

Chapter 9

General discussion

9.1 Main findings from this dissertation

Yellow eels are rather sedentary with a strong site fidelity and limited home range. Previous research indicated that the ranging behaviour of yellow eels varied between 285 m and 5,060 m (Baras et al., 1998; McGovern and McCarthy, 1992; Thibault et al., 2007; Walker et al., 2014). However, large scale movements, such as upstream migration, have been reported (Feunteun et al., 2003). Our results confirmed this, as the average movement range of the tracked yellow eels in the polder area were 3,917 m with the eels having a strong site fidelity as well, but five of the 56 tagged eels showed a movement range between 10 and 20 km (Verhelst et al., 2018d). We could not find any relationship between environmental variables and movement range, which we attribute to the opportunistic feeding behaviour of yellow eels (Lammens et al., 1985; Schulze

et al., 2004; Van Liefferinge et al., 2012). Opportunistic feeding behaviour challenges the existence of disruptive selection, hypothesising that the dichotomous and strongly deterministic characterization into 'broad' and 'narrow' headed eels is erroneous. Indeed, in Chapter 4 we found no proof for disruptive selection, since the head width distribution of 272 eels caught at the weir in Merelbeke had a unimodal head width distribution. Even more, the relative condition increased from narrower headed eels to broader headed eels. Consequently, eels could indeed not be divided in two distinct head-width groups. Instead, their head widths showed a continuum of narrow to broad.

Related to silver eel migration behaviour, in Chapter 5 we illustrated strong evidence that silver eels apply STST in the Schelde Estuary and therefore it is likely that the tides help eels to migrate in a bioenergetically efficient way through estuaries. Also, applying STST suggests eels can make a distinction between ebbing and flooding tide, indicating that cues other than currents play a role in orientation.

Silver eel tracking in a polder and shipping canal obstructed with migration barriers such as weirs, pumping stations, tidal sluices and shipping locks, revealed substantial delays, slow migration speeds and even migration arrests (Verhelst et al., 2018a,c). Consequently, these barriers negatively affect the eel population as delayed eels are more prone to disease and predation. Also, the effect of delays on the fish's fitness is currently unknown and therefore requires further research (Silva et al., 2018).

Finally, the observation that at least part of the silver European eels migrate through the English Channel to exit the North Sea emphasized the importance of large scale international networks to track migratory species over admin-

istrative borders. It also holds important implications for management. Different migration routes may have different bio-energetic implications: some routes may be energetically more demanding, leaving less energy for spawning. As such, management might need to focus more on areas where eels take an energetically favourable route and contribute more to spawning (Huisman et al., 2016) (see Section 9.3.4).

9.2 Eel management revisited

9.2.1 Migration barriers

River continuity is a necessity for fish migration and in particular for diadromous species. Of the 250 diadromous species (Myers, 1949), many have historical low numbers (Limburg and Waldman, 2009). Likely, various factors contributed to their decline, but migration barriers have been considered to be one of the main causes (Limburg and Waldman, 2009). As stated in the introduction, migration barriers prevent both the upstream migration of glass eels, elvers and yellow eels as the downstream migration of silver eels (Drouineau et al., 2018b; Feunteun, 2002; Moriarty and Dekker, 1997). Considering the critical status of the European eel population, effective management to allow safe passage is urgently needed. Various measures are taken to allow the ingress of glass eels into freshwater habitats near coastal areas, such as eel ladders and tidal barrier management (Mouton et al., 2011b; Legault et al., 1990; Benecke, 1884). Yet, to increase the eel abundance further upstream, restocking is the main applied management measure, the efficiency of which is doubtful (see

Section 1.5.2).

Different types of barriers exist such as large barrages, flood-control dams, flood gates, weirs, hydropower stations, shipping locks, tidal sluices, pumping stations and fisheries (Bruijs and Durif, 2009). In this dissertation, we investigated the effect of shipping locks and pumping stations on silver eel migration. Yet, since hydropower stations have a similar effect on silver eels as pumping stations, we will discuss solutions for them as well.

Pumping and hydropower stations

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 instalment of more pumping stations and hydropower turbines (Beatty et al., 2014; Hannah et al., 2007; Hermoso and Clavero, 2011; Maceda-Veiga, 2013). Pumping and hydropower stations cause severe mortality among downstream migrating silver eels. Propeller pumps, for instance, can kill up to 97% of migrating silver eels, while this is near 20% for Archimedes pumps (Buysse et al., 2014, 2015). For turbine stations, among which Kaplan turbines are the most used turbine type in Europe, mortality ranged from 20% to 38% (Hadderingh and Bruijs, 2002; Winter et al., 2007). Note that a river can have multiple hydropower stations, leading to an accumulated silver eel mortality rate along a river stretch.

Despite their severe impact and although the EU Eel Regulation is in place for almost ten years, effective management measures are still lacking. Considering pumping stations, fish-friendly screw-adaptations have been made, but proved ineffective (Buysse et al., 2015). Eel racks (Russon et al., 2010)

and light deflection systems (Hadderingh et al., 1992, 1999) are applied to prevent eels from migrating through hydropower turbines, yet with varying results (Brujjs and Durif, 2009). Solutions enabling safe passage of downstream migrating silver eels through pumping and hydropower stations can act on different fronts. First, development of fish-friendly screws is a pressing issue, as in many cases it is the only possible migration route, especially for pumping stations in polders (Fig. 9.1). In those systems, the water level is below sea level, making gravitational discharge, for instance via fish passes, impossible (see further). The exact cause of damage and subsequent mortality is well known: fish get struck by the first winding of the screw or get stuck/-crushed between the winding of the screw and the inner side of the housing of the screw. Yet, success stories with zero mortality through adapted screws are rare. Even more, in some cases no difference in silver eel mortality was found before and after fish-friendly adaptations to an Archimedes pumping station in a polder in Flanders (Buysse et al., 2015). Related to turbine stations, supposed fish-friendly improvements have been developed over the classic Francis, Kaplan and Archimedes turbines. These include low pressure turbines (<http://fishflowinnovations.nl>), fish-friendly Archimedes turbines (<http://fishflowinnovations.nl>), Alden turbines (Silva et al., 2018), Kaplan turbines with 'Minimum Gap Runner' (MGR) technology (<http://www.voith.com>), DIVE turbines (<http://www.dive-turbine.de>) and Very Low Head (VLH) turbines (<http://www.vlh-turbine.com>). Yet, further testing in the field is required and hence, development of fish-friendly adaptations requires further research and bringing together behavioural ecologists and engineers are necessary to lead to effective solutions. Second, development of downstream fish passes can be a promising management measure to aid silver eel migration.

Fish passes have been successfully applied for upstream migrating fish, as fish can be attracted to an attraction flow of a fish pass near a migration barrier (Bunt et al., 2012; Roscoe and Hinch, 2010; Silva et al., 2018). However, downstream migrating fish follow the main current, making them less prone to attraction flows near the margins of the main river. Consequently, development of fish passes to aid downstream migrating fish is not straightforward, as the main current runs through pumping and hydropower stations. Even more, in case of pumping stations in polders, water is pumped from watersheds with a low water level to a high water level. This leads to a fish pass with water running back into the watershed with the lowest water level, resulting in an incoming attraction flow which is in conflict with silver eels following the downstream current (Buysse et al., 2015). Yet, the delays and exploration behaviour upstream a migration barrier accompanied with deflecting behaviour by eel- and trash-racks may open opportunities to guide eels towards the inlet of a downstream fish pass, especially near turbine stations (Bruijs and Durif, 2009; Gosset et al., 2005; Silva et al., 2018; Verhelst et al., 2018c). Gosset et al. (2005) observed that 56% - 64% of the downstream migrating eels used flap gates located near the end of a trash-rack instead of migrating through a small hydropower station, while the flap gates had a discharge of only 2% - 5% of the turbine discharge. Further, Egg et al. (2017) observed silver eels migrating through an undershot sluice instead of the provided eel pass at a small hydropower station in Germany of which eel migration through the turbines was prevented by an eel rack. In conclusion, due to the lower water level than the sea in polders, the only probable eel migration route is often via the pumping station. Consequently, fish-friendly screw improvements are urgently needed. In case of turbine stations, development of undershot sluice gates or flap gates

could aid downstream fish migration when applied next to the trash- and eel-racks of turbine stations (Fig. 9.1). They would even be more efficient when the turbine station is shut off during migration periods, leading to the main current running via the undershot sluice gate or flap gates (see Section 9.2.3).

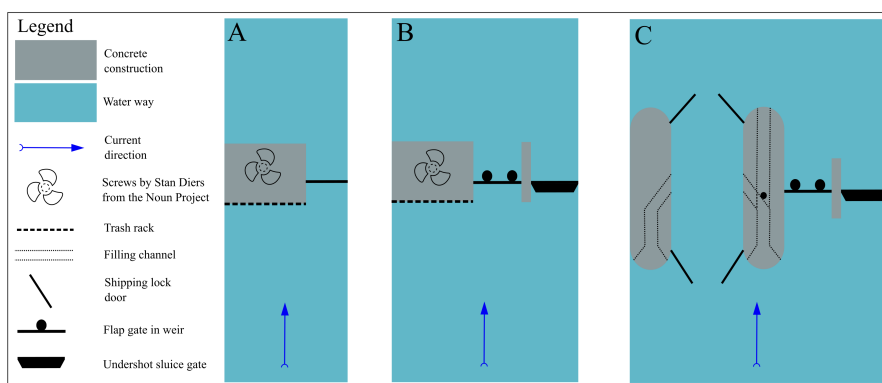


Figure 9.1: Proposed adaptations to enhance safe downstream fish passage at a pumping station in a polder (A), turbine station (B) and a shipping lock complex (C).

Shipping locks

In contrast to pumping and hydropower stations, a direct mortality effect on migrating silver eels has not been shown for shipping locks and tidal sluices (but see Section 9.3.2). Yet, they cause substantial delays, making eels more prone to diseases and predation (Verhelst et al., 2018a). In general, there are three ways to help eels overcome shipping locks: (1) via opening of the lock gates, (2) via channels which transport water from the river/canal into the shipping locks for filling (note that not all shipping locks have these channels)

or (3) via specifically designed fish passage systems. The substantial delays upstream the shipping locks in the Albert Canal indicated that eels had difficulties to overcome the shipping locks (Verhelst et al., 2018a). Consequently, it is likely that the attraction flow generated by opening a shipping lock or filling channel may be insufficient to attract eels (Buysse et al., 2008) or that the filling of shipping locks comes with high levels of turbulence and underwater noise, which may deter eels (Piper et al., 2015; Sand et al., 2000). Therefore, aiding eel passage over shipping locks requires a higher attractiveness of the eels to the shipping locks or passage systems and development of fish-friendly water inlets and filling channels. For example, widening the filling channels may make them prone for eels to find them and move unharmed with a lower (i.e. less turbulent) filling flow (Fig. 9.1). In addition, channels with as few bends as possible, may reduce eel strikes against the channel walls. If it is impossible to widen or straighten the channels, reducing the filling discharge may allow eels to pass safely. Yet, in this case attractiveness is likely to be reduced, but eel deflection systems towards the inlet may help.

Similar to the fish passes near hydropower stations, management could opt to develop undershot sluice gates or specialised passes next to shipping locks to allow silver eel passage. However, flap gates could be integrated in the shipping lock filling channels, with one part of the channel made inaccessible for eels and diverting to the shipping lock for filling, while the other part functions as a corridor to transport the eels to the other side of the shipping lock (Fig. 9.1).

9.2.2 Regulated water flow

Apart from migration barriers, an important feature for efficient migration is the water flow. Various studies observed that silver eel migration is linked with an increase in discharge (Bultel et al., 2014; Travade et al., 2010; Vøllestad et al., 1986). Consequently, a reduction or disruption in natural flow may affect silver eel migration. Indeed, in the studied polder, for instance, eel migration came to a standstill in the Braakman. This was likely caused by the infrequent dewatering of the Braakman: it was only dewatered when the water level of the Schelde Estuary was lower than the Braakman. The resulting water flow however was probably too marginal for the eels to detect and consequently leave the system (Verhelst et al., 2018c).

In the Albert Canal and the Zeeschelde, the tracked migratory eels ($n = 70$ and $n = 58$ respectively) showed substantial different migration successes. Of the 70 tracked silver eels in the Albert Canal, only 12 reached Antwerp (i.e. the most downstream part of the canal near the estuary) during a 27 month study period; another 15 were still migrating towards Antwerp while 35 were considered not showing migration behaviour at all (the remaining 12 eels migrated to the Meuse) (Verhelst et al., 2018a). In contrast, 52 of the 58 migrating eels from the Zeeschelde reached Antwerp within three months. The migration speed between the two groups which reached Antwerp was different as well: the 12 Albert Canal eels migrated on average at 0.01 m s^{-1} (notably, the 15 eels still migrating towards Antwerp migrated at a similar average speed of 0.02 m s^{-1}), while the 52 eels in the Zeeschelde migrated five times as fast (i.e. 0.05 m s^{-1}) (Verhelst et al., 2018b). Yet, the latter eels applied STST and migrated during ebbing tide at an average speed of 0.92 m s^{-1} . Even more, further down-

stream the estuary (i.e. the Westerschelde), eels speeded up substantially (0.42 m s^{-1}), yet with a comparable speed during ebb as in the Zeeschelde (0.95 m s^{-1}). This indicated that eels are less reluctant in their migration behaviour as they descent an estuary. In contrast, the lowest average migration speed for the Albert Canal eels was found at the most downstream section in Antwerp (0.02 m s^{-1} ; in the other sections the speed ranged from $0.06 - 0.18 \text{ m s}^{-1}$, except for the most upstream section (0.003 m s^{-1})). The slower speeds of the Albert Canal eels are probably not only attributed to migration obstruction by the shipping locks, but also to the inconsistent and bidirectional regulated water flow, a.o. due to shipping lock operation resulting in back-and-forth moving waterfronts and turbine operation. Even more, the lowest speeds in the most downstream canal section are likely attributed to a standstill in water flow: the already low water flow distributes over the large area of the docks.

Consequently, to aid silver eel migration, a more consistent downstream flow needs to be generated. In polders, pumping stations are activated when a specific water level threshold is achieved. During heavy rainfall, pumps could be activated over long, uninterrupted periods, creating a consistent, unidirectional flow. Yet, to stimulate pumping over longer periods and consequently silver eel migration, water managers could opt to allow water levels to rise at a higher level or drain a polder until a lower level, if it is raining sufficiently to bring the polder back at its minimum water level. Obviously, in accordance with the agriculture sector and without flooding risks for inhabitants.

However, in highly regulated shipping canals like the Albert Canal, creating a consistent, unidirectional current poses a bigger challenge. A more consistent, unidirectional flow could be achieved by feeding the canal with a

higher proportion of the Meuse discharge. A first plausible solution may be the construction of weirs next to the shipping lock complexes which can allow water passage next to the shipping locks to generate a more unidirectional flow. However, due to economic interests and lack of space, the construction of weirs is not always feasible. Second, a higher discharge could be generated during specific migration windows (see Section 9.2.3). The shipping locks of the Albert Canal operate from Monday morning 6 a.m. till Saturday evening 10 p.m, and remain closed/inactive on Sundays and holidays. Also, due to limitations of nocturnal navigation, the locks mainly operate during daytime. Eels, in their turn, mainly migrate at night and during autumn (Verhelst et al., 2018a). As such, management could opt to increase the discharge running through the Albert Canal via either (slightly) opened shipping locks, undershot sluice gates or constructed weirs at night during, for instance, October, November and December. In addition, to stimulate a unidirectional flow in the lowest canal section (i.e. the docks of Antwerp), a minimum number of tidal sluices to prevent flooding could be opened during the aforementioned migration windows when the water level of the Schelde Estuary is lower than the Albert Canal to stimulate gravitational flow. Acknowledging that the 'Grensmaas' (i.e. the part of the Meuse bordering Belgium and The Netherlands) needs at least a discharge of $10 \text{ m}^3 \text{ s}^{-1}$ (Anonymous, 2002), water supply is unlikely to be the limiting factor as eels migrate during periods of high precipitation and consequently a higher discharge (Stein et al., 2015; Travade et al., 2010).

9.2.3 Migration windows

To make the above mentioned suggestions more effective or since some can only be applied during a restricted time period (i.e. due to economic importance, water scarcity...), it is beneficial to implement them during specific migration windows. Silver eel migration in Western Europe occurs between August and January, mostly at night and during moments of high precipitation and accompanied discharge (Tesch, 2003; Travade et al., 2010; Vøllestad et al., 1986). Consequently, management could strive to apply measures during those specific moments, leading to, for instance, relative more water through undershot sluice gates or flap gates (Egg et al., 2017; Gosset et al., 2005). Notably, management should act within a region (e.g. Western Europe, Northern Europe...) or even within catchments as there are differences in timing of migration between regions (i.e. eels start to migrate in summer in Northern Europe, but in autumn in Western Europe (Durif and Elie, 2008; Haraldstad et al., 1985; Vøllestad et al., 1986)). Obviously, the spatial resolution on which management should act, depends on the knowledge of the managed catchment and could require further research for actions to be effective. This also holds true for the temporal resolution: telemetry data reveals high resolution spatio-temporal data on silver eel migration and allows for a detailed analysis on the migration routes and environmental triggers. Fitting these data into mechanistic models (e.g. individual based models) could result in interesting management tools (Baetens et al., 2013), narrowing down the spatio-temporal migration windows on which management has to act in order to restore the European eel population. Specifically, such tools could allow the prediction of silver eel escapement, aiding water managers on their decision when mitiga-

tion measures need to be taken. Through the collection of more qualitative and quantitative data, the models will become more accurate and even may take into account biotic factors such as species interactions instead of solely abiotic factors.

9.2.4 Individual variability

An important added value of telemetry, is the tracking of individuals, leading to datasets of individual behaviour. Nonetheless, this poses challenges for data analysis (e.g. autocorrelation) and translating the results to a (sub)population level. The latter is especially important since nowadays management often works on a (sub)population level or in some occasions at life stage levels (e.g. adjusted tidal barrier management to improve glass eel colonisation (Mouton et al., 2011b)). This individual variability translates itself to pronounced variability in movement behaviour, such as migration and swim speed, degree of exploratory behaviour, temporal movement variability, route choice... Obviously some might be at least partly intrinsically determined by the eels morphology; larger eels swim faster than smaller eels (Bainbridge, 1958). Yet, many aspects may depend on the eel's 'choice'.

Anthropogenic interference with the animal kingdom results in selection of specific genotypes, leading to the accompanied phenotype. A well-known example is fisheries-induced smaller size at maturity of fish (Law, 2000). Genotype selection may also occur at freshwater obstructions or even fish passes trying to allow free fish movement. In the polder and Albert Canal, substantial individual variability was observed between silver eels approaching a migration barrier (i.e. pumping station, tidal barriers and shipping locks): some eels

were much more reluctant to pass a barrier than others. Although the effect of delays is not well understood (see Section 9.3.3), delayed eels may have a smaller chance to contribute to the spawning population by an increased susceptibility to disease, mortality or a lower fitness. Yet, their more reluctant movement behaviour and accompanied lower migration speed, may be compensated by a higher fertility. Therefore, migration obstructions may have important repercussions to the genetic diversity of the spawning population. The same holds true for possible management measures to make barriers passable, for instance fish passes. Dependent on the construction of fish passes, they may select for strong swimmers, which may not necessarily coincide with high fertility. Although the effect on the genetic diversity of fish populations of migration barriers and management measures to overcome them is still unknown, from a precautionary perspective, we should take as much individuals as possible into account for management. Telemetry data gives researchers insight in the individual behaviour of animals, allowing a more detailed understanding of how species behave. As such, this may help push management further than (sub)population level and start considering measures on an individual level.

9.3 Remaining knowledge gaps

9.3.1 Methodological constraints

Life stage classification

When eels prepare for migration, they turn from yellow into silver eels (Tesch, 2003). The morphological appearance of silver eels is characterised by a vis-

ible lateral line, large, melanised pectoral fins, dark dorsal side, silver-white ventral side and large eyes. Due to the large eyes, the far end of the mouth does not reach beyond the eyes, which is the case for yellow eels. Hence, classifying silver eels based on the aforementioned external characteristics may be subjective. Consequently, we applied a more objective approach by measuring morphometrics (i.e. total length (to the nearest mm), weight (to the nearest g), horizontal and vertical left eye diameter (to the nearest 0.01 mm) and pectoral fin length (to the nearest 0.01 mm) to deduce the maturation stage according to Durif et al. (2005). This method is widely applied in European eel research (Barry et al., 2016a; Bultel et al., 2014; Simon et al., 2012; Stein et al., 2015). Nonetheless we do acknowledge that the method is not 100% conclusive. For example in the Schelde Estuary, six of the 51 (12%) tagged premigratory staged eels (FIII) migrated upon tagging, while another seven (14%) migrated at the following season upon tagging and 38 (74%) eels did not show migration behaviour at all. In contrast, 13 (62%) of the 21 tagged FIV eels migrated upon tagging, with an additional two (10%) a year later (six eels (29%) did not show migration behaviour). For FV eels, even 25 (86%) of 28 eels migrated upon tagging with a single eel (4%) the year after (three eels (11%) did not show migration behaviour). This variability can be attributed to factors other than the migration classification (i.e. morphometric measurement errors, post-handling stress, unfavourable environmental variables, mortality, tag expulsion...). However, since eels were not obstructed in the Schelde Estuary, it is unlikely caused by delays due to migration barriers. On the other hand, these results may point to a revision of the classification method or at least further fine tuning of the FIII-stage. Nonetheless, due to the low number of FIII eels migrating upon tagging, we suggest not to tag that life stage for silver eel

migration studies of less than a year, but preferentially tag FV eels.

Migration behaviour identification

Animal migration is considered a persistent and unidirectional movement, characterized by the temporary inhibition of station keeping responses such as foraging, territorial behaviour and commuting (Kennedy, 1985). Yet, eel migration is often found to be not continuous (Béguer-Pon et al., 2014; Durif et al., 2006, 2002; Stein et al., 2015). This discontinuous migration behaviour can be explained by various reasons such as the absence of required environmental conditions, STST for migration in tidal environments or even trial runs to test their body condition before they leave for the Sargasso Sea (Hain, 1975). Nonetheless, such discontinuous behaviour makes it hard to distinguish between dispersion/ranging events and possible migration events. This difficulty becomes more apparent in systems where migration is obstructed due to migration barriers or regulated water flows: it is hard to distinguish between ranging and a failed migration event. Nonetheless, yellow eels are highly sedentary with a limited home range (285 – 18,248 m) (Baras et al., 1998; Thibault et al., 2007; Verhelst et al., 2018d; Walker et al., 2014), yet, larger scale explorative behaviour may occur (e.g. in their search for wintering habitat (Hammond and Welsh, 2009)). However, not many studies make a distinction between resident and migratory behaviour (Stein et al., 2015), but consider eels in the migratory silver stage based on external morphology (e.g. Aarestrup et al. (2010); Béguer-Pon et al. (2014); Bultel et al. (2014); Davidsen et al. (2011); Piper et al. (2017); Verbiest et al. (2012)). Consequently, the whole dataset is considered migratory silver eel behaviour. In order to identify migration, three different methods

were tested in this dissertation: (1) progression speed, (2) the method of Lavielle (Lavielle, 1999, 2005) and (3) the triplet method.

Progression speeds can be used as a tool to distinguish between residency and migration behaviour, but require a thorough knowledge of the animal of interest (e.g. range distances during the non-migratory life stage and movement speeds) to justify threshold values. Both yellow and silver eels have been studied extensively leading to sufficient literature to support our applied thresholds (Verhelst et al., 2018b). Yet, this method can only be applied at study sites larger than the range distance of the animal during its non-migratory life stage. In addition, aquatic systems with migration barriers delay eels, leading to biased progression speeds and, consequently, inapplicability of this method. Therefore, we applied this method in the Schelde Estuary only, which is free of migration barriers.

Another possible method to delineate migration is via residence times. The method of Lavielle partitions a trajectory in K segments based on homogeneous mean residence times (Lavielle, 1999, 2005; Barraquand and Benhamou, 2008). Since we were interested to distinguish the eels' trajectories into residency and migration, each individual trajectory was split in two segments ($K = 2$). An acknowledged disadvantage of the method is that it is developed for Lagrangian data which have a constant time interval between detections, while acoustic telemetry data has an Eulerian structure (i.e. a moving object passes detection stations) (Merki and Laube, 2012). Consequently, residency times can only be deduced at detection stations and can lead to misclassifying the tipping point of residency into migration behaviour. Nonetheless, we tested the method in a polder area as it is (1) independent of the biased migration

speed due to the present migration barriers in the system and (2) the polder is located relatively close to the marine environment, challenging the minimum distance threshold to distinguish eel migration from ranging (Verhelst et al., 2018c,d).

A third approach was using the set-up of the network: when a fish consequently passes three ALSs, it is considered migratory; a method similar to the approach by Stein et al. (2015) (an eel was considered migratory if it was sequentially detected at two downstream located ALSs). Since acoustic telemetry networks often have an irregular set-up (i.e. the interdistance between ALSs is not constant), fish residing in parts of the network with a higher density of ALSs may be more easily classified as migrants. Nonetheless, when a constant interdistance between the ALSs is applied, this method may be promising to distinguish between resident and migratory behaviour. The reason why this method was still applied in the Albert Canal was due to the large detection ranges (> 1 km), leading to unreliable residence times at ALSs. Also, due to the shipping locks and heavily regulated water flow, migration was much slower than in previously reported studies tackling silver eel progression, making it difficult to apply a method based on progression speed (Verhelst et al., 2018a).

9.3.2 Physical effect of shipping locks

Despite substantial research during the last few decades on Anguillid eels, especially the European eel, many knowledge gaps remain. A lot of attention regarding eel migration focused on pumping and hydropower stations. However, it is still unknown if shipping locks cause physical damage to eels as well. This physical damage is likely dependent on the mechanical structure

and functioning of the shipping lock, especially during filling and emptying. For instance, openings above water can lead to eels smashing on the water surface or even concrete bottoms of the receiving reservoir, leading to possible damage. Obviously, this problem is less prominent when openings are under water. Another possible problem to overcome shipping locks, are the filling channels. Not only may the eels encounter shear stresses when moving through these channels at the high speed of water transport, they may be subjected to substantial changes in pressure, leading to barotrauma. The latter has been observed for salmonids passing pumping stations and hydropower stations (Brown et al., 2014). Finally, the transported ships themselves may cause damage to fish as well, via, for instance, propeller strikes (Brown and Murphy, 2010). If future research would indicate physical damage on fish during movement in or through a shipping lock, the development of these structures need to be revisited to make them fish friendly, if we want to protect our fish populations.

9.3.3 Effect of delays

Another important knowledge gap, is the effect of delays, caused by migration barriers, on the eel's life cycle (Silva et al., 2018). We can assume that a longer residence in a specific area comes hand in hand with a higher chance of disease, predation and consequently mortality. However, since gonads mature during their migration, delays may lead to a mismatch in gonad maturation and arrival at the spawning grounds. Yet, eels may be able to regulate their gonad maturation via diel vertical migrations in the Atlantic Ocean by ascending to shallower, warmer water at night and diving to deeper, colder water during daytime (Aarestrup et al., 2009). Even more, eels may be flexible in their migration strategy as they could adopt a fast migration and arrive at the spawning event following their onset of migration or arrive a year later at the next event (i.e. mixed migration hypothesis) (Righton et al., 2016). Indeed, although migration generally takes place in autumn in Western Europe (Durif and Elie, 2008), spring migrants are often observed in heavy anthropogenically regulated systems (Acou et al., 2008; Deelder, 1954; Feunteun et al., 2000).

Migration delays can even lead to eels postponing their spawning migration and turning from the silver stage back into a so called semiyellow stage (Svedäng and Wickström, 1997). As gonads start to mature prior migration (Durif et al., 2005), postponing their migration comes with a certain cost: either the eels resorb their gonads or they maintain them for the next migration attempt. It is not known what the effect of this cost is on the migration behaviour or the quality of the eggs and sperm and consequently reproductive success. Investigating the gonads and condition of eels caught at both barrier free systems and heavily regulated systems or even ponds and lakes may shed light on

this knowledge gap. Nonetheless, the relative condition of the silver eels (FV) in this dissertation did not differ between the polder, estuary and canal (Fig. S1), but a more thorough analysis (i.e. fat content, liver weight, pollutants...) may reveal a different result.

9.3.4 Spawning and movement behaviour in the marine environment

Although stated in numerous studies that European eels spawn in the Sargasso Sea, there is still no proof that eels effectively spawn in that area, as spawning has never been observed in the wild, nor have eggs. In addition, the migration routes to the presumed spawning ground are largely unknown as well. However, technological improvements related to telemetry allowed recent discoveries such as the tracking of eels from continental Europe till the Azores (Righton et al., 2016), the first evidence of European eels migrating through the Gibraltar Strait to leave the Mediterranean (Amilhat et al., 2016) and the finding of both a Nordic and Southern migration route to exit the North Sea (Huisman et al., 2016; Westerberg et al., 2014). Locating and sampling spawning eels in the wild would answer important questions related to anthropogenic impacts on the eel population and conducted management. Acknowledging that the eel is a panmictic species (Als et al., 2011), they show a remarkable adaptive capacity to various habitats, which is probably the result of genetic polymorphism (Drouineau et al., 2014; Mateo et al., 2017). Hence, it may be possible to deduce where the spawning eels' growing regions were located, allowing to map the geographical regions which contain the majority of the eels contributing to spawning. Next to growing habitats, different migration routes

may have different bio-energetic implications: some routes may be energetically more demanding, leaving less energy for spawning (Huisman et al., 2016). As such, management might need to focus more on those areas where eels with a substantial contribution to the spawning population depart from or take an energetically favourable route. It also holds true the other way around: when spawning eels from specific regions are only marginally contributing to the spawning stock, the reason could be sought for and, if necessary, management could be improved.

Despite eels show a high phenotypic plasticity in habitat use, behavioural movement studies are mainly conducted in freshwater systems (Acou et al., 2008; Piper et al., 2015; Vøllestad et al., 1986; Winter et al., 2006). Yet, a part of the European eel population is oceanodromous and resides in marine and estuarine environments and lagoons during the growing stage (Tsukamoto and Nakai, 1998). This knowledge gap is especially important since the recruitment decline is based on glass eels migrating upstream, neglecting the oceanodromous part of the population. Consequently, the 90 – 99% decline may be an overestimation.

A large knowledge gap persists in the movement biology of yellow eels in marine and estuarine environments, with only a handful of studies been conducted (Daverat et al., 2006; Walker et al., 2014). Daverat et al. (2006) found that a large part of the eels is resident in marine and estuarine environments, but moved into freshwater systems at least once during their life. However, this tendency decreased with latitude, which is in accordance with the hypothesis that catadromous behaviour is a response to tropical, productive rivers, while anadromy is more common at high latitudes (Gross et al., 1988). It is suggested

that mainly glass eels with a lower body condition adopt an oceanodromous life stage, as upstream migration requires more energy (Edeline et al., 2006). Yet, predation and intra-specific competition is lower in temperate freshwater systems (Ibbotson et al., 2002; Jonsson and Jonsson, 1993), leading to a trade-off between oceanodromy and catadromy.

To partly cover the knowledge gap about yellow eel behaviour in estuarine systems, an acoustic telemetry network of 15 ALSs was deployed from July 2016 till August 2017 in the Drowned Land of Saeftinghe, a saltmarsh area part of the Westerschelde. However, after four weeks of fishing with fyke nets in July – August 2016, only one eel (FII, Total length = 570 mm, Weight = 401 g) was caught and subsequently tagged with a V13 coded tag (VEMCO Ltd, Canada). Upon tagging, the eel moved downstream to the edge of the Drowned Land of Saeftinghe with the main channel of the Westerschelde to subsequently move upstream in the saltmarsh area. Unfortunately, tracking stopped after 16 days at that upstream location (Verhelst et al. unpubl. data). Although the fate of the eel remains speculative, it illustrates that saltmarshes may be used by at least some eels as growing areas. In particular, these systems are full of macroinvertebrates and juvenile fish, which are potential prey for eels (Tesch, 2003). Yet, although it is assumed that eel densities are high in estuaries to population diffusion processes, leading mainly to males (Krueger and Oliveira, 1999), we could only catch a single yellow, female eel. The reason for this remains unclear and different possible explanations may hold true: (i) it could be that a better water quality of the Zeeschelde stimulates eels to migrate further upstream (Guelinckx et al., 2008), (ii) the system is too dynamic to hold many eels (i.e. at low water, only the largest ditches and some deep pools contain water), (iii) competition with shore crab (*Carcinus maenas* L.) is

too high (they proved to be highly abundant during the sampling campaign), despite eels eat crabs (Tesch, 2003) or (iv) our fishing methodology was not sufficient or intensive enough. As a result, the study left more research questions than it solved, emphasising the knowledge gaps of marine and estuarine eel behaviour.

Development in marine/estuarine and freshwater habitats may have certain consequences. For instance, growth rate is higher in estuaries at lower latitudes due to a higher productivity and temperature (Fernández-Delgado et al., 2006). Also, eel sex differentiation is mainly attributed to density, with male eels developing when density is high (Krueger and Oliveira, 1999). Consequently, due to the higher density of eels in estuaries and coastal areas (which in itself is the result of population diffusion processes), these areas may lead to the production of a higher proportion of male eels compared to freshwater systems. Even more, recent research suggests that eels may be genetically determined to be either oceanodromous or catadromous (Stacey et al., 2015).

Due to the marine biological knowledge gap, we have limited understanding about the impact of coastal and estuarine anthropogenic activities, such as migration barriers (both physical and chemical), harbours and coastal protection on oceanodromous eels as well. For instance, prevention of freshwater habitat colonisation may increase the proportion of oceanodromous eels (Clavero and Hermoso, 2015), leading to shifts in growth rate, sexual differentiation and perhaps mortality (e.g. via mismatch between genotype and phenotype). However, historical and current abundance and distribution data of eels is scarce or even non-existent, making it difficult to elucidate changes in population dynamics of oceanodromous eels. Nonetheless, water quality im-

provement in the Schelde Estuary is likely the driver of a larger number of yellow eels being caught upstream the estuary (Guelinckx et al., 2008). On the other hand, coastal and estuarine anthropogenic effects may lead to habitat loss and, consequently, a reduction in the number of oceanodromous eels (Drouineau et al., 2018b). Specifically, development of harbours and coastal fortification has reduced the number of estuaries and lagoons substantially (Gros and Prouzet, 2014; Simenstad and Cordell, 2000). Further, it has been stated that pollution accumulation in catadromous eels restrains successful spawning migration (Belpaire et al., 2016), yet pollution at coastal and estuarine harbours may be substantial (Deschutter et al., 2017) and affecting oceanodromous eels as well.

9.4 Future considerations

9.4.1 International networks

Telemetry allows tracking of mobile species over large spatio-temporal scales, even over administrative borders. Development of international networks not only enhances this large-scale tracking, it encourages cooperation over administrative borders and is consequently beneficial for wildlife management (Lennox et al., 2017). Recently, several local aquatic tracking networks, created by individual research groups, have been clustered in large-scale tracking networks allowing the tagged animals of different researchers and different projects to be detected on a larger scale and consequently expanding the study area substantially. Examples of such networks are the Integrated

Marine Observing System (IMOS, Australia), Atlantic Cooperative Telemetry (North America), California Fish Tracking Consortium, Florida Acoustic Cooperative Telemetry (North America) and the Acoustic Tracking Array Platform (South Africa). Many of these networks are on their turn clustered within the global Ocean Tracking Network (OTN). Recently, the European Tracking Network (ETN) was created to unite the different networks in Europe as well (<http://www.lifewatch.be/etn>) (Section 2.3). Further, not only the physical network is an important feature. It is likely that telemetry will play a more prominent role to meet management goals in the near future (Lennox et al., 2017). Creating large-scale networks stimulates cooperation and discussion, and as such, knowledge exchange between researchers of different institutes will be key for future management.

Clustering local tracking networks into large-scale, administrative border-crossing networks allows a better understanding of animal movement behaviour and has recently led to novel insights (Brodie et al., 2018; Huisman et al., 2016; Sequeira et al., 2018). Expanding these physical and social networks will undoubtedly aid future insights in fish migration and lead management towards sustainable and viable populations.

9.4.2 Open source policies

A prerequisite of (international) cooperation between institutes requires open source policies, so animals can be tracked beyond the local tracking network. Currently, some telemetry companies hold patents on their specific hardware and settings, leading to incompatibilities between telemetry equipment of different companies and as a result to less detections and knowledge. Striving for

open source technology allows a larger flexibility of the applied technology in the large-scale network or even combine different techniques of different companies. Even more, supply and demand, as well as competition between companies may lead to faster technological improvements such as smaller transmitters or lower prices, which in their turn result in tagging more individuals of smaller species or life stages.

In parallel with the technological improvements of telemetry are the development of analytical tools and algorithms. Telemetry researchers all over the world face similar problems at different steps of the data analysis: formatting the data, visualisations and data exploration, data analysis... Not only does this require an increasing collaboration between biologists, computer scientists and statisticians, making developed code reusable and publically available will enhance the scientific community substantially (Lennox et al., 2017). Some developments are already ongoing, such as the VTrack (<https://cran.r-project.org/web/packages/VTrack/index.html>) and glatos (<https://gitlab.oceantrack.org/GreatLakes/glatos>) R-packages of which the former is on CRAN (the Comprehensive R Archive Network) and the latter on gitlab. Both packages contain functionalities and algorithms for acoustic telemetry data assimilation, visualisation and analysis. Note that this development does not need to be limited to the telemetry community, but can be picked up by researchers in other fields of interest as well. Nowadays, different platforms exist to make code publically available (e.g. GitHub Inc., Gitlab). Even more, digital object identifiers can be added to the code, so they can be tracked or even added to a published article. And if you want the code to be picked up even faster, you can write a package for it and put it in an open library of the program it was written for (e.g. CRAN). Consequently, users are able to down-

load and use your code and functionalities.

Finally, making the data publically available can aid science and management as analyses can be conducted on data over vaster regions or longer time spans, leading to more well-founded management decisions. An open policy can benefit other end users as well, for example scientists conducting research on global scale distribution patterns of many species (Bosch et al., 2018). Such platforms already exist, for example the Ocean Biogeographic Information System (OBIS) and the Global Biodiversity Information Facility (GBIF). Since the number of telemetry studies is increasing and leads to high resolution spatio-temporal distribution patterns (Hussey et al., 2015), these data are an added value for open species distribution platforms.

However, we should be careful with open data policies as well. Making data publically available allows unprecedented disturbance by people who benefit from the tagged species (Cooke et al., 2017). This can be recreational and commercial fishermen, divers and wildlife photographers, but poachers as well, leading to the opposite effect of conservation. It is therefore crucial to overthink in what form telemetry data can be made publically available (e.g. lowering the spatio-temporal resolution of the detection) and for who (e.g. people registering at a specific website, scientists, policy makers...).

9.4.3 Linking environmental and biological data

The application of telemetry to track aquatic animals dates back to the 70s (Arnold and Dewar, 2001), yet, complex algorithms and models for data analysis have been lagging behind. It is only during the last decade that substantial

improvements have been made on that frontier (Béguer-Pon et al., 2014; Jacoby et al., 2012; Jacoby and Freeman, 2016; Ledee et al., 2015; Pauwels et al., 2014). Nonetheless, many of those studies analyse metrics derived from the movement itself (e.g. arrivals and residence times at ALSs, effect of morphometrics on the movement behaviour, migration speeds and distances...) (Béguer-Pon et al., 2014; Ledee et al., 2015). To analyse effects of the environment on the spatio-temporal animal movement behaviour is not a trivial thing to do, since it requires qualitative and quantitative environmental data and complex algorithms to link those data to telemetry datasets. All the more since the resolution of telemetry data mostly exceeds the resolution of the monitored environmental data (Bruneel et al., 2018). Indeed, many aquatic systems have only one to a handful of environmental data monitoring stations, while telemetry networks often exceed in tens of deployed ALSs over a wide geographical area of the aquatic system of interest (see Chapter 5 and 6). Different solutions for future considerations exist, from the addition of extra environmental sensors in the study area, over the application of transmitters combined with sensors, to the interpolation of environmental variables between different detection stations (Bruneel et al., 2018). Yet, some aquatic systems are currently extensively monitored and the environmental data gaps are filled with interpolation techniques (e.g. the Delft3D model of the Schelde Estuary). It would be of substantial added value to link telemetry data with those systems in the future, not only to improve our insight in animal behaviour, but also to get a more thorough understanding of the impact of system changes to those animals.

This approach could actually be taken a step further. Apart from environmental variables, species interactions can play a significant role in animals' distributions and movements (Verhelst et al., 2016). Many waterways are mon-

itored for macro-invertebrates and fish to assess the water quality (Breine et al., 2004, 2007; Gabriels et al., 2010). Linking these biotic and environmental data to telemetry data may reveal important insights in ecosystem functioning. Even more, it is likely that a higher number of species and individuals will be tracked in the future, leading to more data and more solid models. As such, telemetry will play a more prominent role in efficient management and environmental policy studies (Lennox et al., 2017; McGowan et al., 2017).

9.5 Future recommendations

9.5.1 Management recommendations

To aid conservation and recovery of European eel stocks, 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. Not only is it unknown if this theoretical rate suffices to save the eel population, per country or catchment, it implies understanding (1) of the annual silver eel production and (2) the annual silver eel escapement. Obviously, these aspects are hard to identify, challenging the evaluation of the European Eel Regulation.

Although many knowledge gaps remain, substantial research has been conducted since the establishment of the European Eel Regulation, leading to various studies emphasising the importance of global change on the European eel population (Drouineau et al., 2018b), such as the impact of ocean climate

change (Miller et al., 2015), pollution (Belpaire et al., 2016), movement barriers (Buysse et al., 2014; Verhelst et al., 2018a,c), introduction of non-native parasites (Palstra et al., 2007) and overexploitation (Aarestrup et al., 2010; Dekker, 2018; Moriarty and Dekker, 1997). With the upcoming evaluation of the regulation, additional research is likely to follow (e.g. towards development of downstream fish passes, fine tune migration models, effect of migration delays...), yet, sufficient knowledge is available to take new steps in eel management.

Despite the numerous factors contributing to the European eel decline, the two main management measures taken are fishing limitations and glass eel stocking. Nonetheless, as long as no adequate actions are taken to reduce mortality related to other factors such as habitat loss and movement barriers, climate change, pollution and the effect of non-native parasites, the aforementioned management measures are unlikely to have a substantial effect (Drouineau et al., 2018b). Glass eel stocking, for instance, may only be beneficial at locations with a minimum of migration barriers near the sea. Nonetheless, genetic research is urgently needed to deduce if glass eel relocation is effective, since recent research indicated that the phenotype or phenotypic plasticity may be determined by the genotype (Stacey et al., 2015).

The results of this dissertation clearly illustrate that downstream migrating silver eels are severely impacted by migration barriers such as weirs, pumping stations, tidal sluices and shipping locks. Although more research is needed to understand the effects of delayed migration on reproductive success (Silva et al. 2018), delayed fish are more prone to diseases and predation, indicating the negative effect of migration barriers. Yet, the results showed opportunities for management to improve silver eel escapement during so called "migration

windows". Specifically, silver eels in Belgium primarily migrated at night during autumn under increased discharge conditions, likely a consequence of increased precipitation (Verhelst et al., 2018a,c). At some locations, it may be feasible to temporarily open migration barriers to stimulate a unidirectional flow and consequently silver eel escapement during those environmental conditions during which silver eel migration is most likely to occur. Further, at other locations alternative migration routes may be stimulated by slightly changing the hydrology of the system, allowing eels to take a safer route by, for instance, avoiding passage through pumping stations or hydropower turbines (Verhelst et al., 2018a,c). In case of the Albert Canal, this would imply that it can act as a short cut for eels growing in the upper reaches of the Meuse River and take the canal as an alternative route instead of the longer Meuse with hydropower stations.

However, these actions come with certain costs (e.g. reduction in hydropower, less shipping, higher water levels in polder areas...), so it may not be straightforward to implement the suggested measures. Hence, ecologists and engineers need to work together to strive for win-win situations between both ecology and economy. Obviously, not only the eel population will benefit from taken measures, but other diadromous and potamodromous species as well.

9.5.2 Research recommendations

The European eel has a complex life cycle with fundamental biological questions still being unanswered. Thus far, the exact marine migration routes of silver eels to the spawning grounds have not been elucidated. Yet, recent technological improvement allowed tracking of silver eels until the Azores

(Righton et al., 2016). Mapping these routes and understanding the accompanying behaviour can teach us how Anguillid eels handle their available bio-energy budgets for successful spawning. For instance, Righton et al. (2016) hypothesised that the migration routes at sea may take 1.5 years before reaching the spawning grounds, which has important bio-energetic repercussions considering the species ceases feeding at this life stage (Chow et al., 2010). As stated in Chapter 8, different migration routes may require different energy demands and consequently, contribution to the spawning stock may not be equal for all eels from various locations in Europe. Therefore, management may need to be tailored according to the energy requirements of the escaping population. For instance, yellow eel growing in areas holding a substantial part of the spawning population may require extra attention. However, more information related to the energy requirements for spawning migration is needed. Further, tracking silver eels until the spawning area could not only reveal anthropogenic bottlenecks at sea, but also migratory problems occurring at sea due to anthropogenic influences during the continental phase (e.g. effects of pollution, the non-native swim bladder parasite *Anguillicoloides crassus* and delays near migration barriers on efficient spawning migration and consequently successful spawning). Also, various studies tracking silver eels at sea observed predation by marine mammals, sharks and tunas (Béguier-Pon et al., 2012; Righton et al., 2016). Although a high predation rate may be attributed to the tagging effect, it may also hold true that migrating silver eels serve as an important food source for many marine predators. Silver eel migration is an annual recurring event over a large spatial scale. Consequently, a substantial reduction in silver eels may have important consequences for large marine predator population dynamics.

Another important scientific field which contributes to the many biological enigmas of Anguillid eels is genetic research. Genetic research has improved substantially over the last decades and this trend will likely continue in the near future. Hence, eel research will benefit from this as well. Specifically, although the European eel population is considered panmictic (Als et al., 2011), genetic patchiness among recruits has been observed (Pujolar et al., 2006). Even more, recent genetic research found evidence against panmixia for the Japanese eel (Igarashi et al., 2018). Hence, further elucidating the genetic structure of Anguillid eels could help determine the effective spawning stock (Pujolar et al., 2006). It also may be possible in the future to determine the different growing locations of the spawning stock, enabling a quantification of migrating eels from different continental regions. In light of this genetic patchiness, future research could unravel if glass eels have different genetic adaptations. Specifically, despite decades of glass eel restocking, the implementation has not led to the expected population recovery. The reasons for this are unclear, but it could be that restocking results in a mismatch between genotype and habitat (Stacey et al., 2015). Hence, further understanding related to genetics and adaptive responses is urgently required.

Also our understanding on the effect of migration barriers on fish migration requires further research. The numerous migration barriers result in substantial delays of migratory fish species (Silva et al., 2018; Verhelst et al., 2018a,c). Although chances of disease, predation, fishing and therefore mortality may rise substantially, the effect of delays on the fitness and reproductive success of the animal is unknown. Such research has important implications for management. It would indicate that fish passage not only needs to be sufficient, it needs to be efficient as well.

Finally, Anguillid eels and diadromous species in general show some of the most extensive animal migrations known to man. These migrations are the result of long-term evolutionary trends and natural selection allowed the species to adapt and persist during the changing events of time. However, due to anthropogenic influences, the Earth's climate is changing faster than ever before leading to difficulties for species to adapt and, consequently, extinctions (Visser, 2008; Ceballos et al., 2015). Related to fish migration, climate change will likely lead to different hydrological conditions (Vörösmarty et al., 2000). This may not only result in the construction of migration barriers such as pumping stations, dams, weirs and hydropower plants, but also in conflicts between the migratory behaviour and the altered hydrological conditions. For instance, a dryer climate or higher anthropogenic water retention in reservoirs may lead to less run-off and consequently more limited migration windows.

