

UNRAVELING THE DRIVERS OF RIVER LAMPREY MIGRATION USING TELEMETRY DATA

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A dissertation submitted to Ghent University in partial fulfilment of the requirements for the degree of master in Bioscience Engineering: Environmental Technology.

Academic year: 2025 - 2026

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Gent, 5 June 2026

The promotors,

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Dankwoord

Ik herinner me nog hoe ik op een koude herfstochtend in oktober, om vijf uur 's morgens en in het pikkedonker, stond te wachten op de trein. Op dat moment besepte ik nog niet volledig wat me te wachten stond, maar enkele uren later zouden de golven van de Westerschelde, die we met een klein bootje trotseerden, me meteen wakker schudden. Het was mijn eerste kennismaking met de intrigerende wereld van telemetrieonderzoek. De avontuurlijke boottochten, de wonderlijke vissen die we vingen, de schat aan informatie die daaruit voortkwam en de fascinerende modellen die we ermee konden ontwikkelen: het is nooit gaan vervelen.

Met enorm veel enthousiasme ben ik deze wereld ingedoken, en kijk ik met trots terug op het traject dat ik heb afgelegd. Uiteraard had ik dit nooit alleen kunnen realiseren. Daarom wil ik eerst en vooral mijn allergrootste dank uitbrengen aan mijn begeleiders. Hanna, ik had me geen betere tutor kunnen wensen. Je stond altijd klaar om te helpen, zowel met de thesis als daarbuiten. Professor Baetens, bedankt voor de sturing waar nodig, de waardevolle inzichten en de aangename omgeving om in te werken. Pieterjan, bedankt voor de begeleiding, de interessante gesprekken en inzichten, en de kans om mee het veld in te trekken. Ook bedankt voor de uitdagende cursus 'hoe neem je een paling vast', een vaardigheid die ik, vrees ik, nog steeds niet helemaal onder de knie heb.

Daarnaast wil ik ook Mylan Lyssens, Simon Plaetinck en Nico De Maerteleire bedanken om mij telkens opnieuw enthousiast mee te nemen op leerrijke en avontuurlijke veldwerkdagen. Die dagen brachten me niet alleen waardevolle inzichten en onvergetelijke ervaringen, maar ook vriendschap en heel wat vuile kleren. Ik heb hier enorm veel voldoening uit gehaald.

Tot slot wil ik graag de mensen bedanken die altijd achter me zijn blijven staan. Mama, papa en Lowie, bedankt voor jullie onvoorwaardelijke steun en vertrouwen. En Alexia, bedankt om mijn enthousiaste (en vaak veel te lange) verhalen over vissen te doorstaan, maar vooral om er altijd voor mij te zijn. Jullie betekenen ontzettend veel voor mij.

Dit traject was zonder twijfel een van de meest interessante ervaringen die ik ooit heb mogen beleven, en hopelijk slechts de eerste van vele. Ik kijk er alvast enorm naar uit!

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Use of generative AI

Use of GenAI tools in the master's dissertation:

- ☐ No use of GenAI tools
- ☒ One or more GenAI tools used

Indicate and describe, in case of using one or more GenAI tools, how you have used them:

GenAI tool used as	Description	Used tool(s)
☒ Idea generator	No newly generated ideas, but discussion and insights about personal ideas and thoughts	ChatGPT and Gemini
☒ Search engine	Deep literature search on various topics, identifying literature-derived arguments and counterarguments for used methodologies	Undermind, SciSpace, ChatGPT and Gemini
☒ Writing assistant	Rewording long and/or difficult explanations more simply and clearly	ChatGPT
☐ Designer	/	/
☐ Practice tool	/	/
☐ Data analysis	/	/
☒ Efficiency booster	Helping with debugging and writing long, repetitive code	ChatGPT and Gemini
☒ Used in another way	Generating tables in LaTeX	ChatGPT

List of symbols and abbreviations

- A1** Shipping lock complex in Merelbeke.
- A2** Weir complex at the tidal branch in Merelbeke.
- B** Shipping lock complex in Asper.
- C** Shipping lock complex in Oudenaarde.
- D** Shipping lock complex in Kerkhove.
- AIC** Akaike Information Criterion.
- ETN** European Tracking Network.
- GLMM** Generalized Linear Mixed Model.
- HIC** Hydrological Information Centre.
- IBM** Individual-based model.
- INBO** Research Institute for Nature and Forest.
- IUCN** International Union for Conservation of Nature.
- ODD** Overview, Design concepts, Details.
- PBARN** Permanent Belgian Acoustic Receiver Network.
- PIT** Passive Integrated Transponder.
- VLIZ** Flanders Marine Institute.
- VMM** Flanders Environment Agency.
- WGS** World Geodetic System.

Samenvatting

Wereldwijd gaan ecologisch waardevolle vispopulaties achteruit door antropogene impacten, waarbij rivierfragmentatie door menselijke constructies een van de meest ingrijpende oorzaken is. Deze structuren vormen barrières voor vismigratie en verstoren de levenscyclus van trekkende soorten, zoals de Europese rivierprik (*Lamprolaima fluviatilis*).

In deze thesis onderzochten we de effecten van fragmentatie in de Bovenschelde op stroomopwaarts migrerende individuen van deze soort, met behulp van akoestische telemetrie. Daarnaast analyseerden we factoren die hun gedrag beïnvloedden via gegeneraliseerde lineaire gemengde modellen, in zowel vrij stromende als geblokkeerde riviertrajecten. Finaal bestudeerden we migratiepatronen via overlevingsanalyse en een individu-gebaseerd model (IBM), onder huidige en alternatieve scenario's.

Onze resultaten toonden duidelijk aan dat sluiscomplexen een sterke impact hadden op succesvolle vismigratie en aanzienlijke vertragingen veroorzaakten bij migrerende rivierprikken. Voor individuen die deze barrières wel passeerden, bleken rivierafvoer en operationele regimes van stuwen een belangrijke invloed te hebben op het succes. Vispassages vergemakkelijkten de passage van de beperkte groep individuen die ze konden bereiken. In vrij stromende riviersecties migreerden de rivierprikken vooral 's nachts en nam hun migratiesnelheid later in het seizoen toe.

Het IBM reproduceerde de waargenomen passage-efficiënties en migratievertragingen aan sluiscomplexen nauwkeurig, en de scenarioanalyse benadrukte het belang van vispassages voor migratiesucces en weerbaarheid tegen droogte.

Over het algemeen bevestigden onze bevindingen de negatieve effecten van fragmentatie in de Bovenschelde op migrerende vissoorten. Verder onderstreepten ze het belang van een beter rivierbeheer en mitigatie van barrières via vispassages of aangepast spuibeheer, in het bijzonder met het oog op toekomstige droogteperiodes.

Summary

Across the world, ecologically valuable fish populations are declining due to anthropogenic stressors, with river fragmentation through man-made constructions being one of the most severe contributors. These structures act as barriers to fish migration and disrupt the life cycle of migratory species, such as the European river lamprey (*Lampetra fluviatilis*).

In this dissertation, we investigated the impacts of fragmentation in the Upper Scheldt on upstream migrating individuals of this species, using acoustic telemetry. We further analyzed behavioral drivers using generalized linear mixed models in free-flowing and obstructed river stretches. Finally, we assessed migration patterns using survival analysis and an individual-based model (IBM), under existing and alternative scenarios.

Our results undeniably showed that shipping lock complexes had a strong impact on successful fish migration and caused substantial delays for migrating lampreys. For individuals that passed these barriers, flow conditions and weir operating regimes significantly influenced success. Fishways facilitated passage for the limited number of individuals that reached them. In unobstructed river sections, lampreys mainly migrated at night and increased their migration speed later in the season.

The IBM reproduced the observed passage efficiencies and migration delays at shipping lock complexes accurately, and scenario analysis highlighted the importance of fishways for migration success and resilience to drought.

Overall, our findings reinforced evidence on adverse effects of fragmentation in the Upper Scheldt on migrating fish species. In addition, they highlighted the importance of improved river management and barrier mitigation strategies through fishways and adjusted barrier management, especially with regard to future drought periods.

Introduction

Freshwater ecosystems are among the most biodiverse and productive environments on Earth, yet they are also among the most threatened (Strayer and Dudgeon, 2010). Over the past century, pressures such as pollution, habitat degradation and modification, overexploitation, invasive species, and climate change have driven widespread declines in freshwater biodiversity (Dudgeon et al., 2006; Reid et al., 2019). Among these stressors, river fragmentation, caused by the construction of dams, weirs, hydropower stations, sluices, and other water regulating structures, has shown to be particularly widespread and disruptive (Vörösmarty et al., 2010; Carpenter et al., 2011), with more than 1.2 million barriers fragmenting European rivers (Belletti et al., 2020), leaving less than 10% of those free-flowing (Parasiewicz et al., 2023).

By altering natural flow regimes and interrupting connectivity within river networks, water regulating structures transform ecosystem functioning and threaten the survival of many aquatic species (Vörösmarty et al., 2010; Sabater et al., 2018; Schmutz and Moog, 2018). One of the most visible and well-documented consequences of river fragmentation is its impact on migratory fish (Drouineau et al., 2018; Dean et al., 2023; Chan et al., 2025), as these species depend on unobstructed pathways to complete their life cycle (Lucas and Baras, 2001). When barriers impede these movements, populations may decline or even collapse, despite the presence of suitable habitats elsewhere in the river system (Moser et al., 2021). This is particularly critical for diadromous species, which migrate between freshwater and marine environments. In fact, diadromous fish have severely declined in the last century, with reductions of at least 90% for all species across the northern Atlantic since the early 1900s (Limburg and Waldman, 2009).

In response, efforts to restore connectivity and mitigate river fragmentation have gained increasing attention in policy and management (e.g., the European Nature Restoration Regulation and the Benelux Decree), through measures such as barrier removal and fishways (Verhelst et al., 2021). However, their effectiveness varies widely (Drouineau et al., 2018) and often depends on species-specific behavior, environmental conditions, design or operation, and socioeconomic constraints (Silva et al., 2018). Adaptive management of fishways and water infrastructures, such as temporarily opening barriers during migration peaks, could be a feasible alternative (Mouton et al., 2011; Griffioen et al., 2017).

In this context, research on migratory fish, aimed at uncovering the effects of environmental conditions and water regulating structures on migration, provides valuable insights for conservation and management. Advances in tracking technologies, such as aquatic biotelemetry, have made it possible to gain new ecological knowledge by monitoring individual movements in unprecedented detail (Hussey et al., 2015). The European river lamprey (*Lampetra fluviatilis*) provides a particularly relevant case study. As an anadromous species with a complex life cycle that spans both marine and freshwater environments, it relies heavily on river connectivity for successful reproduction (Kelly and King, 2001; Maitland, 2003; Lucas et al., 2009). However, the species has experienced significant declines, largely due to habitat fragmentation and degradation (Stevens et al., 2009; Lucas et al., 2021). Understanding the factors that influence and impede its migration, is therefore crucial to inform conservation strategies.

This master's dissertation aims to contribute to that understanding by examining the migratory behavior of the river lamprey in the Upper Scheldt River. By combining ecological knowledge with insights from acoustic telemetry, it tries to identify key drivers of migration success in this heavily fragmented river. Moreover, this study develops a data-driven, individual-based model to forecast migration timing and characteristics, based on environmental conditions and barrier operating regimes. By informing management of water regulating structures in the Upper Scheldt River, the model can help to conserve the river lamprey in Flanders. In general, this thesis aims to answer four distinct research questions, related to the migration of the river lamprey:

1. How does the presence of water regulating structures affect migration success and speed (Section 4.1 and 4.2.1, respectively)?
2. How do environmental conditions and water regulating structure operation regimes affect passage success (Section 4.2.2)?
3. How do environmental conditions affect migration speed in unobstructed river sections (Section 4.3)?
4. To what extent do different environmental conditions and management scenarios for water regulating structures influence upstream migration (Section 5.3)?

Chapter 1 provides a general framework on river fragmentation, outlining its ecological impacts with a particular focus on migratory fish, as well as broader consequences for river ecosystem functioning. It then reviews the current legislative context in Europe and Flanders and discusses commonly applied restoration strategies. Special attention is given to methods for studying fish movement, with an emphasis on aquatic biotelemetry. Chapter 2 introduces the European river lamprey

as a model species, describing its life cycle, ecological relevance, and conservation status. It further explores the main factors influencing its upstream migration. Building on this background, Chapter 3 presents the materials and methods used in this study, followed by Chapter 4, which reports the results on movement patterns, environmental drivers of migration, and barrier effects in the Upper Scheldt River, to successfully answer the first three research questions. Finally, Chapter 5 discusses the development of an individual-based model to simulate the upstream migration behavior of the European lamprey under different scenarios, with a view to nature management and conservation.

1. Losing connection: understanding and addressing river fragmentation

Despite ranking among the planet's most biodiverse and productive environments, freshwater ecosystems are severely affected by human activities (Strayer and Dudgeon, 2010). Major threats include overexploitation, invasive alien species, climate change, habitat degradation and destruction, water pollution and flow modification (Dudgeon et al., 2006; Reid et al., 2019). The latter generally serves to control flooding, store water, facilitate transport or generate electricity (Poff et al., 1997), and often results in habitat fragmentation through the development of water regulating structures such as hydropower plants, dams, weirs, sluices and water pumping stations (Belletti et al., 2020).

By disrupting aquatic connectivity and flow regimes, these structures are one of the most severe anthropogenic factors that threaten global freshwater biodiversity and natural river systems (Vörösmarty et al., 2010; Carpenter et al., 2011; Sabater et al., 2018). About 60% of the world's river systems are fragmented by large dams (>15 m) (Nilsson et al., 2005; Grill et al., 2019). At least 1.2 million barriers fragment European rivers, the vast majority being low-head structures smaller than 5 m (23%) or 2 m (68%) rather than large dams exceeding 15 m (1%). These small structures are often poorly mapped or unreported and likely have an even greater impact on river connectivity due to their abundance and cumulative effects (Belletti et al., 2020). Taking this into account, Parasiewicz et al. (2023) estimate that only 10% of European rivers remain free-flowing.

1.1 Impacts of river fragmentation

1.1.1 Effects on migratory fish

Water regulating structures can act as barriers for migrating fish as they move between critical habitats to complete their life cycle. Lucas and Baras (2001) describe fish migration as coordinated movements by individuals of a species, over distances larger than their typical home range, during specific life stages.

Fish migration serves three main functions: reproduction, feeding, and seeking refuge. Depending on the habitats involved, three types of migration are distinguished: oceanodromous (entirely marine), potamodromous (entirely freshwater), and diadromous (movement between freshwater and marine environments) (Lucas and Baras, 2001). As shown in Figure 1.1, diadromy can be further divided into anadromy, where fish feed and grow at sea but reproduce in freshwater, catadromy, where they feed and grow in freshwater but reproduce at sea, and amphidromy, involving movements between fresh and salt water not directly related to spawning (McDowall, 1997).

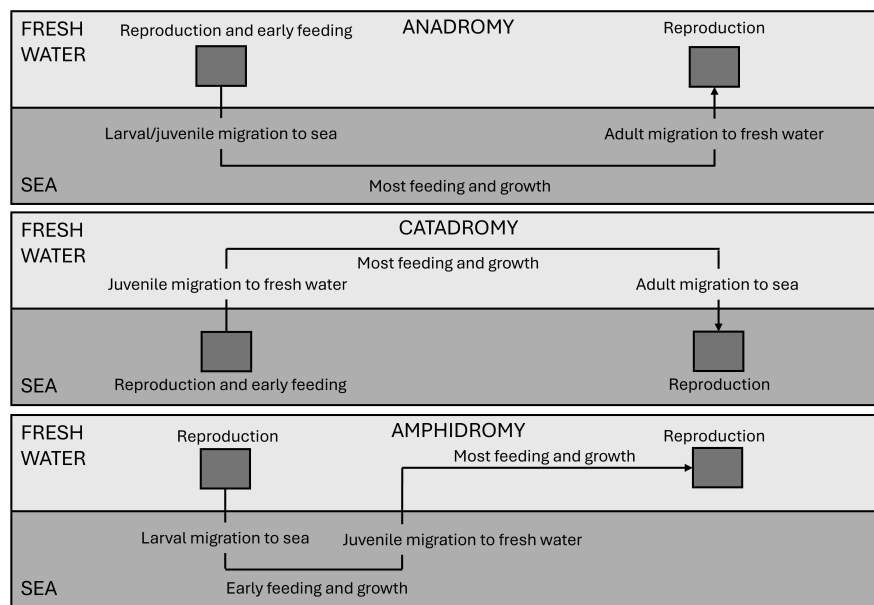


Figure 1.1: The different categories of diadromous fish migration, adapted from McDowall (1997).

Diadromous fish species are of great ecological, economic, and cultural importance and contribute significantly to both freshwater and marine biodiversity worldwide (Drouineau et al., 2018; Ashley et al., 2023). However, their populations have declined in recent decades due to river fragmentation, habitat loss, pollution, climate change, overfishing, invasive alien species and other human-induced pressures (Limburg and Waldman, 2009; Wilson and Veneranta, 2019). Since connectivity between key habitats throughout the life cycle is crucial for their reproduction and survival (Moser et al., 2021), the alarming status of migratory fish is strongly attributed to loss of river continuity (Nieland et al., 2015; Drouineau et al., 2018; Verhelst et al., 2021; Dean et al., 2023; Chan et al., 2025). Even when key habitats are of high ecological quality, fragmentation of the river ecosystem still critically affects these species by preventing them from reaching those habitats (Moser et al., 2021).

Barriers, such as dams and weirs, regulate water flow in rivers and directly affect migratory fish by impairing habitat access, delaying migration and causing injury and mortality (Zydlewski et al., 2023). Large and medium-sized structures

1. Losing connection: understanding and addressing river fragmentation

can form impenetrable barriers to fish migration, while low-head structures might be penetrable under some conditions. However, smaller barriers are considered more problematic overall due to their abundance (Lucas et al., 2009; Belletti et al., 2020). For example, Lucas et al. (2009) document a progressive decline in European river lampreys (*Lampetra fluviatilis*) passing successive barriers during upstream migration (Figure 1.2). Similar cumulative impacts have been reported for lampreys (Foulds and Lucas, 2013; Davies et al., 2021; Jubb et al., 2023b) and other migratory species such as salmonids (Gowans et al., 2003; Gauld et al., 2013; van Rijssel et al., 2024) and eels (Yokouchi et al., 2022).

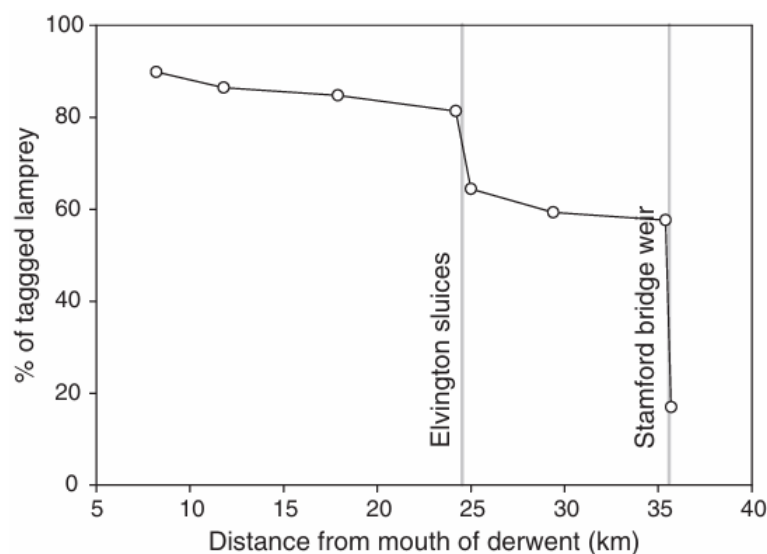


Figure 1.2: Percentage of river lampreys ($n = 56$) that migrated past particular sites up the Derwent River. The percentage shows a clear cumulative reduction coinciding with the vertical bars, which represent two weirs in the river (Lucas et al., 2009).

Dams and weirs are not the only structures that fragment rivers and impede fish migration. Lock complexes delay migration if their operational regimes do not coincide with fish movement (Vergeynst et al., 2019). The same holds for hydropower stations (Piper et al., 2018), and tidal sluices and pumping stations (Wright et al., 2015; Verhelst et al., 2018), with the former becoming increasingly relevant in the green energy transition, and the latter two often being used to control water levels and avoid flooding in wetland and estuary areas. Furthermore, individuals passing through fish-unfriendly pumps or hydroelectric turbines frequently experience severe or mortal injuries and can completely halt their downstream migration (Buysse et al., 2014; Bolland et al., 2019; van Treeck et al., 2022).

Beyond the well-documented impacts on migratory fish, Zydlewski et al. (2023) highlight several less obvious consequences of river barriers. For instance, aggregations of individuals below barriers increase vulnerability to opportunistic and ambush predators. In addition, dams alter local biophysical conditions (Section 1.1.2),

which might create opportunities for invasive non-native species to enter the river system. Demographic changes may also arise, for example through size-selective passage in fishways (Zydlewski et al., 2023). Furthermore, barriers can change the spatial distribution of a population: Lucas et al. (2009) observe a severe spatial mismatch between spawning activity and suitable habitat for river lampreys, and identify restricted upstream migration as the cause of this mismatch. Since these spawners are forced to concentrate in areas downstream of barriers, population vulnerability to catastrophic events increases, especially for self-sustaining populations (Lucas et al., 2009).

1.1.2 Other ecological consequences

The ecological integrity and biodiversity of rivers strongly depend on their natural dynamics. Water regulating structures fundamentally alter hydrological regimes, river geomorphology, and ecosystem functioning (Poff et al., 1997). Consequently, there is broad scientific consensus that human-induced changes to flow regimes have various negative ecological impacts (Poff and Zimmerman, 2010). Schmutz and Moog (2018) consider six main impacts associated with dam construction: loss of river continuity, siltation and clogging of the riverbed, homogenization of habitats, riverbed erosion in downstream sections, change in groundwater exchange and alteration of downstream flow and water quality.

Interruption of river connectivity occurs both longitudinally (up- and downstream) and laterally (river–floodplain). This affects not only fish migration, but also sediment and nutrient transport (Schmutz and Moog, 2018). As barriers retain sediments and nutrients, they reduce downstream loads. The resulting lower nutrient contents diminish productivity, wetland fertility, and carrying capacity (Schmutz and Moog, 2018), while a decrease in suspended material causes sediment-starved streams, enhancing riverbed incision and erosion (Hohensinner et al., 2018). As a consequence, increased incision alters river structure and floodplain connectivity (Hohensinner et al., 2018), whereas increased erosion coarsens or armors the riverbed (Hauer et al., 2018). The latter makes the riverbed more prone to clogging by fine sediments (e.g. from runoff), which degrades invertebrate habitats and reduces fish spawning success, particularly for rheophilic species that rely on gravel beds for spawning (Dubuis and De Cesare, 2023).

Large dams slow down the flow and retain water, thereby converting dynamic lotic habitats into more uniform lentic environments. These altered systems differ in physicochemical conditions, biological communities, and ecological processes. The lower flow velocities enhance nutrient and pollutant retention, raise water temperatures, and promote the deposition of fine sediments and organic matter, increasing susceptibility to eutrophication, oxygen depletion, pollution, acidification, and siltation (Schmutz and Moog, 2018). Moreover, the absence of natural dynamics leads

to habitat homogenization, favoring generalist and invasive species over native specialists (Poff et al., 2007). Migratory fish are especially affected, experiencing severe declines due to lentic conditions, fragmentation, and the loss of critical spawning grounds (Agostinho et al., 2008).

1.2 Legislation in Europe and Flanders

Due to the alarming status of global freshwater biodiversity (Dudgeon et al., 2006; Reid et al., 2019), various international, national and regional legislative frameworks have been established to restore and protect aquatic ecosystems and species. A key example is the European Nature Restoration Regulation (2024/1991). As a core element of the EU Biodiversity Strategy for 2030 and the European Green Deal, it sets several binding targets to restore degraded ecosystems, habitats and species. One specific target is to restore the continuity of at least 25 000 km of rivers by 2030, by removing barriers and restoring floodplains and wetlands. To achieve the objectives of this regulation, member states are required to develop National Restoration Plans by 2026.

The Habitats Directive (92/43/EEC) aligns its goals with those of the Nature Restoration Regulation, by aiming to protect a wide range of threatened, vulnerable, rare or characteristic habitats and species in Europe. For their conservation, habitats and species listed respectively in Annex I and II of the Habitats Directive require special areas of conservation (SACs), which form a part of the Natura 2000 network of protected European sites. EU member states are legally obligated to identify, protect and sustain these SACs. Furthermore, species listed in Annex IV must be strictly protected by EU member states, even outside their designated conservation areas.

The framework of the EU Habitats Directive is implemented in Flanders through the Nature Decree (21/10/1997), while the protection of relevant species is executed by the Flemish Government through the Species Decision (15/06/2009). Several diadromous fish species are listed in the Habitats Directive, and the following diadromous species are subsequently protected through the Flemish Nature Decree: Atlantic salmon (*Salmo salar*), twaite shad (*Alosa fallax*) and river lamprey (*Lampetra fluviatilis*). In addition, the diadromous European eel (*Anguilla anguilla*) is protected in Flanders through the European Eel Regulation (1100/2007). To conserve migratory fish species listed in the Habitats Directive, the Benelux Decision (M.2009.01) requires Flanders to eliminate all fish migration bottlenecks by 2027.

Another key example of European legislation dealing with the deterioration of freshwater ecosystems is the Water Framework Directive (2000/60/EC). This directive aims at reaching and maintaining a good ecological and chemical status of freshwater ecosystems. The ecological status of a water body is assessed using bio-

logical, hydromorphological, and physicochemical parameters, while the chemical status relies on environmental quality standards. Following the ‘one out, all out’ principle, the overall status is determined by the lowest-scoring parameter. Therefore, improvement requires enhancing all elements, by reducing pollution and improving hydromorphology and water quality. The EU Water Framework Directive is implemented in Flanders through the Flemish Decree on Integrated Water Policy (18/07/2003).

One specific way in which the objectives of the Water Framework Directive align with those of the Nature Restoration Regulation and Habitats Directive, is through river continuity restoration. As mentioned above, hydromorphology is an important aspect of the ecological status of a water body. Specifically for rivers, this relates to natural hydrological regimes (quantity, dynamics and connection to groundwater), morphology (depth, width, structure of the riparian zone and structure and substrate of the river bed) and river continuity. Hydromorphological improvements therefore include river continuity restoration, which remains one of the priorities in the conservation of diadromous fish (Drouineau et al., 2018; Verhelst et al., 2021).

1.3 Restoration of river connectivity

The negative consequences of river fragmentation have been increasingly acknowledged in recent decades (Section 1.1), resulting in various legislative frameworks (Section 1.2) and subsequent restoration plans that try to address this problem. Methods to mitigate barrier effects include barrier removal, fish passages, and changes in barrier and fish passage operations (Verhelst et al., 2021). However, connectivity restoration measures have often led to mixed results (Drouineau et al., 2018). Management of diadromous species might only be successful if, along with connectivity restoration, additional measures are taken, such as habitat restoration, fish restocking and fisheries management (Verhelst et al., 2021).

1.3.1 Barrier removal, fish passages and trap-and-transport

If possible, the preferred method of river connectivity restoration is barrier removal (Verhelst et al., 2021). Removing obstructions in rivers can restore natural flow regimes, sediment and nutrient transport, and habitat structure, which improves overall ecosystem functioning (Bubb et al., 2021; Dietrich et al., 2025). In addition, fish movements become unhindered again, which often results in re-establishment of populations up- and downstream of the removed barrier (Hogg et al., 2013; Birnie-Gauvin et al., 2017; Bubb et al., 2021; Kukuła and Bylak, 2022). Since many (low-head) barriers in Europe are old and obsolete, there exist numerous opportunities to restore continuity (Belletti et al., 2020). However, to maximize the efficiency

1. Losing connection: understanding and addressing river fragmentation

of restoration efforts, removal should be coordinated rather than focused on individual watersheds (Neeson et al., 2015).

Since the 1990s, more than 9000 barriers have been removed in Europe (Dam Removal Europe, 2025). Although barrier removal is now a common approach and considered a priority, it should be approached with caution. For example, barriers might prevent invasive species from entering systems (Kerby et al., 2005; Walter et al., 2021). Moreover, removal might not always be considered feasible, due to excessive costs or loss of barrier functions such as energy production and flood protection. Therefore, alternatives should be considered.

A common alternative for barrier removal is fishway construction, i.e., structures that allow fish movement across obstacles. Designs vary from technical structures, to nature-like and purpose-specific designs (Silva et al., 2018). Technical fishways however, are often designed for a narrow range of species (such as salmonids) resulting in low passage efficiency for other species. In addition, fishways often fail to facilitate downstream passage, since downstream migrants generally follow the main flow (Katopodis and Williams, 2012). Furthermore, general performance remains low in some regions due to lack of biological knowledge and design or operation flaws (Silva et al., 2018). For instance, several studies report low fishway passage efficiency for lampreys, due to insufficient attraction flows or velocities exceeding swimming capacity (Lucas et al., 2009; Huysecom et al., 2012; Foulds and Lucas, 2013; Lothian et al., 2024). Although nature-like fishways show more promise in allowing fish passage across a broad range of species (Aronsuu et al., 2015; Silva et al., 2018), the presumed beneficial effect for some species still appears to be limited (Abersons et al., 2025).

Another alternative for river connectivity restoration is catching fish and transporting them over barriers (trap-and-transport), although this method is considered costly and labor intensive, and causes stress to the animals (Verhelst et al., 2021). Furthermore, not all individuals might be caught, and its success depends largely on environmental conditions and habitat quality (Aronsuu et al., 2019).

1.3.2 Uncovering fish movement patterns

If traditional methods to restore river connectivity are impossible or insufficient, alternative methods should be explored. One possibility is to create operational conditions that increase fishway efficiency, such as increased attraction flows or reduced velocities (Johnson et al., 2012). Another option is to temporarily shut off pumping stations or open barriers during periods of increased migration (Mouton et al., 2011; Griffioen et al., 2017; Silva et al., 2017a). However, to allow fishway, pump, or barrier regimes to act in concert with fish movements, one needs to be able to forecast the timing of migration peaks, which depends on seasonal and en-

vironmental factors. Therefore, a deeper understanding of fish behavior and their interactions with the environment is necessary. The following sections elaborate on various techniques for gaining knowledge on fish movement, behavior and migration.

1.3.2.1 Aquatic biotelemetry

Aquatic biotelemetry has emerged as one of the most widely used methods for monitoring fish movements, largely due to technological advancements over recent decades that have enhanced its practicality and accessibility (Hockersmith and Beeman, 2012; Hussey et al., 2015). Although costly (Brownscombe et al., 2022), this technique allows for the detailed and large-scale study of individual movements and locations, without the need for direct observation or recapture of fish, therefore offering major advantages over traditional approaches (Hockersmith and Beeman, 2012). It involves placing electronic devices in or on animals, after which these devices transmit data signals to fixed receiver stations or satellites (i.e., passive methods), or to receiver stations following the individual (i.e., active methods) (Hussey et al., 2015; Brownscombe et al., 2019). To unlock the true potential of this technology, various national and international telemetry projects have been established, such as the permanent Belgian acoustic receiver network (Reubens et al., 2019) and the European Tracking Network (Abecasis et al., 2018).

The main biotelemetry methods applied in freshwater include acoustic telemetry (acoustic signals), radio telemetry (radio signals) and passive integrated transponder or PIT telemetry (inductive electromagnetic signals) (Verhelst et al., 2023). Telemetry signals are unique to the individual, and locations are derived from the location of the tag relative to the receiver. If the device contains sensors, environmental conditions or physiological state can be measured and transmitted as well (Hockersmith and Beeman, 2012; Hussey et al., 2015). Since station-based, passive acoustic telemetry (Figure 1.3) appears to be the most popular method in fish movement studies (Brownscombe et al., 2022) and is the most relevant to this thesis (Chapter 3), it will be the focus of this section.

An important advantage of acoustic telemetry over radio or PIT telemetry is the possibility to use it in seas and estuaries, as radio and PIT signals are weakened by saline waters and acoustic signals are not (Verhelst et al., 2023). However, acoustic and radio tags rely on internal batteries, which make them relatively large compared to PIT tags (Verhelst et al., 2023). Consequently, acoustic and radio tags have a limited lifespan and only allow the study of individuals that are sufficiently large or at a specific life stage. Furthermore, the performance of acoustic telemetry is rather poor in turbulent conditions compared to radio telemetry (Hockersmith and Beeman, 2012).

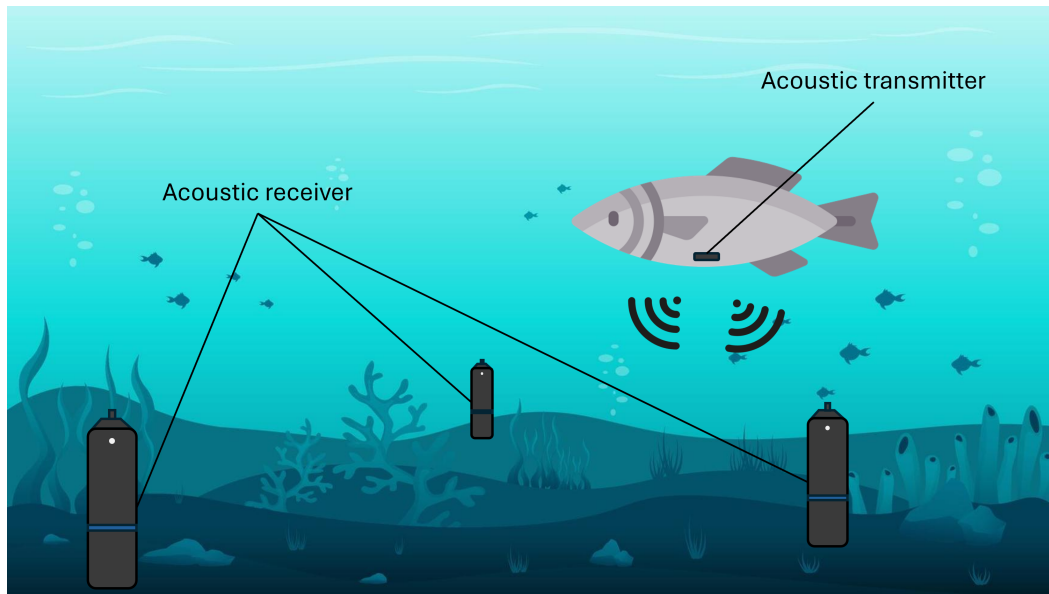


Figure 1.3: Illustration of the mechanism of station-based, passive acoustic telemetry.

If an individual is detected by a stationary acoustic receiver, it is located within the detection range of that receiver. If multiple receivers are placed in a compact grid such that their detection ranges overlap, the location can be precisely determined using triangulation (Brownscombe et al., 2019). If receivers are organized in a line and detection ranges do not overlap, the exact position becomes uncertain since the detected individual might be located anywhere within the spherical detection area of the receiver. Although the latter approach is less precise, it is more commonly used, and is suitable for mapping large-scale movements and habitat identification (Brownscombe et al., 2019).

The detection range of an acoustic receiver depends on various environmental factors (Brownscombe et al., 2020), such as the tidal cycle, water velocity, water depth and wind speed (Bruneel et al., 2023). Although they are often not considered in acoustic telemetry studies, detection ranges are essential for data interpretation and receiver network design (Kessel et al., 2014). In fact, false or even contradictory conclusions are possible depending on whether or not the detection range is taken into account, due to correlations between detection efficiency and environmental variables (Payne et al., 2010).

1.3.2.2 Other techniques

An interesting alternative to biotelemetry is biologging, which relies on tags carried by fish, and allows for continuous environmental and migrational data collection over larger spatial and temporal scales. To retrieve logged data, tags send a signal to the Argos satellite system when surfacing, or need to be manually recovered

after washing ashore (Cooke et al., 2012). However, their applications are limited, as biologgers are relatively large and expensive, and data retrieval can be difficult (Verhelst et al., 2023).

Methods for understanding fish movement other than electronic tracking include observation and interception (e.g., mark-and-recapture), analysis of environmental DNA (eDNA), and otolith microchemistry. On the one hand, the spatial and temporal resolution of these methods is relatively low compared to electronic tracking techniques (Verhelst et al., 2023). On the other hand, advantages include the lower cost of mark-and-recapture, the fact that eDNA does not require fish capture, or the possibility to study fish of all life stages and sizes with these methods (Verhelst et al., 2023). Moreover, one method can be used to complement and reinforce another method, e.g. telemetry data might increase accuracy and precision of mark-and-recapture data (Jubb et al., 2023a; Badger et al., 2024).

2. An ancient traveler: the European river lamprey as a case study

Lampreys (order Petromyzontiformes) are among the oldest living vertebrates on Earth and have existed for over 360 million years (Gess et al., 2006; Xu et al., 2016). They belong to the Agnatha, an ancient group of jawless, primitive, fish-like vertebrates. Lampreys are characterized by their eel-shaped bodies, round sucker-like mouths, and seven pairs of breathing holes instead of gills. They lack jaws, scales, and pelvic fins, and their skeleton is composed of cartilage (Kelly and King, 2001). Although not strictly accurate in taxonomic terms, the word 'fish' will be used synonymously with 'lamprey' throughout this thesis.

The European river lamprey, *Lampetra fluviatilis* (Linnaeus, 1758), is a parasitic, anadromous species within the family Petromyzontidae. It migrates from marine to freshwater habitats to spawn. Its distribution is limited to European waters, ranging from southern Norway along the Baltic and North Sea coasts to the Atlantic shores of Britain, Ireland, France, and Portugal, and into the western Mediterranean along France and western Italy (Wilson and Veneranta, 2019). The river lamprey holds considerable ecological, scientific, cultural, and economic importance but faces multiple anthropogenic threats. As a result, it is protected under several European legislative frameworks, emphasizing the need for effective conservation strategies based on a sound understanding of its life cycle and behavior.

2.1 Ecology and role of the European river lamprey

2.1.1 Life cycle

The life cycle of the river lamprey is schematically presented in Figure 2.1. Adult river lampreys spawn in a nest known as a redd, which is usually an excavated, shallow depression in a riverbed consisting of sand and gravel. The eggs are fertilized externally and stick to the edge of the nest (Wünstel et al., 1996). They hatch after 15-30 days, depending on the water temperature (Maitland, 2003). After hatching, the larvae, also known as ammocoetes, drift downstream at night and burrow into soft silt beds (Maitland, 2003; Zvezdin et al., 2017). Ammocoetes are filter feeders and therefore they mainly consume fine particulate matter, such

as organic detritus and diatoms (Sutton and Bowen, 1994; Maitland, 2003). Larval burrows are typically found at the edges of rivers or behind obstructions, in slow flowing and shaded areas with sandy silt bottoms and accumulating organic matter (Maitland, 2003; Dawson et al., 2015).

The larval stage of a river lamprey lasts about 4 years, after which metamorphosis starts (Maitland, 2003). This process can be triggered by changes in water temperature and day length, and involves the development of a silvery color, functional eyes, a sucker mouth and the ability to osmoregulate (Manzon et al., 2015). The newly transformed, sexually mature and non-feeding adults, known as macrophthalmia, then begin their downstream migration towards the sea. Downstream movement is mainly nocturnal (Potter and Huggins, 1973) and primarily stimulated by increased discharge and water levels (Quintella et al., 2005; Pavlov et al., 2017; Baer et al., 2018), although decreasing temperatures can also have an effect (Dawson et al., 2015; Baer et al., 2018). In the Scheldt basin, downstream migrating lampreys are found between February and April, with a peak of macrophthalmia in February (Maes and Ollevier, 2005).

Once individuals enter the sea, their parasitic, adult life stage initiates. Adult river lampreys feed on fish tissue and blood. They attach their sucker-like mouth to their prey, and inflict wounds using their sharp rasping tongue and teeth. Additionally, the mouth of the river lamprey contains glands that secrete an anticoagulant, preventing blood clotting and dissolving muscle tissue (Kelly and King, 2001). Parasitic river lampreys feed on various fish species, including species that occur along the Belgian coast, such as herring (*Clupea* spp.) and flounder (*Platichthys flesus*) (Stevens et al., 2009). The adults remain parasitic for about 1-2 years, after which they stop feeding and begin their upstream spawning migration (Maitland, 2003).

The spawning migration is nocturnal (Maitland, 2003) and can be divided into three phases: (1) movement from the marine environment into rivers, (2) freshwater holding before spawning, and (3) upstream movement to reach spawning grounds (Clemens et al., 2010). The timing and extent of this migration appears to be highly variable, depending on location, environmental factors and river obstructions. In general, upstream migration in Europe occurs during the autumn and winter months (Moser et al., 2015). Based on cooling water samples from the Doel nuclear power plant, Maes and Ollevier (2005) report that adult river lampreys start their migration up the Scheldt River from October to January. Buysse et al. (2004) record migrating adults between December and May, in front of migration barriers in the Scheldt River near Ghent, Asper, and Oudenaarde.

The onset of spawning is primarily determined by water temperature, typically occurring when it reaches 10–11 °C (Kelly and King, 2001). In British rivers, spawning takes place between March and May (Kelly and King, 2001; Lucas et al., 2009). Before spawning, adults excavate shallow, oval nests at the tails of pools and glides

2. An ancient traveler: the European river lamprey as a case study

(Maitland, 2003) or before migration barriers (Kelly and King, 2001). River lampreys lose their negative phototactic behavior during spawning and can be seen equally often during the day and at night (Jang and Lucas, 2005). Spawning habitat requires water flowing through sand and gravel river bottoms. Furthermore, backwaters with silt beds for larvae should be in the vicinity of the spawning location (Maitland, 2003; Johnson et al., 2015). Adults spawn in groups, after which they move downstream and eventually die (Jang and Lucas, 2005; Johnson et al., 2015), thus completing their life cycle.

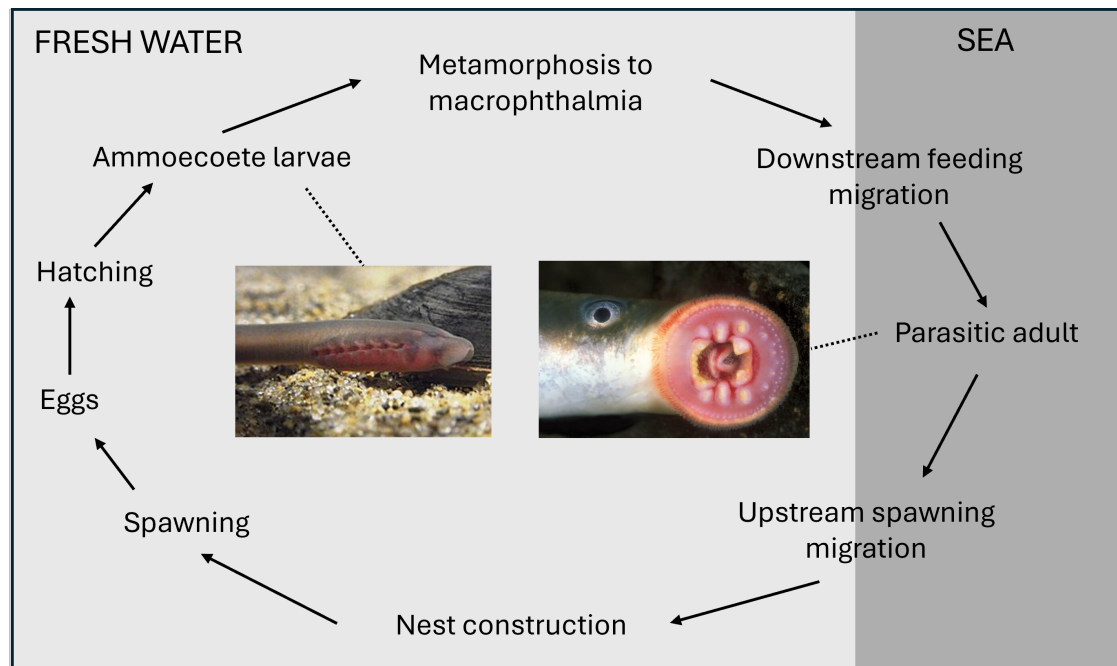


Figure 2.1: The life cycle of the European river lamprey, *Lampetra fluviatilis*. Left image from Loki Austanfell (2011). Right image from Ecopedia (n.d.).

2.1.2 Relevance

Lampreys play vital ecological roles. During nest building, adults act as ecosystem engineers by increasing habitat complexity and promoting the spread of pollution-sensitive benthic invertebrates (Hogg et al., 2014). For example, the digging activity of nest-building lampreys significantly alters the mean particle size of sediments (Sousa et al., 2012). The filter-feeding and burrowing larvae also engineer habitats, by oxygenating and softening the streambed, increasing particulate organic matter levels near the streambed, and altering microbial communities (Shirakawa et al., 2012; Boeker and Geist, 2016). Owing to their complex life cycle and sensitivity to habitat integrity, the river lamprey serves as an indicator species (e.g. in Water Framework Directive assessments) for good water quality, river connectivity and ecological functioning of estuaries (Breine et al., 2008).

Since larvae can make up a large fraction of the biomass in streams where they are abundant, they may serve as an important food source for various animals. This is especially the case during emergence from the nest or scouring events that dislodge them from their burrows (Close et al., 2002). Carcasses of post-spawning adults transfer marine nutrients to freshwater ecosystems, supporting food webs during nutrient-scarce periods (Nislow and Kynard, 2009; Weaver et al., 2018). A significant proportion of the carcasses can be transported to the riparian zone, where they serve as an important food source for riparian scavengers (Dunkle et al., 2020).

Beyond ecology, lampreys hold cultural and scientific importance. Pacific lampreys (*Entosphenus tridentatus*) are a traditional religious food source for Native American tribes in the mid-Columbia River Plateau (Close et al., 2002), while lampreys more broadly serve as model organisms in evolutionary and biomedical research due to their ancient evolutionary history, regenerative abilities and anticoagulant compounds (York et al., 2019; Hanel et al., 2022). Economically, lampreys remain valuable in various fisheries for consumption and as bait (Kelly and King, 2001; Almeida et al., 2021). Despite the relevance of native lamprey species, their reputation has often been overshadowed by that of their invasive counterparts (Lucas et al., 2021). For example, invasive sea lampreys in the Laurentian Great Lakes caused major fishery collapses by the 1950s, and shifted research focus toward control efforts (Kelly and King, 2001; Lucas et al., 2021; Hanel et al., 2022).

2.1.3 Threats and conservation

Although river lampreys used to be widespread throughout Europe, their numbers have declined in recent decades due to anthropogenic pressures (Kainua and Valtonen, 1980; Ojutkangas et al., 1995; Kelly and King, 2001; Maitland, 2003; Mateus et al., 2012; Zvezdin et al., 2023). Consequently, the European river lamprey is considered a ‘near threatened’ species by the European IUCN Red List (Ford, 2024) and is listed in Annexes II (and V) of the EU Habitats Directive. Lucas et al. (2021) consider habitat fragmentation, habitat degradation, pollution and exploitation to be the main threats to lampreys. Conservation priorities therefore include, but are not limited to, mapping populations, enhancing water and habitat quality, and mitigating the effect of barriers.

Migration barriers are considered the most important problem for the recovery and conservation of the river lamprey in Flanders (Maes and Ollevier, 2005; Stevens et al., 2009). Unlike the European list, the Flemish IUCN Red List considers the river lamprey to be ‘vulnerable’ (Verreycken et al., 2014), suggesting that the species is regionally more threatened than at the European scale. For river lamprey conservation in Flanders, Stevens et al. (2009) suggest to prioritize resolving migration barriers and restoring larval and spawning habitat.

2.2 Factors influencing upstream migration

2.2.1 Obstacles and individual characteristics

River barriers undoubtedly affect the upstream migration of river lampreys by delaying or even halting it (Lucas et al., 2009; Mateus et al., 2012). The success of passing these barriers depends not only on environmental conditions (e.g., river discharge, Section 2.2.3) and the presence of fishways, but also on the characteristics of individual lampreys. For example, Keefer et al. (2009a) show that Pacific lampreys with a large body size migrate further into the river system, and are two to four times more likely to pass barriers compared to smaller individuals. Furthermore, males tend to arrive earlier at the spawning site (Kelly and King, 2001; Johnson et al., 2015), indicating a difference in migration timing between sexes.

2.2.2 Larval pheromones

Although lampreys do not necessarily have a homing instinct (Bergstedt and Seelye, 1995), larvae of the sea lamprey *Petromyzon marinus* release pheromones that strongly attract adults (Wagner et al., 2009; Vrieze et al., 2010). Vrieze et al. (2011) state that this pheromone plume may be important in initially finding the river mouth along the shoreline. Larvae of the river lamprey produce the same pheromones (Fine et al., 2004) and adults prefer streams with ammocoetes (Gaudron and Lucas, 2006), indicating the same chemotactic behavior (i.e., attraction to certain molecules) in the river lamprey.

2.2.3 Flow regime and velocity

Rheotactic behavior (i.e., attraction to water flows) during migration is frequently described in literature. Increased river discharge generally leads to an increase in migration activity (Masters et al., 2006; Aronsuu et al., 2015; Kerr et al., 2025) and the success of passing barriers (Lucas et al., 2009; Foulds and Lucas, 2013; Silva et al., 2017a; Davies et al., 2022; Lothian et al., 2024). The same holds for increased water levels (Kelly and King, 2001; Davies et al., 2021; Lothian et al., 2024). Binder et al. (2010) hypothesize that this behavior ensures that lampreys can reach sheltered spawning grounds or pass difficult areas more easily. Although increased flow rates are needed to stimulate migratory behavior, too high flow rates make access to spawning grounds difficult and may reduce migration success (Masters et al., 2006; Kemp et al., 2010). This is likely related to water velocity, as the maximum swimming speed of river lampreys lies between 1.75 and 2.12 m/s (Russon and Kemp, 2011).

Movements of migrating adults become more directed and persistent with increased flow velocities (>0.1 m/s) (Kerr et al., 2023). Using hydrodynamic flow models in combination with bathymetric mapping and fine-scale acoustic telemetry, Griffin et al. (2025) demonstrate that sea lampreys follow paths along the thalweg, typically the deepest and fastest-flowing part of the river. These paths prove to be the most energy-efficient, yet sufficiently safe from nocturnal predators. Kerr et al. (2025) show that sea lampreys not only prefer routes with low turbulence and high velocity, but also rely on their short-term memory for navigation, as their orientation depends on the mean flow direction they recently experienced, rather than the present direction.

At the river mouth, the plume of larval pheromones becomes wider and thicker as the flow rate increases (Vrieze et al., 2011), making it easier to detect. This indicates a possible interaction between the known chemotactic and rheotactic behaviors. Although higher flow rates can also dilute the pheromone plume, which can weaken its effect, Wagner et al. (2009) demonstrate that differences in pheromone concentration only become relevant when they change by an order of magnitude. As the propagation of the plume is determined by the branching pattern of the stream, the structure of the river network itself can influence the migratory behavior of adults, and consequently the occurrence of larvae (Neeson et al., 2011b).

Wind speed and direction may also have an important effect on migration success. During onshore wind events, more lampreys migrate into the rivers, possibly due to the formation of currents that speed up migration or increase river plume dispersal (Aronsoo et al., 2015). However, tidal currents may not play a significant role in the behavior of *L. fluviatilis*, as Silva et al. (2017b) report no evidence of selective tidal stream transport in migrating lampreys within the Ouse estuary.

2.2.4 Temperature

Besides river discharge, temperature, rather than photoperiod, appears to be one of the main factors that trigger upstream migration (Moser et al., 2015). This temperature-dependent behavior might ensure that lampreys reach the spawning grounds when river temperatures are suitable for reproduction (Binder et al., 2010). In British and Finnish rivers, temperature ranges of roughly 2-16°C have been documented during migration periods (Masters et al., 2006; Aronsoo et al., 2015), although most activity might occur below 8-12°C (Lucas et al., 2009; Baer et al., 2018).

However, the effect of temperature within the suitable range for migration is not very clear. Some studies report that, contrary to discharge, water temperature itself does not have a significant influence (Masters et al., 2006; Foulds and Lucas, 2013; Aronsoo et al., 2015). Others report that higher water temperatures (within the

appropriate range) increase migratory activity (Silva et al., 2017b) and the success of passing barriers (Lothian et al., 2024). Moreover, the magnitude and rate of temperature change may also play a role. As rivers cool faster and more strongly, migration activity can be stimulated (Aronsuu et al., 2015), which is a behavior opposite to that of sea lampreys (Binder et al., 2010).

2.2.5 Light intensity

Lampreys exhibit negative phototaxis (i.e. aversion to light) and are generally considered nocturnal during their spawning migration (Maitland, 2003). However, Silva et al. (2017b) observe that river lampreys migrate in the Ouse River both during the day and at night. Although the observed migration rate is higher at night, this contradicts strictly nocturnal behavior. The authors suggest high turbidity reducing light intensity as a possible explanation. River lampreys can also lose their nocturnal behavior during their search for a passage through obstacles (Lothian et al., 2024).

At increased flows, the water level generally rises and the water becomes more turbid, reducing light intensity. This may be another possible explanation for the increased migration activity at high river discharge (Aronsuu et al., 2015; Lothian et al., 2024). Moonlight intensity appears to be negatively correlated with the number of lampreys passing through the river. Cloud cover weakens this negative effect, suggesting that migration behavior is effectively influenced by moonlight illumination rather than the lunar cycle. Additionally, river lampreys tend to stop their migration next to artificial light sources, such as illuminated bridges (Aronsuu et al., 2015).

3. Materials and methods to investigate lamprey migration

The management of diadromous fish species in fragmented river landscapes requires detailed knowledge on the impact of water regulating structures on migration, as well as on the passage efficiency across migration barriers (Verhelst et al., 2021; Mawer et al., 2023). Therefore, the main objective of this master's dissertation is to elucidate the effects of environmental factors and migration barriers on the upstream migration of the diadromous European river lamprey in fragmented Flemish rivers. For this purpose, acoustic telemetry constitutes a powerful approach (Hussey et al., 2015). However, its effective application requires a well-defined acoustic receiver network, carefully executed tagging procedures, and transparent data processing and analysis.

This chapter discusses the data collection, processing and analysis steps used in this study to (1) characterize the effect of water regulating structures on migration success and speed, (2) uncover the relation between environmental drivers, water regulating structure operation and passage success across shipping lock complexes, and (3) identify the environmental drivers of migration speed in unobstructed river sections.

3.1 Study area

The study area comprises a 43 km stretch of the Upper Scheldt River, extending from Avelgem at the Walloon border to downstream of the tidal locks in Merelbeke, where river lampreys were caught and released (Figure 3.1). This release site in Merelbeke is the most upstream location of the Scheldt River that is influenced by the tides. Since only upstream migration is investigated, stretches further downstream are not considered. Tributaries of the Scheldt are also not taken into account, as the receiver network only covers the main stream. During their upstream migration, river lampreys encounter four shipping lock complexes, potentially acting as fish migration barriers.

The first and most downstream shipping lock complex is located in Merelbeke, close to the release location. Lampreys can follow two possible routes to pass this shipping lock complex: (A1) the main lock complex, which consists of two weirs and

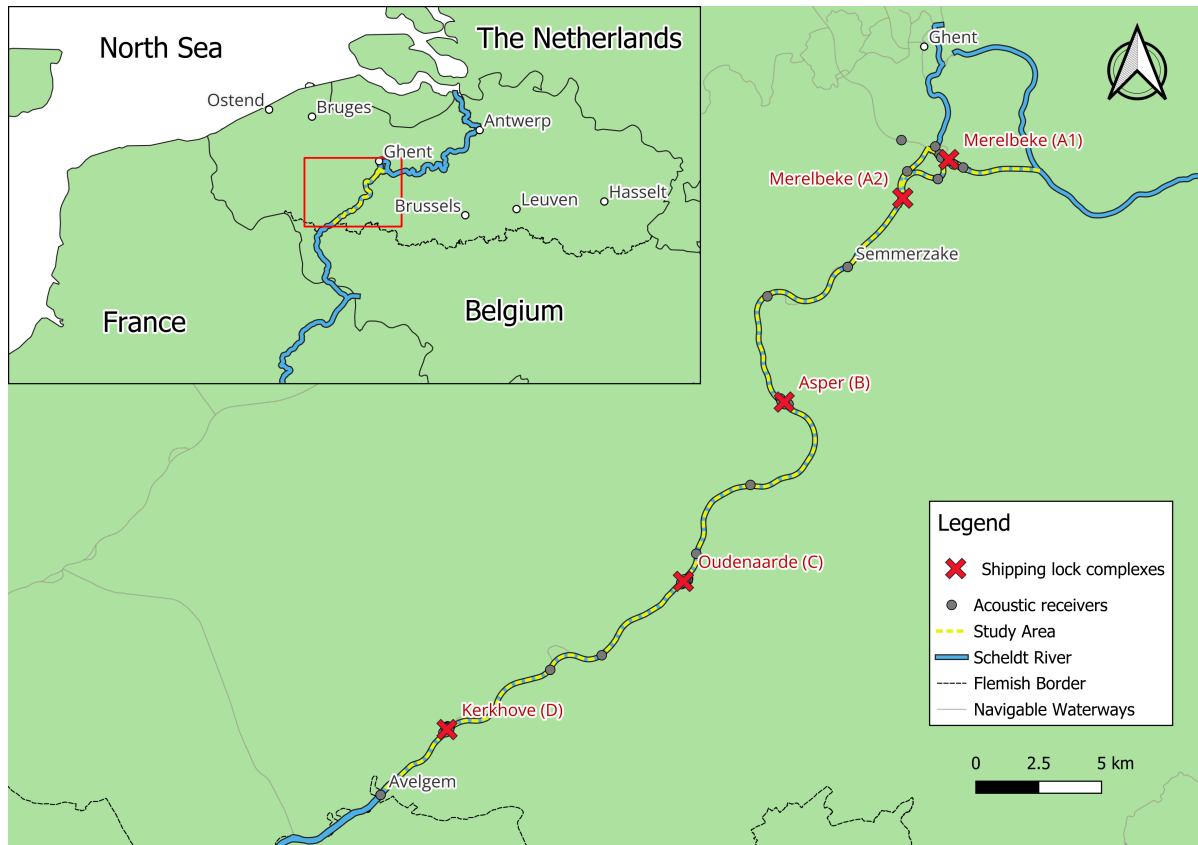


Figure 3.1: Study area and shipping lock complexes, each shown by the city in which they are located, followed by a unique letter code (A1/A2, B, C, D). Note that in Merelbeke, lampreys can pass through the shipping lock complex itself (A1) or via an old meander of the Scheldt containing only two weirs (A2). Grey points represent the receiver network in the study area.

two navigation locks, allowing boats to pass through, and (A2) the ‘tidal branch’, an old unnavigable meander of the Scheldt, which is blocked by two weirs. The second shipping lock complex (B) appears in Asper, about 16 km upstream of the lock complex in Merelbeke, and includes one navigation lock and two weirs. Although this section contained a fish passage in the past, the passage is closed down and therefore not functional during the study period. The third migration barrier (C) occurs 11 km further upstream, in Oudenaarde, and consists of one navigation lock, two weirs, and one functional fish passage. The final shipping lock complex (D) is located in Kerkhove, another 12 km further upstream. It comprises one navigation lock, a functional fish passage, and two weirs. An overview of the different shipping lock complexes in the study area is shown in Table 3.1.

3. Materials and methods to investigate lamprey migration

Table 3.1: Overview of shipping lock complexes and their associated structures in the study area. Numbers of weirs, locks and fishways present are reported. The distance column corresponds to the distance (km) from the lamprey release location.

Complex ID	Location	Distance (km)	Weirs	Locks	Fishways
A1	Merelbeke	0	2	2	0
A2	Merelbeke	3	2	0	0
B	Asper	16	2	1	0
C	Oudenaarde	27	2	1	1
D	Kerkhove	39	2	1	1

3.2 Tagging procedure

In December 2024, 20 river lampreys were caught directly downstream of the weirs in Merelbeke using double fyke nets. During November and December 2025, another 30 river lampreys were caught at the same location. The individuals were first sedated by placing them in a water basin with 0.3 mL/L clove oil (Figure 3.2a). After sedation, total length (mm) and body weight (g) were measured. Individuals were suitable for tagging if the weight of the acoustic transmitter was less than 2% of the individual's body weight (> 95 g).

Acoustic transmitters (6×21 mm, weight in air 1.9 g, random delay around 50 s, life time 8 months, power output 137 dB, frequency 69 kHz) from Thelma Biotech, Norway, model 2LP6, were implanted using a small abdominal incision (Figure 3.2b). During tagging, 21 males and 29 females were identified by inspecting their gonads. The incisions were closed using a biodegradable thread, after which the lampreys were placed in an oxygenated recovery basin. After recovery, the tagged individuals were released downstream of the Merelbeke weirs near their capture location.

3.3 Acoustic receiver network

In 2014, Ghent University, the Research Institute for Nature and Forest (INBO) and the Flanders Marine Institute (VLIZ) initiated a collaboration to permanently track movements of fish throughout Belgian aquatic and marine systems using passive acoustic telemetry. This resulted in the Permanent Belgian Acoustic Receiver Network (PBARN) (Reubens et al., 2019). In this study, PBARN was used to track river lampreys during their upstream migration. Throughout free-flowing river sections, the detection range of receivers was assumed to cover the full channel width (Bruneel et al., 2023). Therefore, using a single receiver to check passage in these sections was considered appropriate. At each shipping lock complex, multiple receivers were used: two receivers per barrier type (downstream and upstream of



(a) River lamprey in the sedation basin.



(b) Abdominal incision for transmitter insertion.

Figure 3.2: Two steps of the tagging procedure.

the obstruction), and three receivers per fishway (the downstream, middle, and upstream part of the passage). One important exception was location A2, where no receivers were present upstream of the weirs. Figure 3.3 shows the location of shipping lock complex C in Oudenaarde and the corresponding barrier and receiver arrangement in detail.

In total, the study area contained 41 passive acoustic receivers of various models (the TBR800 from Thelma Biotel, Norway, and the VR2W and VR2Tx from Innovasea, USA). All receivers operated at 69 kHz.

3.4 Data acquisition and processing

3.4.1 Raw acoustic telemetry data and environmental data

The acoustic receivers were collected and data was extracted two to three times a year, after which the data was uploaded to the European Tracking Network (ETN). The raw acoustic data included individual detections with their respective timestamps, transmitter ID, receiver ID, and receiver spatial coordinates (WGS 84). The

3. Materials and methods to investigate lamprey migration



Figure 3.3: Aerial photo of shipping lock complex C in Oudenaarde, with marked river constructions and acoustic receivers. The relative position of upstream and downstream receivers is indicated in their names ('DS' for downstream, 'MID' for middle section, 'US' for upstream).

entire data set contained 676 678 detections, with lampreys being tracked from 4 December 2024 to 19 April 2026.

For analysis, the raw data were first downloaded from the ETN and subsequently preprocessed. Preprocessing included adding individual metadata (species, sex, length, and weight) and calculating trajectory characteristics (direction, distance traveled and average swimming speed). Furthermore, detections were merged in the case of multiple consecutive observations at the same receiver within an hour (resulting in 'at-receiver' residence times). The at-receiver residences resulted in an 'arrival' and 'departure' timestamp for each observation. Given the focus on upstream migration, downstream return movements after spawning or abandonment were excluded from the analysis. In addition, observations of deceased individuals were removed.

Environmental data timeseries were recovered from the Hydrological Information Centre (HIC) through its web service (<https://hicws.vlaanderen.be>), and included discharge (m^3/h), oxygen concentration (mg/L), rainfall (mm), water temperature ($^{\circ}\text{C}$) and water level (m). Additional rainfall timeseries from the Flanders Environment Agency (VMM) were retrieved using the R-package `waterInfo` (Van Hoey,

2025). Since the absolute discharge and water level values depended on the distance to the river mouth and we were only interested in deviations, these variables were scaled. For discharge and water level, only measuring stations outside the tidal zone were taken into account. Conversely, to determine the tidal phase (ebb or flood), the first order derivative of the water level was calculated for the nearest monitoring station in the tidal zone downstream of the release location.

The photoperiod (h) and moment of the day (dawn, day, dusk and night) corresponding with detection timestamps were determined using the R-package `suncalc` (Thieurmél and Elmarhraoui, 2022). ‘Dawn’ corresponded to the times from the beginning of astronomical twilight till sunrise, ‘day’ to the times between sunrise and sunset, and ‘dusk’ to the times from the sunset till the end of astronomical twilight. The photoperiod was defined as the time difference between sunrise and sunset.

3.4.2 Weir operational data

Operational data of the weirs at each shipping lock complex location were retrieved through Flanders Hydraulics Research, and included the water level directly up- and downstream of the weirs, and the top and bottom valve positions. Weir overflow (Q_k) and underflow rates (Q_s) in m^3/s could be calculated from these data using (Flanders Hydraulics Research, pers. comm., 2026):

$$Q_k = C_k B_s h_k^{3/2}, \quad (3.1)$$

$$Q_s = C_s B_s h_s \sqrt{2g (H_o - H_a)}, \quad (3.2)$$

where C_k [-] and C_s [-] denote the flow coefficients for overflow and underflow, equal to 1.9 and 0.7, respectively, B_s is the horizontal width of a weir, equal to 12.5 m, h_k [m] is the top valve position, relative to the water level immediately upstream of the weir, h_s [m] is the bottom valve position, relative to the bottom of the weir channel, H_o and H_a [mTAW] are the water levels directly up- and downstream of the weir, respectively, and g is the gravitational acceleration on Earth (9.81 m/s^2). The physical meaning of these parameters, and the different operational scenarios under which the weirs can operate, are schematically represented in Figure 3.4.

During periods of high river discharge an additional scenario could take place in Merelbeke (only A1), in which the weirs were lifted from the stream, therefore temporarily creating free-flowing conditions. In 2002, these conditions existed for at least 4 h per day, during 33 days per year (Buysse et al., 2008). During the study period, free-flowing conditions were assumed to occur if the calculated weir over- and underflow rates clearly ‘jumped’ to rates above $200 \text{ m}^3/\text{s}$. These calculated values were considered unrealistic for weir flow rates, since the yearly 99th percentile

3. Materials and methods to investigate lamprey migration

discharge of the Upper Sea Scheldt itself fluctuates around 200 m³/s (Nicolai et al., 2023).

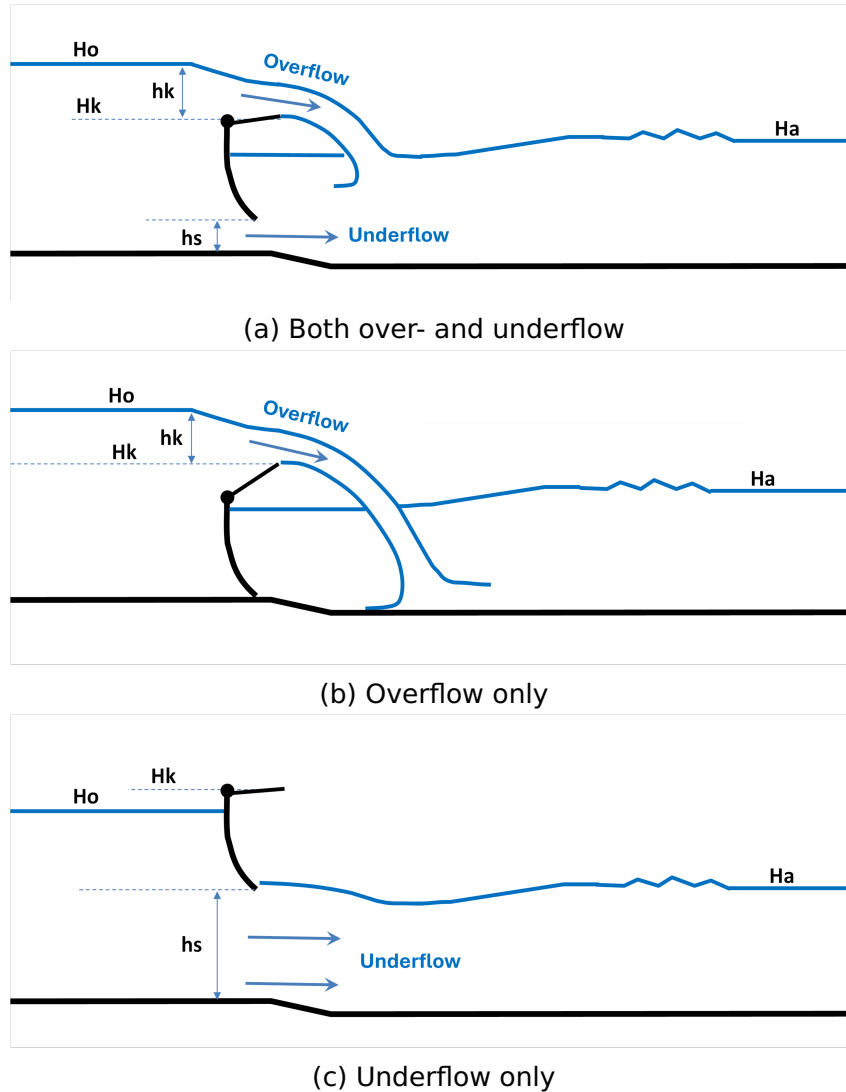


Figure 3.4: Schematic overview of a weir structure and its operating conditions, adapted from Flanders Hydraulics Research (pers. comm., 2026). The weir can operate under three scenarios: (a) exerting both over- and underflow, (b) exerting only overflow, and (c) exerting only underflow. H_o and H_a [mTAW] represent the upstream and downstream water levels, respectively, H_k [mTAW] is the absolute upper valve position, h_k [m] is the relative upper valve position, and h_s [m] is the relative lower valve position.

3.4.3 Behavioral data characterization

3.4.3.1 Movement characteristics

To identify the effects of shipping lock complexes on migration characteristics, the specific routes that river lampreys followed through these complexes (i.e., via navigation locks, weirs or fishways) were reconstructed. An overall shipping lock com-

plex ‘migration speed’ was defined using the time between the first most downstream detection and the last most upstream detection at that shipping lock complex, and the corresponding distance. This speed represents an average, whereby the individual can be in three behavioral states: rest, search for a passage (‘searching’), and actually pass an obstacle or swim through a fishway (‘crossing’). Here, only searching and crossing states were considered, since resting cannot be distinguished from the searching state in the data.

An individual was assumed to be searching for an opening when the data showed repeated detections downstream of a shipping lock complex. Conversely, a crossing event was assumed to take place when an individual was detected downstream of a shipping lock complex, followed by the next observation immediately upstream of that shipping lock complex. Due to overlapping detection ranges, individuals could be detected simultaneously at both downstream and upstream receivers during crossing (which we refer to as ‘ping-pong’ detections). At shipping lock complex location A2, searching and crossing states could not be determined due to an unsuitable receiver arrangement.

In addition to movement behavior at shipping lock complexes, migration in unobstructed river sections was characterized. Here, free migration speed was calculated as the distance between the departure and arrival of two subsequent receivers divided by the migration time. Thus, overall, three types of behavioral data were distinguished: (1) shipping lock complex migration speeds, (2) searching and crossing times at specific barriers, and (3) unobstructed migration speeds.

3.4.3.2 Merging environmental variables and weir data

To merge environmental data with migration speeds over shipping lock complexes and unobstructed river sections, a temporally aggregated value was calculated for each observation over the entire periods during which these speeds were defined, as described above. For searching behavior, it was possible to construct a long data format, such that the high temporal resolution of environmental variables was retained: the entire searching period was divided into hourly intervals and an aggregated value was calculated for each hour. For rainfall, the aggregation corresponded to the median, since precipitation data were skewed and contained extreme outliers (i.e., the majority was equal to 0 mm, but some extreme peaks occurred). Other continuous variables were aggregated using the mean, while the mode was used for categorical data.

For crossing behavior, however, it was difficult to rigorously define aggregation time periods for each barrier. The absence of an upstream receiver at location A2 in particular made it impossible to determine an exact crossing time, even though this was an important route through which 37% of the crossing individuals passed.

3. Materials and methods to investigate lamprey migration

Furthermore, the crossing times defined at other locations were highly dependent on the layout of the receiver network, for instance due to the occurrence of 'ping-pong' detections. Therefore, assuming that actual crossing events occurred during a limited time period, a predefined 30-minute time interval was chosen to link environmental variables to crossing events. For shipping lock complex A2, this was 30 minutes after the last downstream detection of the barrier, while for the other locations it was 30 minutes before the first upstream detection of the barrier. However, fish passages differed fundamentally from other river constructions, and crossing events over them took a relatively long time (up to 42 hours). To account for this and at the same time avoid an overrepresentation of fishway presence, the aggregation there occurred over the entire crossing period rather than over a 30-minute interval or long format.

Next to the temporal aggregation, continuous environmental data required a spatial weighting procedure. Each observation in the behavioral data frames always contained a starting and an ending timestamp, corresponding to their own receivers. Therefore, the point in space to which the environmental variables were linked was located along the thalweg, exactly halfway between these two receivers. The precipitation was calculated through inverse distance weighting with respect to this halfway point, using the median values of different measuring stations over the time period discussed.

Other continuous environmental variables were linked to the telemetry datasets using the following procedure. Inverse distance weighting (along the thalweg) was performed with the nearest measuring stations downstream and upstream of the halfway point, using the averages of both stations over the time period in question. If there was no measuring station downstream, or no measuring station upstream, the data from the single other station was used. The linking process resulted in a data frame with an average environmental variable for each observation over the time periods discussed above. Categorical data did not require spatial weighting, as tidal phase was measured at only one station, and circadian phase was always determined at the average of the coordinates of all receivers in the study area.

Unlike environmental variables, weir operation data did not require spatial weighting. The relevant weir that corresponded to the location at which the lamprey was observed was selected, its data was temporally aggregated over the discussed time periods using the mean, and this aggregated value was subsequently merged to the observation. For analysis, the weir over- and underflow rates were normalized to a threshold value of 200 m³/s.

3.5 Data analysis

The three research questions regarding lamprey behavior were answered using three different generalized linear mixed models (GLMMs), in which the transmitter ID always served as a random effect (only intercept), reflecting individual variability. The R-packages nlme (Pinheiro et al., 2026) and glmmTMB (Brooks et al., 2017) were used for the regression analysis. In some cases, random intercept variance was close to zero, indicating singularity (i.e., negligible individual variability compared to residual variability). However, since the main purpose of these models was to estimate the significance of the fixed effects while still accounting for individual interdependency, these singular fits were retained.

If multiple models with different sets of predictors were possible, the best performing model was selected using the Akaike Information Criterion (AIC) (Akaike, 1974), following a backward stepwise selection (Bolker et al., 2009; Zuur et al., 2009). This procedure began with a ‘full’ model containing all variables, after which ecologically meaningful submodels were constructed, and the ones with the lowest AIC were retained. To validate each of the constructed models, relevant assumptions were checked (linearity, normality of residuals, homoscedasticity, independence of residuals, and normality of random effects). Multicollinearity among predictors was identified using the correlation matrix, with correlations greater than 0.7 removed from the model structure (Dormann et al., 2013), and the choice of the removed variable based on expert knowledge. In addition, after fitting, the overdispersion ratio and variance inflation factors were checked using the performance-package (Lüdtke et al., 2021), to respectively check expected variance structure and identify strong correlations between optimal predictors. All statistical tests were performed on the 5% significance level.

3.5.1 The effects of shipping lock complexes on migration speed

To describe how the presence of shipping lock complexes affected the average migration speed, a Gaussian GLMM with an identity link was used. Since this model was primarily intended to detect statistically significant differences between average migration speeds in unobstructed stretches and across shipping lock complexes, while accounting for consecutive, dependent observations of the same individual, no environmental variables were included. The model therefore only accounted for the presence of shipping lock complexes and fish passages. The variance in migration rate differed drastically between different predictor categories. Therefore, to avoid severe heteroscedasticity, the migration speed response variable was log-transformed.

3.5.2 Relation between environmental conditions, weir operation and shipping lock complex passage success

Success in crossing barriers was modeled using a logistic GLMM with a logit link, where the probability of crossing a barrier was the response variable. Observations in which individuals were searching for an entrance were assigned a response value of 0, while observations in which individuals actually crossed the barrier corresponded with a response value of 1. No correlations between environmental variables exceeded the 0.7 threshold, leading to an initial set of predictors that included water temperature, discharge, oxygen concentration, water level, rainfall and photoperiod. Regarding the characteristics of the shipping lock complexes, the presence of fish passages and the operating regimes (underflow rates, overflow rates and free-flowing conditions) of the relevant weirs were taken into account as predictors. The model was constructed such that, under free-flowing conditions, over- and underflow rates did not contribute to passage success, as their calculated values had no physical meaning anymore. In addition, the tidal phase at location A1/A2, the circadian phase at all shipping lock complexes, and the presence of free-flowing conditions specifically at location A1 were checked for any significant effects on passage success.

3.5.3 Environmental drivers of free migration speed

To investigate the effect of various environmental variables on the average migration speed in unobstructed river sections, a Gaussian GLMM with an identity link was used. Here, the migration speed (m/h) served as the response variable. The initial set of predictor variables included water temperature, discharge, oxygen concentration, water level, rainfall and photoperiod. Naturally, several variables were mutually correlated. For example, photoperiod was positively correlated with temperature ($\rho = 0.579$) and negatively correlated with discharge ($\rho = -0.479$). Furthermore, oxygen concentration was correlated with discharge and photoperiod ($\rho = -0.661$ and 0.529 , respectively). However, given the threshold value of 0.7, no predictor variables were removed prior to model selection.

4. Insights into the spawning migration in the Scheldt River

As discussed in Chapter 3, the river lamprey was tracked during its upstream spawning migration through the fragmented upper Scheldt River using acoustic telemetry. This chapter reports the results derived from the analysis of these acoustic telemetry data, in which the relationships between movement patterns, environmental data and barrier operation were examined, with the aim of identifying the impact of water regulating structures and environmental factors on the spawning migration of the river lamprey. In particular, three research questions are answered:

1. How does the presence of water regulating structures affect migration success and speed (Section 4.1 and 4.2.1, respectively)?
2. How do environmental conditions and water regulating structure operation regimes affect passage success (Section 4.2.2)?
3. How do environmental conditions affect migration speed in unobstructed river sections (Section 4.3)?

4.1 Individual characteristics and general migration patterns

Average body weight and length for all tagged lampreys were respectively 95.5 ± 12.8 g and 379.8 ± 16.5 mm. For the 2024 batch, these were 100.6 ± 15.7 g and 385.4 ± 19.4 mm, while for the 2025 batch, these were 92.1 ± 9.2 g and 376.1 ± 13.4 mm, respectively. The total body weight and length of an individual appeared to be strongly correlated ($\rho = 0.82$), and both were significantly greater in females than in males (Wilcoxon rank sum test: $p = 0.006$, and $p = 0.018$, respectively).

Of the 50 tagged individuals, 54% ($n = 27$) were able to pass the first shipping lock complex in Merelbeke (A1 or A2). All lampreys passed through weir structures, except four, which passed through the navigation lock. The next shipping lock complex in Asper (B) was penetrable for only 12.5% ($n = 3$) of the individuals that reached it, with all three lampreys passing through the navigation lock. However, these three individuals all managed to pass the subsequent shipping lock

complexes in Oudenaarde (C) and Kerkhove (D), and remarkably they all did so via the fish passages (Figure 4.1).

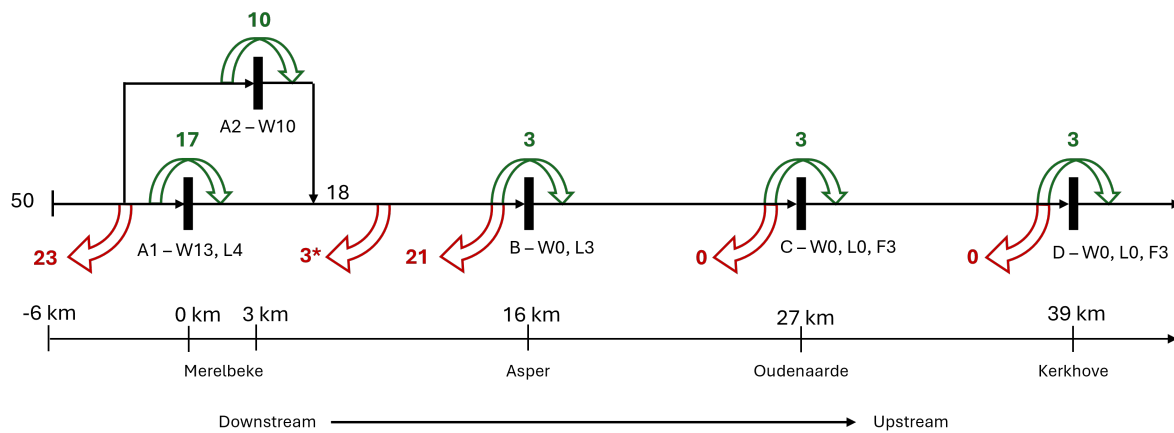


Figure 4.1: Schematic representation of the migration routes followed by the 50 tagged lampreys, with distance to the release location along the river (km) shown below. The thick vertical bars indicate shipping lock complexes (Merelbeke, Asper, Oudenaarde, and Kerkhove). Below each complex is a code: the first symbol represents the shipping lock complex itself (A1/A2, B, C, or D), and the following symbols indicate the type of barrier (W for weirs, L for navigation locks, F for fish passages), each immediately followed by the number of individuals that passed the shipping lock complex via this type of barrier. Furthermore, red arrows indicate that individuals could not pass, while green arrows indicate that they could. If there is a '*' next to a number, migration was not stopped by shipping lock complexes, but by an unknown cause.

Note that these results were based on two separate lamprey batches (i.e., the first 20 individuals captured and released in 2024, and the last 30 captured and released in 2025) that differed strongly from each other. In 2024-2025, Merelbeke was passable for 18 of the 20 tagged individuals (90%), while Asper was passable for only 3 of the 15 individuals that reached it (20%). However, in 2025-2026, Merelbeke was passable for 9 of the 30 tagged individuals (30%), and Asper was not penetrable for a single individual.

Success in passing the Asper shipping lock complex (B) barriers appeared to be significantly related to an individual's length (Wilcoxon rank sum test: $p = 0.017$), with larger lampreys crossing more frequently (Figure 4.2). Although this pattern was not significant for body weight (Wilcoxon rank sum test: $p = 0.094$), the same effect was expected due to its correlation with the total length. No significant relation between passage success and length or weight was present for the Merelbeke complex (A1/A2) (Wilcoxon rank sum test: $p = 0.204$ and $p = 0.188$, respectively). Since the passage in Oudenaarde (C) and Kerkhove (D) was 100% successful, no correlation could be established between the success of passage and body size.

4. Insights into the spawning migration in the Scheldt River

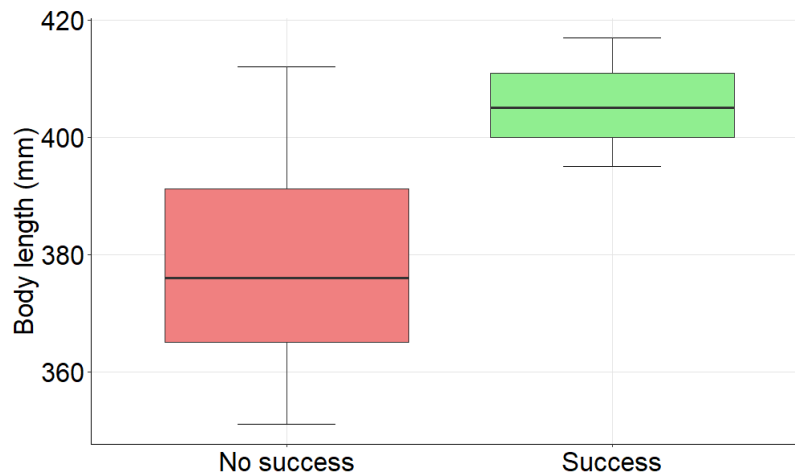


Figure 4.2: Boxplots showing the total body length (mm) for individuals not successful (red, $n = 21$) and successful (green, $n = 3$) in passing the Asper shipping lock complex.

The majority of the lampreys that abandoned their migration traveled considerable distances downstream along the Scheldt River on their return. One lamprey even reached the Westerschelde (120 km downstream from the release site). The data did not reveal whether these movements were the result of active swimming or passive drifting, nor did they indicate whether these retreating individuals survived or not.

Remarkably, however, after abandoning their migration at the shipping lock complex near Merelbeke, three individuals returned, swam into a different river system (the Rupel and the adjoining Nete) and migrated approximately between 14 and 27 km upstream to a point at least 77 to 90 km from the release site, after which contact was lost. Three other individuals did the same: after failing to pass the shipping lock complex at Asper, they swam back downstream, passed the shipping lock complex at Merelbeke again, but this time in the opposite direction, and reached the Rupel and Nete, in which they swam another 7 to 21 km upstream and reached a point 70 to 86 km from the release site. Although strictly speaking this was also upstream migration, these river systems were not included in the study due to limited data and the fact that the Rupel and the Nete were not part of the study area. Furthermore, interestingly, three individual lampreys interrupted their migration and returned after reaching Semmerzake, located on a river section between Merelbeke (shipping lock complex A1/A2) and Asper (shipping lock complex B) that was considered unobstructed.

4.2 The barrier effect

4.2.1 The effects of shipping lock complexes on migration speed and behavior

The optimal linear mixed model structure to analyze the effect of shipping lock complexes on migration speeds was:

$$^{10}\log(\text{Speed}_{ij}) = \beta_0 + \beta_1 D_{\text{unobstructed}_j} + \beta_2 D_{\text{fishway}_j} + b_i + \varepsilon_{ij}, \quad (4.1)$$

where β_0 denotes the intercept, β_1 and β_2 are the regression coefficients for the dummy variable ‘unobstructed’ (0 when a barrier is present, 1 when the river section is unobstructed) and the dummy variable ‘fishway’ (0 when there is no fishway, 1 when there is one), respectively, b_i represents the random intercept for individual i , and ε_{ij} is the residual error for observation j of individual i . The presence of a shipping lock complex was found to have a significant effect on migration speed ($p < 0.0001$), with unobstructed sections resulting in a speed approximately 250 times higher than that of obstructed sections ($\beta_1 = 2.40$). The presence of fish passages also significantly accelerated migration ($p = 0.008$) by a factor of approximately 6 ($\beta_2 = 0.78$).

This was reflected in overall migration speeds and times (Figure 4.3). The mean migration speed over shipping lock complex locations was 14.6 ± 26.4 m/h, with a respective minimum and maximum value of 0.3 and 141.7 m/h, resulting in a mean overall passage time of 458.8 ± 512.27 h. This speed differed between shipping lock complexes with fishways (27.8 ± 22.6 m/h, resulting in a passage time of 23.3 ± 14.5 h) and without those (11.9 ± 26.7 m/h, resulting in a passage time of 548.9 ± 519.2 h), and both were substantially lower than observed migration speeds in unobstructed river sections (see further, Figure 4.8).

Shipping lock complex migration times could be subdivided into searching and crossing states (see Section 3.4.3.1). The mean searching and crossing times at any shipping lock complex, with the exception of A2 (see Section 3.4.3.2), were respectively 410.7 ± 575.8 h and 7.3 ± 15.2 h. Interestingly, search times at shipping lock complexes with fishways (9.6 ± 15.0 h) were lower than at those without fishways (537.3 ± 609.4 h). Conversely, crossing times at shipping lock complexes with fishways (13.4 ± 15.5 h) were slightly longer than at those without (5.3 ± 14.9 h), as presented in Figure 4.4.

4. Insights into the spawning migration in the Scheldt River

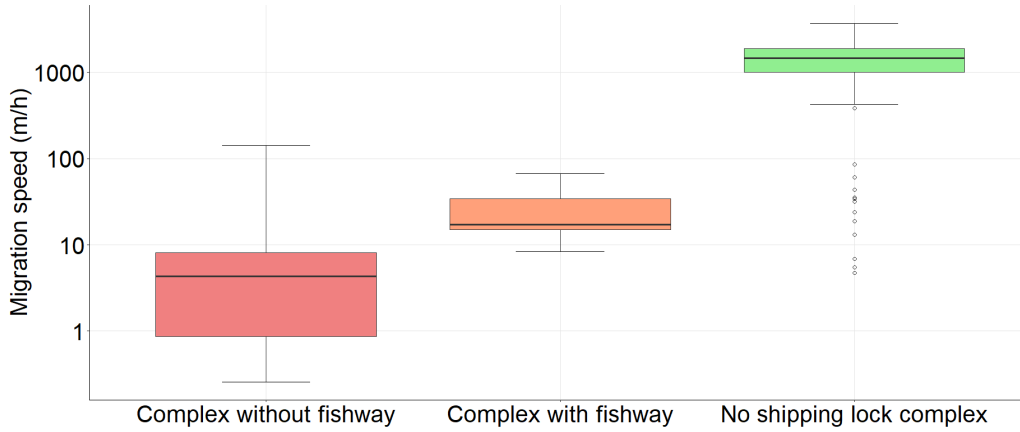


Figure 4.3: Boxplots representing the migration speed (m/h, logarithmic scale) of river lampreys through shipping lock complexes without (red) and with (orange) fishways, and barrier-free river segments (green). Only upstream movement is considered.

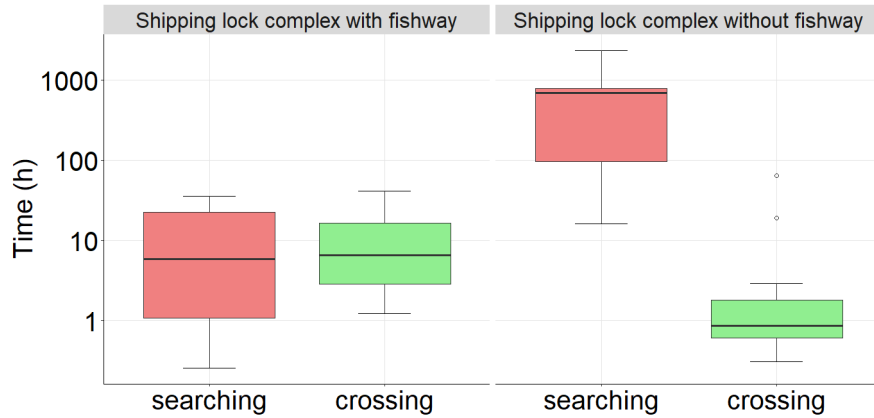


Figure 4.4: Boxplots representing the searching (red) and crossing (green) times (h, logarithmic scale), at shipping lock complexes with fishways (left) and without them (right).

4.2.2 Relation between environmental conditions, weir operation and shipping lock complex passage success

The optimal GLMM structure to describe the effect of environmental variables and barrier operation on passage success was:

$$\begin{aligned}
 \text{logit}(P_{\text{success}_{ij}}) = & \beta_0 + \beta_1 \text{Discharge}_j + \beta_2 \text{Waterlevel}_j \\
 & + \beta_3 (1 - D_{\text{free flow}_j}) \text{Overflow}_j \\
 & + \beta_4 (1 - D_{\text{free flow}_j}) \text{Underflow}_j \\
 & + \beta_5 D_{\text{free flow}_j} + \beta_6 D_{\text{fishway}_j} + b_i + \varepsilon_{ij},
 \end{aligned} \tag{4.2}$$

where β_0 denotes the intercept, β_1 , β_2 , β_3 and β_4 are the regression coefficients for scaled discharge, scaled water level, normalized total weir overflow rate and normalized total weir underflow rate respectively, β_5 is the coefficient of the dummy variable ‘free flow’ (0 when no free-flowing conditions occur, 1 when they do occur), β_6 is the coefficient of the dummy variable ‘fishway’ (0 when there is no fishway, 1 when there is one), b_i represents the random intercept for individual i , and ε_{ij} is the residual error for observation j of individual i . $P_{\text{success}_{ij}}$ represents the probability of a successful shipping lock complex passage for observation j of individual i (0 for searching observations, 1 for crossing observations).

Although the presence of free flow appeared to increase the odds of passage by a factor 2.56, it did not seem to have a significant effect on passage success ($\beta_6 = 0.94$, $p = 0.072$). However, the presence of fishways strongly increased the odds of passage by a factor 123.6, with a significant effect of $\beta_5 = 4.82$ ($p < 0.0001$). Furthermore, discharge, water level, weir overflow rate and weir underflow rate all had significant effects, with p-values of < 0.0001 , 0.002, < 0.001 , and < 0.0001 , and β -values of 1.21, 0.28, 4.93, and -6.68, respectively, meaning that an increase in the former three predictors enhanced the odds of passage, while an increase in the latter predictor lowered it. In Figure 4.5, the positive discharge effect is visually supported for lampreys passing weirs, but not for other barrier types.



Figure 4.5: Boxplots representing the searching (red) and crossing (green) events, corresponding with unsuccessful and successful passage, respectively, and the scaled discharge during these events, at different barrier types through which lampreys crossed. Weirs are split up in those that can experience free flow (location A1), and those that cannot (all other locations).

About 77% of the cases in which lampreys passed through the barriers in Merelbeke (A1/A2) occurred at night, indicating a significant effect of the circadian phase on crossing behavior (chi-square test with simulated p -values and circadian proportions: $p < 0.001$). Although other locations could not be statistically tested due to an insufficient number of crossing events, the latter all again occurred during

4. Insights into the spawning migration in the Scheldt River

dusk or at night. Furthermore, at the shipping lock complex in Merelbeke (A1/A2), where tides influence the downstream area, 65% of crossing attempts occurred during flood, resulting in a significant tidal effect on crossing behavior (chi-square test with simulated p -values and tidal proportions: $p < 0.001$). Finally, the majority of crossing events (75%) at the Merelbeke weirs (only A1) occurred during free-flowing conditions, when the weirs were lifted from the stream (chi-square test with simulated p -values and free flow proportions: $p < 0.001$).

Migration speed across shipping lock complexes was slightly correlated with total body length and weight ($\rho = 0.48$ and 0.37 , respectively). Of all continuous environmental variables, discharge showed the strongest correlation with overall migration speed ($\rho = 0.53$; Figure 4.6). Furthermore, observations at shipping lock complexes occurred equally during the day and night (Figure 4.7, right).

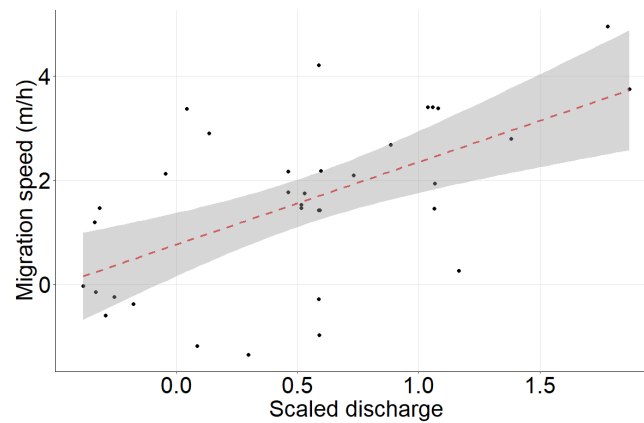


Figure 4.6: Relation between scaled discharge and overall shipping lock complex migration speed. The red dotted line represents a fitted linear regression curve, while gray bands represent the 95% confidence interval.

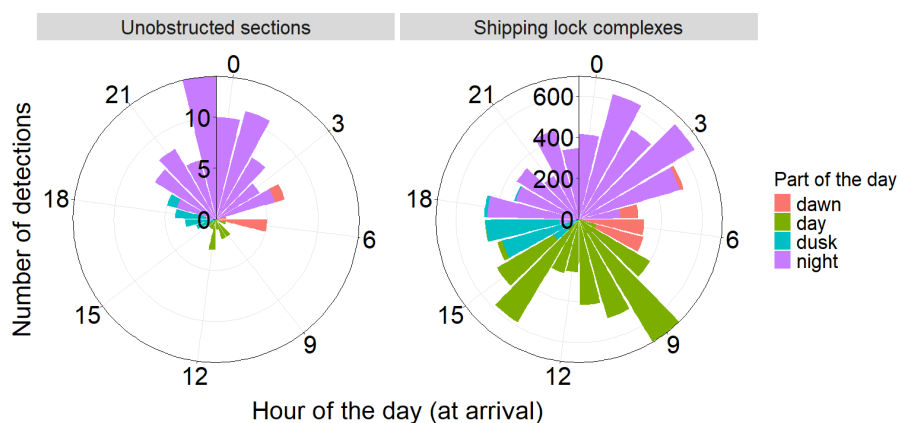


Figure 4.7: Radial plot showing the number of observations (bar length) that occurred in unobstructed river sections (left) and at shipping lock complexes (right), at a specific hour during the day, with the colors representing the corresponding circadian phase. For each observation, the detection timestamp in the plot corresponds to the arrival at that observation.

4.3 Migration in unobstructed river sections

The average migration speed in unobstructed river segments, which could be calculated for 26 lampreys, was 1438.8 ± 820.0 m/h, with a minimum and maximum value of 4.7 and 3735.6 m/h, respectively. There was considerable variability between successive stretches, although the average speed increased as the individuals moved further upstream (Figure 4.8). Moreover, the standard deviation in migration speeds per individual decreased in these upstream sections. Each time lampreys entered the last unobstructed river section before the next shipping lock complex, their migration speed appeared to decrease slightly, with the largest change between the receiver in Semmerzake and the shipping lock complex in Asper.

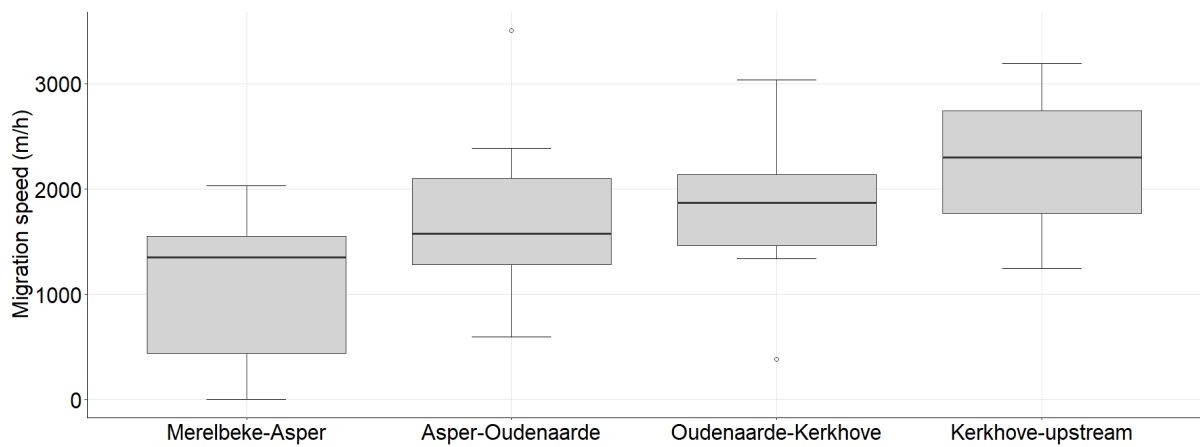


Figure 4.8: Boxplots showing the average migration speeds calculated between consecutive receivers occurring in unobstructed river sections.

The model selection procedure resulted in the following optimal linear mixed model structure to relate migration speed to environmental predictors:

$$\text{Speed}_{ij} = \beta_0 + \beta_1 \text{Temperature}_j + \beta_2 \text{Rainfall}_j + \beta_3 \text{Photoperiod}_j + b_i + \varepsilon_{ij}, \quad (4.3)$$

where β_0 denotes the intercept, β_1 , β_2 and β_3 are the regression coefficients for temperature, rainfall and photoperiod, respectively, b_i represents the random intercept for individual i , and ε_{ij} is the residual error for observation j of individual i . The photoperiod had a significant effect on migration rate ($p < 0.001$), with $\beta_3 = 225.11$. Conversely, temperature ($\beta_1 = 64.75$) and rainfall ($\beta_2 = 3246.25$) had no significant effect ($p = 0.136$ and $p = 0.143$, respectively).

In contrast to shipping lock complexes, most observations of arrivals in free-flowing river sections occurred at night (Figure 4.7, left), indicating nocturnal behavior. The same plot was constructed with departure times for each observation, which gave similar results. No correlations were found between migration speed and total body length ($\rho = 0.03$) and weight ($\rho = 0.11$).

4.4 Discussion

4.4.1 Passage across shipping lock complexes

In general, shipping lock complexes undeniably reduced numbers of migrating lampreys, with the largest reduction at the second shipping lock complex in Asper (87.5%), and the second largest reduction at the first complex in Merelbeke (46%). However, the final two shipping lock complexes in Oudenaarde and Kerkhove did not show any reduction. This observation did not correspond with the typical cumulative reduction reported in literature (Lucas et al., 2009), and was the consequence of the functional fishways at these two final shipping lock complexes. Although several studies suggest that technical and even nature-like fishway designs are not sufficient to sustain lamprey passage (Lucas et al., 2009; Abersons et al., 2025), our results suggested the opposite, i.e., the nature-like fishway in Oudenaarde (Huysecom et al., 2012), and the V-shaped weir and pool fishway in Kerkhove (Vercruysse et al., 2024) ensured 100% lamprey passage. However, while fishways significantly increased passage probability, the observed patterns should be interpreted with particular caution, as they only covered the three individuals that managed to pass Asper. Moreover, it might be possible that these individuals were already more fit than others, such that a successful passage in Asper was naturally linked to a successful passage across the fishways further upstream.

A clear relation between body size and passage success was present at the shipping lock complex in Asper, similar to patterns found for Pacific lampreys (Keefer et al., 2009a). The smaller average size of the 2025 batch compared to the 2024 batch might have caused the lower passage efficiencies observed in 2025-2026. As females were generally larger than males, this size effect might lead to an imbalance between sexes present at spawning (Zydlewski et al., 2023). A possible explanation for the absence of the size effect in Merelbeke was the recurring free-flowing regime at location A1, which might have been less size selective than passage through the weir itself. However, when excluding individuals passing through the weirs at site A1, the size effect in Merelbeke was found to be stronger, yet still insignificant. Furthermore, these results should again be interpreted with particular caution, as the significant size effect in Asper covered 21 unsuccessful and only 3 successful individuals.

The effect of barrier presence on migration speed was found to be significant and considerable, with speeds at shipping lock complexes decreasing more than 250 times compared to unobstructed sections. Searching behavior at barriers could be considered migration delays and accounted on average for more than 83.2% (17 ± 24 days) of the total migration time over shipping lock complexes. These delays were of the same order of magnitude as in other studies (Huysecom et al., 2012; Davies et al., 2021, 2022; Lothian et al., 2024). Furthermore, similar to the ob-

servations of Davies et al. (2022), delay times at specific barriers clearly showed bimodal or multimodal distributions, with some individuals passing relatively fast (≤ 100 h) and others only passing later (≥ 700 h), often during moments of relatively high discharge. These strong delays may result in misalignment with natural cycles and other spawning individuals, high energetic losses, and even death (Zydlewski et al., 2023). Interestingly, fishways did not only ensure passage, but also substantially reduced searching times compared to other barriers, therefore counteracting the delay. This indicates that lampreys found the entrance to the fishway relatively quickly, which is often regarded one of the major challenges in fish passage science (Mawer et al., 2023; Verhelst et al., 2023).

Shipping lock complex passage success increased with discharge and water level, as suggested by several studies (Lucas et al., 2009; Foulds and Lucas, 2013; Silva et al., 2017a; Davies et al., 2022; Lothian et al., 2024). The majority of lampreys passed Merelbeke through weirs (both at locations A1 and A2). Individuals that passed via A1 mainly did this during periods of high discharge, often when the weirs were lifted from the river (i.e., free-flowing conditions). Furthermore, contrary to the observation that lock gates often do not provide a suitable passage for fish (Vergeynst et al., 2019), the three fish that passed through Asper always swam through the locks. This may suggest that lampreys effectively need an open channel to migrate through, rather than through a small opening above or below a weir. Although our optimal regression model did not find a significant effect of free-flowing conditions, a location-specific test considering only the weirs at location A1 did find significant results for free flow.

However, another fraction of individuals (37%) passed Merelbeke via location A2, where free flow never occurred. They also did this during periods of high discharge, water level and weir overflow rates, indicating that lampreys could effectively pass weirs, even if the barriers were not completely lifted from the stream, as supported by literature (Lucas et al., 2009; Davies et al., 2021). In contrast to overflow, higher underflow rates appeared to reduce passage success. This may be explained by the high water velocities associated with large underflow, which can exceed the swimming capacity of lampreys (Russon and Kemp, 2011). A similar negative effect likely also occurred at high overflow rates, but was only detected for underflow because large underflow events were more frequently represented in the data than large overflow events. Therefore, a quadratic relationship for both weir over- and underflow might represent the underlying process better (Masters et al., 2006). To evaluate this hypothesis, an alternative regression model with quadratic effects for both predictors was estimated, yielding coefficients that showed a parabolic relationship with an optimum, thus supporting the hypothesis. However, it also led to multicollinearity, such that the model was regarded unacceptable.

Finally, it is important to note that the size of the estimated regression coefficients in Eq. (4.1) and (4.2) should be approached carefully. As tracked individuals showed

limited crossing events, especially at shipping lock complexes with fishways (i.e., Oudenaarde and Kerkhove), coefficients such as the one for fishway presence could suffer from overfitting. Furthermore, while the effects of most predictors in Eq. (4.2) were considerable, the baseline probability of passage (evaluated at average discharge, average water level, absence of fishways, and absence of free flow, overflow and underflow), was very low ($\beta_0 = -8.84$, so close to 0). In other words, for a small increase in probability, large coefficients were needed.

4.4.2 Unobstructed migration

The speed at which individuals migrated between shipping lock complexes increased as they moved further upstream. Combined with lower standard deviations of the speed per individual in these upstream reaches, this might point to a more directed migration the closer lampreys got to their destination. One explanation might be the effects of environmental drivers, such as seasonal increase in water temperature and decrease in discharge (see below). Alternatively, lampreys may be strongly attracted to a higher concentration of larval pheromones closer to potential larval nurseries and subsequent spawning areas beyond Avelgem, leading to accelerated migration (Gaudron and Lucas, 2006). Unfortunately, as discussed before, not one individual from the second round of tagged lampreys passed Asper, such that this pattern could not be confirmed for more than three individuals.

Regarding the regression model with unobstructed migration speed as response variable (Eq. 4.3), the photoperiod was consistently the only environmental factor that appeared to have a significant and positive effect. The majority of literature on lamprey ecology reports evidence on seasonal variation in migration timing and intensity (e.g., Buysse et al., 2004; Masters et al., 2006; Moser et al., 2015; Baer et al., 2018), but not in migration speed. As these seasonal variations in speed are often attributed to changes in discharge and temperature (Keefer et al., 2009b), a possible reason for the significant effect of photoperiod might be its correlation with both of these environmental drivers, although this was not the case in our data. Another reason could be that the lampreys swam faster as they approached their destination (e.g., due to larval pheromones, see above). This led to higher speeds in the latter part of the study period, when the photoperiod was longer than at the beginning. Finally, our optimal regression model may have mainly captured the gradually varying seasonal factors affecting migration speed, while neglecting patterns that occurred on shorter time scales (e.g., discharge peaks), due to aggregation of environmental predictors over relatively long time periods.

Although rainfall was included in the optimal regression model, it did not show any significant effects. Furthermore, its indirect consequences, i.e. discharge and water level, were not included in the optimal regression model at all, and even if included, always showed insignificant (and negative) effects, except when serving as the sole

predictors. In lamprey migration studies, discharge and water level are often found to have a positive effect on migration activity (Masters et al., 2006; Aronsuu et al., 2015), suggesting that higher flow rates stimulate migration and lead to more directed movements (Kerr et al., 2023). However, this does not necessarily mean that a higher discharge increases the migration speed itself, since lampreys experience higher energetic costs under these conditions (Kemp et al., 2010). In fact, Almeida et al. (2002) report that higher discharge increases catch per unit effort of sea lampreys, but also decreases their migration speed, while Keefer et al. (2009b) observe slower movements at higher discharge for Pacific lampreys. Both studies confirm the negative (yet insignificant) relations we found between discharge and migration speed in the unreported (suboptimal) regression models.

While water temperature was also included in the optimal regression model, it did not show any significant relation with the response variable. Active migration during the study period occurred at water temperatures of 1.9-13.3 °C, which was within the suitable range reported by other studies (Masters et al., 2006; Aronsuu et al., 2015). Some authors contradict our findings of an insignificant temperature effect, and report positive correlations between temperature and lamprey swimming speed (Keefer et al., 2009b; Kemp et al., 2010; Silva et al., 2017b), while others support an insignificant temperature effect, although they focus on catch per unit effort rather than migration speed (Masters et al., 2006; Aronsuu et al., 2015).

Migration through unobstructed river sections clearly showed nocturnal patterns, which aligns with observations that migrating river lampreys exhibit negative phototactic behavior (Maitland, 2003). Although detections at shipping lock complexes occurred throughout the entire day, as also described by Lothian et al. (2024), effective barrier crossing events still occurred mainly at night, suggesting that even at migration barriers, nocturnal activity persisted. This aligns with observations of Pacific lampreys showing strong nocturnal behavior in complex, turbulent environments with high risk of predation (Keefer et al., 2013).

Interestingly, lampreys always slowed down slightly in the last unobstructed river section before the appearance of a shipping lock complex (average speed 853.2 m/h), compared to other sections (average speed 1749.3 m/h). Two reasons for this apparent delay are possible: (1) lampreys already ‘feel’ the presence of the shipping lock complex before effectively encountering it, through changes in natural flow, leading to less directed migration behavior, and (2) the receivers at shipping lock complexes fail to immediately detect lampreys the moment they arrive. The latter is deemed unlikely because this required individuals to remain undetected in Asper for an average of 10 hours.

4.4.3 Potential spawning grounds

The slowing effect in the unobstructed river section between Semmerzake and Asper (average speed 747.8 m/h) was much stronger than in other unobstructed river sections with delaying effects (average speed 1362.7 m/h), and occurred throughout the entire study period. This might be explained by (1) the presence of a chemical pollution barrier (Maitland, 2003), illumination barrier (Aronsuu et al., 2015) or a physical submerged structure that affects lamprey navigation, (2) the presence of smaller side streams with sufficient periodic discharge to attract lampreys and allow them to enter, and (3) the presence of larval nurseries and subsequent spawning grounds in one of the many side streams in this section, to which lampreys might be strongly attracted and consequently delayed. All three hypotheses can be supported by the fact that three lampreys passed Semmerzake, subsequently 'disappeared' in the river section between Semmerzake and Asper, and finally returned back downstream after relatively long periods ($\geq$ two months for two individuals), passing Semmerzake in the other direction. If these lampreys had reached Asper, they should have been frequently detected there, like all other individuals.

One counterargument against the third hypothesis is that the 'disappeared' individuals already returned downstream before half March, while typical spawning events in the Scheldt River system presumably occur in April-May (Huysecom et al., 2012). Therefore, it is unlikely that these lampreys effectively spawned. Moreover, the mismatch between arrival at potential spawning grounds and spawning season might have been observed for other individuals as well: from the three lampreys that reached Avelgem (past which spawning habitat is suspected to occur), only one individual resided there in April, while the two other individuals already arrived and returned downstream before the beginning of March. This is inconsistent with the findings of Jang and Lucas (2005), which show that lampreys reaching spawning grounds may remain there for several months before actual spawning. The observed return behavior might be a consequence of migration barriers beyond Avelgem (e.g., the Spiere shipping lock complex). In other words, from the 50 individuals initially tagged in our study, only 1 lamprey (2%) may have had the chance to effectively reproduce, although it might also have been blocked by further migration barriers, thus abandoning migration similar to all other tracked lampreys.

The presence of spawning grounds between Semmerzake and Asper, and beyond Avelgem, seems an interesting research opportunity, as current spawning areas in the Scheldt River are still unknown despite intensive search efforts (Stevens et al., 2011). Furthermore, since multiple lampreys entered the Rupel and Nete rivers after abandoning their migration in the fragmented Scheldt River, it might be interesting to investigate whether spawning grounds exist in these river systems. Knowledge about spawning grounds and larval nurseries could be invaluable for the conservation of these species in Flanders (Stevens et al., 2009).

5. An individual-based model of lamprey migration

Although the insights into river lamprey migration presented in Chapter 4 provide valuable knowledge about the movement behavior of this species in a fragmented river system, translating this knowledge into effective management remains a challenge (Drouineau et al., 2018; Verhelst et al., 2021). To support conservation and river management, it is therefore important to estimate migration timing and barrier passage efficiency under both current and alternative environmental or management scenarios.

To translate acoustic telemetry observations of a limited number of individuals into complex population dynamics and evaluate alternative scenarios, process-based modeling approaches such as individual-based models (IBMs) are promising (Mawer et al., 2023). Building on the behavioral patterns identified in Chapter 4, this chapter therefore develops an IBM of river lamprey migration in the Upper Scheldt River. Using this model, we investigate how variability in barrier management and environmental conditions can influence the timing and success of migration, to support future diadromous fish management.

5.1 Introduction

Individual-based models (IBMs), also known as agent-based models, are a modeling approach in which discrete individuals are explicitly represented. Each individual is assigned a set of attributes that may vary through time, such as spatial location and behavioral traits (DeAngelis and Grimm, 2014). Interactions among individuals, as well as between individuals and their environment, arise from adaptive, fitness-seeking behavior (i.e., responses that enhance survival and reproductive success). These local interactions lead to emergent patterns at the population level (Grimm and Railsback, 2005). For this reason, IBMs are often described as bottom-up population models, since population-level dynamics arise from the behavior of individuals rather than being imposed a priori.

A key advantage of IBMs is their ability to represent complex ecological processes, including inter-individual variability, within-individual variation across the life cycle,

local interactions between individuals, and adaptive behavioral responses (DeAngelis and Grimm, 2014). In contrast, classical differential equation-based models rely on top-down parameterization, assume homogeneously mixed populations (i.e., the mean-field assumption), and depend on assumptions embedded within the equations (Berec, 2002; DeAngelis and Grimm, 2014). Due to their relaxed assumptions and increased realism, IBMs have greater predictive capacity and improved transferability to new study areas compared to traditional and correlative approaches (Stillman et al., 2015; Mawer et al., 2023). However, IBMs are often complex and difficult to analyze mathematically, resulting in a lack of standardized theoretical frameworks (Grimm and Railsback, 2005; Cornell et al., 2019).

Since the 1990s, advances in computational power have facilitated the application of IBMs in ecology (i.e., individual-based ecology), particularly in studies of animal populations (Grimm and Railsback, 2005; DeAngelis and Grimm, 2014). IBMs have been widely applied in fish ecology, especially in management and the study of movement and population dynamics (Railsback et al., 1999; Hubbard et al., 2004; Baetens et al., 2013; Jager and DeAngelis, 2018). Furthermore, they are well suited for investigating fish migration in fragmented river systems, including passage through barriers and fishways (Mawer et al., 2023). Still, relatively few studies apply IBMs specifically to the upstream migration of lampreys. Kerr et al. (2023) develop a fine-scale IBM of river lamprey behavior near instream structures, while Kerr et al. (2025) extend this approach to an intermediate spatial scale for sea lampreys. Moreover, Neeson et al. (2011a,b) develop an IBM of the sea lamprey life cycle. To the best of our knowledge, however, no individual-based model simulating large-scale upstream migration of the river lamprey in highly fragmented river systems has been developed.

5.2 The individual-based migration model

This section provides a brief overview of the purpose, patterns and design of the developed individual-based migration model. For a more comprehensive and detailed description, we refer to Appendix A.

5.2.1 Purpose and patterns

The purpose of the IBM is to reproduce fish migration patterns in the Upper Scheldt River under current and new scenarios, including changing environmental conditions and different management of water regulating structures. In Section 4.2.2, the presence of fish passages and flow-related conditions (discharge, water level, and weir flow rates) were found to be important factors influencing lamprey passage through shipping lock complexes. Furthermore, the Upper Scheldt River is

5. An individual-based model of lamprey migration

particularly vulnerable to climate-induced drought (Yimer, 2025). Therefore, six scenarios related to fish passages and drought are considered (Table 5.1).

Table 5.1: Scenarios considered, with S_0 corresponding to the current baseline scenario.

Scenario	Drought	Presence of fishways in			
		Merelbeke	Asper	Oudenaarde	Kerkhove
S_0	No	No	No	Yes	Yes
S_1	Yes	No	No	Yes	Yes
S_2	No	Yes	Yes	Yes	Yes
S_3	No	No	No	No	No
S_4	Yes	Yes	Yes	Yes	Yes
S_5	Yes	No	No	No	No

The drought scenarios assume an average decrease of 13% in the annual discharge of the Upper Scheldt River due to climate change, during the period 2077–2100 (compared to 1961–1990) (Willems et al., 2011). While in reality, future drought effects might be seasonal and peak-dependent (Willems et al., 2011), for the sake of simplicity, the reduction in discharge is assumed to be constant and corresponds to an equal reduction in water level and weir over- and underflow rates. In addition, lower flow rates at the weirs mean that free-flowing conditions occur less frequently in Merelbeke.

As Chapter 4 showed that shipping lock complexes in the Scheldt River form major migration barriers, they are from now on referred to as ‘bottlenecks’. The specific output patterns that this model seeks to reproduce are primarily passage efficiencies across bottlenecks, and migration delay distributions. Analyzing these migration patterns under the proposed scenarios could help inform management and conservation of the European river lamprey and other diadromous fish species.

5.2.2 General model description

The IBM simulates the upstream spawning migration of 1000 European river lampreys within a 43 km section of the Upper Scheldt River. The latter corresponds to the study area (Figure 3.1) and is represented as a one-dimensional continuous space containing four shipping lock complexes that act as migration bottlenecks: A (Merelbeke, with A1/A2 combined for simplification), B (Asper), C (Oudenaarde), and D (Kerkhove). All individuals are initialized 3 km downstream of the first bottleneck in Merelbeke, and are simulated from 1 December 2024 to 31 May 2025, using time steps of 15 minutes. The simulation ends for an individual when it reaches the last point in the study area (Avelgem), abandons its migration, or when the simulation period ends.

Behavior of in silico lampreys is governed by two submodels that are calibrated using processed telemetry data. In unobstructed river sections, migration speed is

determined by a swimming submodel based on the linear mixed regression model developed in Section 4.3 (Eq. 4.3). In contrast, when individuals encounter a bottleneck, a survival submodel based on competing risk theory is triggered. This submodel evaluates the probabilities of two mutually exclusive events: (1) bottleneck passage and (2) return (i.e., migration abandonment). Passage probabilities depend on wait time, discharge, water level, weir flow conditions, and fishway presence through Cox's proportional hazards regression (Cox, 1972), whereas return probabilities depend only on time. Both submodels incorporate individual variability through random effects.

By updating individual positions, travel times, and bottleneck decisions at each time step, the IBM generates migration trajectories, from which passage efficiencies, migration delays, and overall migration success can be derived under different scenarios. To account for stochasticity and obtain robust estimates, each scenario is simulated 250 times with a population of 1000 individuals.

5.3 Results and discussion

In this section, simulation results are presented and discussed. First, results for the baseline scenario are reported (Section 5.3.1), after which we perform a scenario analysis to investigate how alternative environmental conditions and fishway configurations affect migration patterns. More specifically, the impact of drought is discussed (Section 5.3.2.1), after which our attention shifts to fishways and their effects under both normal flow conditions and drought (Section 5.3.2.2). Finally, the interaction between fishways and reduced flow conditions is investigated (Section 5.3.2.3).

5.3.1 Baseline scenario

In the baseline scenario (S_0), we assumed that all 1000 *in silico* lampreys started their migration in the Upper Scheldt River on 1 December 2024, approximately 3 km downstream of the first bottleneck in Merelbeke. In addition, fishways only occurred at the bottlenecks in Oudenaarde and Kerkhove. The simulated passage efficiencies and delays at the different shipping lock complexes are reported in Table 5.2. Asper appeared to be the most problematic bottleneck, with the lowest passage efficiency and long delays of several months. The shipping lock complex in Merelbeke showed a higher passage efficiency, with approximately half of the arriving individuals successfully passing through. Furthermore, delays before returning were considerably longer in Asper compared to Merelbeke, while delays before passing showed the opposite pattern. In Oudenaarde and Kerkhove, *in silico* passage efficiencies were close to 100% and delays were relatively short.

5. An individual-based model of lamprey migration

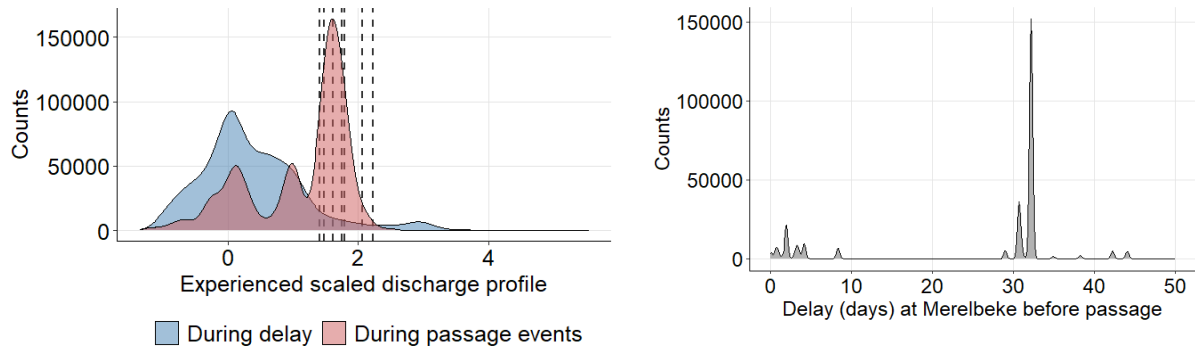
Table 5.2: In silico lamprey passage efficiencies and wait times before passage or returning, at different shipping lock complexes (bottlenecks) in the Upper Scheldt River, between 01/12/2024 and 31/05/2025, and under the baseline scenario (S_0). Values are reported as mean $\pm$ standard deviation.

Bottleneck	Passage efficiency (%)	Wait time before passage (days)	Wait time before returning (days)
Merelbeke	55.4 $\pm$ 1.5	26.7 $\pm$ 15.2	27.5 $\pm$ 24.6
Asper	29.6 $\pm$ 1.9	20.8 $\pm$ 19.9	42.2 $\pm$ 30.3
Oudenaarde	99.2 $\pm$ 0.7	0.4 $\pm$ 0.7	0.6 $\pm$ 0.3
Kerkhove	98.1 $\pm$ 1.1	1.1 $\pm$ 2.5	2.7 $\pm$ 5.5

To model the effects of environmental factors and weir operation on passage probability, the IBM applied a survival submodel using Cox regression (see Appendix A, Section A.6.1). The regression coefficients showed positive values for scaled discharge ($\beta_1 = 0.60$, $p < 0.001$), scaled water level ($\beta_2 = 0.43$, $p < 0.001$), normalized weir overflow ($\beta_3 = 3.48$, $p = 0.044$), free-flowing conditions ($\beta_5 = 0.76$, $p = 0.095$), and the presence of a fish passage ($\beta_6 = 3.7$, $p < 0.001$), while weir underflow was assigned a negative value ($\beta_4 = -2.75$, $p = 0.016$). In other words, the ‘hazard’ of passage increased under free-flowing conditions, in the presence of fish passages, and with higher discharge, water level, and overflow, while it decreased with larger underflow, consistent with previous results in Chapter 4.

In general, these coefficients resulted in frequent passage during discharge peaks. For instance, Figure 5.1a shows the discharge distributions individuals experienced during delay and at passage events in Merelbeke. There, a significant proportion of the in silico lampreys passed within a narrow range of high scaled discharge (approximately 1.5–2.5). This was likely due to the free-flowing conditions that prevailed at the weirs in Merelbeke during these high-discharge events. Consequently, 50% of the simulated individuals that passed Merelbeke did so within a relatively short period, between 31 December 2024 and 7 January 2025. This intense passage is visible in the delay plot for Merelbeke under S_0 (Figure 5.1b) as a sharp peak around 30 days.

At other bottlenecks, the discharge experienced by individuals during passage was similarly higher compared to discharge during delay, although the pattern was less pronounced than in Merelbeke. Moreover, most in silico lampreys at Oudenaarde happened to arrive there during a higher discharge than at other locations, which might explain the shorter waiting times compared to Kerkhove (see Table 5.2). Although the focus here is on discharge, similar conclusions can be drawn for water level and weir flow rates.



(a) Distribution of scaled discharge during delay (blue) and passage (red) at the Merelbeke shipping lock complex. Dotted vertical lines represent in silico passage events where free-flowing conditions occurred at the weirs.

(b) Distribution of simulated delays before passing the Merelbeke shipping lock complex.

Figure 5.1: Relation between discharge, passage and delay at the Merelbeke shipping lock complex under S_0 .

In total, $16.0 \pm 36.6\%$ of the in silico lampreys migrated past Avelgem, and therefore had the best chance to reach potential spawning grounds. The time it took individuals to reach Avelgem followed a multimodal distribution (Figure 5.2), with three peaks after 7, 36, and 63 days. Simulated arrivals at potential spawning grounds often occurred several months before the presumed spawning period in April–May, therefore aligning with field observations (Jang and Lucas, 2005). However, since other bottlenecks may exist upstream of Avelgem (e.g., the Spiere shipping lock complex), arriving there was no guarantee of successful spawning. The multimodal nature was likely due to individual variation combined with discharge peaks, allowing large numbers of migrants to pass through at once after long delays, especially in Merelbeke (see above). Of the 84.0% of lampreys that did not reach Avelgem, the majority (82.0%) abandoned their migration, while the remaining portion (2.0%) was still swimming or waiting at the end of the simulation.

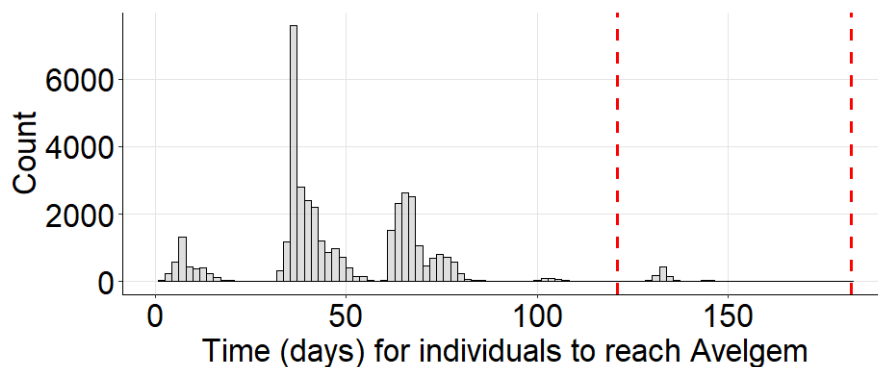


Figure 5.2: Distribution of in silico migration times for S_0 , from the start (3 km downstream of the first bottleneck in Merelbeke) to the farthest point in the study area (43 km upstream of the start location, in Avelgem). Red vertical dotted lines represent the presumed spawning period of the European river lamprey in the Upper Scheldt River (April to May).

5.3.2 Scenario analysis

5.3.2.1 The effect of drought

The effects of drought (i.e., reduced river discharge, water level and weir flow rates) under the current fishway configuration are represented in S_1 . Corresponding simulation results are shown in Table 5.3. Under this scenario, passage efficiency decreased in Merelbeke and Asper, while the complexes in Oudenaarde and Kerkhove remained passable for most of the individuals that reached them. Passage in Merelbeke again mainly occurred during periods of high discharge and free-flowing conditions, between 31 December 2024 and 7 January 2025, resulting in simulated passage waiting times comparable to those under S_0 . However, because discharge peaks were reduced and free-flowing conditions occurred less frequently, a smaller fraction of individuals was able to pass. Waiting times before passage at Asper did not change much compared to S_0 , whereas they almost doubled in Oudenaarde and Kerkhove.

Table 5.3: In silico lamprey passage efficiencies and wait times before passage or returning, at different shipping lock complexes (bottlenecks) in the Upper Scheldt River, between 01/12/2024 and 31/05/2025, and under future projected drought conditions (S_1). Values are reported as mean $\pm$ standard deviation.

Bottleneck	Passage efficiency (%)	Wait time before passage (days)	Wait time before returning (days)
Merelbeke	38.5 $\pm$ 1.6	29.1 $\pm$ 17.6	36.5 $\pm$ 28.8
Asper	20.7 $\pm$ 2.1	21.8 $\pm$ 21.0	44.0 $\pm$ 30.4
Oudenaarde	98.5 $\pm$ 1.4	0.8 $\pm$ 1.5	1.6 $\pm$ 3.9
Kerkhove	97.0 $\pm$ 2.0	1.9 $\pm$ 4.4	6.3 $\pm$ 9.0

Compared to S_0 , the simulated waiting times before lampreys returned were about ten days longer in Merelbeke, while they remained roughly the same in Asper. This may indicate that individuals that were able to pass Merelbeke under normal conditions, but failed to do so under drought, continued waiting for quite some time before returning. Moreover, waiting times before return in both Oudenaarde and Kerkhove more than doubled compared to S_0 . Finally, the climate-induced decline in flow conditions reduced overall migration success. Although a multimodal pattern in migration timing similar to S_0 could be observed (Figure 5.3), only $7.6 \pm 26.5\%$ of the in silico lampreys reached Avelgem, less than half the number in S_0 . Overall, the IBM therefore indicated that future drought could have negative consequences for populations of diadromous fish in the Scheldt River.

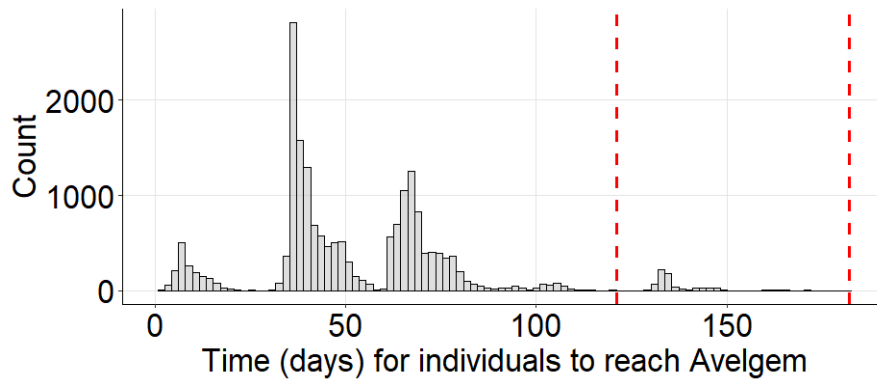


Figure 5.3: Distribution of in silico migration times for S_1 , from the start (3 km downstream of the first bottleneck in Merelbeke) to the farthest point in the study area (43 km upstream of the start location, in Avelgem). Red vertical dotted lines represent the presumed spawning period of the European river lamprey in the Upper Scheldt River (April to May).

In S_1 , the drought effect was incorporated multiple times, as all predictors were simultaneously reduced by the same drought factor (i.e., water level, discharge, and weir flow rates). To assess which predictors were responsible for the observed drought effect, three additional model versions were tested. In the first version, only discharge and water level were reduced. Under these conditions, passage efficiency decreased by an amount similar to that previously observed in S_1 . In the second version, only weir flow rates were reduced, resulting in a minor to no decrease in passage efficiency. And finally, the third version considered only the complete removal of free flow events in Merelbeke. Here, reductions in passage were considerable, but smaller compared to those observed in S_1 .

These results suggested that changes in river discharge and water level, and the loss of free flow in Merelbeke, likely had a greater impact on migration than changes in weir flow rates. This may appear counterintuitive, as reduced weir flow rates were associated with fewer free-flowing conditions. However, lampreys were able to pass in large groups during such events. Consequently, during drought, substantial passage could still occur at rare free flow events, implying that only their complete removal had significant adverse effects. Furthermore, as discussed in Section 4.4.1, not only very low but also excessively high under- and overflow rates may hinder passage. A moderate reduction in weir flow rates may therefore have little negative effect, or may even improve passage conditions by reducing flow velocities at the weirs. This could explain the minor change in passage efficiency observed at lower weir flow rates. In contrast, natural discharge and water level likely reflected the overall accessibility of shipping lock complexes better than local flow velocities.

Note that increased discharge peaks during winter might be an alternative consequence of climate change (Yimer, 2025). Since our primary objective was to assess drought effects, this was not taken into account. However, incorporating seasonal effects on river flow may lead to different results.

5.3.2.2 The fishway effect

In S_2 , all bottlenecks contained fishways, whereas in S_3 , no fishways were present in the study area. Consequently, in S_2 , fishways were introduced at Merelbeke and Asper, while in S_3 , the existing ones at Oudenaarde and Kerkhove were removed. Table 5.4 shows changes in results at the relevant shipping lock complexes for both scenarios, relative to S_0 . Introducing fishways in Merelbeke and Asper drastically increased passage success and decreased delays before passing and returning. In contrast, removing existing fishways from the bottlenecks in Oudenaarde and Kerkhove resulted in a strong reduction in passage efficiency and increase in delays.

Table 5.4: Changes in simulated lamprey passage efficiencies and wait times before passage or returning, for S_2 and S_3 , compared to S_0 . S_2 corresponds to the installation of a new fishway in Merelbeke and Asper, while S_3 corresponds to the disappearance of existing fishways in Oudenaarde and Kerkhove. Values are reported as mean $\pm$ standard deviation.

Bottleneck	Scenario comparison	Δ Passage eff. (%)	Δ Wait time passage (days)	Δ Wait time return (days)
Merelbeke	$S_2 - S_0$	$+42.4 \pm 1.5$	-25.6 ± 15.3	-25.9 ± 25.0
Asper	$S_2 - S_0$	$+68.9 \pm 1.9$	-20.0 ± 20.0	-40.2 ± 30.7
Oudenaarde	$S_3 - S_0$	-54.2 ± 4.1	$+18.4 \pm 21.5$	$+37.4 \pm 29.3$
Kerkhove	$S_3 - S_0$	-67.2 ± 5.5	$+19.4 \pm 23.6$	$+37.9 \pm 29.8$

When each shipping lock complex contained a fish passage (S_2), $93.2 \pm 24.3\%$ of the in silico lampreys reached Avelgem. Conversely, when no functional fishways were present in the entire study area (S_3), only $2.3 \pm 14.8\%$ of individuals reached their destination. Furthermore, Figure 5.4 shows that for S_2 , the shape of the arrival curve in Avelgem changed from a multimodal pattern to a single peak. This was probably the result of enhanced passage that did not depend entirely on discharge peaks, and subsequent shorter delays at Merelbeke and Asper. However, when fishways were removed from the study area under S_3 , arrival times at Avelgem were spread throughout the entire study period, a pattern similar to that observed for migrating eels in strongly regulated rivers arriving at sea (Verhelst et al., 2025).

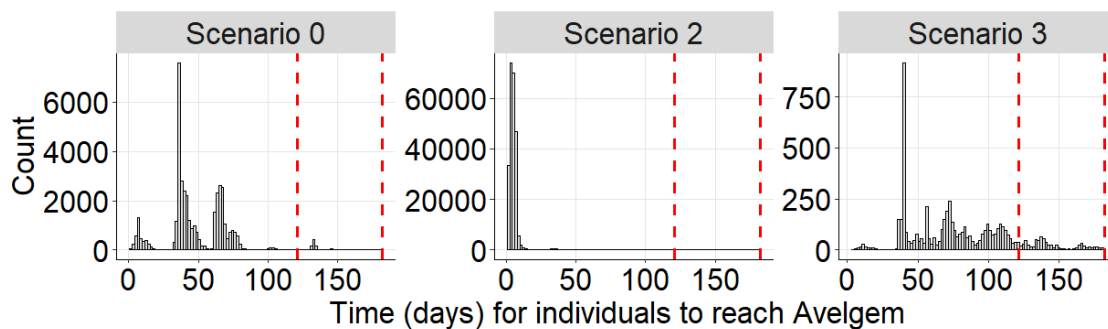


Figure 5.4: Distribution of in silico migration times, from the start to the farthest point in the study area (Avelgem), for S_0 (baseline), S_2 (fishways at all bottlenecks) and S_3 (no fishways). Red vertical dotted lines represent the spawning period.

S_4 and S_5 similarly considered alternative fishway configurations, but under drought conditions. In S_4 , each bottleneck contained a fishway, while in S_5 , no fishways were present in the study area. Table 5.5 shows changes in results at the relevant shipping lock complexes for both scenarios, relative to the baseline drought scenario S_1 . Here, similar effects of fishways were observed, i.e., their introduction at Merelbeke and Asper increased passage and reduced delay, while their removal in Oudenaarde and Kerkhove did the opposite. Moreover, when all bottlenecks contained fishways under drought (S_4), $89.5 \pm 30.6\%$ of in silico lampreys reached Avelgem. However, when no fishways were present at any bottleneck (S_5), only $0.5 \pm 7.1\%$ were successful. Furthermore, changes in arrival timing patterns (Figure 5.5) were similar to those reported under normal flow conditions (Figure 5.4).

Table 5.5: Changes in simulated lamprey passage efficiencies and wait times before passage or returning, for S_4 and S_5 , compared to S_1 . S_4 corresponds to the installation of a new fishway in Merelbeke and Asper under drought conditions, while S_5 corresponds to the disappearance of existing fishways in Oudenaarde and Kerkhove under drought. Values are reported as mean $\pm$ standard deviation.

Bottleneck	Scenario comparison	Δ Passage eff. (%)	Δ Wait time passage (days)	Δ Wait time return (days)
Merelbeke	$S_4 - S_1$	$+57.8 \pm 1.7$	-26.9 ± 18.1	-31.2 ± 29.9
Asper	$S_4 - S_1$	$+76.6 \pm 2.2$	-20.2 ± 21.3	-39.3 ± 31.4
Oudenaarde	$S_5 - S_1$	-67.1 ± 5.6	$+20.3 \pm 22.3$	$+39.6 \pm 30.1$
Kerkhove	$S_5 - S_1$	-76.4 ± 8.6	$+21.2 \pm 24.9$	$+35.4 \pm 30.6$

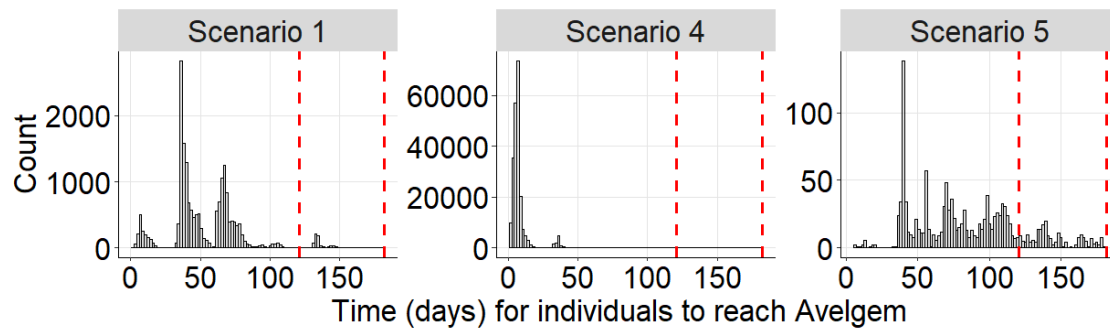


Figure 5.5: Distribution of in silico migration times, from the start to the farthest point in the study area (Avelgem), for S_1 (drought baseline), S_4 (fishways at all bottlenecks under drought) and S_5 (no fishways under drought). Red vertical dotted lines represent the spawning period.

In general, our results indicated that fishways at the upstream bottlenecks in Oudenaarde and Kerkhove alone (S_0) had a limited effect on overall migration success. Compared to a study area without fishways (S_3), they increased the proportion of in silico lampreys reaching Avelgem from 2.3% to 16.0%. In contrast, when fishways were also present at the downstream bottlenecks in Merelbeke and Asper (S_2), overall migration success increased to 93.2%. Similar conclusions could be drawn from the drought scenarios. This aligns with previous studies that suggest impassable downstream barriers limit the benefits of passable upstream barriers,

as only a few individuals are able to reach the latter (O’Hanley and Tomberlin, 2005; Kemp and O’Hanley, 2010; Nunn and Cowx, 2012). In addition, delays at successive bottlenecks can lead to cumulative energetic costs that further reduce passage success (Lucas et al., 2009; Kemp and O’Hanley, 2010; Garcia de Leaniz and O’Hanley, 2022).

Thus, our results suggested that fishway management in the Upper Scheldt River should prioritize downstream bottlenecks. This is particularly relevant, as plans are currently underway regarding the installation of a fish passage at the Merelbeke shipping complex (Visser et al., 2024), and erosion of the existing fishway in Asper resulted in its shutdown (Vercruysse et al., 2024).

5.3.2.3 Interaction between fishways and drought

Fishway-related changes in passage efficiencies and delays appeared to be different under normal flow conditions (Table 5.4) compared to drought conditions (Table 5.5), suggesting a potential interaction effect. To assess the interaction between fishways and drought, i.e., whether fishways have a different effect on passage and delay under dry conditions compared to normal flow, these tables should be mutually compared. However, since both tables reported absolute changes, based on different baseline values (S_0 versus S_1), relative differences rather than absolute ones should be compared. For this purpose, two indices were defined:

$$I_{4,2} = \left| \frac{\left(\frac{y(S_4) - y(S_1)}{y(S_1)} \right)}{\left(\frac{y(S_2) - y(S_0)}{y(S_0)} \right)} \right| \quad \text{for Merelbeke and Asper and} \quad (5.1)$$

$$I_{5,3} = \left| \frac{\left(\frac{y(S_5) - y(S_1)}{y(S_1)} \right)}{\left(\frac{y(S_3) - y(S_0)}{y(S_0)} \right)} \right| \quad \text{for Oudenaarde and Kerkhove.}$$

Here, $y(S_i)$ corresponds to the output data for scenario i , $I_{4,2}$ is the relative, beneficial effect of fishway *introduction* during drought compared to normal flow, and $I_{5,3}$ is the relative, adverse effect of fishway *removal* during drought compared to normal flow. A value of > 1 means the fishway effect was stronger under drought conditions, and vice versa. Calculated values for these indices are reported in Table 5.6. Since all indices corresponding to passage efficiency were > 1 , effects of fishway introduction and removal on passage success were stronger during drought compared to normal conditions. The most clear interaction appeared in Merelbeke and Asper (introduction) rather than in Oudenaarde and Kerkhove (removal). In contrast, indices for delays were consistently < 1 . This indicated that the effect of fish passages on delays was stronger under normal conditions compared to drought, especially in Oudenaarde and Kerkhove (removal), where indices were the lowest.

Table 5.6: Interaction indices between drought and the impact of fish passages. If $I_{4,2} > 1$, then the positive effects of fishway *introduction* are stronger during drought compared to normal flow conditions. If $I_{5,3} > 1$, then the negative effects of fishway *removal* are stronger during drought conditions. Values are reported as mean $\pm$ standard deviation.

Bottleneck	Scenario comparison	Passage efficiency (-)	Wait time for passage (-)	Wait time for returning (-)
Merelbeke	$I_{4,2}$	1.97 ± 0.13	0.97 ± 0.0004	0.91 ± 0.003
Asper	$I_{4,2}$	1.61 ± 0.24	0.97 ± 0.0007	0.94 ± 0.003
Oudenaarde	$I_{5,3}$	1.25 ± 0.14	0.56 ± 0.01	0.44 ± 0.07
Kerkhove	$I_{5,3}$	1.16 ± 0.16	0.61 ± 0.03	0.40 ± 0.04

One possible explanation for the passage efficiency interaction (with indices > 1) lies in the flow regimes at barriers and fishways. Under normal conditions, lamprey passage occurred primarily during periods of high discharge, often when there was for instance free flow at Merelbeke. During drought, however, discharge peaks in our model were less frequent or smaller, meaning that fishways became more necessary to help lampreys pass. Moreover, lower discharge may reduce turbulence and flow velocity within fishway channels, potentially making them easier to traverse (Silva et al., 2018). This would mean that overall, passages across fishways actually decrease at too high flows. The same reasoning may apply to the removal of fish passages in Oudenaarde and Kerkhove, where reductions in passage efficiency were more severe under drought.

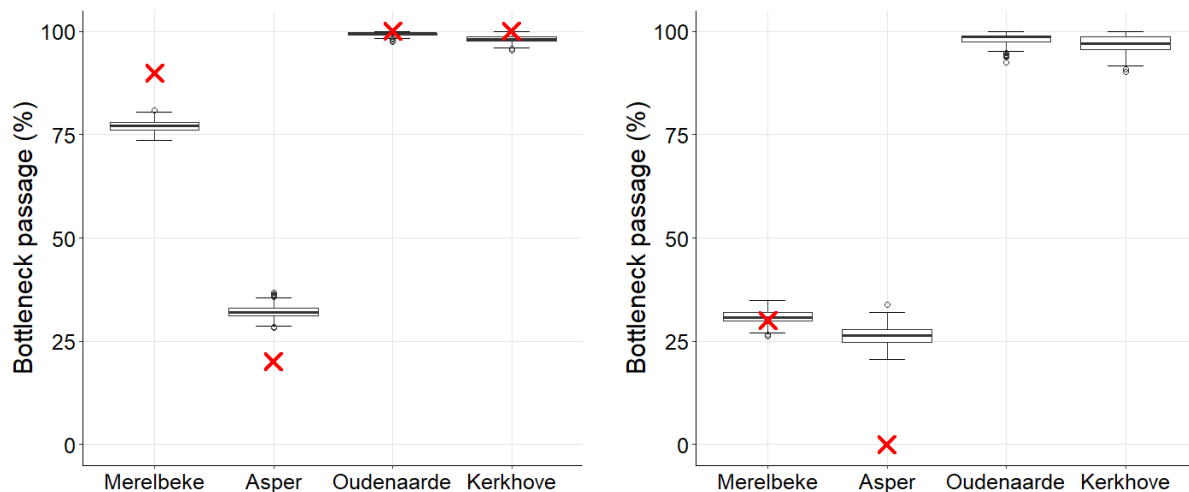
In other words, fishway presence generally increased passage success, but the effect was more noticeable during droughts, since high-flow events supporting passage over barriers occurred less frequently. However, in contrast to this hypothesis, some studies show that fishway performance declines under low-flow conditions (Foulds and Lucas, 2013; Castro-Santos et al., 2017), although they mainly focus on fishway attraction and entrance rather than traversal, or only consider limited flow ranges.

The wait time interaction (with indices < 1) might be explained by rheotaxis-driven behavior of lampreys at bottlenecks. Under normal conditions, fishways reduce delays. However, during drought, attraction flows at the entrance of fishways may be weaker, causing lampreys to search longer (Foulds and Lucas, 2013; Castro-Santos et al., 2017). Removal of these fishways on the other hand increases migration delays under normal conditions, but during drought, the attraction flow is already low, so removing the fishway only increases wait times to a limited extent. In other words, bottlenecks with fishways may lead to more delays during droughts than under normal conditions, even though they eventually allow more individuals to pass over time. Although attraction to fishways was not explicitly modeled in our IBM, the survival submodel might have incorporated this indirectly through its regression coefficients, as lower discharge resulted in longer searching behavior.

5.4 Qualitative model validation

Because empirical observations were limited, quantitative validation (e.g., cross validation) and parameter optimization were not feasible. Validation therefore primarily focused on checking whether the model was able to reproduce the observed patterns in the calibration data. This was done by qualitatively comparing simulated and observed passage efficiencies and migration delays for both tagged lamprey batches.

Passage efficiencies for the 2024 and 2025 batches are shown in Figure 5.6a and 5.6b, respectively. In general, observations aligned relatively well with predicted passage success. For instance, the IBM accurately reproduced the observed difference in passage efficiencies across batches for Merelbeke. In Section 4.4.1, this difference was hypothesized to be a consequence of the smaller average size of the second batch. However, in the IBM, a population of 1000 individuals was simulated, where a size bias was no longer present because it had not been included in the model. The difference was therefore likely a result of the lower river discharge in December 2025 (average 20.9 m³/s) compared to December 2024 (average 47.5 m³/s), and not of differences in lamprey size.



(a) Simulated and observed passage efficiencies for the 2024 lamprey batch, from 4 December 2024 to 5 April 2025.

(b) Simulated and observed passage efficiencies for the 2025 lamprey batch, from 27 November 2025 to 16 May 2026.

Figure 5.6: Boxplots represent 250 *in silico* passage efficiencies per bottleneck, each calculated from a population of 1000 individuals. Red crosses denote the passage efficiencies for the two lamprey batches observed in the telemetry data.

Although both discharge and weir overflow experienced by the second batch in Asper during the initial months were lower than for the first batch, the model appeared to overestimate passage for the second batch in Asper. This may indicate the presence of an underlying factor other than flow effects, that was not included in the predictor structure (for example, a size effect after all). Alternatively, the

observed data might just have been too limited to reproduce accurate effects at Asper, since only three tagged individuals from the first batch, and none from the second batch could pass.

In silico and observed delay times lampreys experienced at the Merelbeke and Asper bottlenecks before they returned or passed are shown in Figure 5.7. Similar to literature and our own telemetry observations, delays showed multimodal patterns (Davies et al., 2022). While some details were not captured by the model, such as the initial abandonment peak at short waiting times in Asper, overall delay time patterns were reproduced by the IBM.



Figure 5.7: In silico and observed delays in front of the Merelbeke and Asper bottlenecks. The histograms represent telemetry observations of waiting times in front of bottlenecks before returning (red) or passing (green), while the dotted lines are the corresponding simulation results. The 2024 and 2025 batch observations and simulations are grouped together in this plot, such that it consists of 250 simulations of each 2000 individuals.

Note that, since calibration data coincided with validation data, the assessment of the model's performance might be overly optimistic. Moreover, our model was parametrized using a limited number of individuals, and made use of two correlative regression submodels. Correlative and statistical approaches are limited in their ability to capture study sites or conditions other than those for which they are calibrated (Mawer et al., 2023). Therefore, the robustness of the model structure and coefficients should be further verified using additional telemetry data collected in the future, both in the Upper Scheldt River and in other fragmented river systems (e.g., the Leie).

5. An individual-based model of lamprey migration

Furthermore, the underlying model assumptions should also be evaluated, as they influence the results. An example is the three lampreys that returned between Semmerzake and Asper (see Chapter 4). These individuals may have abandoned migration without encountering a bottleneck, or may have entered sidestreams associated with potential spawning habitat. However, the model assumes that abandonment only occurs at bottlenecks and not in free-flowing sections (e.g., due to predation), and that lampreys do not enter sidestreams with intermediate potential spawning habitat before Avelgem. In addition, return movements and subsequent migrations into other river systems (e.g., the Nete) are also not considered. These assumptions are currently regarded reasonable given the limited occurrence of such behavior and the focus on bottleneck passage. However, if future telemetry data show repeated instances of these patterns, the assumptions should be revisited.

Conclusion and perspectives

In this study, we primarily investigated the effect of river fragmentation on the spawning migration of the diadromous European river lamprey in the Upper Scheldt River, using acoustic telemetry. More specifically, we analyzed (1) the effects of barrier presence on migration success and speed, (2) the extent to which environmental conditions and weir operation influence passage success, and (3) environmental drivers of free migration speed. In addition, we developed an individual-based model (IBM) for migration, to evaluate current and alternative scenarios.

Our results clearly showed adverse impacts of river fragmentation, both in terms of migration success and delays. At the shipping lock complexes of Merelbeke and Asper, drastic reductions in numbers and long waiting times were observed, with only 6% able to pass through both. However, the next two shipping lock complexes in Oudenaarde and Kerkhove, that both contain fish passages, reduced delay and sustained 100% passage for the limited number of individuals that reached them.

Lampreys were more successful in passing shipping lock complexes during high river discharge, water level and weir overflow, while they were less successful at higher weir underflow rates, indicating a velocity barrier effect. Furthermore, our data suggested that the rare occurrences of free-flowing regimes in Merelbeke, when weirs were lifted from the stream during peak discharge conditions, were essential to enable passage of large numbers of river lampreys.

During unobstructed migration, the river lamprey visibly exhibited nocturnal behavior, and the few individuals that reached far upstream appeared to swim both faster and more directed when the migration season advanced and they got closer to their potential spawning grounds.

Finally, the IBM could reproduce observed migration patterns and allowed for scenario analysis. Drought decreased passage efficiency over shipping lock complexes, and generally increased migration delays, although the effect was smaller when fish passages were present. If the latter were introduced at the migration barriers in Merelbeke or Asper, passage efficiency increased and delay decreased, whereas their removal in Oudenaarde and Kerkhove did the opposite. Furthermore, fish passages interacted with drought, since their effect on passage efficiency and migration delay was stronger during dry and normal flow conditions, respectively.

Since this study covered a limited number of individuals, with only three lampreys reaching shipping lock complexes with fish passages, results and conclusions should be approached with particular caution, especially regarding fishway effects. Therefore, to validate our findings on migration patterns and passage efficiencies, further research using the developed methodology on a larger sample size of tagged river lampreys is needed. Annual tagging studies conducted by INBO are currently ongoing, meaning that available telemetry data will continue to increase over time. In addition, passage efficiencies should not be generalized to other diadromous species, as passage mechanisms differ among taxa (Kemp et al., 2010; Russon et al., 2011). Ongoing research into other diadromous species may further clarify differences in fishway efficiency across species.

While our research answered several important questions regarding the spawning migration of the river lamprey in the Upper Scheldt River, some remain. For instance, further fine-scale telemetry could help identify the mechanisms underlying passage behavior and explain the differences in weir passage success between Asper and Merelbeke (at location A2). Although previous research indicates that river lampreys do not exhibit selective tidal stream transport in unobstructed sections (Silva et al., 2017b), our results suggest that at the bottleneck in Merelbeke, a significant fraction of individuals passed during flood. This contrasts with Asper, where tidal influence is absent, and requires further investigation. Additional explanatory factors may include differences in barrier characteristics and local flow regimes.

Fishway efficiencies were remarkably high, and while the number of individuals reaching them was limited, this still emphasizes their importance. However, these fishways were only present at the most upstream shipping lock complexes, whereas our scenario analysis indicated that improving passage at downstream bottlenecks could lead to substantial benefits. This suggests that future fishway management in the Upper Scheldt River should prioritize downstream bottlenecks such as the ones in Merelbeke and Asper. Together, our findings may contribute to improved management of fish passages and weirs in the Upper Scheldt River, for example through optimized flow conditions or adjusted barrier management.

Finally, this dissertation may provide indications regarding the location of lamprey spawning areas, both within the Upper Scheldt and in other river systems, such as the Grote Nete and Demer. Previous efforts to identify larval nurseries and spawning habitats were unsuccessful (Stevens et al., 2011), making these observations particularly interesting. Alternatively, because river lampreys are known to spawn with the satellite species brook lamprey (*Lampetra planeri*) (Lasne et al., 2010; Staponkus and Kesminas, 2014), these migration patterns may instead indicate the presence of brook lamprey spawning grounds attracting river lampreys. Brook lamprey populations are currently known to reside in several river systems, including the Grote Nete (Van Thuyne et al., 2016). Identifying spawning habitats and nurseries of both species remains essential for effective conservation.

Bibliography

- Abecasis, D., Steckenreuter, A., Reubens, J., Aarestrup, K., Alós, J., Badalamenti, F., Bajona, L., Boylan, P., Deneudt, K., Greenberg, L., Breve, N., Hernandez, F., Humphries, N., Meyer, C., Sims, D., Thorstad, E., Walker, A., Whoriskey, F., and Afonso, P. (2018). A review of acoustic telemetry in Europe and the need for a regional aquatic telemetry network. *Animal Biotelemetry*, 6:12.
- Abersons, K., Raibarte, P., Elferts, D., and Dimante-Deimantovica, I. (2025). Weak reproductive response of European river lamprey to a newly built fishway—a case study from Latvia. *River Research and Applications*, 42(1):284–292.
- Agostinho, A., Pelicice, F., and Gomes, L. (2008). Dams and the fish fauna of the Neotropical region: Impacts and management related to diversity and fisheries. *Brazilian journal of biology*, 68:1119–1132.
- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19(6):716–723.
- Almeida, P., Quintella, B., and Dias, N. (2002). Movement of radio-tagged anadromous sea lamprey during the spawning migration in the River Mondego (Portugal). *Hydrobiologia*, 483(1–3):1–8.
- Almeida, P. R., Arakawa, H., Aronsuu, K., Baker, C., Blair, S.-R., Beaulaton, L., Belo, A. F., Kitson, J., Kucheryavyy, A., Kynard, B., Lucas, M. C., Moser, M., Potaka, B., Romakkaniemi, A., Staponkus, R., Tamarapa, S., Yanai, S., Yang, G., Zhang, T., and Zhuang, P. (2021). Lamprey fisheries: History, trends and management. *Journal of Great Lakes Research*, 47:S159–S185. Supplement on Sea Lamprey International Symposium III (SLIS III).
- Aronsuu, K., Marjomäki, T., Tuohino, J., Wennman, K., R., V., and Ojutkangas, E. (2015). Migratory behaviour and holding habitats of adult river lampreys (*Lampetra fluviatilis*) in two Finnish rivers. *Boreal Environment Research*, 20:120–144.
- Aronsuu, K., Vikström, R., Marjomäki, T. J., Wennman, K., Pakkala, J., Mäenpää, E., Tuohino, J., Sarell, J., and Ojutkangas, E. (2019). Rehabilitation of two northern river lamprey (*Lampetra fluviatilis*) populations impacted by various anthropogenic pressures: Lessons learnt in the past three decades. Jyväskylän yliopiston bio- ja ympäristötieteiden laitoksen tiedonantoja (2/2019), University of Jyväskylä.

-
- Ashley, M., Murillas, A., Muench, A., Marta-Pedroso, C., Rodwell, L., Rees, S., Rendle, E., Bašić, T., Copp, G. H., Díaz, E., Nachón, D. J., Lambert, P., and Lassalle, G. (2023). An evidence base of ecosystems services provided by diadromous fish in the European Atlantic Area. *Ecosystem Services*, 64:101559.
- Badger, J. J., Johnson, D. S., Baird, R. W., Bradford, A. L., Kratofil, M. A., Mahaffy, S. D., and Oleson, E. M. (2024). Incorporating telemetry information into capture-recapture analyses improves precision and accuracy of abundance estimates given spatiotemporally biased recapture effort. *Methods in Ecology and Evolution*, 15(10):1847–1858.
- Baer, J., Hartmann, F., and Brinker, A. (2018). Abiotic triggers for sea and river lamprey spawning migration and juvenile outmigration in the River Rhine, Germany. *Ecology of Freshwater Fish*, 27(4):988–998.
- Baetens, J., Van Nieuland, S., Pauwels, I., De Baets, B., Mouton, A., and Goethals, P. (2013). An individual-based model for the migration of pike (*Esox lucius*) in the river Yser, Belgium. *Ecological Modelling*, 258:40–52.
- Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., Bund, W., Aarestrup, K., Barry, J., Belka, K., Berkhuysen, A., Birnie-Gauvin, K., Bussettini, M., Carolli, M., Consuegra, S., Dopico, E., Feierfeil, T., Fernández, S., and Zalewski, M. (2020). More than one million barriers fragment Europe’s rivers. *Nature*, 588:436–441.
- Berec, L. (2002). Techniques of spatially explicit individual-based models: construction, simulation, and mean-field analysis. *Ecological Modelling*, 150(1):55–81.
- Binder, T. R., McLaughlin, R. L., and McDonald, D. G. (2010). Relative importance of water temperature, water level, and lunar cycle to migratory activity in spawning-phase sea lampreys in Lake Ontario. *Transactions of the American Fisheries Society*, 139(3):700–712.
- Birnie-Gauvin, K., Larsen, M. H., Nielsen, J., and Aarestrup, K. (2017). 30 years of data reveal dramatic increase in abundance of brown trout following the removal of a small hydrodam. *Journal of Environmental Management*, 204:467–471.
- Boeker, C. and Geist, J. (2016). Lampreys as ecosystem engineers: Burrows of *Eudontomyzon* sp. and their impact on physical, chemical, and microbial properties in freshwater substrates. *Hydrobiologia*, 777:171–181.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., and White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24(3):127–135.
- Bolland, J. D., Murphy, L. A., Stanford, R. J., Angelopoulos, N. V., Baker, N. J., Wright, R. M., Reeds, J. D., and Cowx, I. G. (2019). Direct and indirect impacts of pumping

- station operation on downstream migration of critically endangered European eel. *Fisheries Management and Ecology*, 26(1):76–85.
- Breine, J., Stevens, M., Simoens, I., and Van den Bergh, E. (2008). A reference list of fish species for a heavily modified estuary and its tributaries: the River Schelde. Rapporten van het Instituut voor Natuur- en Bosonderzoek 2008 (INBO.R.2008.4), Instituut voor Natuur- en Bosonderzoek, Brussels, Belgium.
- Breslow, N. (1972). Discussion on professor Cox's paper. *Journal of the Royal Statistical Society: Series B (Methodological)*, 34(2):202–220.
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., and Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2):378–400.
- Brownscombe, J., Lédée, E., Raby, G., Struthers, D., Gutowsky, L., Nguyen, V., Young, N., Stokesbury, M., Holbrook, C., Brenden, T., Vandergoot, C., Murchie, K., Whoriskey, K., Mills Flemming, J., Kessel, S., Krueger, C., and Cooke, S. (2019). Conducting and interpreting fish telemetry studies: considerations for researchers and resource managers. *Reviews in Fish Biology and Fisheries*, 29:369–400.
- Brownscombe, J. W., Griffin, L. P., Brooks, J. L., Danylchuk, A. J., Cooke, S. J., and Midwood, J. D. (2022). Applications of telemetry to fish habitat science and management. *Canadian Journal of Fisheries and Aquatic Sciences*, 79(8):1347–1359.
- Brownscombe, J. W., Griffin, L. P., Chapman, J. M., Morley, D., Acosta, A., Crossin, G. T., Iverson, S. J., Adams, A. J., Cooke, S. J., and Danylchuk, A. J. (2020). A practical method to account for variation in detection range in acoustic telemetry arrays to accurately quantify the spatial ecology of aquatic animals. *Methods in Ecology and Evolution*, 11(1):82–94.
- Bruneel, S., Goossens, J., Reubens, J., Pauwels, I., Moens, T., Goethals, P., and Verhelst, P. (2023). Turning the tide - understanding estuarine detection range variability via structural equation models. *Animal Biotelemetry*, 11:38.
- Bubb, D. H., Birnie-Gauvin, K., Tummers, J. S., Aarestrup, K., Jepsen, N., and Lucas, M. C. (2021). Short-term effects of low-head barrier removals on fish communities and habitats. *Frontiers in Ecology and Evolution*, 9:697106.
- Buysse, D., Coeck, J., and Maes, J. (2008). Potential re-establishment of diadromous fish species in the River Scheldt (Belgium). *Hydrobiologia*, 602(1):155–159.
- Buysse, D., Martens, S., Baeyens, R., and Coeck, J. (2004). Onderzoek naar de migratie van vissen tussen Boven-Zeeschelde en Bovenschelde. Rapporten van het Instituut voor Natuurbehoud (IN.R.2004.02), Instituut voor Natuurbehoud, Brussels, Belgium.

-
- Buyse, D., Mouton, A., Stevens, M., Van den Neucker, T., and Coeck, J. (2014). Mortality of European eel after downstream migration through two types of pumping stations. *Fisheries Management and Ecology*, 21(1):13–21.
- Carpenter, S. R., Stanley, E. H., and Vander Zanden, M. J. (2011). State of the world's freshwater ecosystems: Physical, chemical, and biological changes. *Annual Review of Environment and Resources*, 36(Volume 36, 2011):75–99.
- Castro-Santos, T. and Haro, A. (2003). Quantifying migratory delay: a new application of survival analysis methods. *Canadian Journal of Fisheries and Aquatic Sciences*, 60(8):986–996.
- Castro-Santos, T., Shi, X., and Haro, A. (2017). Migratory behavior of adult sea lamprey and cumulative passage performance through four fishways. *Canadian Journal of Fisheries and Aquatic Sciences*, 74(5):790–800.
- Chan, J. C. F., Lam, B. Y. K., Dudgeon, D., and Liew, J. H. (2025). Global consequences of dam-induced river fragmentation on diadromous migrants: a systematic review and meta-analysis. *Biological Reviews*, 100(5):2020–2037.
- Clemens, B. J., Binder, T. R., Docker, M. F., Moser, M. L., and Sower, S. A. (2010). Similarities, differences, and unknowns in biology and management of three parasitic lampreys of North America. *Fisheries*, 35(12):580–594.
- Close, D. A., Fitzpatrick, M. S., and Li, H. W. (2002). The ecological and cultural importance of a species at risk of extinction, Pacific lamprey. *Fisheries*, 27(7):19–25.
- Cooke, S., Hinch, S., Lucas, M., and Lutcavage, M. (2012). Biotelemetry and biologging. In Zale, A., Parrish, D., and Sutton, T., editors, *Fisheries Techniques 3rd ed.*, pages 819–881. American Fisheries Society, Bethesda, Maryland.
- Cornell, S. J., Suprunenko, Y. F., Finkelshtein, D., Somervuo, P., and Ovaskainen, O. (2019). A unified framework for analysis of individual-based models in ecology and beyond. *Nature Communications*, 10(1).
- Cox, D. R. (1972). Regression models and life-tables. *Journal of the Royal Statistical Society: Series B (Methodological)*, 34(2):187–202.
- Dam Removal Europe (2025). Home - dam removal europe. <https://damremoval.eu/>. Accessed 22 October 2025.
- Davies, P., Britton, J. R., Nunn, A. D., Dodd, J. R., Bainger, C., Velterop, R., and Bolland, J. D. (2021). Cumulative impacts of habitat fragmentation and the environmental factors affecting upstream migration in the threatened sea lamprey, *Petromyzon marinus*. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(9):2560–2574.

- Davies, P., Britton, J. R., Nunn, A. D., Dodd, J. R., Bainger, C., Velterop, R., and Bolland, J. D. (2022). Individual movement variation in upstream-migrating sea lamprey *Petromyzon marinus* in a highly fragmented river. *Freshwater Biology*, 67(4):643–656.
- Dawson, H., Quintella, B., Almeida, P., Treble, A., and Jolley, J. (2015). The ecology of larval and metamorphosing lampreys. In Docker, M. F., editor, *Lampreys: Biology, Conservation and Control: Volume 1*, pages 75–137. Springer Netherlands, Dordrecht.
- Dean, E. M., Infante, D. M., Yu, H., Cooper, A., Wang, L., and Ross, J. (2023). Cumulative effects of dams on migratory fishes across the conterminous United States: Regional patterns in fish responses to river network fragmentation. *River Research and Applications*, 39(9):1736–1748.
- DeAngelis, D. L. and Grimm, V. (2014). Individual-based models in ecology after four decades. *F1000Prime Reports*, 6(39).
- Dietrich, J., Rickard, A., Sethi, S. A., Cuppett, S., and Sullivan, P. (2025). Aquatic habitat response to small dam removal demonstrates recovery in three years. *Ecosphere*, 16(6):e70323.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., and Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1):27–46.
- Drouineau, H., Carter, C., Rambonilaza, T., Beaufaron, G., Bouleau, G., Gassiat, A., Lambert, P., Floch, S., Tétard, S., and De Oliveira, E. (2018). River continuity restoration and diadromous fishes: Much more than an ecological issue. *Environmental Management*, 61:671–686.
- Dubuis, R. and De Cesare, G. (2023). The clogging of riverbeds: A review of the physical processes. *Earth-Science Reviews*, 239:104374.
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D., Stiasny, M. L. J., and Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, 81(2):163–182.
- Dunkle, M. R., Lampman, R. T., Jackson, A. D., and Caudill, C. C. (2020). Factors affecting the fate of Pacific lamprey carcasses and resource transport to riparian and stream macrohabitats. *Freshwater Biology*, 65(8):1429–1439.
- Ecopedia (n.d.). Rivierprik (*Lampetra fluviatilis*). <https://www.ecopedia.be/dieren/rivierprik>. Accessed 22 May 2026.

-
- Fine, J., Vrieze, L., and Sorensen, P. (2004). Evidence that Petromyzontid lampreys employ a common migratory pheromone that is partially comprised of bile acids. *Journal of chemical ecology*, 30:2091–2110.
- Ford, M. (2024). *Lampetra fluviatilis* — the IUCN red list of threatened species. <https://www.iucnredlist.org/species/11206/135088436>. Accessed 15 September 2025.
- Foulds, W. L. and Lucas, M. C. (2013). Extreme inefficiency of two conventional, technical fishways used by European river lamprey (*Lampetra fluviatilis*). *Ecological Engineering*, 58:423–433.
- Garcia de Leaniz, C. and O’Hanley, J. R. (2022). Operational methods for prioritizing the removal of river barriers: Synthesis and guidance. *Science of The Total Environment*, 848:157471.
- Gaudron, S. M. and Lucas, M. C. (2006). First evidence of attraction of adult river lamprey in the migratory phase to larval odour. *Journal of Fish Biology*, 68(2):640–644.
- Gauld, N., Campbell, R., and Lucas, M. (2013). Reduced flow impacts salmonid smolt emigration in a river with low-head weirs. *Science of The Total Environment*, 458-460:435–443.
- Gess, R., Coates, M., and Rubidge, B. (2006). A lamprey from the Devonian period of South Africa. *Nature*, 443:981–984.
- Gowans, A. R. D., Armstrong, J. D., Priede, I. G., and Mckelvey, S. (2003). Movements of Atlantic salmon migrating upstream through a fish-pass complex in Scotland. *Ecology of Freshwater Fish*, 12(3):177–189.
- Griffin, K. R., Holbrook, C. M., Zielinski, D. P., Cahill, C. L., and Wagner, C. M. (2025). Not all who meander are lost: migrating sea lamprey follow river thalwegs to facilitate safe and efficient passage upstream. *Journal of Experimental Biology*, 228(4):jEB249539.
- Griffioen, A., Winter, H., and van Hal, R. (2017). Prognose visstand in en rond het Haringvliet na invoering van het Kierbesluit in 2018. Wageningen Marine Research rapport C081/17, Wageningen Marine Research, Netherlands.
- Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M., Meng, J., Mulligan, M., and Zarfl, C. (2019). Mapping the world’s free-flowing rivers. *Nature*, 569:215–221.
- Grimm, V. and Railsback, S. (2005). *Individual-based modeling and ecology*. Princeton University Press.

- Grimm, V., Railsback, S. F., Vincenot, C. E., Berger, U., Gallagher, C., DeAngelis, D. L., Edmonds, B., Ge, J., Giske, J., Groeneveld, J., Johnston, A. S., Milles, A., Nabe-Nielsen, J., Polhill, J. G., Radchuk, V., Rohwäder, M.-S., Stillman, R. A., Thiele, J. C., and Ayllón, D. (2020). The ODD protocol for describing agent-based and other simulation models: A second update to improve clarity, replication, and structural realism. *Journal of Artificial Societies and Social Simulation*, 23(2):7.
- Hanel, L., Andreska, J., and Dyldin, Y. (2022). Lampreys in human life, their cultural and folklore importance. *Humanities and Social Sciences*, 10(5):290–305.
- Hauer, C., Leitner, P., Unfer, G., Pulg, U., Habersack, H., and Graf, W. (2018). The role of sediment and sediment dynamics in the aquatic environment. In Schmutz, S. and Sendzimir, J., editors, *Riverine Ecosystem Management: Science for Governing Towards a Sustainable Future*, pages 151–169. Springer, Cham.
- Hockersmith, E. and Beeman, J. W. (2012). A history of telemetry in fishery research. In Adams, N. S., Beeman, J. W., and Eiler, J. H., editors, *Telemetry techniques: A user guide for fisheries research*, pages 7–19. American Fisheries Society, Bethesda, Maryland.
- Hogg, R., Coghlan Jr., S. M., and Zydlewski, J. (2013). Anadromous sea lampreys recolonize a Maine coastal river tributary after dam removal. *Transactions of the American Fisheries Society*, 142(5):1381–1394.
- Hogg, R. S., Coghlan Jr, S. M., Zydlewski, J., and Simon, K. S. (2014). Anadromous sea lampreys (*Petromyzon marinus*) are ecosystem engineers in a spawning tributary. *Freshwater Biology*, 59(6):1294–1307.
- Hohensinner, S., Hauer, C., and Muhar, S. (2018). River morphology, channelization, and habitat restoration. In Schmutz, S. and Sendzimir, J., editors, *Riverine Ecosystem Management: Science for Governing Towards a Sustainable Future*, pages 41–65. Springer, Cham.
- Hubbard, S., Babak, P., Sigurdsson, S. T., and Magnússon, K. G. (2004). A model of the formation of fish schools and migrations of fish. *Ecological Modelling*, 174(4):359–374.
- Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., Harcourt, R. G., Holland, K. N., Iverson, S. J., Kocik, J. F., Flemming, J. E. M., and Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Science*, 348(6240):1255642.
- Huysecom, S., Mouton, A., Buysse, D., Gelaude, E., Baeyens, R., Jacobs, Y., Stevens, M., Van den Neucker, T., Robberechts, K., Pauwels, I., and Coeck, J. (2012). Evaluatie van de visnevengeulen bij de stuwen van Asper en Oudenaarde in de Bovenschelde. Rapporten van het Instituut voor Natuur- en Bosonderzoek 2012 (INBO.R.2012.66), Instituut voor Natuur- en Bosonderzoek, Brussels, Belgium.

-
- Jager, H. I. and DeAngelis, D. L. (2018). The confluences of ideas leading to, and the flow of ideas emerging from, individual-based modeling of riverine fishes. *Ecological Modelling*, 384:341–352.
- Jang, M.-H. and Lucas, M. C. (2005). Reproductive ecology of the river lamprey. *Journal of Fish Biology*, 66(2):499–512.
- Johnson, E. L., Caudill, C. C., Keefer, M. L., Clabough, T. S., Peery, C. A., Jepson, M. A., and Moser, M. L. (2012). Movement of radio-tagged adult Pacific lampreys during a large-scale fishway velocity experiment. *Transactions of the American Fisheries Society*, 141(3):571–579.
- Johnson, N., Buchinger, T., and Li, W. (2015). Reproductive ecology of lampreys. In Docker, M. F., editor, *Lampreys: Biology, Conservation and Control: Volume 1*, pages 265—303. Springer Netherlands, Dordrecht.
- Jubb, W., Noble, R., Dodd, J., Nunn, A., Lothian, A., Albright, A., Bubbs, D., Lucas, M., and Bolland, J. (2023a). Acoustic telemetry informs conditional capture probability of an anadromous fish. *Fisheries Research*, 264:106737.
- Jubb, W., Noble, R., Dodd, J., Nunn, A., Lothian, A., Albright, A., Bubbs, D., Lucas, M., and Bolland, J. (2023b). Understanding the impact of barriers to onward migration; a novel approach using translocated fish. *Journal of Environmental Management*, 335:117488.
- Kainua, K. and Valtonen, T. (1980). Distribution and abundance of European river lamprey (*Lampetra fluviatilis*) larvae in three rivers running into Bothnian Bay, Finland. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(11):1960–1966.
- Katopodis, C. and Williams, J. G. (2012). The development of fish passage research in a historical context. *Ecological Engineering*, 48:8–18. Ecohydraulic Approaches for Restoring Habitat Connectivity and Suitability.
- Keefer, M. L., Caudill, C. C., Peery, C., and Moser, M. L. (2013). Context-dependent diel behavior of upstream-migrating anadromous fishes. *Environmental Biology of Fishes*, 96(6):691 – 700.
- Keefer, M. L., Moser, M. L., Boggs, C. T., Daigle, W. R., and Peery, C. A. (2009a). Effects of body size and river environment on the upstream migration of adult Pacific lampreys. *North American Journal of Fisheries Management*, 29(5):1214–1224.
- Keefer, M. L., Moser, M. L., Boggs, C. T., Daigle, W. R., and Peery, C. A. (2009b). Variability in migration timing of adult Pacific lamprey (*Lampetra tridentata*) in the Columbia River, U.S.A. *Environmental Biology of Fishes*, 85(3):253–264.
- Kelly, F. and King, J. (2001). A review of the ecology and distribution of three lamprey species, *Lampetra fluviatilis* (L.), *Lampetra planeri* (Bloch) and *Petromyzon*

- marinus* (L.): A context for conservation and biodiversity considerations in Ireland. *Biology and Environment*, 101:165–185.
- Kemp, P. S. and O'Hanley, J. R. (2010). Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. *Fisheries Management and Ecology*, 17(4):297–322.
- Kemp, P. S., Russon, I. J., Vowles, A. S., and Lucas, M. C. (2010). The influence of discharge and temperature on the ability of upstream migrant adult river lamprey (*Lampetra fluviatilis*) to pass experimental overshoot and undershot weirs. *River Research and Applications*, 27(4):488–498.
- Kerby, J. L., Riley, S. P., Kats, L. B., and Wilson, P. (2005). Barriers and flow as limiting factors in the spread of an invasive crayfish (*Procambarus clarkii*) in southern California streams. *Biological Conservation*, 126(3):402–409.
- Kerr, J., Tummers, J., Benson, T., Lucas, M., and Kemp, P. (2023). Modelling fine scale route choice of upstream migrating fish as they approach an instream structure. *Ecological Modelling*, 478:110210.
- Kerr, J. R., Zielinski, D. P., Goodwin, R. A., Holbrook, C. M., and McLaughlin, R. L. (2025). Upriver migrating sea lamprey exhibit similar responses to hydrodynamic features as other up and downriver-moving species. *Frontiers in Freshwater Science*, 3:1528481.
- Kessel, S., Cooke, S., Heupel, M., Hussey, N., Simpfendorfer, C., Vagle, S., and Fisk, A. (2014). A review of detection range testing in aquatic passive acoustic telemetry studies. *Rev Fish Biol Fisheries*, 24:199–218.
- Kleinbaum, D. G. and Klein, M. (2005). *Survival Analysis: A Self-Learning Text*. Springer, New York.
- Kukuła, K. and Bylak, A. (2022). Barrier removal and dynamics of intermittent stream habitat regulate persistence and structure of fish community. *Scientific Reports*, 12:1512.
- Lasne, E., Sabatié, M.-R., and Evanno, G. (2010). Communal spawning of brook and river lampreys (*Lampetra planeri* and *L. fluviatilis*) is common in the Oir River (France). *Ecology of Freshwater Fish*, 19(3):323–325.
- Limburg, K. E. and Waldman, J. R. (2009). Dramatic declines in North Atlantic diadromous fishes. *BioScience*, 59(11):955–965.
- Lin, D. Y. (2007). On the Breslow estimator. *Lifetime Data Analysis*, 13(4):471–480.
- Loki Austanfell (2011). Ammocoetes larva of Eastern brook lamprey (*Lethenteron cf. mitsukurii*). Wikimedia Commons. Available at https://commons.wikimedia.org/wiki/File:Ammocoetes-l_reissneri-01.jpg (Accessed 22 May 2026). Licensed under CC BY-SA 3.0.

-
- Lothian, A., Bolland, J., Albright, A., Jubb, W., Bubb, D., Noble, R., Nunn, A., Dodd, J., Tummers, J., and Lucas, M. (2024). Factors influencing European river lamprey passage at a tidal river barrier. *Hydrobiologia*, 851:4803–4820.
- Lucas, M. and Baras, E. (2001). *Migration of Freshwater Fishes*. Blackwell Science, Oxford.
- Lucas, M. C., Bubb, D. H., Jang, M.-H., Ha, K., and Masters, J. E. G. (2009). Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lampreys. *Freshwater Biology*, 54(3):621–634.
- Lucas, M. C., Hume, J. B., Almeida, P. R., Aronsuu, K., Habit, E., Silva, S., Wang, C. J., and Zampatti, B. (2021). Emerging conservation initiatives for lampreys: Research challenges and opportunities. *Journal of Great Lakes Research*, 47:S690–S703. Supplement on Sea Lamprey International Symposium III (SLIS III).
- Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., and Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6(60):3139.
- Maes, J. and Ollevier, F. (2005). Impact van baggeractiviteiten in de Beneden-Zeeschelde op de ecologie van de rivierprik. Studierapport in opdracht van de afdeling maritieme toegang, Katholieke Universiteit Leuven, Belgium.
- Maitland, P. S. (2003). *Ecology of the River, Brook and Sea Lamprey*. Conserving Natura 2000 Rivers Ecology Series No. 5. English Nature, Peterborough.
- Manzon, R., Youson, J., and Holmes, J. (2015). Lamprey metamorphosis. In Docker, M. F., editor, *Lampreys: Biology, Conservation and Control: Volume 1*, pages 139–214. Springer Netherlands, Dordrecht.
- Masters, J. E., Jang, M.-H., Ha, K., Bird, P., Frear, P., and Lucas, M. (2006). The commercial exploitation of a protected anadromous species, the river lamprey (*Lampetra fluviatilis* (L.)), in the tidal River Ouse, north-east England. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 16(1):77–92.
- Mateus, C., Rodríguez-Muñoz, R., Quintella, B., Alves, M., and Almeida, P. (2012). Lampreys of the Iberian Peninsula: Distribution, population status and conservation. *Endangered Species Research*, 16(2):183–198.
- Mawer, R., Pauwels, I. S., Bruneel, S. P., Goethals, P. L., Kopecki, I., Elings, J., Coeck, J., and Schneider, M. (2023). Individual based models for the simulation of fish movement near barriers: Current work and future directions. *Journal of Environmental Management*, 335:117538.
- McDowall, R. M. (1997). The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. *Reviews in Fish Biology and Fisheries*, 7(4):443–462.

- Moore, D. F. (2016). *Applied Survival Analysis Using R*. Springer, Cham.
- Moser, M. L., Almeida, P. R., Kemp, P. S., and Sorensen, P. W. (2015). Lamprey spawning migration. In Docker, M. F., editor, *Lampreys: Biology, Conservation and Control: Volume 1*, pages 215–263. Springer Netherlands, Dordrecht.
- Moser, M. L., Almeida, P. R., King, J. J., and Pereira, E. (2021). Passage and freshwater habitat requirements of anadromous lampreys: Considerations for conservation and control. *Journal of Great Lakes Research*, 47:S147–S158. Supplement on Sea Lamprey International Symposium III (SLIS III).
- Mouton, A., Stevens, M., Van den Neucker, T., Buysse, D., and Coeck, J. (2011). Adjusted barrier management to improve glass eel migration at an estuarine barrier. *Marine Ecology Progress Series*, 439:213–222.
- Neeson, T. M., Ferris, M. C., Diebel, M. W., Doran, P. J., O’Hanley, J. R., and McIntyre, P. B. (2015). Enhancing ecosystem restoration efficiency through spatial and temporal coordination. *Proceedings of the National Academy of Sciences*, 112(19):6236–6241.
- Neeson, T. M., Wiley, M. J., Adlerstein, S. A., and Riolo, R. L. (2011a). How river network structure and habitat availability shape the spatial dynamics of larval sea lampreys. *Ecological Modelling*, 226:62–70.
- Neeson, T. M., Wiley, M. J., Adlerstein, S. A., and Riolo, R. L. (2011b). River network structure shapes interannual feedbacks between adult sea lamprey migration and larval habitation. *Ecological Modelling*, 222(17):3181–3192.
- Nicolai, R., Gensen, M., Stolp, T., Thant, S., Michielsen, S., Messens, F., Van de Moortel, I., Boudewijn, T., van de Haterd, R., van der Jagt, H., de Jong, J., Middelveld, R. P., Van Echelpoel, W., and Bruneel, S. (2023). Analyserapport. T2021-rapportage Schelde-estuarium. Technical report, HKV / Antea Group / Universiteit Gent / Bureau Waardenburg, Nederland / België.
- Nieland, J. L., Sheehan, T. F., and Saunders, R. (2015). Assessing demographic effects of dams on diadromous fish: a case study for Atlantic salmon in the Penobscot River, Maine. *ICES Journal of Marine Science*, 72(8):2423–2437.
- Nilsson, C., Reidy, C. A., Dynesius, M., and Revenga, C. (2005). Fragmentation and flow regulation of the world’s large river systems. *Science*, 308(5720):405–408.
- Nislow, K. and Kynard, B. (2009). The role of anadromous sea lamprey in nutrient and material transport between marine and freshwater environments. *American Fisheries Society Symposium*, 69:485–494.
- Nunn, A. D. and Cowx, I. G. (2012). Restoring river connectivity: Prioritizing passage improvements for diadromous fishes and lampreys. *AMBIO*, 41(4):402–409.

-
- O’Hanley, J. R. and Tomberlin, D. (2005). Optimizing the removal of small fish passage barriers. *Environmental Modeling & Assessment*, 10(2):85–98.
- Ojutkangas, E., Aronen, K., and Laukkanen, E. (1995). Distribution and abundance of river lamprey (*Lampetra fluviatilis*) ammocoetes in the regulated river Perhonjoki. *Regulated Rivers: Research & Management*, 10(2-4):239–245.
- Parasiewicz, P., Belka, K., Łapińska, M., Ławniczak, K., Prus, P., Adamczyk, M., Buras, P., Szlakowski, J., Kaczkowski, Z., Krauze, K., O’Keeffe, J., Suska, K., Ligieza, J., Melcher, A., O’Hanley, J., Birnie-Gauvin, K., Aarestrup, K., Jones, P., Jones, J., and Wiśniewolski, W. (2023). Over 200,000 kilometers of free-flowing river habitat in Europe is altered due to impoundments. *Nature Communications*, 14:6289.
- Pavlov, D., Zvezdin, A., Kostin, V., Tsimbalov, I., and Kucheryavyy, A. (2017). Temporal characteristics of downstream migration of smolts of the European river lamprey *Lampetra fluviatilis* in the Chernaya river. *Biology Bulletin*, 44:290–295.
- Payne, N., Gillanders, B., Webber, D., and Semmens, J. (2010). Interpreting diel activity patterns from acoustic telemetry: The need for controls. *Marine Ecology Progress Series*, 419:295–301.
- Pinheiro, J., Bates, D., and R Core Team (2026). *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-169.
- Piper, A. T., Rosewarne, P. J., Wright, R. M., and Kemp, P. S. (2018). The impact of an Archimedes screw hydropower turbine on fish migration in a lowland river. *Ecological Engineering*, 118:31–42.
- Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegard, K. L., Richter, B. D., Sparks, R. E., and Stromberg, J. C. (1997). The natural flow regime. *BioScience*, 47(11):769–784.
- Poff, N. L., Olden, J. D., Merritt, D. M., and Pepin, D. M. (2007). Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences*, 104(14):5732–5737.
- Poff, N. L. and Zimmerman, J. K. H. (2010). Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology*, 55(1):194–205.
- Potter, I. C. and Huggins, R. J. (1973). Observations on the morphology, behaviour and salinity tolerance of downstream migrating river lampreys (*Lampetra fluviatilis*). *Journal of Zoology*, 169(3):365–379.
- Quintella, B. R., Andrade, N. O., Espanhol, R., and Almeida, P. R. (2005). The use of PIT telemetry to study movements of ammocoetes and metamorphosing sea lampreys in river beds. *Journal of Fish Biology*, 66(1):97–106.

- Railsback, S. F., Lamberson, R. H., Harvey, B. C., and Duffy, W. E. (1999). Movement rules for individual-based models of stream fish. *Ecological Modelling*, 123(2):73–89.
- Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K. A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K., Vermaire, J. C., Dudgeon, D., and Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94(3):849–873.
- Reubens, J., Verhelst, P., van der Knaap, I., Wydooghe, B., Milotic, T., Deneudt, K., Hernandez, F., and Pauwels, I. (2019). The need for aquatic tracking networks: The permanent Belgian acoustic receiver network. *Animal Biotelemetry*, 7:2.
- Russon, I. J. and Kemp, P. S. (2011). Experimental quantification of the swimming performance and behaviour of spawning run river lamprey *Lampetra fluviatilis* and European eel *Anguilla anguilla*. *Journal of Fish Biology*, 78(7):1965–1975.
- Russon, I. J., Kemp, P. S., and Lucas, M. C. (2011). Gauging weirs impede the upstream migration of adult river lamprey *Lampetra fluviatilis*. *Fisheries Management and Ecology*, 18(3):201–210.
- Sabater, S., Bregoli, F., Acuña, V., Barceló, D., Elosegí, A., Ginebreda, A., Marcé, R., Muñoz, I., Sabater-Liesa, L., and Ferreira, V. (2018). Effects of human-driven water stress on river ecosystems: A meta-analysis. *Scientific Reports*, 8(1).
- Schmutz, S. and Moog, O. (2018). Dams: Ecological impacts and management. In Schmutz, S. and Sendzimir, J., editors, *Riverine Ecosystem Management: Science for Governing Towards a Sustainable Future*, pages 111–127. Springer, Cham.
- Shirakawa, H., Yanai, S., and Goto, A. (2012). Lamprey larvae as ecosystem engineers: Physical and geochemical impact on the streambed by their burrowing behavior. *Hydrobiologia*, 701:312–322.
- Silva, A. T., Lucas, M. C., Castro-Santos, T., Katopodis, C., Baumgartner, L. J., Thiem, J. D., Aarestrup, K., Pompeu, P. S., O'Brien, G. C., Braun, D. C., Burnett, N. J., Zhu, D. Z., Fjeldstad, H.-P., Forseth, T., Rajaratnam, N., Williams, J. G., and Cooke, S. J. (2018). The future of fish passage science, engineering, and practice. *Fish and Fisheries*, 19(2):340–362.
- Silva, S., Lowry, M., Macaya-Solis, C., Byatt, B., and Lucas, M. C. (2017a). Can navigation locks be used to help migratory fishes with poor swimming performance pass tidal barrages? A test with lampreys. *Ecological Engineering*, 102:291–302.
- Silva, S., Macaya-Solis, C., and Lucas, M. (2017b). Energetically efficient behaviour may be common in biology, but it is not universal: A test of selective tidal stream transport in a poor swimmer. *Marine Ecology Progress Series*, 584:161–174.

-
- Sousa, R., Araújo, M. J., and Antunes, C. (2012). Habitat modifications by sea lampreys (*Petromyzon marinus*) during the spawning season: effects on sediments. *Journal of Applied Ichthyology*, 28(5):766–771.
- Staponkus, R. and Kesminas, V. (2014). Confirmation of hybridisation between river lamprey *L. fluviatilis* and brook lamprey *L. planeri* from in situ experiments. *Polish Journal of Natural Sciences*, 29(1):49–54.
- Stevens, M., Van den Neucker, T., Gelaude, E., Baeyens, R., Jacobs, Y., Mouton, A., Buysse, D., and Coeck, J. (2011). Onderzoek naar de trekvissoorten in het Schelde-estuarium. Voortplantings- en opgroei-habitat van rivierprik en fint. Rapporten van het Instituut voor Natuur- en Bosonderzoek 2011 (INBO.R.2011.14), Instituut voor Natuur- en Bosonderzoek, Brussels, Belgium.
- Stevens, M., Van den Neucker, T., Mouton, A., Buysse, D., Martens, S., Baeyens, R., Jacobs, Y., Gelaude, E., and Coeck, J. (2009). Onderzoek naar de trekvissoorten in het stroomgebied van de Schelde. Rapporten van het Instituut voor Natuur- en Bosonderzoek 2009 (INBO.R.2009.9), Instituut voor Natuur- en Bosonderzoek, Brussels, Belgium.
- Stillman, R. A., Railsback, S. F., Giske, J., Berger, U., and Grimm, V. (2015). Making predictions in a changing world: The benefits of individual-based ecology. *BioScience*, 65(2):140–150.
- Strayer, D. L. and Dudgeon, D. (2010). Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society*, 29(1):344–358.
- Sutton, T. M. and Bowen, S. H. (1994). Significance of organic detritus in the diet of larval lampreys in the Great Lakes basin. *Canadian Journal of Fisheries and Aquatic Sciences*, 51(11):2380–2387.
- Therneau, T. M. (2026). *A Package for Survival Analysis in R*. R package version 3.8-6.
- Thieurmél, B. and Elmarhraoui, A. (2022). *suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase*. R package version 0.5.1.
- Van Hoey, S. (2025). *waterInfo: Download Time Series Data from Waterinfo.be*. R package version 0.3.0.9065.
- van Rijssel, J. C., Breukelaar, A. W., de Leeuw, J. J., van Puijenbroek, M. E. B., Schilder, K., Schrimpf, A., Vriese, F. T., and Winter, H. V. (2024). Reintroducing Atlantic salmon in the river Rhine for decades: Why did it not result in the return of a viable population? *River Research and Applications*, 40(7):1164–1182.

- Van Thuyne, G., Coeck, J., and Verreycken, H. (2016). Advies over de soortbeschermingsprogramma's voor beekprik, kleine modderkruiper en rivierdonderpad. Adviezen van het Instituut voor Natuur- en Bosonderzoek (INBO.A.3477), Instituut voor Natuur- en Bosonderzoek, Brussels, Belgium.
- van Treeck, R., Radinger, J., Smialek, N., Pander, J., Geist, J., Mueller, M., and Wolter, C. (2022). Comparative assessment of hydropower risks for fishes using the novel European fish hazard index. *Sustainable Energy Technologies and Assessments*, 51:101906.
- Vercruysse, J., Visser, K., Goormans, T., Depreiter, D., Claeys, S., Vereecken, H., and Buysse, D. (2024). Vispassage kerkhove: Validatiemeting en optimalisatie ontwerpmethodiek bekkenvormige vispassage. Versie 4.0 WL Rapporten 22_030_1, Waterbouwkundig Laboratorium, Antwerpen.
- Vergeynst, J., Pauwels, I., Baeyens, R., Coeck, J., Nopens, I., De Mulder, T., and Mouton, A. (2019). The impact of intermediate-head navigation locks on downstream fish passage. *River Research and Applications*, 35(3):224–235.
- Verhelst, P., Brys, R., Cooke, S., Pauwels, I., Rohtla, M., and Reubens, J. (2023). Enhancing our understanding of fish movement ecology through interdisciplinary and cross-boundary research. *Reviews in Fish Biology and Fisheries*, 33:111–135.
- Verhelst, P., Buysse, D., Reubens, J., Pauwels, I., Aelterman, B., Van Hoey, S., Goethals, P., Coeck, J., Moens, T., and Mouton, A. (2018). Downstream migration of European eel (*Anguilla anguilla* L.) in an anthropogenically regulated freshwater system: Implications for management. *Fisheries Research*, 199:252–262.
- Verhelst, P., Reubens, J., Buysse, D., Goethals, P., Van Wichelen, J., and Moens, T. (2021). Toward a roadmap for diadromous fish conservation : the Big Five considerations. *Frontiers in Ecology and the Environment*, 19(7):396–403.
- Verhelst, P., Righton, D., Aarestrup, K., Almeida, P. R., Bašić, T., Bolland, J. D., Carter, L., Coeck, J., Costa, J. L., Dainys, J., Davidsen, J. G., Domingos, I., Dorow, M., Feunteun, E., Frankowski, J., Griffioen, A. B., Monteiro, R. M., Moore, A., Oldoni, D., Piper, A. T., Quintella, B. R., Reeds, J., Trancart, T., Verschelde, P., Winter, H. V., and Reubens, J. (2025). The seaward migration of European eel at a continental scale: A Europe-wide biotelemetry meta-analysis. *Fish and Fisheries*, 26(4):651–668.
- Verreycken, H., Belpaire, C., {Van Thuyne}, G., Breine, J., Buysse, D., Coeck, J., Mouton, A., Stevens, M., {Van den Neucker}, T., {De Bruyn}, L., and Maes, D. (2014). IUCN red list of freshwater fishes and lampreys in Flanders (north Belgium). *Fisheries Management and Ecology*, 2014(21):122–132.
- Verweij, P. J. M. and Van Houwelingen, H. C. (1994). Penalized likelihood in Cox regression. *Statistics in Medicine*, 13(23-24):2427–2436.

-
- Visser, K. P., Buysse, D., Goormans, T., Vanderkimpen, P., and Viaene, P. (2024). Vertical slot vispassage op de Schelde te Merelbeke: Hydraulisch ontwerp. Versie 4.0 WL Rapporten 18_144_1, Waterbouwkundig Laboratorium, Antwerpen.
- Vittinghoff, E. and McCulloch, C. E. (2007). Relaxing the rule of ten events per variable in logistic and Cox regression. *American Journal of Epidemiology*, 165(6):710–718.
- Vrieze, L. A., Bergstedt, R. A., and Sorensen, P. W. (2011). Olfactory-mediated stream-finding behavior of migratory adult sea lamprey (*Petromyzon marinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 68(3):523–533.
- Vrieze, L. A., Bjerselius, R., and Sorensen, P. W. (2010). Importance of the olfactory sense to migratory sea lampreys *Petromyzon marinus* seeking riverine spawning habitat. *Journal of Fish Biology*, 76(4):949–964.
- Vörösmarty, C., McIntyre, P., Gessner, M., Dudgeon, D., Proussevitch, A., Green, P., Glidden, S., Bunn, S., Sullivan, C., Reidy Liermann, C., and Davies, P. (2010). Global threats to human water security and river biodiversity. *Nature*, 467:555–561.
- Wagner, C. M., Twohey, M. B., and Fine, J. M. (2009). Conspecific cueing in the sea lamprey: do reproductive migrations consistently follow the most intense larval odour? *Animal Behaviour*, 78(3):593–599.
- Walter, L. M., Dettmers, J. M., and Tyson, J. T. (2021). Considering aquatic connectivity trade-offs in Great Lakes barrier removal decisions. *Journal of Great Lakes Research*, 47:S430–S438. Supplement on Sea Lamprey International Symposium III (SLIS III).
- Weaver, D., Coghlan Jr, S., Greig, H., Klemmer, A., Perkins, L., and Zydlewski, J. (2018). Subsidies from anadromous sea lamprey (*Petromyzon marinus*) carcasses function as a reciprocal nutrient exchange between marine and freshwaters. *River Research and Applications*, 34(7):824–833.
- Whoriskey, K., Martins, E. G., Auger-Méthé, M., Gutowsky, L. F. G., Lennox, R. J., Cooke, S. J., Power, M., and Mills Flemming, J. (2019). Current and emerging statistical techniques for aquatic telemetry data: A guide to analysing spatially discrete animal detections. *Methods in Ecology and Evolution*, 10(7):935–948.
- Willems, P., Baguis, P., Ntegeka, V., and Roulin, E. (2011). Climate change impact on hydrological extremes along rivers and urban drainage systems in Belgium “CCI-HYDR” Final Report. Research programme science for a sustainable development, Belgian Science Policy, Brussels.
- Wilson, K. and Veneranta, L. (2019). Data-limited diadromous species – review of european status. ICES Cooperative Research Report No. 348, International Council for the Exploration of the Sea.

- Wright, G., Wright, R., and Kemp, P. (2015). Impact of tide gates on the migration of adult European eels, *Anguilla anguilla*. *Estuaries and Coasts*, 38:2031–2043.
- Wünstel, A., Mellin, A., and Greven, H. (1996). Zur Fortpflanzungsbiologie des Flußneunauges, *Lampetra fluviatilis* (L.), in der Dhünn, NRW. *Fischökologie*, 10:11–46.
- Xu, Y., Zhu, S.-W., and Li, Q.-W. (2016). Lamprey: a model for vertebrate evolutionary research. *Zoological Research*, 37:263–269.
- Yimer, E. (2025). *From drought deficits to climate resilience: Coupled surface-groundwater modelling and nature-based solutions for drought assessment and mitigation*. PhD thesis, Vrije Universiteit Brussel, Belgium.
- Yokouchi, K., Itakura, H., Wakiya, R., Yoshinaga, T., Mochioka, N., Kimura, S., and Kaifu, K. (2022). Cumulative effects of low-height barriers on distributions of catadromous Japanese eels in Japan. *Animal Conservation*, 25(1):137–149.
- York, J. R., Lee, E. M.-J., and McCauley, D. W. (2019). The lamprey as a model vertebrate in evolutionary developmental biology. In Docker, M. F., editor, *Lampreys: Biology, Conservation and Control: Volume 2*, pages 481–526. Springer Netherlands, Dordrecht.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer-Verlag New York.
- Zvezdin, A., Kucheryavyy, A., Kolotei, A., Polyakova, N., and Pavlov, D. (2023). European river lamprey *Lampetra fluviatilis* (Petromyzontidae) of the Pskov lakeland: Current state of isolated populations. *Journal of Ichthyology*, 63:1080–1091.
- Zvezdin, A., Pavlov, D., Kucheryavyy, A., and Tsimbalov, I. (2017). Experimental study of the European river lamprey, *Lampetra fluviatilis* (L.), migratory behavior in the period of initial dispersion of juveniles. *Inland Water Biology*, 10:209–218.
- Zydlewski, J., Coghlan, S., Dillingham, C., Figueroa-Muñoz, G., Merriam, C., Smith, S., Smith, R., Stich, D., Vogel, S., Wilson, K., and Zydlewski, G. (2023). Seven dam challenges for migratory fish: insights from the Penobscot River. *Frontiers in Ecology and Evolution*, 11:1253657.

A. Appendix

In the following sections, the developed migration model is reported according to the ODD (Overview, Design concepts, Details) protocol, which refers to a standardized framework for describing IBMs proposed by Grimm et al. (2020). Note that the model purpose and patterns are already covered in Chapter 5 (Section 5.2.1).

A.1 Entities, state variables and scales

This section summarizes the objects represented in the model (entities), the set of attributes that characterize these entities (state variables), and the spatial and temporal dimensions of the model (scale).

1. Entities:

- (a) Individuals: lampreys
- (b) Environment: continuous, one-dimensional space representing the Upper Scheldt River along the thalweg

2. State variables:

- (a) Individuals: ID (static), total distance traveled (dynamic), total time traveled (dynamic), located at bottleneck (binary, dynamic), current bottleneck name (dynamic), waiting time at current bottleneck (dynamic), number of bottlenecks passed (dynamic), did the individual permanently abandon its migration (binary, dynamic), and did the individual reach the last point in the study area (Avelgem) (binary, dynamic)
- (b) Environment: four shipping lock complexes (bottlenecks) with the presence of fishways specified (binary, static), and with defined coordinates along the river (static), weir over- and underflow rates at the bottlenecks (dynamic), and discharge, water level, temperature, rainfall and photoperiod (dynamic in time, static in space)

3. Scale:

- (a) Spatial: a continuous, 43 km section of the Upper Scheldt River corresponding to the study area (Figure 3.1), which includes four bottlenecks: A (Merelbeke, A1/A2 combined for simplification), B (Asper), C (Oude-naarde), and D (Kerkhove), respectively located at 3, 16, 27 and 39 km from the start location. When passing the 43 km point (Avelgem), the simulation for that individual is stopped.
- (b) Temporal: the time step Δt is fixed and equal to 15 minutes, to ensure high temporal resolution of environmental and weir data. Unless stated otherwise, the model simulates migration during 6 months (from 1 December 2024 to 31 May 2025), covering the entire spawning migration in the Upper Scheldt River (Buysse et al., 2004).

A.2 Process overview and scheduling

In Algorithm 1, a pseudocode of the IBM is shown. At each time step, it checks whether an individual reaches a point closer than 300 m downstream of the bottleneck (see Section A.5). If this is the case, the individual is assumed to be ‘influenced’ by the barrier. At that point, the survival submodel (Section A.6.1) is triggered, where we assume that two distinct events may occur at the bottleneck: (1) passage or (2) return (i.e., migration abandonment). To determine whether either event occurs, and if so which one, the survival submodel proceeds in two steps. First, it calculates and evaluates the probability that any event occurs. If no event occurs, the individual continues waiting at the bottleneck. If an event does occur, the submodel then calculates and evaluates the conditional probability that the event is passage, given that an event has occurred. Based on this probability, the event is classified as either passage or return.

In the latter case, the simulation is stopped for that individual. In contrast, if lampreys experienced a bottleneck passage event in the previous time step, or are not located at any bottleneck, the free migration speed is calculated using the swimming submodel (Section A.6.2). If an individual reaches Avelgem and beyond (> 43 km), the simulation for that individual is stopped as well. The IBM is coded in R, and for each scenario, the simulation is repeated 250 times to account for stochastic variability in the system and to obtain robust model estimates.

Algorithm 1: Pseudocode of the lamprey migration IBM

for each time step t do**for each individual i do**

Skip inactive individuals

if individual reached destination OR returned then

└ next

Increase total traveling time with Δt

Update migration state (bottleneck or unobstructed)

if distance(individual, next barrier) < 300 m then

Survival submodel

Compute passage hazard h_{pass} and return hazard h_{return} With these, compute $P(\text{event})$ over $[t, t + \Delta t]$ **if random number in $[0,1] < P(\text{event})$ then**└ Compute $P(\text{passage}|\text{event})$ **if random number in $[0,1] < P(\text{passage}|\text{event})$ then**

└ Remove barrier for individual

└ Update next barrier

└ Reset bottleneck waiting time to 0

else

└ Mark individual as inactive (returned)

else└ Increase bottleneck waiting time with Δt **else**

Swimming submodel

Compute free migration speed from environmental conditions

Update total traveled distance

if distance > 43 km then

└ Mark individual as inactive (reached destination)

A.3 Design concepts

Basic principles: The model is based on ecological principles related to the spawning migration and barrier passage behavior of the European river lamprey. Environmental drivers and effects of water regulating regimes are identified by regression models using real-life telemetry observations. Individuals migrate upstream until they either reach their destination or abandon migration. At barriers, passage

and return events are governed by probabilities that depend on waiting time, environmental conditions, and weir operation, while in unobstructed river sections, movement speed is determined by environmental drivers. In both cases, individual-specific variability is accounted for using random effects.

Emergence: From individual migratory behavior, such as swimming speed and decisions at barriers, population dynamics regarding overall passage success, timing of migration and bottleneck delays emerge.

Sensing: Individuals sense environmental variables and weir flow conditions available at the current time step. In addition, they can perceive their own time delay at bottlenecks, their own location, and subsequently the ‘barrier limit’, i.e., the distance at which a barrier starts to influence their behavior (300 m).

Adaptation: Lampreys respond to barriers and environmental conditions through dynamic changes in migration speed, governed by water temperature, rainfall and photoperiod, and passage probability, governed by water level, discharge, weir flow regimes and fishway presence.

Objectives: Individual lampreys try to reach potential spawning grounds without losing too much time or energy during bottleneck passage, so, they try to maximize upstream migration success within their own physical capabilities.

Stochasticity: The model is inherently stochastic, as decisions made by individuals in front of barriers are probabilistic (i.e., staying, passing or returning).

Observation: Model outputs include individual migration trajectories (i.e., number of bottlenecks passed, and traveling time and distance), migration status (i.e., whether an individual reached its destination, returned or is still migrating), waiting times at barriers, and passage success at each bottleneck.

Learning, prediction, interaction and collectives: No learning, memory, or predictive behavior is included. Lampreys migrate mutually independent and only interact with their environment.

A.4 Initialization

The lamprey populations were initialized by creating a data frame with 1000 unique, active individuals. As the primary purpose of this model was to evaluate fish passage at bottlenecks, all *in silico* lampreys started at the same location, 3000 m downstream from the first bottleneck in Merelbeke (A1/A2 combined for simplicity), meaning they started in an unobstructed river section. Each lamprey received three random intercepts: one for the swimming speed, one for the return hazard, and one for the bottleneck passage hazard (see Section A.6).

A.5 Input data

Processed telemetry data described in Chapter 3 were used as external input data to calibrate the submodels. More specifically, the behavioral data frames linked to environmental variables and weir data (Section 3.4.3) were used to estimate the regression coefficients and random intercepts in both the swimming and survival submodels.

During the simulation period, raw discharge, temperature and photoperiod data were obtained from the monitoring station in Gavere, located between Merelbeke and Asper. Although these data did not cover the entire study area, measurements from this station were highly correlated with those at other stations ($\rho > 0.7$), and were therefore assumed to be representative for the entire study area. Water level showed weaker correlations between stations ($\rho < 0.7$) and was consequently obtained from the measuring station corresponding to the bottleneck where an individual resided. Discharge and water level were scaled, while weir over- and under-flow rates were obtained from the corresponding bottlenecks and normalized to 200 m³/s. Precipitation data were obtained from the three monitoring stations closest to the study area (Zingem, Maarke-Kerkem and Elst), and values at an individual's location were estimated using inverse distance weighting.

In the model, the distance downstream from the bottleneck at which individuals switch from free swimming behavior to 'obstructed behavior' (i.e., intensive searching activity and delays in front of bottlenecks) is referred to as the 'barrier limit'. When lampreys crossed this threshold distance, the survival submodel was initiated to determine if individuals stay, return or pass. A default value of 300 m was selected, which approximately equals the receiver detection ranges at which 5% of lampreys are still detected (Bruneel et al., 2023). Thus, the barrier limit accounted for detection range effects in behavioral data. The sensitivity of the passage efficiency to this parameter choice was assessed over a range of 0 to 3000 m and at different bottlenecks, via linear regression. Slopes did not exceed 0.002 % m⁻¹. Moreover, distributions of migration delays did not appear to change much, suggesting that the model results were robust against the value of the barrier limit.

A.6 Submodels

A.6.1 The survival submodel

A.6.1.1 Theoretical considerations

Bottleneck passage success and its important driving factors were estimated in Section 4.2.2 through a logistic GLMM with a logit link (Eq. 4.2). In the IBM we implement here, however, realistic passage must depend on the time spent in front of the bottleneck (e.g., when the arbitrary timestep-size changes, passage probabilities evaluated at each timestep should change accordingly to keep passage rates constant). For this purpose, we resort to survival analysis (Castro-Santos and Haro, 2003; Whoriskey et al., 2019). Next to bottleneck passage, however, other time-dependent events can happen in front of barriers, such as migration abandonment. Competing risk theory is an extension of survival analysis that is able to deal with the occurrence of multiple events (Moore, 2016; Kleinbaum and Klein, 2005).

In survival analysis, one considers (1) observations that correspond to a certain event happening at a certain time T , and (2) observations in which no events happen, referred to as ‘censored’ observations. From this, one can define the time-dependent survival function $S(t)$, which gives the probability that the event has not occurred up until time t :

$$S(t) = P(T > t), \quad 0 < t < \infty, \quad (\text{A.1})$$

where $S(0) = 1$ and $S(\infty) = 0$. Moreover, one needs to define the time-dependent hazard function $h(t)$, which gives the instantaneous failure rate (i.e., the instantaneous potential that the event occurs, given that it did not occur up to time t):

$$h(t) = \lim_{\Delta t \rightarrow 0} \frac{P(t < T < t + \Delta t \mid T > t)}{\Delta t}, \quad (\text{A.2})$$

where $h(t) \geq 0$. The hazard and survival functions are linked through Bayes’ rule, leading to the following relation:

$$h(t) = -\frac{1}{S(t)} \frac{dS(t)}{dt} = \frac{1}{S(t)} \frac{dF(t)}{dt}, \quad (\text{A.3})$$

with $F(t) = 1 - S(t) = P(T \leq t)$ the cumulative risk function. When solving Eq. (A.3), one gets an expression that allows us to transform the hazard function into the corresponding survival function:

$$S(t) = \exp \left(- \int_0^t h(u) du \right) = \exp(-H(t)), \quad (\text{A.4})$$

with $H(t)$ the cumulative hazard function up to time t . In other terms, to derive the survival function $S(t)$ (or the cumulative risk function $F(t)$), one needs to estimate the cumulative hazard function $H(t)$ from the data. However, our model considers multiple possible events, namely bottleneck passage and return, which requires competing risk logic.

One accepted method for the evaluation of competing risks, with K different types of events (here $K = 2$), is cause-specific hazard analysis (Moore, 2016). In this approach, each of the K events is considered individually and assumed to be independent. Consequently, only observations corresponding to the event of interest are effectively regarded as an event, while all other observations, including the $K - 1$ other event types, are considered to be ‘censored’. This results in K cause-specific cumulative hazard functions $H_k(t)$, one for each type of event. The overall cumulative hazard function $H(t)$ can then be estimated as follows:

$$H(t) = \sum_{k=1}^K H_k(t), \quad (\text{A.5})$$

from which the overall survival function can be obtained through Eq. (A.4).

A.6.1.2 Derivation of survival probabilities

To estimate the effects of environmental covariates and barrier regimes on the hazard of bottleneck passage, $h_1(t)$, while accounting for variation among individuals, Cox’s proportional hazard regression (Cox, 1972) with frailty terms was used:

$$h_{1,i}(t) = h_{1,0}(t) e^{x_i(t)\beta + b_{1,i}}, \quad (\text{A.6})$$

where $b_{1,i} \sim \mathcal{N}(0, \sigma_1^2)$ is the random intercept for individual i , referred to as the frailty term, which reflects individual variation, σ_1 is the estimated standard deviation of the random intercept, $h_{1,0}(t)$ is the baseline hazard function (i.e., the hazard function if all covariates and random intercepts would be equal to 0), $x_i(t)$ is the covariate vector, [Discharge, Waterlevel, Weir overflow rate, Weir underflow rate, $D_{\text{free flow}}$, D_{fishway}], corresponding with the observation for individual i at time t , and β is the regression coefficient vector for these covariates $[\beta_1, \beta_2, \beta_3, \beta_4, \beta_5, \beta_6]^T$. Note that the regression coefficients and random intercept in Eq. (A.6) followed the optimal structure identified via the AIC in Section 4.2.2

We assumed that the hazard of return $h_2(t)$ only depended on time and individual variation. Frailty terms for return were estimated as follows:

$$h_{2,i}(t) = h_{2,0}(t) e^{b_{2,i}}, \quad (\text{A.7})$$

where $b_{2,i} \sim \mathcal{N}(0, \sigma_2^2)$ is the frailty term for individual i , σ_2 is the estimated standard deviation of the random intercept, and $h_{2,0}(t)$ is the baseline hazard function.

The subsequent cumulative baseline hazard functions for passage events, $H_{1,0}(t)$, and return events, $H_{2,0}(t)$, could be estimated using the Breslow estimator (Breslow, 1972; Lin, 2007):

$$\begin{aligned} H_{1,0}(t) &= \sum_{t_k \leq t} \left(\frac{d_k}{\sum_{j \in R(t_k)} e^{x_j(t_k)\beta + b_{1,j}}} \right), \\ H_{2,0}(t) &= \sum_{t_k \leq t} \left(\frac{d_k}{\sum_{j \in R(t_k)} e^{b_{2,j}}} \right), \end{aligned} \quad (\text{A.8})$$

with $R(t_k)$ the risk set (i.e., all individuals that have not yet undergone the event before time t_k), and d_k the number of events at that time t_k .

Cox regression coefficients and frailty terms in Eq. (A.6) and (A.7), and cumulative baseline hazards in Eq. (A.8) were estimated from the linked searching and crossing data (see Section 3.4.3) using the survival-package (Therneau, 2026). To prevent overfitting, Cox regression with ridge-penalization considering eight outcome events per predictor was applied (Verweij and Van Houwelingen, 1994; Vittinghoff and McCulloch, 2007). Using the estimated values for these parameters, the total cumulative hazard increment ΔH over the time interval $[t, t + \Delta t]$ could be obtained:

$$\Delta H_i = \Delta H_{1,i} + \Delta H_{2,i} = \Delta H_{1,0} e^{x_i\beta + b_{1,i}} + \Delta H_{2,0} e^{b_{2,i}}. \quad (\text{A.9})$$

Here, x_i is the constant covariate vector for individual i at time interval $[t, t + \Delta t]$, and the cumulative baseline hazard increments are

$$\begin{aligned} \Delta H_{1,0} &= H_{1,0}(t + \Delta t) - H_{1,0}(t), \\ \Delta H_{2,0} &= H_{2,0}(t + \Delta t) - H_{2,0}(t). \end{aligned} \quad (\text{A.10})$$

Through Bayes' rule and Eq. (A.4), one can show that the probability of *any* event occurring at a time interval $[t, t + \Delta t]$ and for each individual, given that it did not occur before, is:

$$P(t \leq T_{\text{any}} \leq t + \Delta t \mid T_{\text{any}} \geq t, \text{ individual} = i) = 1 - \exp(-\Delta H_i), \quad (\text{A.11})$$

with T_{any} the time at which any event occurs. To subsequently determine which event occurred (given that *any* event occurred in front of a bottleneck during $[t, t + \Delta t]$ at all), the probability of passage can be expressed with the ratio of the cause-specific hazard for passage over the total hazard:

$$P(\text{passage} \mid \text{event}, \text{individual} = i) = \frac{h_{1,i}(t)}{h_{1,i}(t) + h_{2,i}(t)}. \quad (\text{A.12})$$

This relation assumes that, during the time interval $[t, t + \Delta t]$, the ratio of cause-specific hazards is constant, which is effectively the case for the IBM. Hence, the hazards in Eq. (A.12) can be replaced by the incremental cumulative hazards $\Delta H_{1,i}$ and $\Delta H_{2,i}$.

A.6.2 The swimming submodel

When lampreys were in unobstructed river sections, or alternatively, after they passed bottlenecks, their migration speed was modeled using the optimal linear mixed regression model given by Eq. (4.3). To account for individual variability, each lamprey was assigned a random intercept following a normal distribution $\mathcal{N}(0, \sigma_3^2)$, with σ_3 the estimated standard deviation for the random intercept. Predicted migration speeds were bounded by a minimum and maximum value, since swimming speeds lower than 0 m/h were assumed to never occur, and speeds higher than 7000 m/h were deemed physically impossible (Russon and Kemp, 2011).