were tagged with acoustic transmitters. Due to the transmitter size and our restriction not to allow tags to exceed 2 % of the fish weight, the tagged eels were all large and considered to be females (minimum TL of 495 mm and minimum weight of 246 g) (Laffaille et al., 2003), as males are smaller than the minimum size handled in this study (<450 mm (Durif et al., 2005)). Movement behaviour of yellow eels may provide insight in the amount of space yellow eels require to grow. Consequently, the results can inform managers about sufficient qualitative and quantitative growing habitat. Once metamorphosing in silver eels, knowledge about their spatio-temporal migration behaviour is crucial for effective management trying to achieve a higher escapement-rate. The latter may consist of temporal elevation of migration barriers to the development of downstream fish passes. Consequently, the following general research questions are the focus of this dissertation, with more specific questions under the different chapters and subchapters:

- What is the spatio-temporal movement behaviour of the European eel during the sedentary, yellow eel stage?

- What is the spatio-temporal movement behaviour of migrating eels in:
  - a system free of anthropogenic migration barriers?
  - moderately (e.g. polders) and severely (e.g. shipping canals) regulated systems?

Chapter 2 - Acoustic telemetry

Acoustic telemetry was the technique used to study spatio-temporal movement behaviour of European eels in this dissertation. In chapter two we explain the concept, applicability and some constraints of the technique.

Chapter 3 - Movement behaviour of large female yellow European eel (*Anguilla anguilla* L.) in a freshwater polder area

In this chapter, we analysed the movement behaviour of female yellow eels in a freshwater polder system, characterized by interconnected canals, polder ditches and ponds. A high density network of acoustic listening stations (ALSs) allowed to investigate (i) when yellow eels were most active in terms of circadian inter-ALS movements and seasonal swim distance patterns, including effects of temperature, (ii) the size of the movement range and (iii) what environmental variables determined movement. In addition, (iv) an effect of habitat type (i.e., canal, polder ditch and pond) on (ii) and (iii) was analysed.

Chapter 4 - Unimodal head-width distribution of the European eel (*Anguilla anguilla* L.) from the Zeeschelde does not support disruptive selection

The following chapter handles head width distribution of eels in the Schelde Estuary. Being opportunistic feeders, we hypothesize that eels from a single river drainage do not show disruptive selection related to eel head width by assessing four sub-hypotheses: (i) Head width variation follows a unimodal distribution and (ii) this distribution does not differ between different maturation stages; (iii) body condition does not differ according to head width, and (iv) eels with a narrower head width migrate at a similar speed as eels with a broader head width.

Chapter 5 - Selective tidal stream transport in silver European eel (*Anguilla anguilla* L.) – Migration behaviour in a dynamic estuary
The fifth chapter related to spatio-temporal migration behaviour deals with movement in a system free of physical anthropogenic barriers, i.e. the Schelde Estuary, and can consequently be regarded as the baseline. Specifically, we investigated (i) if migratory eels apply STST and (ii) at what speed they migrate through the estuary.

Chapter 6 - Downstream migration of European eel (*Anguilla anguilla* L.) in an anthropogenically regulated freshwater system: Implications for management
In this chapter, we analysed the migration behaviour of female silver eels in a moderately regulated system, i.e. a polder. We analysed (i) if eels take different migration routes, (ii) if their behaviour changes significantly in the vicinity of barriers, (iii) if migration follows a circadian pattern, (iv) if migration starts at a specific point in time, and (v) what environmental variables influence migration.

Chapter 7 - European silver eel (*Anguilla anguilla* L.) migration behaviour in a highly regulated shipping canal
Chapter 7 deals with eel migration in a highly regulated shipping canal i.e. the Albert Canal, characterised by seven shipping lock complexes, turbine stations

and tidal sluices. In this chapter, we analysed if (i) eels are able to migrate out of the system, (ii) if they are delayed in their migration, and (iii) how their behaviour related to eel migration behaviour in other systems.

Chapter 8 - Heading south or north: novel insights on European silver eel *Anguilla anguilla* migration in the North Sea
The majority of eel telemetry research is conducted in freshwater and estuarine habitats. Consequently, the exact migration routes and destination of European eels are still unknown. In chapter 8, we describe a newly discovered marine migration route based on eels tagged in three different European countries (i.e. Belgium, Germany and The Netherlands).

Chapter 9 - General discussion
In the general discussion, first some nuances are made related to the applied methodology in this dissertation such as eel life stage classification and migration identification. Next, we discuss what the results can mean for future management, research and development. Finally, remaining knowledge gaps important for future research and management are discussed.

Chapter 10 - Conclusion
The conclusion states more of a plea why European eel management is failing and what needs to happen to be successful.